

germination. We evaluated the seed–recruit relationship using linear regression of log transformed values of  $R + 1$  and  $S + 1$  to normalize residuals. In these regressions, the fitted constant  $b$  takes values of less than 1 if the per seed probability of recruitment is inversely related to seed density.

Species were excluded from regression analyses if (1) seeds passed through the 1-mm trap mesh, (2) seeds or recruits were recorded at fewer than 10 stations, or (3) seed or recruit density varied less than a factor of four among stations. Fifty-three species remained including 28 trees, 20 lianas and five shrubs. These 53 focal species account for 60.3% of the seed rain and 80.4% of recruits. None of the 53 species persist for more than one year in the soil seed bank.

To insure that the regression results were not spurious or artefactual, we conducted several additional tests. First, some traps received many more seeds than could possibly recruit into adjacent seedling plots (simple space limitation). Second, in many instances, seedlings of a given species recruited into some seedling plots, but no seeds of that species were found in the adjacent seed traps. Either or both of these effects would lower  $b$ -value estimates and inflate the apparent importance of density dependence. Third, empty stations, lacking both seeds and recruits, introduce an opposing bias, and raise the  $b$ -value estimates. To control for the effect of space limitation, we conducted analyses excluding stations in which single species seed densities exceeded the maximum single species recruit density ( $66 \text{ seedlings m}^{-2}$ ). To control for the other biases, we conducted analyses after excluding stations lacking conspecific seed. We then eliminated all of these effects by including only stations with non-zero seed densities less than  $66 \text{ seed m}^{-2}$ . Finally, the addition of 1 before taking logarithms gives  $b$  values a downward bias. This effect can be large, particularly when the ratio of seeds to recruits is large. To evaluate the effect of this final potential bias, we compared 95% confidence intervals of the observed  $b$  values with  $b$  values predicted in the absence of density dependence. Observed  $b$  values were significantly less than predicted  $b$  values for every species. In all cases, these more conservative tests substantiated the pervasive and strong effects of negative density dependence on seedling recruitment.

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## The evolution of syntactic communication

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Animal communication is typically non-syntactic, which means that signals refer to whole situations<sup>1–7</sup>. Human language is syntactic, and signals consist of discrete components that have their own meaning<sup>8</sup>. Syntax is a prerequisite for taking advantage of combinatorics, that is, “making infinite use of finite means”<sup>9–11</sup>. The vast expressive power of human language would be impossible without syntax, and the transition from non-syntactic to syntactic communication was an essential step in the evolution of human language<sup>12–16</sup>. We aim to understand the evolutionary dynamics of this transition and to analyse how natural selection can guide it. Here we present a model for the population dynamics of language evolution, define the basic reproductive ratio of words and calculate the maximum size of a lexicon. Syntax allows larger repertoires and the possibility to formulate messages that have not been learned beforehand. Nevertheless, according to our model natural selection can only favour the emergence of syntax if the number of required signals exceeds a threshold value. This result might explain why only humans evolved syntactic communication and hence complex language.

The uniqueness of language has been compared to that of the elephant’s trunk<sup>13</sup>. Human language is as different from animal communication as the elephant’s trunk is from other animals’ nostrils. Yet few biologists worry about the evolution of the elephant’s trunk (which is a most complex organ that consists of about 6,000 individual muscles and that can perform an unparalleled variety of mechanical tasks), whereas many philosophers, linguists and biologists have great difficulties in imagining how language could have arisen by darwinian evolution<sup>17–21</sup>.

A challenge for evolutionary biology, therefore, is to provide a detailed mathematical account of how natural selection can enable the emergence of human language from animal communication. Animal communication is based on three basic designs: a finite repertoire of calls (territorial calls or warning of predators); a continuous analogue signal (for example, the dance of bees); and a series of random variations on a theme (such as the song of birds). All natural animal communication appears to be non-syntactic; some caution, however, seems appropriate as the final verdict on complex vocalization patterns of certain primate species or dolphins has not been reached. In contrast, human language is clearly syntactic: messages consist of components that have their own meaning. We compare non-syntactic and syntactic communication and evaluate their relative performance in an evolutionary setting.

