Could arbitrary imitation and pattern completion have bootstrapped human linguistic communication?

Citation for published version:
Theamariz, M 2011, ‘Could arbitrary imitation and pattern completion have bootstrapped human linguistic communication?’ Interaction Studies, vol. 12, no. 1, pp. 36-62. DOI: 10.1075/is.12.1.02tam

Digital Object Identifier (DOI):
10.1075/is.12.1.02tam

Link:
Link to publication record in Edinburgh Research Explorer

Document Version:
Peer reviewed version

Published In:
Interaction Studies

Publisher Rights Statement:
© Tamariz, M. (2011). Could arbitrary imitation and pattern completion have bootstrapped human linguistic communication?. Interaction Studies, 12(1), 36-62. 10.1075/is.12.1.02tam

General rights
Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and/or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.
Could arbitrary imitation and pattern completion have bootstrapped human linguistic communication?

Monica Tamariz

Language Evolution and Computation research unit

School of Psychology, Philosophy and Language Sciences

The University of Edinburgh

monica@ling.ed.ac.uk
Abstract

The present study explores the idea that human linguistic communication co-opted a pre-existing population-wide behavioural system that was shared among social group members and whose structure reflected the structure of the environment. This system is hypothesized to have emerged from interactions among individuals who had evolved the capacity to imitate arbitrary, functionless behaviour. A series of agent-based computer simulations test the separate and joint effects of imitation, pattern completion behaviour, environment structure and level of social interaction on such a population-wide behavioural system. The results support the view that a system that could be co-opted for linguistic communication might arise in a population of agents equipped with arbitrary imitation for the purposes of pattern completion interacting in certain kinds of structured environments. Such pre-linguistic behavioural system could have bootstrapped communication and paved the way for biological capacities widely believed to be necessary for communication, such as shared intentionality and symbolicity, to evolve.

Author’s biographical note: Monica Tamariz is researcher at the Language Evolution and Computation research unit at Edinburgh University, where she is involved in two research projects, one funded by AHRC and another one by ESRC. She did her PhD (2005) followed by an ESRC Postdoctoral Fellowship and a Leverhulme Early Career Fellowship in the same research unit. Her research focuses on systematicity in cultural systems resulting from evolutionary pressures.
1 Introduction

Much of human socially transmitted culture arguably depends on arbitrarily copying learnt patterns whose function or origin is often unknown to the learner. This idea is clearly illustrated by Gergely and Csibra (2006) Sylvia’s ham recipe story: Sylvia always cut the end of the ham when she cooked it because that is the way her mother did it; when the mother saw her do that, and asked why, Sylvia told her: “Because that is the way you always did it”. The mother explained that her pan was too small to hold a whole ham, and that was why she had to cut off the end. Children also engage in mindless imitation of elaborate actions even when they are obviously irrelevant for the desired goal (Horner & Whiten, 2005; Lyons, Young & Keil, 2007; Whiten et al., 1996), or even for no apparent goal, as illustrated by the personal observation, which partly inspired the present study, of a 24-month-old who, after seeing his mother clap her hands to try to catch moths on multiple occasions, interrupted his playing to clap when he saw a moth in the room, even if the moth was so far away he could not possibly catch it – and in fact he did not even attempt to.

This paper explores the role of mindless imitation in the origin of linguistic communication in our species. Recent approaches to the evolution of language propose that the hominin lineage evolved a unique biological adaptation, a socio-cognitive capacity characterized as “understanding others as intentional agents like the self” (Tomasello, 1999: 7) or as symbolic reference, the capacity to share conventional meanings for signals in a community (Deacon, 1997). These two biological adaptations presuppose and rely on non-communicative behaviour being already in place (Tomasello, Call & Gluckman. 1997). During the transition to language, previously non-communicative behaviour would come to be understood as
a reflection of others’ meanings or intentions. Imitation, or mimesis, has been proposed as one capacity that preceded and may have afforded the evolution of communicative behaviour (Donald, 1991; Zlatev, 2007). The study presented here is concerned with the origin of the pre-linguistic imitative behaviour system; it explores the characteristics it needed to have in order to have bootstrapped communication, the function it could have served and the conditions under which it could have appeared.

The computer simulations presented below model the cultural evolution of behaviour systems (which would have emerged from the biological evolution of the capacity to do arbitrary imitation for pattern completion). Specifically, the simulations test the hypothesis that a population whose members have the capacity for arbitrary imitation could develop a behaviour system that reflects the structure of the environment and is coordinated in the population; these two features would allow such system to bootstrap communication.

Tomasello (1999) has claimed that only human cultural behaviour involves true imitation, that is, replication of the means that another individual employed to obtain an end or function, as opposed to emulation, or achieving the same function as the other individual, regardless of the means employed. The present paper focuses on the kind of mindless imitation mentioned above, involving the replication of behaviour irrespective of whether the behaviour can be identifiable as a means to an end or not. Therefore, mutual interpersonal attention or intentionality (Uzgiris, Broome & Kruper, 1989) lies outside the scope of our definition of imitation. It can be argued that this kind of mindless or “function-independent” imitation is present in non-human species, particularly suboscine birds (Slater, 2003), which produce songs where elements of other songs are learned and then produced in novel combinations.
In these birds, the imitated vocal elements have no clear proximate function (Hindmarsh, 1986), even if the whole production does serve an ultimate function such as marking territory or attracting mates. It is interesting to note that at least in some of these animal groups, imitation is mediated by neural mechanisms homologous to those underlying human motor speech instructions (Jarvis, 2006; Haesler et al., 2007). The implication here is that bird song possesses some important prerequisites for linguistic function. This is reminiscent of Darwin’s musical protolanguage hypothesis (Darwin, 1871) whereby humans would have developed complex vocal imitation in the form of song to which meaning would then become associated.

