ORIGINAL PAPER

A game theoretical approach to the evolution of structured communication codes

José F. Fontanari · Leonid I. Perlovsky

Abstract Structured meaning-signal mappings, i.e., mappings that preserve neighborhood relationships by associating similar signals with similar meanings, are advantageous in an environment where signals are corrupted by noise and sub-optimal meaning inferences are rewarded as well. The evolution of these mappings, however, cannot be explained within a traditional language evolutionary game scenario in which individuals meet randomly because the evolutionary dynamics is trapped in local maxima that do not reflect the structure of the meaning and signal spaces. Here we use a simple game theoretical model to show analytically that when individuals adopting the same communication code meet more frequently than individuals using different codes—a result of the spatial organization of the population—then advantageous linguistic innovations can spread and take over the population. In addition, we report results of simulations in which an individual can communicate only with its K nearest neighbors and show that the probability that the lineage of a mutant that uses a more efficient communication code becomes fixed decreases exponentially with increasing K. These findings support the mother tongue hypothesis that human language evolved as a communication system used among kin, especially between mothers and offspring.

J. F. Fontanari (✉)
Instituto de Física de São Carlos,
Universidade de São Paulo, Caixa Postal 369,
São Carlos, SP 13560-970, Brazil
e-mail: fontanari@ifsc.usp.br

L. I. Perlovsky
Harvard University, 33 Oxford St, Rm 336,
Cambridge, MA 02138, USA
e-mail: leonid@seas.harvard.edu

Introduction

The notion that words compete and languages evolve in analogy to individuals and populations was already familiar in the nineteenth century as expressed in this quotation by the famous Darwin contemporary philologist Max Müller, "A struggle for life is constantly going on amongst the words and grammatical forms in each language. The better, the shorter, the easier forms are constantly gaining the upper hand, and they owe their success to their own inherent virtue" (Radick 2002). A more suitable analog to language, however, is that of a parasitic species since language does not exist without speakers, just like parasites do not exist without hosts (Deacon 1997, Chap. 4). In fact, the propagation of linguistic innovations through a population depends solely on the interaction between individuals and, as we will show here, the meeting practices of the speakers can hamper or facilitate the spread of new words or grammatical forms, regardless of their worth.

The debate on language evolution has centered mainly on the apparent gap between animal communication systems and human language (see e.g., Pinker and Bloom 1990). In fact (non-human) animals use non-syntactic or holistic communication codes, i.e., signals refer to whole situations, in contrast to human language which is characterized by signals formed by discrete components that have their own meaning. As pointed out by Deacon (1997), no "simple" language which uses some elementary form of syntax or words combination has ever been found either in

humans or in animals (see, however, Gordon 2004 for a possible exception—the puzzling language of the Pirahã people which lacks subordinate clauses as well as words associated with time, color and numbers). This discontinuity is behind the notion of a "language organ" exclusive of the human species which was originally designed to carry out combinatorial calculations (Chomsky 1972; Fodor 1983). According to Chomsky (1972), language is an example of true emergence—the appearance of a qualitatively different phenomenon at a specific stage of complexity of organization. The burden of identifying the selective pressures accountable for the emergence of syntax falls to those who hold the biological-oriented perspective that human language has evolved gradually from a simpler precursor—a proto-language—by means of the usual natural selection process. The demands of the social life of early hominids have been pointed as a probable source of selective pressures for the evolution of syntactic communication (Dunbar 1996).

Even the evolution of simple holistic communication, which can be viewed as a one-to-one mapping between meanings and signals, has to confront some fundamental difficulties (Dawkins and Krebs 1978; Fitch 2004). In fact, from the perspective of the signaller, passing useful information to another individual is an altruistic act and so its maintenance in nature is problematic, whereas from the receiver viewpoint deciding whether a signal is honest (in the sense of conveying accurate information) or not is a difficult problem, the solution of which is thought to depend on the cost paid by the signaller to emit the signal (Zahavi 1993). This is the essence of the "handicap principle", namely, honest signals are retained only when the signaller pays a high cost when emitting them (Zahavi 1975). The relevance of this principle to the evolution of communication, however, has been defied by Noble (2000) who showed that a necessary condition for efficient communication to evolve is that both sender and receiver are benefited equally in the case of mutual understanding. By an efficient communication code we mean a Saussurean communication system that maps meanings unambiguously onto signals and then back into the original meanings (Hurford 1989; Oliphant 1996).

Rather than focusing on the evolution of Saussurean communication (see Hurford 1989; Nowak and Krakauer 1999; Nowak et al. 1999; Oliphant 1996; Noble 2000 for work on this line), in this paper we consider that one such a code is already established in the population and study the conditions under which a more robust communication system can take over. The breaking of the degeneracy between distinct Saussurean codes—essentially the $n!/(n-m)!$ different manners to associate m meanings to $n \geq m$ signals—is achieved by introducing errors in the

perception of signals as well as by rewarding the inference of meanings close to the intended ones (Nowak and Krakauer 1999; Zuidema 2003; Fontanari and Perlovsky 2007). This amounts to considering structured meaning-signal mappings in which neighborhood relationships are preserved (see Sect. 2).