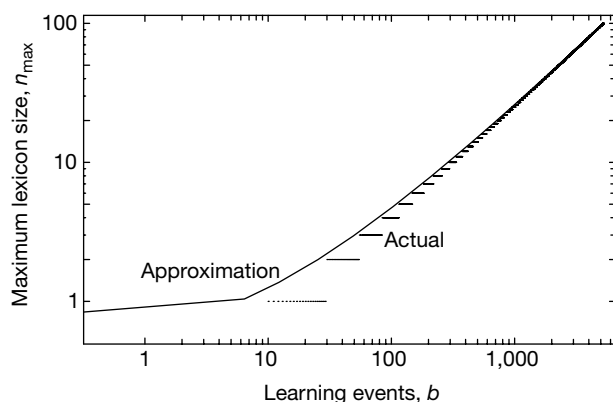
First, we formulate a mathematical model for the population dynamics of language evolution. Suppose a language contains  $n$

words. Each individual is born not knowing any of the words, but can acquire words by learning from other individuals. Individuals are characterized by the subset of words that they know. The general equations for the resulting evolutionary dynamics are complicated (see Methods), but an analytical approach is possible if we describe the process in terms of independent, elementary steps on the basis of two assumptions: first, in any one interaction between two individuals only a single new word can be learned; second, words are memorized independently of each other. With these assumptions, we obtain for the population dynamics of  $x_i$ , which is the relative abundance of individuals who know word  $W_i$

$$\dot{x}_i = R_i x_i (1 - x_i) - x_i \quad (1)$$

where  $i = 1, \dots, n$ . The abundance of word  $W_i$  spreads by the interaction of people who know the word with people who do not know the word; hence its rate of increase is proportional to the product  $x_i(1 - x_i)$ . The rate constant,  $R_i = bq\phi_i$ , is the basic reproductive ratio of word  $W_i$ . This is the average number of individuals who acquire word  $W_i$  from one individual who knows it. The parameter  $b$  is the total number of word-learning events per individual per lifetime. The parameter  $q$  is the probability of memorizing a single word after one encounter, and  $\phi_i$  is the frequency of occurrence of word  $W_i$  in the (spoken) language. The term  $-x_i$  denotes a constant death rate, setting the average lifetime of each individual as one time unit.

For a word to be maintained in the lexicon of the population, its basic reproductive ratio must exceed one, which implies that  $\phi_i > 1/(bq)$ . Suppose  $W_i$  is the least frequent word. We certainly know that  $\phi_i$  is less than  $1/n$ , which is the frequency of a word if all words have the same frequency. Thus the maximum number of words is  $n_{\max} = bq$ . Note that this number is always less than the total number of words,  $b$ , that are presented to a learning individual. Hence, the lexicon of the population cannot exceed the total number of word-learning events for each individual.



**Figure 1** How many word-learning events per individual are required for a population to maintain a certain number of words in its combined lexicon assuming that word frequencies follow Zipf's law? Zipf's law states that the frequency  $\phi_i$  of occurrence of a word is inversely proportional to its position,  $i$ , in a frequency ranking. Zipf's law seems to be a very good approximation for every human language. Nobody knows its significance. It can be shown, however, that a random source emitting symbols and spaces also generates word frequency distributions following Zipf's law<sup>23</sup>. Assuming that  $n$  words follow a frequency distribution as in Zipf's law,  $\phi_i = C_n/i$  where  $C_n = 1/\sum_{i=1}^n (1/i)$ , the maximum number of words that can be maintained,  $n_{\max}$ , is the largest integer,  $n$ , which fulfils the inequality  $\phi_n = C_n/n > 1/bq$ . The figure shows  $n_{\max}$  versus  $b$  for  $q = 0.1$ . The exact relationship is a step function because both  $b$  and  $n_{\max}$  are integers. The equation  $n_{\max}(\gamma + \ln n_{\max}) = bq$  is an excellent approximation (continuous line). Here we have used Euler's gamma which is  $\gamma = 0.5772\dots$ . For example, to maintain a lexicon of 100 words, we need about  $bq = 520$  successful word-learning events per individual. For  $q = 0.1$ , this implies that a total of roughly  $b = 5,200$  word-learning events per individual are required.

Assuming that word frequency distributions follow Zipf's law<sup>22,23</sup>,  $\phi_i = C/i$ , where  $C$  is a constant, we find that the maximum number of words is roughly given by the equation  $n_{\max} \ln(n_{\max}) = bq$  (Fig. 1).