Imitation of functionless components of behaviour in the great apes, which are phylogenetically closer to humans and therefore more relevant to the study of the evolution of communication, is not clear from an analysis of the literature (Tomasello, 1996; Whiten et al., 2004). The consensus seems to be that if they can do it, it is only to a very limited degree. Apes have been found to imitate behaviour sequences in order to obtain rewards, and indeed, diffusion chain studies have discovered that apes imitate sequences from conspecifics (Horner et al. 2006). However, imitation happens only when the sequence is either visibly functional or, if it is non-functional, only if this fact is not known to the subject (Horner & Whiten, 2005; see also discussion in Gergely & Csibra, 2006). In other words, chimpanzees learn behaviour sequences that they perceive as functional, since they achieve the desired goal. If they discover that an element of the sequence is not relevant to the efficiency of the mechanism, they stop producing that element.

Function-independent imitation is present in humans, as anecdotically illustrated by Sylvia’s ham recipe and the moth-clapping stories above. In those cases, the
replicated behaviour is not functional but it is nevertheless copied, perhaps because of a conformity bias or a pattern completion bias. Additionally, irrelevant or unnecessary elements of functional behaviours are also imitated. In the study mentioned above, Horner & Whiten (2005) also tested 4-year old children in the same tasks as the chimpanzees, and found that the children imitated the irrelevant actions to a higher degree than the chimpanzees. This adds to other studies where children who are presented with an apparatus and shown how to operate it in one of several possible ways tend to copy the procedure they have observed (Meltzoff, 1988, Flynn & Whiten, 2008). Here, the form of the imitated behaviour is arbitrary, but the behaviour is functional. Another set of studies that are relevant to the question of arbitrary imitation in humans includes Asch’s (1955) conformity experiments (although these are arguably modulated by more complex social motivations). In these experiments naïve participants give obviously wrong responses to questions in order to conform to the majority opinion. Although these studies focus on phenomena that are qualitatively different and involve much more complex factors including group dynamics, social prestige etc, they share with the above-reviewed work on mindless imitation the fact that imitated behaviours are non-functional. Here, the bias to imitate the majority behaviour is strong enough to override rationality and functionality and result in the production of arbitrary, non-functional behaviour.

The proposed driver of pre-linguistic functionless imitation is conformity emerging from pattern completion behaviour. Pattern completion relies on the activation of a complete representation upon exposure to a partial representation. A pattern can be the recurrent correlation of a number of stimuli, including objects and individuals in the environment and behaviour produced by oneself or by others,
during an individual’s experience. If the behaviour component is missing from an (incomplete) instance of a pattern learnt by an individual, this individual may, under a pattern-completion bias, produce the missing behaviour, thus completing the pattern. When the behaviour produced is a copy of the same behaviour previously observed in another individual, and if the behaviour itself has no current function other than to complete the pattern, we have an instance of arbitrary imitation for pattern completion.

Pattern completion is invoked as the fundamental cognitive mechanism in approaches to learning and cognition such as Sign Gestalt Expectancy (Tolman, 1932) and connectionism (Bishop, 1995; Ripley, 1996). It explains experimental results, from visual processing (Maloney et al. 2005), to language, with Pickering and Garrod (2007) proposing that during comprehension, the language production system acts as a simulator, constantly activating the most likely continuations of the present input (or completions of the current pattern), likelihood relating to predictability given previous experience. Pattern completion behaviour may be motivated by the drive reduction or secondary reinforcement (Mowrer 1956, Miller & Dollar, 1941; Osgood, 1953) that follows it. Secondary reinforcement refers to the relief and satisfaction experienced when an acquired negative emotion is reduced. Pattern completion behaviour releases the tension created by the discrepancy between a stored complete pattern and its current partial activation by actively resolving the discrepancy. This kind of secondary reinforcement may be pathologically exacerbated in the involuntary tics observed in some neurological conditions; compulsive behaviour and involuntary tics have been reported to be triggered by the need to correct feelings of “incompleteness” or “imperfection” that are relieved by the pathological behaviour in obsessive-
compulsive disorder (Janet, 1903; Rasmussen & Eisen, 1992; Summerfeldt, 2004) and Tourette syndrome and, especially, in patients suffering from both disorders simultaneously (Prado et al., 2008). Secondary reinforcement has also been proposed to be behind human fondness of music (Keller & Schoenfeld, 1950) in the form of fulfilling the expectations about the rhythmical and melodic structure that the input stream generates. Additionally, pattern completion can respond to cognitive pressures, as an associative learning mechanism benefits from preferential exposure to complete patterns because exposure to incomplete patterns introduces noise in the categorisation and processing of complete patterns (McClelland, 2001).