We take up the evolutionary language game approach (Nowak et al. 1999) to study the competition between two communication codes or strategies: a perfectly structured meaning-signal mapping (strategy 1) and a random meaning-signal mapping (strategy 2). This study is primarily motivated by the failure of the traditional language game scenario to explain the evolution of structured communication codes starting from a population composed of individuals who use distinct communication codes, so the chance that a signal emitted by an individual is correctly interpreted by another individual is $1/m$ (Fontanari and Perlovsky 2007). This is so because the evolutionary dynamics is very likely to get trapped in the local maxima—the random meaning-signal mappings—and once a communication code is fixed in the population it cannot be changed even if a small fraction of the population adopts the more efficient structured code. This is essentially the Allee effect (1931) of population dynamics that asserts that intraspecific cooperation might lead to inverse density dependence, resulting in the extinction of some (social) animal species when their population size becomes small. The situation is different, however, in the case of weak selection (i.e., the fitness of the individual is scarcely influenced by its communicative performance) in finite populations, in which more efficient communication codes are favored, in the sense of exhibiting a fixation probability greater than the inverse of the population size—the neutral value (Pawlowitsch 2007; Nowak et al. 2004).

Instead of using the genetic algorithm to simulate the population dynamics, here we use an analytical approach based on the game theoretical formulation of Eshel and Cavalli-Sforza (1982), which allows us to derive explicit conditions for the minimum size of the population that adopts a structured code to invade an established population of individuals adopting a sub-optimal communication system. In particular, we show that useful linguistic innovations can spread and take over the population if the meeting of individuals using the same communication strategy is more likely than the encounter of individuals using different strategies—a natural consequence of imposing a spatial structure to the population since individuals are more likely to communicate with those close to them than with those farther away. Additional support to this finding is obtained through the explicit simulation of a spatially organized population in which the individuals can interact with their K-nearest neighbors only. Our

findings support the "mother tongue" assumption that human language evolved as a communication system used among kin, especially between parents and their offspring (Fitch 2004).

Meaning-signal mapping

Here we adopt the view that language is a mapping between meanings (or objects) and signals. In most previous studies of evolutionary language games this mapping is structureless or random: the metrics (if any) of the meaning and signal spaces play no role in the properties of the mapping and hence on the nature of the evolved communication codes (Hurford 1989; Nowak and Krakauer 1999; Nowak et al. 1999; Oliphant 1996; Noble 2000). This contrasts with a more recent approach that put emphasis on the properties of the meaning-signal mapping and, in particular, focus on structured mappings that preserve neighborhood relationships, i.e., nearby meanings in the meaning space are likely to be associated to nearby signals in signal space (Smith et al. 2003; Zuidema 2003; Brighton et al. 2005; Fontanari and Perlovsky 2007).

This notion of structured mappings seems contradictory to the well-established fact that the relation between a word (signal) and its meaning is arbitrary (Petitto 1994). In fact, as pointed out by Pinker (1994) "babies should not, and apparently do not, expect cattle to mean something similar to battle, or singing to be like stinging, or coats to resemble goats". On the other hand, a code that preserves neighborhood relationships is clearly advantageous in an environment where signals are likely to be altered by noise. Consider for instance the Vervet monkey alarm calls (Seyfarth et al. 1980): misinterpreting a snake alarm for a leopard one, and hence running to a tree instead of standing up and looking in the grass, is clearly much better than misinterpreting it for an eagle call. In addition, sentences like *John walked* and *Mary walked* have parts of their semantic representation in common (someone performed the same act in the past) and so the meaning of these sentences must be close in the meaning space. Since both sentences contain the word *walked* they must necessarily be close in signal space as well (Smith et al. 2003; Brighton et al. 2005). It should be noted that the very notion of meaning similarity in contraposition to meaning identity is a highly controversial issue in cognitive science (see, e.g., Churchland (1998), Fodor and Lepore (1999), Abbott (2000). However, within a connectionist perspective in which meanings are neural activation patterns, the concept of meaning similarity follows naturally and the neural modeling fields theory systematically exploits this

similarity (see Perlovsky 2007 for an overview). In this contribution, we take the stand that in simple (nonhuman) communication structured meaning-signal mappings are likely to be relevant even at the elementary level of the object-word pairing, whereas in human language these mappings may play a role at the meaning-sentence level and in word morphology (e.g., ring-rung, walk-walked, meaning-meaningful).