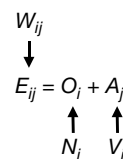
We now use this mathematical framework to analyse how natural selection can guide the transition from non-syntactic to syntactic communication. Imagine a group of individuals who communicate about events in the world around them. Events are combinations of objects, places, times and actions. (We use 'object' and 'action' in a general way to represent everything that can be referred to by nouns and verbs of current human languages.) For notational simplicity, suppose that each event consists of one object and one action. Thus, event  $E_{ij}$  consists of object  $i$  and action  $j$ . Non-syntactic communication uses words for events, whereas syntactic communication uses words for objects and actions (Fig. 2). Events occur at different rates, which are specified by the entries of an 'event rate matrix',  $\Gamma$ .

For natural selection to operate on language design, language must confer fitness. A plausible assumption is that correct communication about events provides a fitness advantage to the interacting individuals. In terms of our model, the fitness contribution of a language can be formulated as the probability that two individuals know the correct word for a given event summed over all events and weighted with the rate of occurrence of these events.

The population dynamics of non-syntactic communication are again given by equation (1) with word  $W_{ij}$  referring to event  $E_{ij}$ . As before, the maximum number of words that can be maintained in the population is limited by  $bq$ . We calculate the fitness of individuals using non-syntactic communication (see Methods).

We now turn to syntactic communication. Noun  $N_i$  refers to object  $i$  and verb  $V_j$  refers to action  $j$ , hence the event  $E_{ij}$  is described by the sentence  $N_i V_j$ . For the basic reproductive ratios we obtain  $R(N_i) = (b/2)q_s \phi(N_i)$  and  $R(V_j) = (b/2)q_s \phi(V_j)$ . Here  $\phi(N_i)$  and  $\phi(V_j)$  denote the frequency of occurrence of noun  $N_i$  and verb  $V_j$ , respectively. The factor  $1/2$  appears because either the noun or the verb is learned in any one of the  $b$  learning events. The probability of memorizing a noun or a verb is given by  $q_s$ . We expect  $q_s$  to be smaller than  $q$ , which simply means that it is a more difficult task to learn a syntactic signal than a non-syntactic signal. For both signals, the (arbitrary) meaning has to be memorized; for a syntactic signal one must also memorize its relation to other signals (whether it is a noun or a verb, for example).

For noun  $N_i$  to be maintained in the lexicon of the population, its basic reproductive ratio must exceed one, implying that  $\phi(N_i) > 2/(bq_s)$ . Similarly, for verb  $V_j$  we find  $\phi(V_j) > 2/(bq_s)$ . This means that the total number of nouns plus verbs is limited by  $bq_s$ , which is always less than  $b$ . The maximum number of grammatical sentences, however, which consist of one noun and one verb, is given by  $(bq_s)^2/4$ . Hence syntax makes it possible to maintain more sentences than the total number of sentences,  $b$ , encountered by a learning individual. All words have to be learned, therefore, but syntactic signals enable the formulation of 'new' sentences that have not been learned beforehand.



**Figure 2** To understand the essence of the evolution of syntax, we imagine a world where each event consists of one object and one action. Event  $E_{ij}$  consists of object  $O_i$  and action  $A_j$ . A non-syntactic language has words,  $W_{ij}$ , that refer to events,  $E_{ij}$ . A syntactic language has words for objects and actions,  $N_i$  and  $V_j$ . Words for objects are called nouns, words for actions are called verbs. Our mathematical analysis can also be adapted to more complicated situations, where events consist of several objects, actions, places or times, but the equations become more clumsy. The principles remain the same.

For calculating the fitness of syntactic communication, note that two randomly chosen individuals can communicate about event  $E_{ij}$  if they both know noun  $N_i$  and verb  $V_j$ . If we denote the relative abundance of individuals who know  $N_i$  and  $V_j$  by  $x(N_i V_j)$ , we obtain

$$\begin{aligned} \dot{x}(N_i V_j) = & R(N_i)x(N_i)[x(V_j) - x(N_i V_j)] \\ & + R(V_j)x(V_j)[x(N_i) - x(N_i V_j)] - x(N_i V_j) \end{aligned} \quad (2)$$

The abundance of individuals who know noun  $N_i$  and verb  $V_j$  increases if someone who knows  $N_i$  meets someone who knows  $V_j$  but not  $N_i V_j$ . Similarly, the abundance increases if someone

who knows verb  $V_j$  meets someone who knows  $N_i$  but not  $N_i V_j$ . We calculate the equilibrium abundances and thence the fitness of individuals using syntactic communication (see Methods). Figure 3 shows the fitness of syntactic and non-syntactic communication as a function of  $b$  for different examples of the event rate matrix,  $\Gamma$ .