Imitative pattern completion behaviour requires that individuals are capable of making two kinds of cognitive abstractions. First, abstracting means away from function, or decoupling of behaviour from its iconic or primary utility function. This relates to pattern completion, as the functionality of behaviour resides in being the missing bit that completes the current context pattern. Second, it requires individuals to abstract behaviour away from the producer of the behaviour. This relates to imitation, as the individuals must assume that a token of a behaviour produced by oneself is equivalent to a token of the same behaviour produced by another individual. Two behaviour tokens are equivalent, for example, in the sense that both are equally good completions of a pattern. This is precisely the kind of abstraction that the mirror neuron system (Rizzolatti et al., 2001) can mediate.

The behaviours resulting from arbitrary imitation for pattern completion can be described as a form of cultural niche construction (Odling Smee, Laland & Feldman, 2003). Behaviours produced under this regime consistently correlate with other stimuli (those in the incomplete stimulus pattern) and thus increase the level of
structure of the environment that is perceived and processed by other members of the social group. These behavioural productions are structured patterns that are off-loaded onto the environment and result in the construction of a social niche or “external scaffold”. According to the situated and embodied cognition view (Clark, 1997), human communication and cognition rely heavily on this social niche. The new informational structure of the social environment, if properly exploited, may have benefits for the population, such as improving individual’s power of prediction. Thus the social niche may pose a selective pressure for (genetically specified) learning mechanisms to evolve and adapt to it.

The study described below assumes that arbitrarily imitative behaviour for pattern completion evolved biologically in hominin social groups prior to the appearance of linguistic communication. This assumes only a general cognitive change in the direction of relaxing the ties between representations; now individuals can play with behaviours without reference to their usual or original function or performer. However, the possible functions of such change and the evolutionary pressures it may have been responding to are outside the scope of the present study. Computer simulations are used to address one main question, namely whether the behavioural system resulting from that kind of imitation could have been co-opted for linguistic communication. Features of a system that can help bootstrap communication include bidirectional unambiguous mappings between representations of observed events (meanings) on the one hand, and behaviours (potential signals) on the other, which, according to Hurford (1989) are essential for the development of viable communication systems. It would also help if the mappings learned by the different individuals in a population were similar across individuals so that a
behaviour produced by an individual is associated to the same object (potential referent) by both producer and observer; this way, the association has a head start in the path towards conventionalisation. With such systematic, coordinated system in place, an individual’s behaviour would serve as a cue to potentially important environmental information. Observers no doubt would take advantage of those cues, as chimpanzees, for instance, do (Call, Agnetta & Tomasello, 2000). The ensuing near-communicative environment would pose a selective pressure for intentional modulation of one’s own behavioural responses to direct information more selectively, for instance to avoid giving away too much information to enemies or to make it more available to kin.

Two final assumptions implicit in the above-stated hypotheses are that there must be social contact among the individuals in a population to provide opportunities for observation of each other’s behaviours in context and that the environment is structured to some degree – the very process of learning as storage of information from current experience in order to guide future behaviour only makes sense if aspects of experience are likely to repeat themselves. We will examine the effects of the degree of contact among agents and the environment structure on the resulting systems’ potential to bootstrap communication.

The remainder of this paper describes a computer simulation study designed to test the hypothesis that arbitrary imitative behaviour for pattern completion could result in a system of (as yet functionless) mappings between objects and behaviours that could bootstrap communication. The focus is in the separate and joint impact of imitation, pattern completion, environment structure and social contact on mapping
coordination in the population and on the potential adequacy of these mappings both for production and comprehension in communication.

2 Research methodology

2.1 Agent-based computer simulation

The computer simulations employed to test the above hypotheses involve agents learning about their environment and producing their own behaviour. In this respect, they resemble many agent-based computational models of language evolution (e.g. Steels, 1997; Batali, 1998; Cangelosi & Parisi, 1998; Kirby, 2002; Vogt, 2005; see also Briscoe, 2002 for a review). Unlike most of those simulations, the present model does not involve shared goals, explicit symbolicity or intentional communication, and therefore it does not include mechanisms that help form conventional, shared mappings between objects and behaviours, such as the corrective feedback or knowledge transfer (e.g. Steels, 1997; Vogt, 2005) or the homonymy and synonymy dampers proposed by De Beule, de Vylder and Belpaeme (2006). For the same reason, the simulations also exclude grammar induction algorithms (e.g. Kirby 2002; Vogt 2005; Niyogi, 2006). Indeed, the aim of these simulations is to see if anything resembling a shared system of conventional mappings emerges in the absence of such processes, which can only be justified in terms of symbolicity or intentional communication.

The agents are exposed to successive contexts that contain objects from the environment and behaviours produced by themselves and by other agents present, and store information about what objects and behaviours cooccur in the same context. One parameter in the simulation is whether agents do imitation or not. This is implemented
by letting the agents have access to other agents’ behavioural productions or blocking that access, leaving everything else equal. Behaviour production is guided either by a pattern completion heuristic, which maximises the systematicity of the agents’ internal representation of the world in order to optimise correct pattern completion, or is produced randomly. Agents have a simple Hebbian associative learning algorithm (Hebb, 1949), akin to cross-situational learning (Siskind, 1996; Smith, Smith, Blythe & Vogt, 2006) based on cooccurrence: the level of association between two percepts (objects in the environment and behaviours) is proportional to the frequency with which they have cooccurred in the same context in an individual’s experience. In order to keep assumptions to a minimum, stored information is not processed or cleaned in any way (e.g. no lateral inhibition). Each agent’s memory is a symmetrical square matrix storing the cooccurrence counts between every pair of percepts (see Fig. 1).