We represent the signals (sentences or words) as well as the meanings by single symbols (labels)—only the "distance" between these entities will reflect the complex inner structure of the signal and meaning spaces. For instance, suppose there are only two words that we represent, without lack of generality, by 0 and 1 so that a binary sequence or, equivalently, its decimal representation stands for any sentence in this language. Here the relevant distance between two such sentences is the Hamming distance rather than, e.g., the result of the subtraction between their labeling integers. This notion, of course, generalizes trivially to the case where the sentences are composed of more than two types of words. As pointed out before, the representation of meanings is a much vaguer issue, but within a connectionist stand we can think of meanings also as patterns of 1s and 0s representing the arrangement of active and inactive neurons in the neural region activated by the signal.

For simplicity, in this paper we consider the case where both signals and meanings are represented by integer numbers and the relevant distance in both signal and meaning space is the result of the usual subtraction between integers. In addition, we consider the case where the number of signals equals the number of meanings
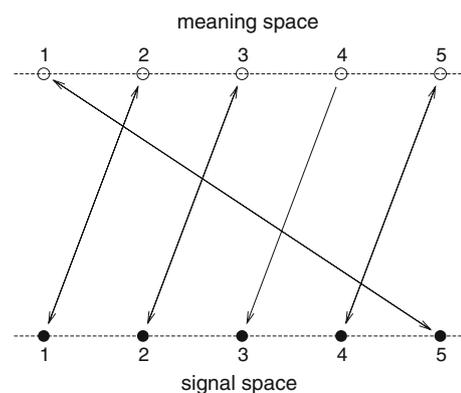

Fig. 1 Illustration of a meaning-signal mapping for $n = 5$. The integers here are viewed as labels for complex entities (e.g., sentences). The metric of the signal space is such that signal 3 is at a distance of one unit from signals 2 and 4. This space has periodic boundary conditions so that signal 5 is at a distance of one unit from signal 1. This metric applies to the meaning space as well. Because nearby meanings in the meaning space are associated to nearby signals in signal space this is a structured mapping

$m = n$. Figure 1 illustrates a structured meaning-signal mapping in the case of $n = 5$ signals. For n signals there are only $2n$ structured mappings out of the $n!$ possible mappings. A random mapping is obtained simply by assigning meanings to signals randomly. A quantitative measure of the structure of a mapping is given by the degree to which the distances between all the possible pairs of meanings correlates with the distance between their corresponding pairs of signals, a quantity known as Pearson's correlation coefficient (Brighton et al. 2005). Since here we will focus on the competition between two communication strategies given a priori—structured and random mapping—we will not consider these partially structured mappings which play a fundamental role when the issue is the emergence of structured mappings from an initial population of random mappings (Fontanari and Perlovsky 2007).

A mapping that preserves the topology of the meaning and signal spaces was termed a compositional mapping in previous works (Smith et al. 2003; Zuidema 2003; Brighton et al. 2005; Fontanari and Perlovsky 2007). Here we use the term structured mapping instead, to avoid confusion with the well-established concept of compositionality which is defined as the property that the meaning of a complex expression is determined by the meanings of its parts and the rules used to combine them. In fact, Fodor and Lepore (1999) even claim that the notion of meaning similarity excludes the possibility of compositionality (see, however, Abbott 2000; Perlovsky 2006). In an artificial scenario in which there is a prescription to derive the meaning of the whole given the meaning of the elementary parts, however, there is a direct connection between structured and compositional meaning-signal mappings since in this case the distance between any two composite meanings could be inferred by comparing their components and, consequently, by introducing a metric in the meaning space.

Our choice of the particular one-dimensional meaning-signal mapping displayed in Fig. 1 aims mainly at simplifying the derivation of the mathematical expressions for the strategy payoffs—the theme of next section. High dimensional mappings in which meanings and signals are defined as strings of symbols drawn from distinct alphabets (Smith et al. 2003; Brighton et al. 2005) lead to complex rugged payoff landscapes where neutral connected regions may substantially influence the dynamics of agent-based simulations (Reidys and Stadler 2001; Schuster and Stadler 2002). However, since our focus here is on the outcome of infinitely many interactions between individuals using distinct communication codes, averaged over the entire meaning-signal mapping, those subtleties of the payoff landscape are simply washed out.

Strategy payoffs

To explore the structure of the meaning-signal mapping (see Fig. 1) we must admit the possibility of errors in the perception of the signals as well as the alternative of rewarding the inference of meanings close but not equal to the meaning intended by the signaller.

It is reasonable to assume that in the earlier stages of the evolution of communication the signals were likely to be noisy and so they could be easily mistaken for each other. The relevance of the structure of the signal space becomes apparent when we note that the closer two signals are, the higher the chances that they are mistaken for each other. In particular, here we will consider the simple case in which there is a nonzero probability ε in [0, 1/2] that a signal, say signal j, be mistaken for one of its nearest neighbors $j - 1$ or $j + 1$. So, in the example of Fig. 1, signal 5 can be mistaken for signal 4 with probability $\varepsilon/2$ or for signal 1 with probability $\varepsilon/2$. Of course, the probability that a signal is not corrupted by noise is $1 - \varepsilon$.