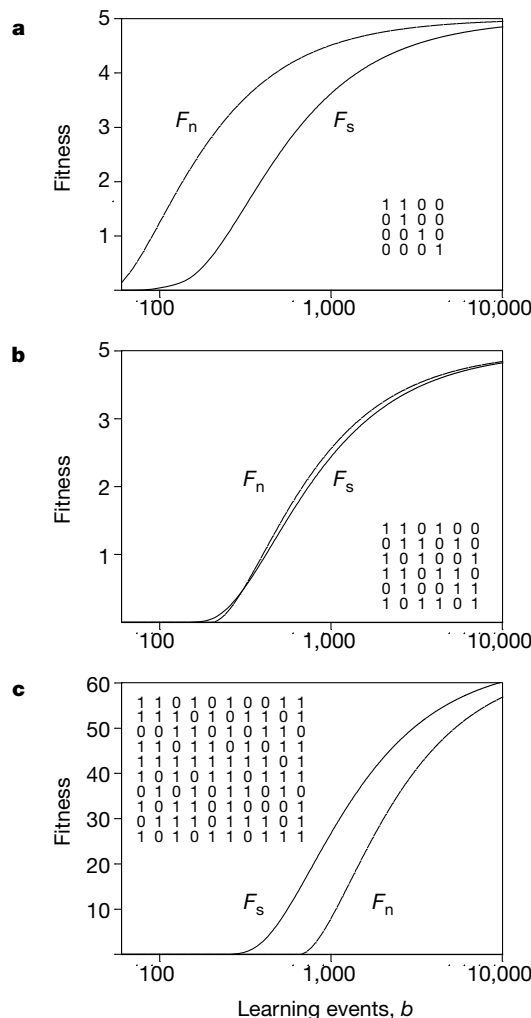
When does syntactic communication lead to a higher fitness than non-syntactic communication? Suppose there are  $n$  objects and  $m$  actions. Suppose a fraction,  $p$ , of these  $mn$  events occur (all at the same frequency), and the other events do not occur. In this case,  $R(W_{ij}) = bq/(pmn)$  for those events that occur. Making the (somewhat rough) assumption that all nouns and all verbs, respectively, occur on average at the same frequency, we obtain  $R(N_i) = bq_s/(2n)$  and  $R(V_j) = bq_s/(2m)$ . If all involved basic reproductive ratios are well above one, the fitness of syntactic communication exceeds the fitness of non-syntactic communication provided  $(m^2n + mn^2)/(m^2 + mn + n^2) > (2q)/(pq_s)$  (see Methods). If this inequality holds then syntactic communication will be favoured by natural selection; otherwise non-syntactic communication will win. Observe that  $m \geq 3$  and  $n \geq 3$  are necessary conditions for the evolution of syntax. For  $m = n$ , the relevant condition is

$$n > 3q/(pq_s) \quad (3)$$

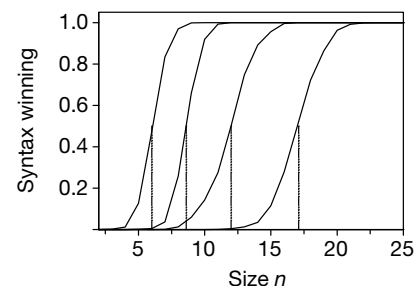
Hence, the size of the system has to exceed a critical value for syntactic communication to evolve. For example, if it is twice as hard to memorize a syntactic signal than a non-syntactic signal,  $q/q_s = 1/2$ , and if a fraction  $p = 1/3$  of all noun verb combinations describe meaningful events, then at least an  $18 \times 18$  system is required for syntactic communication to have any chance of evolving. Figure 4 shows the excellent agreement between our approximative analytical results and exact numerical computations.

The parameter  $p$  quantifies to what extent the perceived world has a compositional structure. A small  $p$  means that events often consist of unique pairings of objects and actions. The smaller the value of  $p$ , the harder it is for syntactic communication to evolve (the critical  $n$  in equation (3) is large).