The cooccurrence count for a pair of objects is increased by one for each time the two objects occur together in the same context. For a pair of item types (A, B) with \( n \) and \( m \) tokens respectively in the context, the cooccurrence frequency count is increased by \( n \times m \). The cooccurrence frequency count of an item type with itself is only increased if two or more tokens of the same item occur in the same context, in which case the self-cooccurrence count is increased by \( n \times (n - 1) \).
The simulation consists of a number of interactions in which the agents observe and interact with their environment. Each *interaction* consists of the following processes:

1. **Observer and producer selection.** The simulations are run with ten agents. At each interaction, a proportion of those ten agents in the population are randomly selected as *observers* of the current context (this proportion is a parameter in the simulation relating to social contact). Observers are present in the current interaction and will update their memory matrices at the end of it. One half of the observers are randomly selected as *producers* of behaviour, so in addition to observing, they will also contribute behaviours to the context.

2. **Context construction.** A *current context* is constructed by randomly selecting eight object tokens (which may be repeated) from a set of four object types.

3. **Behaviour selection and production.** Each producer in turn observes the current environment and selects an item from its behaviour repertoire applying either the pattern completion heuristic or the random heuristic (see 2.2.2). After all the producers have made their selections, the behaviours may be added to the context or not, depending on whether there is imitation or not (see 2.2.1).

4. **Memory matrix update.** After every producer has selected one behaviour, all behaviours are added to the context and then every observer increases the cooccurrence frequency count for each pair of element tokens (objects and behaviours) in the current context (that is, between each and every other element) in their memory matrix. (Self-cooccurrence of a token with itself is not counted.) Producers always have access to their own productions, and even in
the no-imitation condition they increase the correlation frequency counts of their own productions and other items in the context. See 2.2.1.

2.2 Factors

2.2.1 Imitation of others

In the pre-communication scenario simulated in these computer runs, we implement a simple form of imitation which does not involve intentionality or, obviously, communicative purpose. This factor models whether agents can abstract away a behaviour from its producer. An agent who has imitation considers that a behaviour produced by another individual is essentially identical, or has the same value (for example, to complete a pattern) as the same behaviour produced by itself. Conversely, an agent with no imitation will not see his own productions as equivalent to others’ productions of the same behaviour. This is implemented in relation to observational access to others’ behaviours.

In the imitation condition, each producer observes the objects in the context and selects a behaviour from its repertoire according to its heuristic (pattern completion or random). Note that at a given timestep, a producer’s behaviour selection does not take into account the other producers’ current behaviours, and behaviour selections are based only on the objects in the context. Once all producers have made their selections, crucially, all selected behaviours are added to the context. All observers then update the co-occurrence counts of the entire context in their memory matrices.

In the no imitation condition, the behavioural productions are not added to the common context and observers do not see other agents’ behavioural productions.
They only update the cooccurrence counts among objects, and between objects and their own (if any) productions.

2.2.2. Heuristic for the selection of behaviour for production

The second factor is the heuristic employed by the agents to select their behaviour: in the pattern completion heuristic condition, producers select and produce the behaviour that will lead to a memory matrix update that optimises pattern completion. This is implemented by selecting the behaviour that maximises the systematic structure of the overall cooccurrence matrix resulting from their individual experience over successive contexts. The metric of systematicity is based on RegMap (Tamariz & Smith, 2008), a quantification of the regularity of the mappings between two domains (e.g. between signals and meanings in a language). This metric is an information theoretical (Shannon 1948) formalisation of associative learning. It is based on conditional entropy $H(X|Y)$ (see Equation 1), a measure of uncertainty about one variable when another variable is known. This metric is closely related to de Jong’s (2000) measures of specificity and coherence, also used by Vogt & Coumans (2003). The main difference between them is that de Jong’s metrics are based on joint entropy, and are applied to each word (in our case, behaviour) or meaning (in our case, object) independently, while RegMap is based on conditional entropy and is applied to all behaviours or all objects at once. Equations 2 and 3 give the two directions of systematicity of one domain given the other. Equation 4 combines the previous two equations to obtain a measure of systematicity of the whole system. The conditional entropy is normalized between 0 and 1 by dividing by the logarithm of the number of elements in the first domain ($n_x$ in equation 2 and $n_y$ in equation 3) so that we can compare across systems of different sizes. This is then subtracted from one to

15
turn uncertainty levels into confidence levels. The overall systematicity $\text{Syst}(X, Y)$ is the geometric mean of the two conditional systematicities.

\begin{align*}
(1) \quad H(X \mid Y) &= - \sum_x \sum_y p(y)p(x \mid y) \log_2(p(x \mid y)) \\
(2) \quad \text{Syst}(X \mid Y) &= 1 - \frac{H(X \mid Y)}{\log(n_x)} \\
(3) \quad \text{Syst}(Y \mid X) &= 1 - \frac{H(Y \mid X)}{\log(n_y)} \\
(4) \quad \text{Syst}(X, Y) &= \sqrt{\text{Syst}(X \mid Y) \times \text{Syst}(Y \mid X)}
\end{align*}

In the control random heuristic condition producers select a random item from their behaviour repertoire. Comparing these two conditions tells us whether a pattern-completion bias has an effect on our two dependent variables, namely the coordination of the mappings and mapping systematicity, or the potential of the agents’ mental representations to bootstrap communicative production and comprehension.