The individuals in the population can adopt either strategy 1 (structured meaning-signal mapping) or strategy 2 (random meaning-signal mapping). The interaction—a communication event—between a pair of individuals, say individuals I and J, comprises two stages: first I plays the role of signaller (so J is the receiver) and then I and J exchange roles. Both individuals receive the same payoff value. In particular, we assume that both signaller and receiver are rewarded with 1/2 unity of payoff whenever the receiver interprets correctly the meaning of the emitted signal. In addition, both agents are rewarded with $r/2$ unity of payoff, where r in [0, 1], if the inferred meaning is one of the nearest neighbors of the intended meaning. We note that giving value to decisions which are not the best ones is a common assumption in decision and game theory (Fudenberg and Tirole 1991) and, it seems to be consistent with what is actually observed in nature since, as illustrated by the Vervet monkey alarm calls example, not every misinterpretation is equally harmful (see e.g., Zuidema 2003). The factors 1/2 appear here because, as pointed out before, a communication event comprises two stages in which the individuals interchange the roles of signaller and receiver. So, both individuals gain 1 unity of payoff in case communication was successful in both stages.

Next we calculate the average payoff F_{ij} accrued to a pair of individuals using strategies i and j during a communication event. First, let us consider the interaction between two individuals who both have strategy 1. The average payoff of the individual playing the signaller is $(1 - \varepsilon) \times 1/2 + \varepsilon \times r/2$ which, by symmetry, happens to be the same average payoff it receives when playing the receiver role. Hence

$$F_{11} = 1 - \epsilon(1 - r). \tag{1}$$

In the case both individuals have strategy 2, the average payoff of the signaller is $(1 - \epsilon) \times 1/2 + \epsilon \times 2/(n - 1) \times r/2$ where the factor $2/(n - 1)$ accounts for the fact that the reward $r/2$ is obtained only if the inferred meaning is one of the two neighbors of the correct meaning. Hence the average payoff accrued to both individuals in a communication event is

$$F_{22} = 1 - \epsilon + \frac{2\epsilon}{n - 1} r. \tag{2}$$

This reasoning is valid for $n > 2$ only: for $n = 2$ each meaning has a single neighbor and so the correct expression is $F_{22} = 1 - \varepsilon(1 - r)$. Finally, in the case the individuals have different strategies the probability the receiver infers correctly the signaller intentions is simply $1/n$ and the probability that it infers a meaning which is a neighbor of the intended one is $2/(n - 1)$. The average payoff of this communication event is then

$$F_{12} = \frac{1}{n} + \frac{2r}{n - 1}. \tag{3}$$

and $F_{21} = F_{12}$.

For $n \geq 3$ we have $F_{11} \geq F_{22}$ where the equality holds for $n = 3$ as well as for the trivial cases $\varepsilon = 0$ or $r = 0$. In addition, $F_{11} > F_{12}$ for $n > 2$. We will show in the following section that, except for $n = 4$ and ε close to its maximum value $1/2$, we have $F_{22} > F_{12}$. These inequalities are important to determine the local stability of the two strategies.

Population dynamics

As pointed by Ferdinand de Saussure "language is not complete in any speaker; it exists only within a collectivity... only by virtue of a sort of contract signed by members of a community" (Saussure 1966). Translated into the biological jargon, this assertion means that language is not the property of an individual, but the extended phenotype of a population (Nowak et al. 2002). So a suitable approach to language evolution must take into account the population dynamics. In what follows we build on the game theoretical formulation of Eshel and Cavalli-Sforza (1982) to investigate analytically the evolution of structured communication codes.

Let x in [0,1] be the proportion of individuals in a population of infinite size that use the structured communication code (strategy 1). To calculate the expected payoff of individuals adopting a particular strategy we need to make some assumption about the frequency of encounters between any two individuals. Let u_{ij} with $i,j = 1,2$ be the probability that an individual using strategy i encounters an individual that uses

strategy j. Since the game rules are such that an individual must encounter a partner to interact with, we have $u_{i1} + u_{i2} = 1$ for $i = 1,2$. In addition, since the average number of encounters between individuals using different strategies can be written either as $x\,u_{12}$ or $(1 - x)u_{21}$ we have the equality $u_{12}/u_{21} = (1 - x)/x$. Hence a single encounter probability, say u_{11}, determines all other encounter probabilities: $u_{12} = 1 - u_{11}$, $u_{21} = x(1 - u_{11})/(1 - x)$, and $u_{22} = (1 - 2x + xu_{11})/(1 - x)$. In the case encounters are random and independent of the communication code we have $u_{11} = x$ so that $u_{12} = u_{22} = 1 - x$ and $u_{21} = x$.