Our results suggest that the crucial step that guided the transition from non-syntactic to syntactic communication was an increase in the number of relevant events that could be referred to. 'Relevant event' means there is a fitness contribution for communication about this event. As the number of such 'relevant communication topics' increased, natural selection could begin to favour syntactic



**Figure 3** The fitness of non-syntactic and syntactic communication,  $F_n$  and  $F_s$ , as function of the total number of word learning events per individual,  $b$ , for three different choices of the event rate matrix,  $\Gamma$ . The entries of  $\Gamma$  are the numbers  $\gamma_{ij}$  which characterize the rates at which the various events occur. **a**, There are four objects and four actions. Each object is associated with a specific action; in addition object 1 also occurs with action 2. All possible events occur at the same rate. Thus the event rate matrix is a binary  $4 \times 4$  matrix with 5 non-zero entries,  $p = 5/16$ . For  $b$  ranging from 50 to 10,000,  $F_n$  always exceeds  $F_s$ . **b**, There are six objects and six actions, the event rate matrix has 20 non-zero entries,  $p = 5/9$ . For values of  $b$  less than 400, syntactic communication has a higher fitness than non-syntactic communication. For values of  $b$  above 400, non-syntactic communication wins. Hence, for medium-sized systems the emergence of syntactic communication can be prevented by increasing the number of learning events per individual. **c**, There are 10 objects and 10 actions, 65 of 100 combinations occur,  $p = 13/20$ . In this case, syntactic communication wins for any choice of  $b$ . Each panel shows  $F_n$  and  $F_s$  as function of  $b$  and illustrates the chosen event rate matrix,  $\Gamma$ .



**Figure 4** Numerical validation of the approximate threshold condition given by equation (3). If this inequality holds then syntax will be favoured by natural selection. There is communication about  $n$  objects and  $m$  actions. A fraction,  $p$ , of the  $nm$  object-action combinations refers to events that occur in the world. The parameters  $q$  and  $q_s$  denote, respectively, the probability of memorizing a non-syntactic and a syntactic signal after a single occurrence. We choose  $n = m$ ,  $b = 5,000$  and  $q = 0.1$ . The values of  $n$  range from 2 to 25. For each  $n$  we compute  $F_s$  and  $F_n$  for 1,000 randomly chosen event-rate matrices  $\Gamma$ , whose entries are 1 with probability  $p$  or 0 otherwise. The y-axis shows the fraction of times when  $F_s$  exceeds  $F_n$ . From left to right the curves correspond to the parameter values  $p = 0.5$ ,  $q_s = 0.1$ ;  $p = 0.5$ ,  $q_s = 0.07$ ;  $p = 0.25$ ,  $q_s = 0.1$ ;  $p = 0.25$ ;  $q_s = 0.07$ . The straight lines indicate the predicted threshold values  $n = 6, 8.6, 12, 17.1$ .

communication and thereby lead to a language design where messages could be formulated that were not learned beforehand. Syntactic messages can encode new ideas or refer to extremely rare but important events. Our theory, however, does not suggest that syntactic communication is always at an advantage. Many animal species probably have a syntactic understanding of the world, but natural selection did not produce a syntactic communication system for these species because the number of relevant signals was below the threshold illustrated by equation (3). Presumably the increase in the number of relevant communication topics was caused by changes in the social structure<sup>24</sup> and interaction of those human ancestors who evolved syntactic communication. □

## Methods

Suppose there are  $n$  words. Individuals are characterized by the subset of words they know. There are  $2^n$  possibilities for the internal lexicon of an individual. Internal lexica are defined by bit strings: 1 means that the corresponding word is known; 0 means it is not. Let us enumerate them by  $I = 0, \dots, \nu$  where  $\nu = 2^n - 1$ . The number  $I$  is the integer representation of the corresponding bit string. (For example,  $I = 6$  represents the string 000...0110.) Denote by  $x_I$  the abundance of individuals with internal lexicon  $I$ . The population dynamics can be formulated as

$$\dot{x}_I = \delta_I - x_I + b \sum_{J=0}^{\nu} \sum_{K=0}^{\nu} (x_J x_K Q_{JKI} - x_I x_J Q_{IJK}) \quad (4)$$

where  $I = 0, \dots, \nu$ . We have  $\delta_0 = 1$  and  $\delta_I = 0$  otherwise; thus all individuals are born not knowing any of the words. Individuals die at a constant rate, which we set to 1, thereby defining a time scale. The quantities  $Q_{IJK}$  denote the probabilities that individual  $I$  learning from  $J$  will become  $K$ . Equation (4) is a general framework for the population dynamics of the lexical aspects of language. Assuming that in any one interaction between two individuals only a single new word can be acquired and that words are memorized independently of each other, we obtain the specific system described by equation (1).