2.2.3 Environment structure

The third factor, environment structure, includes three conditions. In the control, random condition, the environment has no structure. The probability of an object appearing in the current context of an interaction is equal to that of, and independent of, the appearance of, other objects (all objects are equally frequent). For object set $O = \{1, 2, 3, 4...n\}$, in the random condition, $\forall x \in O \rightarrow p(x) = \frac{1}{n}$. In the frequency-structured environment condition, the object set has an exponential frequency
distribution: $\forall x \in O \rightarrow p(x) = \frac{1}{2^x}$ (some objects are much more frequent than others). In the dependency-structured environment condition, the presence of some objects in the context condition the presence of others. In the simulations described below there are 4 types of objects in the environment $O = \{O_1, O_2, O_3, O_4\}$. During the construction of the current context, tokens of those types are added to the context. In the dependency-structured environment, whenever a token of object $O_1$ is added to the context, one token of object $O_3$ is also added; similarly, whenever a token of object $O_2$ is added to the context, one token of object $O_4$ is also added. This dependency is not symmetrical, so adding tokens of objects $O_3$ or $O_4$ do not imply adding tokens of any other objects. A comparison of the mapping coordination and mapping systematicity between agents obtained in these three conditions informs about the type of environmental structure where communication is more likely to have emerged given the assumptions in this study.

2.2.4 Social contact

Finally, the degree of social contact is manipulated: simulations are run with different proportions of the population present in each interaction (levels .2, .4, .6, .8 and 1). In every interaction in the simulation, only half of the agents present produce behaviour, the other half only observe. The simulations in the study reported below include ten agents, so for social contact value 0.2, two agents are present but only one produces behaviour at each interaction. At the other extreme, for social contact value 1, all ten agents are present and 5 produce behaviour.

2.3 Data analysis

2.3.1 Coordination of the mappings in the population
Two dependent variables are measured at the end of each run of the simulation based on the agent’s memory matrices. The first one is the level of mapping coordination, measuring the degree to which individuals in the population have reached similar mapping matrix subset states. This is quantified as the average of the correlation (Pearson’s $r$) between the mapping matrix subsets over agent pairs in the population. The second one is the systematicity of the mappings (see next section).

**2.3.2 Systematicity of the mappings**

Mappings that could be co-opted for communication need to be apt both for confident production and comprehension. The metric of systematicity in Equation 4 can conveniently be broken down into two components, shown in Equations 2 and 3. Given an agent’s experience, reflected in its memory matrix, $Syst(B|O)$ relates to confidence of production, as it reflects how confidently an agent can select behaviour when presented with an object. $Syst(O|B)$ relates to comprehension, as it reflects how confidently an agent can be of his selection of a referent for an observed behaviour.

The measures of systematicity for production and for comprehension are independent of each other, as illustrated in Fig 2. An individual with the experience stored in the cooccurrence matrix in Fig. 2 (left) can be relatively confident of his choice of behaviour when presented with an object, as reflected in the higher $Syst(B|O)$ value. For instance, for object 2 he can be relatively confident that producing behaviour B is correct, because 191 is so much higher than the other values in the row, that it is unlikely to be so due to chance. However, in comprehension he will not be as confident of his selection of object when observing a behaviour, as reflected by the lower $Syst(O|B)$. For example, for behaviour C, objects 3 or 4 will be selected, but with low confidence level, because all the values in that column are very
similar and differences may be due to chance. The memory matrix in Fig. 2 (right), in contrast, represents a near-optimal situation for communication, where the mappings between behaviours and objects approach one-to-one, with each behaviour being uniquely associated with a single object (and vice versa) with high confidence.

Insert Figure 2 about here.

The potential adequacy of the agents’ mappings at the end of the simulations under different conditions is assessed after examining the three systematicity metrics $Syst(B|O)$, $Syst(O|B)$ and $Syst(B,O)$.

Summing up, each simulation is run with 10 agents; at each interaction, the context includes 8 object tokens selected from a repertoire of 4 object types; of the agents present at each interaction (observers) half only observe and the other half also produce behaviour. The speaking agents have a repertoire of 4 behaviours to select from. Each simulation is run for 500 interactions, at the end of which the average coordination and systematicity of the agents’ mapping subset of their memory matrices are recorded.

The experiment design exhaustively combines two imitation conditions (imitation and no imitation); two heuristics to select and produce behaviour (pattern completion and random); three environment structures (random, frequency-structured and dependency-structured) and five levels of social contact (.2, .4, .6, .8 and 1). The simulations were run 135 times in each factor combination in the $2 \times 2 \times 3 \times 5$ design.
3 Results and discussion

Fig. 3 shows the mapping subsets of two agents out of the ten at the end of a simulation run for each imitation x pattern completion x environment structure condition. All shown matrices are obtained in social contact condition 0.6. Two agents from each run are shown to illustrate the degree of coordination among agents (the exact coordination value for the run is also given in the figure). The systematicity values are calculated as indicated in Fig. 2; Fig. 3 illustrates what drives these values in each case. The effects of all independent variables on each of the two dependent variables are discussed in sections 3.1 and 3.2 below, respectively. There will be extensive references to Fig. 3 throughout those sections to illustrate the different results.

Insert Figure 3 about here.