The expected payoff for individuals using strategy $i = 1,2$ is $F_i(x) = u_{i1} F_{i1} + u_{i2} F_{i2}$ or, explicitly,

$$F_1(x) = F_{12} + (F_{11} - F_{12})u_{11}(x) \tag{4}$$

$$F_2(x) = F_{22} + (F_{12} - F_{22}) \frac{x}{1 - x}[1 - u_{11}(x)]. \tag{5}$$

A simple deterministic population dynamics model that describes the competition of the two strategies is obtained by assuming that the proportion of individuals using strategy 1 in generation $t + 1$ is proportional to the relative payoff of that strategy in generation t, i.e.,

$$x_{t+1} = \frac{x_t F_1(x_t)}{x_t F_1(x_t) + (1 - x_t)F_2(x_t)} \equiv f(x_t), \tag{6}$$

which essentially implies that mastery of a public communication system adds to the reproductive potential of the individuals (Hurford 1989). This model is equivalent to the standard genetic algorithm (Mitchell 1996) procedure with an infinite population size. As expected, $x = 0$ and $x = 1$ are always fixed points of the recursion equation (6). The issue is to determine their stability and, in the case that both fixed points are stable, their basins of attraction. As usual, the condition for the stability of a fixed point x^* is simply $f'(x^*) < 1$ (see e.g., Maynard Smith 1982).

Random encounters

This is the typical scenario used in most computational models for the evolution of communication (Hurford 1989; Nowak and Krakauer 1999) and, in particular, Fontanari and Perlovsky (2007) have considered an agent-based simulation aiming at exploring the plausibility of the emergence of structured codes in a random encounter situation. As already mentioned, random encounters are described by $u_{11} = x$. The stability condition of the fixed point $x = 0$ associated to strategy 2 (random meaning-signal mapping), namely, $f'(0) < 1$ yields $F_{22} > F_{12}$ or, more explicitly,

$$r < \frac{n - 1}{2}\left[1 - \frac{1}{n(1 - \epsilon)}\right]. \tag{7}$$

Since $r \leq 1$ and $\varepsilon \leq 1/2$ this condition is violated only if $n = 4$ and $\varepsilon > 1/4$. Similarly, the fixed point $x = 1$,

associated to strategy 1 (structured meaning-signal mapping), is stable provided $f'(1) < 1$, that leads to the condition $F_{11} > F_{12}$ which is satisfied for $n > 2$ regardless of the values of r and ε. In most cases (e.g., $n > 4$) the fixed points $x = 0$ and $x = 1$ are stable and so there is an inner unstable fixed point x_u that delimits the basins of attractions of the two stable fixed points. It is given by the condition $F_1(x_u) = F_2(x_u)$ which yields

$$x_u = \left(1 + \frac{F_{11} - F_{12}}{F_{22} - F_{12}}\right)^{-1}. \tag{8}$$

This quantity is the minimum initial fraction of individuals using strategy 1 above which this strategy dominates the population. Expression (8) corrects the estimate given in Fontanari and Perlovsky (2007). In Fig. 2 we illustrate the dependence of x_u on the parameters of the model. As already pointed out, since for $n = 4$ the Saussurean fixed point is unstable in the range $r > \frac{3}{2}[1 - 1/4(1 - \epsilon)]$ we have $x_u = 0$ in this regime. For $n \to \infty$ we find $x_u = [2 + \epsilon r/(1 - \epsilon)]^{-1}$.

Nonrandom encounters

Nonrandomness of encounters are usually modeled by imposing some spatial structure to the population in which the individuals are fixed to lattice sites and so can interact only with their nearest neighbors or then isolated in groups (see e.g., Oliphant 1996; Noble 2000; Cangelosi 2001, for this type of approach within the evolution of communication context). An alternative formulation of nonrandom encounters which keeps the mathematics simple is to assume that the frequency of meetings between individuals using strategy 1 is

$$P_{11} = (1 - m)x^2 + mx \tag{9}$$

where m in [0,1] is the aggregation parameter (Wright 1921; Eshel and Cavalli-Sforza 1982). In fact, the probability that an individual using strategy 1 encounters another of its kind is $u_{11} = P_{11}/x = m + (1 - m)x$, from which we obtain $u_{22} = m + (1 - m)(1 - x)$. Hence m represents the portion of the population that meets an individual of the same strategy, whereas the fraction $1 - m$ meets randomly. The situation of random encounters is obtained by setting $m = 0$.