Let us now assume that the world is made up of events  $E_{ij}$  consisting of objects  $i$  and actions  $j$ . The 'event rate matrix',  $\Gamma$  has the entries  $\gamma_{ij}$  which specify the relative rate of occurrence of event  $E_{ij}$ . Denote by  $\phi_{ij}$  the frequency of occurrence of event  $E_{ij}$ . We have  $\phi_{ij} = \gamma_{ij} / \sum_{ij} \gamma_{ij}$ .

Non-syntactic communication uses words,  $W_{ij}$ , for events  $E_{ij}$ . The basic reproductive ratio of  $W_{ij}$  is given by  $R(W_{ij}) = b\phi_{ij}$ . If  $R(W_{ij}) > 1$ , the word  $W_{ij}$  will persist in the population, and at equilibrium the relative abundance of individuals who know this word is given by  $x^*(W_{ij}) = 1 - 1/R(W_{ij})$ .

The fitness contribution of a language can be formulated as the probability that two individuals know the correct word for a given event summed over all events and weighted with the rate of occurrence of these events. Hence, at equilibrium, the fitness of individuals using non-syntactic communication is given by

$$F_n = \sum_{ij} [x^*(W_{ij})^2] \gamma_{ij}. \quad (5)$$

For syntactic communication, we assume the event  $E_{ij}$  is described by the sentence  $N_i V_j$ . The population dynamics of individuals knowing both  $N_i$  and  $V_j$  are described by equation (2). The basic reproductive ratios are given by  $R(N_i) = (b/2)q_i \phi(N_i)$  and  $R(V_j) = (b/2)q_j \phi(V_j)$ . The frequencies of occurrence are  $\phi(N_i) = \sum_j \phi_{ij}$  and  $\phi(V_j) = \sum_i \phi_{ij}$ . If the basic reproductive ratios,  $R(N_i)$  and  $R(V_j)$ , are greater than one, the equilibrium frequency of individuals who know both  $N_i$  and  $V_j$  is given by

$$x^*(N_i V_j) = \frac{[1 - 1/R(N_i)][1 - 1/R(V_j)]}{1 - 1/[R(N_i) + R(V_j)]} \quad (6)$$

At equilibrium, the fitness of syntactic communication is given by

$$F_s = \sum_{ij} [x^*(N_i V_j)]^2 \gamma_{ij}. \quad (7)$$

Assuming there are  $n$  objects and  $m$  actions that give rise to  $pnm$  meaningful events that all occur at the same frequency, we obtain  $R(W_{ij}) = bq/(pnm)$ . If we also assume that the combinations of objects and actions are arranged in a way that all nouns and all verbs, respectively, have about the same frequency, we can write  $R(N_i) = bq_i/(2n)$  and  $R(V_j) = bq_j/(2m)$ . For the fitness values, we obtain  $F_n = pnm[1 - 1/R(W_{ij})]^2$  and  $F_s = pnm[1 - 1/R(N_i)]^2[1 - 1/R(V_j)]^2/[1 - 1/(R(N_i) + R(V_j))]^2$ . Assuming that all involved basic reproductive ratios are well above one, we obtain for  $F_s < F_n$  the condition  $(m^2 n + mn^2)/(m^2 + mn + n^2) > (2q)/(pq_s)$ . Defining the ratio,  $\alpha = m/n$ , we can rewrite this condition as

$$n > \frac{2q}{pq_s} \left( 1 + \frac{1}{\alpha} - \frac{1}{\alpha + 1} \right). \quad (8)$$

Hence the size of the system has to exceed a critical threshold for syntax to be favoured by natural selection.

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# Glutamate spillover suppresses inhibition by activating presynaptic mGluRs

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Metabotropic glutamate receptors (mGluRs) found on synaptic terminals throughout the brain are thought to be important in modulating neurotransmission<sup>1,2</sup>. Activation of mGluRs by synaptically released glutamate depresses glutamate release from excitatory terminals<sup>3–5</sup> but the physiological role of mGluRs on inhibitory terminals is unclear. We have investigated activation of mGluRs on inhibitory terminals within the cerebellar glomerulus, a structure in which GABA ( $\gamma$ -aminobutyric acid)-releasing inhibitory terminals and glutamatergic excitatory terminals are in close apposition and make axo-dendritic synapses onto granule cells<sup>6</sup>. Here we show that 'spillover' of glutamate, which is released from excitatory mossy fibres, inhibits GABA release from Golgi cell terminals by activating presynaptic mGluRs under physiological conditions. The magnitude of the depression of the