3.1 Coordination of the mappings

Fig. 4 shows the effects of imitation, pattern completion, environment structure and social contact on the mapping coordination, which measures the degree to which the mapping subsets of the agents’ memory matrices are correlated on average.
Comparing the upper-left graphs in Figs. 4a, 4b and 4c shows the isolated effect of the environment structure on coordination (one-way ANOVAs for all five social contact conditions return $p<0.001$). The random environment (Fig. 4a) returns values around 0, indicating that agents have not converged onto similar mapping matrices. In contrast, the structured environments (Figs. 4b and 4c) return significantly higher correlation values, indicating that the environment structure alone is enough to make mapping matrices converge even when agents produce behaviours in a non-imitative, random way. The skewed frequency distribution of the objects in the frequency environment is clearly reflected in agents’ mappings (see the mappings resulting from the frequency environment in Fig. 3(I)), which are therefore highly coordinated (Fig. 4b). The mappings arising from dependencies between objects (see mappings from the dependency environment in Fig. 3(I)) are better coordinated between agents than those arising from random structure, but less than those arising from the frequency structure (Fig. 4c).

By comparing the results in the upper left with the upper-right graphs in Figs. 4a, 4b and 4c, we can isolate the effect of pattern completion in the absence of imitation in each environment. In the pattern completion condition each agent behaviour production seeks to maximise the systematicity of its whole memory matrix. Without observation of one another’s production (“no imitation”), each agent finds its own solution, which is on average different from other agents’ solutions. This
is clear in all the mapping matrices on Fig. 3(II). Here, the agents participating in the same simulation run have reached equally valid, but differently structured solutions to the maximisation problem posed by the pattern completion heuristic. Mapping coordination is therefore very low. In the case of the random environment, the pattern completion heuristic alone changes the results only a little: 2-tailed t-tests in the five social contact conditions are significant for social contact values 0.8 and 1 only (compare the upper left and upper right graphs in Fig. 4a). The underlying mapping matrices, however, are quite different; in the baseline condition (random environment) all the mappings in an agent’s matrices have similar values, as can be seen the top two matrices in Fig. 3(I). When pattern completion is present (Fig. 3(II), top row), the values in one of the columns in each matrix are very high, but the high-value column is different for different agents. (Note that a given agent in many cases produces the same behaviour for all objects. This maximises the memory matrix’s systematicity for production Syst(B|O), and therefore increases the overall systematicity Syst(B,O). This behaviour is deleterious to one-to-one mappings, but these agents have no pressure for such mappings since they are not trying to communicate). In the case of the frequency and dependency-structured environments, pattern completion almost completely removes the strong positive effects of environment structure (compare the upper left with the upper right graphs in Fig. 4b and 4c). The matrices in the second and third rows in Fig. 3(II) illustrate why: here, too, one or two behaviours are produced most of the time, and the others almost never, and different agents have different preferred behaviours, which lowers the coordination values. However, traces of the environment structure (different frequencies or dependencies between objects)
are still noticeable in the matrices’ rows. Since agents share the environment, the coordination values do not drop to zero as they do in the random environment.

The lower-left graphs in Figs. 4a, 4b and 4c show the effect of imitation in the absence of pattern completion in the three environment structures. Imitation, as expected, has a strong impact on coordination (2-tailed t-tests of the effect of imitation on mapping coordination return $p<0.001$ for all social contact values in the three environment structures). Fig. 3(III) illustrates how the two matrices in each row reflect the structure of the relevant environment, and now they are also very similar to each other.

The lower right plots in Figs. 4a, 4b and 4c illustrate the interaction between pattern completion and imitation. Mapping coordination levels are significantly higher under the combined effect of these two factors in the three environment structures (the significance of the interaction is significant at $p<0.001$ level for all social contact conditions). Fig. 3(IV) show how in each run the agents produce one or two behaviours in the majority of cases, and these behaviour(s) are the same in all the agents in the population. Here, the very high coordination levels are driven not only by heuristic and the initial environment structure, but also by the fact that the behaviour that each agent produces (in a non-random way, following a pattern completion heuristic) becomes part of the environment that is observed and learned by the population, thus increasing its level of structure.

The effect of social contact is observed in all graphs in Fig. 4. Importantly, in the runs with imitation and pattern completion, linearly higher levels of social contact yielding mapping coordination values that are exponentially higher in value and present lower variances. Higher levels of social contact mean that within a simulation
run, agents, in effect, receive more exposures. The same results might therefore be achieved by running the same simulations with low levels of social contact for longer periods of time. This indicates that when these two factors are in place, very high coordination can be obtained with relatively little social contact, or in relatively little time.

3.2 Adequacy of the mapping structure for communication

For a behavioural system to be able to bootstrap communication it has to be coordinated in the population (see previous section) and also, the mappings between objects and behaviours have to be one-to-one. In other words, they have to be systematic both for production and for comprehension. Systematicity of the mappings for production, for comprehension as well as the overall systematicity in all condition combinations are explored in this section.

These results suggest that the interaction of pattern completion and imitation has the strongest positive impact on mapping coordination in all environment structures.

3.2.1 Mapping systematicity for production

Fig. 5 shows the levels of Syst(B|O), measuring the confidence of agents in their choice of produced behaviours, in all the studied conditions.

Insert Figure 5 about here.

Comparing the upper left graphs in Figs. 5a, 5b and 5c shows that the environment structure makes no difference to the level of Syst(B|O). We can
conclude that the environment structure alone is not enough to generate mapping systemicity for production at any social contact level. Moreover, the results for the different combinations of imitation and pattern completion are very similar in the three environments.