Now the conditions for the stability of the fixed points $x = 0$ and $x = 1$ become $F_{22} > m F_{11} + (1 - m) F_{12}$ and $F_{11} > m F_{22} + (1 - m) F_{12}$, respectively. Since $F_{11} > F_{22}$ and $F_{11} > F_{12}$ for $n > 2$ the fixed point $x = 1$ is always stable regardless of m. The situation for the fixed point $x = 0$, however, changes considerably, as illustrated in Fig. 3 that shows the regions of stability of this fixed point in the plane (m,r). Large values of m can, as expected, destabilize this fixed point. By setting the parameters so as
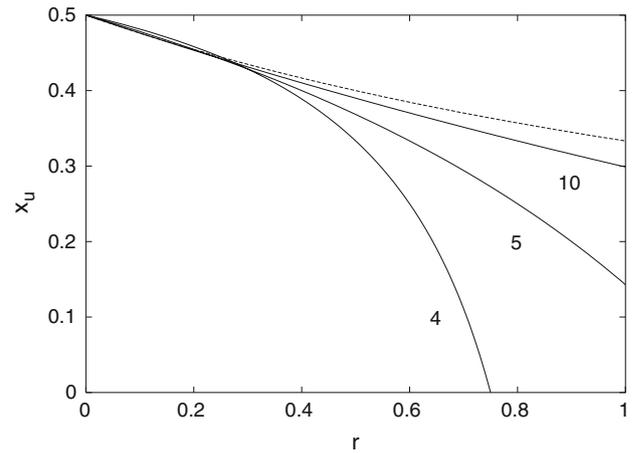
Fig. 2 Minimum fraction of individuals using structured codes necessary for this strategy to dominate the population in the case of random encounters for $\varepsilon = 0.5$ and n as indicated in the figure. The *dashed curve* is the result for $n \to \infty$

to maximize the advantage of strategy 1, i.e., $r = 1$ and $\varepsilon = 1/2$, we find that the stability of $x = 0$ is guaranteed provided that $m < m_s$ with $m_s = 1 - \frac{1}{2}n(n - 3)/(n^2 - 4n + 1)$ for $n > 4$. Note that m_s in [1/6,1/2] as n increases from 5 to ∞.

In the case both fixed points $x = 0$ and $x = 1$ are stable, the inner unstable fixed point is still given by the condition $F_1(x_u) = F_2(x_u)$ which now yields

$$x_u = \frac{1}{1 - m}\left(1 - m\frac{F_{11} - F_{12}}{F_{22} - F_{12}}\right)\left(1 + \frac{F_{11} - F_{12}}{F_{22} - F_{12}}\right)^{-1}. \tag{10}$$
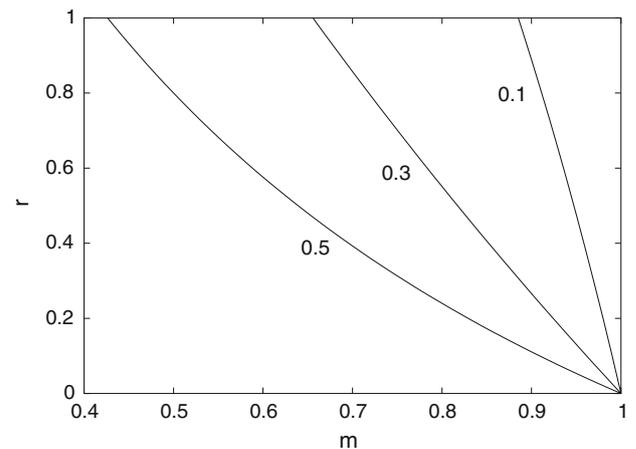

Fig. 3 Phase diagram in the plane (m,r) showing the regions where the fixed point $x = 0$ associated to the random meaning-signal mapping is unstable (above the curves) so the individuals using the structured communication code can dominate the population even when their initial frequency is vanishingly small. The parameters are $n = 10$ and $\varepsilon = 0.1, 0.3, 0.5$ as indicated in the figure
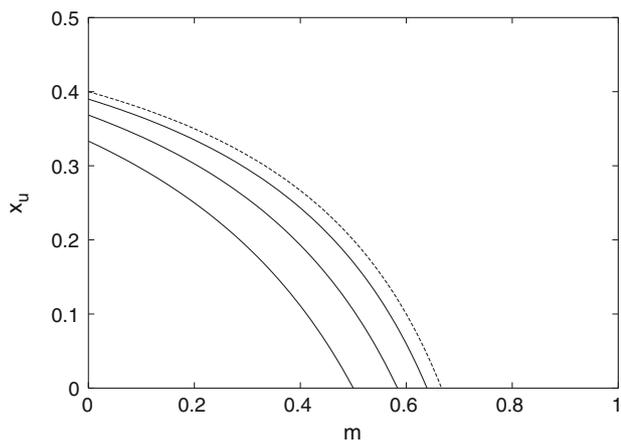
Fig. 4 Minimum fraction of individuals using structured communication necessary for this strategy to dominate the population in the case of nonrandom encounters for $\varepsilon = r = 0.5$ and (*solid curves from bottom to top*) $n = 4$, 5, and 10. The *dashed curve* is the result for $n \to \infty$

Figure 4, which exhibits the dependence of the threshold frequency x_u on the aggregation parameter m, reinforces the fact that $x_u = 0$ in the regions of the space of parameters where the fixed point associated with the random mapping strategy is unstable.