The most striking result in Fig. 5 is the difference between the two graphs on the left in each of Figs. 5a, 5b and 5c and those on the right. This points to the crucial effect of pattern completion on mapping systemicity for production. When pattern completion is not in place, the systemicity of the mappings for production is negligible; when it is in place, we observe high values across the board. This is not surprising given that (a) the pattern completion heuristic makes sure that agents maximise the systemicity of their memory matrix and (b) the only action agents can take is produce behaviours. This result confirms that maximising the systemicity of the whole memory matrix also maximises the systemicity (for production) of the mapping subset of the memory matrix.

Focusing on the simulation runs where pattern completion is in place (graphs on the right-hand side of Figs. 5a, 5b and 5c), imitation (lower right graphs) increases the range of results in all environment conditions. This reflects the fact that when agents do not observe each other (no imitation), the pattern completion heuristic allows each agent to find its own individual matrix configuration with high systemicity for production, with no interference from other agents’ solutions. We saw in section 3.1 that imitation –observing each other’s productions– leads to very high mapping coordination values. Sometimes the “consensus” mapping shared by the population will be more systematic for production than the mapping the average individual attains (in the no imitation condition) and sometimes it will be worse. The
distribution of $Syst(B|O)$ values in the imitation and pattern completion conditions therefore shows a clear bimodality (Fig. 6).

Insert Figure 6 about here

Imitation also accentuates the effect of social contact. When imitation is present, at social contact level 0.2, for instance, only two agents are present at each interaction, and only one of them produces behaviour. An agent is thus exposed to the productions of another agent who may initially have very different mappings from its own, and therefore may produce different behaviours in a given context. During cross-situational learning, this means that for each agent, an object may become associated with several different behaviours, and the certainty of which behaviour should be selected when prompted by an object decreases. In a few cases, however, when all agents independently converge on the same object-behaviour mappings by chance, observing other’s behaviours reinforces the mappings, and the systematicity for production will be higher than with no imitation. At higher social contact levels this effect is not so strong. For instance, at contact level 0.6, six agents are present at each interaction and three of them produce behaviours. Crucially, the likelihood of two or more producers in the same interaction sharing the same mappings increases with social contact level. Producers with the same mappings will produce the same behaviour in a given context, and observers’ counts of that majority behaviour then increase, so that the same behaviour in turn is more likely to be produced in response to the same context when the observer becomes a producer in a future interaction (in other words, selection of a behaviour for production is more confident: higher $Syst(B|O)$).
These results suggest that pattern completion strongly contributes to mapping systematicity for production in all environment structures.

3.2.2 Mapping systematicity for comprehension

Figure 7 shows the levels of $Syst(O|B)$, measuring the confidence that objects are unambiguously related to behaviours in all the studied conditions.

The most salient result in Fig. 7 is the effect of environment structure on mapping systematicity for comprehension $Syst(O|B)$. Comparing the upper left graphs in Figs. 7a, 7b and 7c we see the isolated effect of this factor. Frequency structured and, to a lesser extent, dependency structure, return mapping systematicity for comprehension levels that are significantly different from those in the random environment (one-way ANOVAs return $p<0.001$ for all social contact levels).

$Syst(O|B)$, calculated on the mapping matrices as illustrated in Fig. 2, measures the confidence of selecting objects given behaviours, a task on which agents are not evaluated or are not maximising in the simulations. Consider the upper left quadrant in Fig. 4. In the top row we have matrices from the random environment. Given for instance behaviour A, object 1 is selected because it has the highest cooccurrence count in that column, but the confidence of that selection is very low, as all the figures in the column are very similar. In the middle row (frequency-structured environment), given any behaviour A, B, C or D, object 4 will always be selected, with a fair amount of confidence, hence the $Syst(O|B)$ value 0.18. In the bottom row (dependency-
structured environment), the variance in each column is higher than in the top row, returning slightly higher confidence values.

This pattern repeats itself for the frequency environment in all imitation and pattern completion conditions (Fig. 7b). And neither pattern completion nor imitation has any effect in the random environment (Fig. 7a). We therefore focus on the dependency-structured environment (Fig. 7c) for the remainder of this discussion.

**Pattern completion** alone greatly increases $Syst(O|B)$. The mapping matrices in Fig. 3(II) (bottom row), if far from having one-to-one correspondences between objects and behaviours, show increased confidence of choice of an object given a behaviour at least in two of the columns. For instance, in the left-hand column for behaviour C we can be very confident that it does not map onto object 4, and for behaviour D, we can be very confident that it maps onto behaviours 1 or 2. The uncertainty is greatly reduced with respect to the other two environments, hence the higher $Syst(O|B)$ level of 0.43.

**Imitation** alone (lower left graph in Fig. 7c) has no effect on $Syst(O|B)$, but it interacts with pattern completion (lower right graph in Fig. 7c). As we saw earlier, imitation enhances the mapping coordination between agents and this results in a wider range of systematicity values. Under the imitation and pattern completion conditions, the distribution of $Syst(O|B)$ values shows a clear bimodality but only in the dependency-structured environment (Fig. 8). In the simulation run illustrated in Fig. 3(IV) (bottom row), this lead to a near-consensus mapping matrix that returns a $Syst(O|B)$ of 0.30. However, many runs returned matrices where only one behaviour was ever produced, much like in the random condition, with $Syst(O|B)$ values around 0.
Social contact does not affect the level of mapping systematicity for comprehension, since the social dynamics do not alter the main factor driving that level, namely the underlying structure of the environment.