Spatially structured populations

In support to the findings of the previous section, here we report results of agent-based simulations where the spatial organization of the population is explicitly taken into account. In particular, we assume that N individuals are placed in equidistant sites on a ring (one individual per site), and each individual can interact with its Kth nearest neighbors only. The fully connected situation (i.e., an individual interacts with the $N - 1$ remaining individuals in the population) is recovered by setting $K = (N - 1)/2$. As before, the individuals can use either strategy 1 or strategy 2 and the payoff resulting from their interactions are given by Eqs. (1)–(3). We recall that each interaction comprises two events in which the individuals exchange roles as signaler and receiver.

The fitness of an individual is evaluated by computing the total payoff it obtains when interacting with its K nearest neighbors. Once the fitness of all individuals are known, we compute the total fitness of the population and then the relative fitness of each individual. The next step is to choose a single individual, say I, for replication with probability proportional to its relative fitness. The copy of I then replaces one of the $2K + 1$ individuals that belong to the neighborhood of influence of I and I itself. The choice of the individual to be discarded is done randomly without regard to their fitness values. This selection procedure is

essentially Moran model of population genetics (Ewens 2004), except for the fact that the offspring is placed in the region of influence of its parent, resulting in a situation where neighbors are likely to be genetically similar (Oliphant 1996). The repetition of this procedure for N times defines the time unit (one generation) of the dynamics. At the initial generation ($t = 0$), all individuals adopt strategy 2, except for a single mutant that uses strategy 1.

Figure 5 illustrates the time evolution of the fraction of individuals that use strategy 1 for four independent runs in the case an individual can interact only with its two first nearest neighbors ($K = 1$). We should note that these are not typical runs, since in a typical run the mutant lineage goes extinct in the very first generations. This figure highlights the stochastic character of the dynamics—the same initial setting can lead to very different outcomes, namely, the fixation or the extinction of the mutant lineage. To make this observation quantitative we record the outcome of 10^8 independent runs and present in Fig. 6 the fraction of them (P_s) that resulted in the fixation of the mutant lineage, i.e., of the structured communication code.

The most relevant information revealed by Fig. 6 is that the probability of invasion decreases exponentially with increasing K. In particular, for the data exhibited in the figure we find $P_s = a \exp(-bK)$ where $a \approx 0.03 + 0.47r - 0.23r^2$ is an increasing function of r in [0,1] whereas $b \approx 1.2(1 - r) + 0.46r^2$ decreases with increasing r in [0,1]. The results for different values of the noise parameter ε exhibit the same qualitative behavior. In addition, in the range of K considered here, we have found that the fixation probability P_s is practically insensitive to the population size N. According to Nowak et al. (2004), selection is said to oppose the replacement of the resident
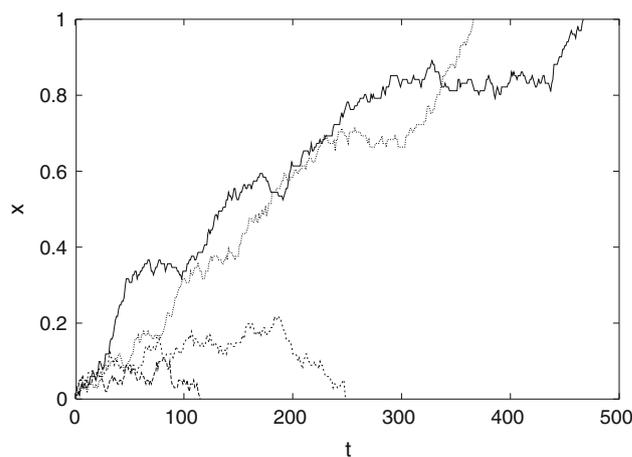

Fig. 5 Fraction of individuals that use strategy 1 in four population samples of $N = 101$ individuals placed in equidistant sites on a ring. Each individual can interact only with its first nearest neighbors ($K = 1$). The initial condition is $x_0 = 1/N$ and the parameters are $r = 1$, $\varepsilon = 0.5$, and $n = 10$
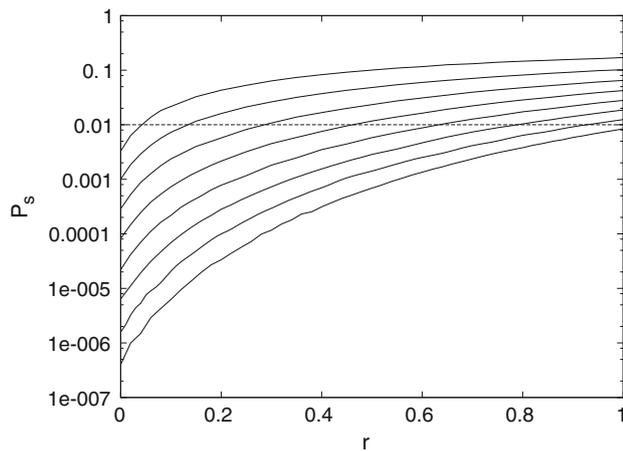
Fig. 6 Probability that the lineage of a single mutant that uses strategy 1 overtakes the resident population in a chain with $N = 101$ individuals, where each individual interacts with the $2K$ closest individuals (the Kth nearest neighbors). The parameters are $\varepsilon = 0.5$, $n = 10$ and (*top* to *bottom*) $K = 1,2,...,8$. The horizontal line represents the probability of invasion of a single mutant in the case of neutral selection ($P_s = 1/N$)

Fig. 7 Per capita growth rate of individuals using the structured communication code as function of the fraction of the population which adopts that strategy for $m = 0$ and $m = 0.9$ as indicated in the figure. The parameters are $n = 10$ and $\varepsilon = r = 0.5$

strategy if the probability of fixation of the single mutant is greater than the neutral value, $1/N$ (Ewens 2004), represented in Fig. 6 by the dashed horizontal line. In this context, for $K \geq 8$ selection opposes invasion by strategy 1, despite of this being the more efficient communication strategy, regardless of the value of the reward accrued to wrong meaning inferences.

In agreement with the findings of the previous section, the aggregation of individuals using the same communication system is ultimately the mechanism that lead to the spread of advantageous linguistic innovations in a population.

Discussion

Understanding how innovations that increase the expressive power of individuals can spread through a population and eventually become fixed is the essence of any evolutionary explanation to language evolution. However, the finding that the adoption of any particular trait (a structured communication code, in the present context) is better for a population, in the sense it yields an higher overall payoff, is no guarantee that such trait will actually spread in the population. As pointed out by Cavalli-Sforza and Feldman (1983), since communication takes place between two or more individuals, the selective process is frequency dependent and so communication cannot evolve in a simple scenario in which the individuals meet randomly. Those authors have argued that such obstacle can be removed, however, if the communication events occur predominantly
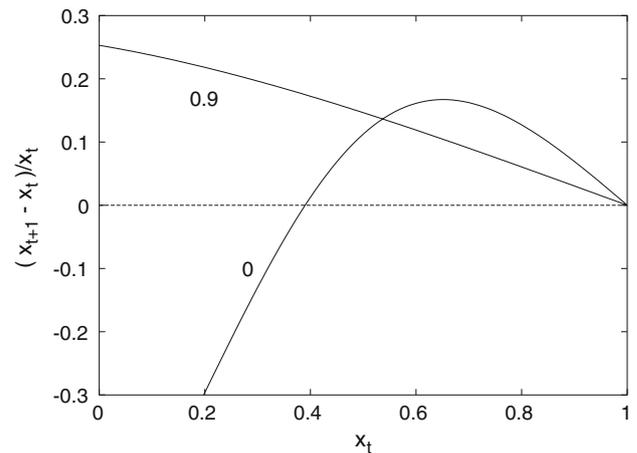
within the family or among close relatives. Interestingly, this same idea reappeared about ten years later as the "mother tongue" scenario, which purports that language evolved as a communication system used among kin, especially between mothers and their offspring, so as to resolve the difficulties inherent to the altruistic behavior of the signaller when passing relevant information to the receiver (Fitch 2004). This scenario is backed by recent experiments on young infants which provide evidence that the prejudice against other languages and, consequently, against speakers of other languages is innate: babies seem to promptly figure out which languages and accents belong to their own group and then show preference to speakers using their language and accent rather than to foreign speakers (Kinzler et al. 2007).

The paradox of the evolution of communication in a panmitic population is, in fact, an older idea: the very notion that intraspecific cooperation might lead to an inverse density dependence on the growth rate of some social animals is the essence of the Allee effect (Allee 1931) (see Courchamp et al. 1999 for a review). This effect is also referred to as the cost of rarity, which buffers an established community from invasion by other types and plays an essential role in the origin of sex theories (Michod 1995). Figure 7 illustrates the Allee effect, i.e., the inverse density dependence of the per capita growth rate in the case of random encounters ($m = 0$) as well as the usual density dependence in the case of strong assortative meetings ($m = 0.9$). The inverse density dependence is characterized by the part of the $m = 0$ curve for which the per capita growth rate is an increasing function of the density. This dependence is unusual since one expects that competition for limited resources should slow down the population growth as the number of individuals increases, a

phenomenon that actually happens when the density x_t becomes sufficiently large. Extinction is certain whenever the population of individuals who have strategy 1 reaches a frequency value for which the growth rate is negative.

In this contribution, we have expanded the work of Cavalli-Sforza and Feldman (1983) by showing that the emergence of different communication codes, even when clearly advantageous in comparison with the code adopted by the resident population, is likely to be established only if some aggregation (or segregation) mechanism is acting on the population. There is vast evidence of this process in the linguistic literature, the more recent is probably the development of the Black English Vernacular dialect in black ghettos in America (Pinker 1994). Our finding that, irrespective of the population organization, one of the communication codes will ultimately reach fixation in the population is at variance with the widespread dialect diversity observed in human society. Extra-linguistic factors (e.g., social motivation) seem to be necessary to explain this diversity (Nettle 1999; Patriarca and Leppanen 2004).

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