These results indicate that the environment structure has a strong impact on mapping systematicity for comprehension, with the highest levels of systematicity obtained in the dependency-structured environment.

It is important to note, however, that systematicity for comprehension never attains very high values like mapping systematicity for production does (Fig. 5). This is because the effect of pattern completion heuristic on the former is stronger than that of the environment on the latter. Other kinds of environment structure might well result in very high mapping systematicity for comprehension values.

3.2.3 One-to-one mappings

In the previous sections we have seen that pattern completion in conjunction with imitation return levels of both $Syst(B|O)$ and $Syst(O|B)$ that are significantly different from chance in the structured environments.

In the frequency-structured environment, however, the mappings are far from being one-to-one. Close inspection of the matrices that return the highest $Syst(B|O)$ and $Syst(O|B)$ values in the frequency structured environment (Fig. 3(II) and (IV), middle row) reveal that the same object will be selected for no matter what behaviour, and the same behaviour will be selected for no matter what object. Only in the
dependency-structured does something approaching one-to-one mappings ever arise. Here, a more varied repertoire of behaviours unambiguously can be associated to specific objects, a crucial advantage if communication is to build on the system.

We therefore focus on the simulation runs in the dependency-structured environment, with imitation and pattern completion in place. It is under these conditions that we saw bimodal distributions of mapping systematicity values both for production and for comprehension. Fig. 9 indicates that there is a trade-off between $Syst(B|O)$ and $Syst(O|B)$.

Insert Figure 9 about here

Bimodal distributions only occur in the dependency-structured environment, but not in the other two (Fig. 9). Here, two clusters of values are apparent: one with very high $Syst(B|O)$ and very low $Syst(O|B)$ and another one with lower (but still significantly higher than the control, random environment condition) $Syst(B|O)$ and higher $Syst(O|B)$ around 0.30. The values in the latter cluster, with a better balance of $Syst(O|B)$ and $Syst(B|O)$, represent situations that might bootstrap communication.

4 Conclusion

The objective of the present study was to explore the effect of a hypothesized capacity for function-independent or arbitrary imitation for pattern completion on the emergence of a behavioural system with the potential to bootstrap linguistic communication. The requirements for such behavioural systems are systematic mappings between behaviours and objects that could be useful both for production and comprehension (one-to-one mappings where distinct behaviours are associated...
with distinct objects) and coordination of those mappings in the population. It was argued that given such a behaviour system, behaviour productions could subsequently be used by observers as cues; this would pose selective pressure for the producer’s intentional modulation of their own productions, leading to the emergence of communication.

The analysis of the results of the computer simulation study indicates that (a) imitation leads to high coordination of the mappings in the population, given enough social contact; (b) pattern completion enhances mapping systematicity for production; (c) environment structure – whether frequency or dependency related – results in systematic mappings for comprehension; (d) in a dependency-structured environment, distinct behaviour-object mappings arise about half of the times even though there is no pressure for them to be in place and they are not serving a specific function; (e) under optimal conditions, a relatively low degree of social contact is enough to achieve high mapping coordination as well as mapping systematicity for production and comprehension. All of this suggests that human communication may have built on a pre-existing shared public behavioural system arising from imitation for the purposes of pattern completion in a dependency-structured environment.

It is important to note that even under the best conditions, one-to-one mappings that would obtain maximal systematicity values are never attained. This could perhaps be remedied if the associative learning mechanism included lateral inhibition or another synonymy-damper mechanism. This was not explored in this study so as to minimise assumptions of mechanisms usually related to communication, but it is worth exploring in future research.
The pivotal biological adaptation necessary for the emergence of coordinated, systematic mappings in a population is arbitrary imitation. This capacity is absent in our closes relatives, non-human primates. It requires an assumption of independence between behaviour and its producer so that a behaviour produced by oneself is equivalent to the same behaviour produced by another individual. It also requires abstracting away behaviour from its utility, primary or iconic, function, which allows a more arbitrary pattern-completion function to drive behaviour production. The present study illustrates how arbitrary imitation for pattern completion could generate a population-wide, highly systematic behaviour system that could have bootstrapped communication. Moreover, it illustrates how this kind of arbitrary imitation could have preceded shared intentions, symbolicity and other socio-cognitive capacities, a possibility that should inform the study of the evolution of communication, language and culture.

Acknowledgements

This research was funded by a Leverhulme Early Career Fellowship. The author also wishes to acknowledge helpful comments to the manuscript by Dan Dediu and three anonymous reviewers.

References


Figure captions

Figure 1. An agent’s memory matrix at timestep 300 of a simulation run. The figures indicate the number of times that the agent has observed the two elements occur simultaneously in the same context. The upper left shaded area corresponds to the object-object associations; the lower right shaded area corresponds to the behaviour-behaviour associations; the two white areas correspond to the object-behaviour associations or mappings. It is the latter that may potentially bootstrap linguistic communication. Note that the complete matrix and the object and behaviour matrix subsets are symmetrical; each mapping matrix subset is not, but both mapping subsets are mirror images of each other.

Figure 2. Systematicity measured in the object-behaviour subsets of two memory matrices. Overall systematicity $\text{Syst}(B,O)$ is broken down into $\text{Syst}(O|B)$ (comprehension) and $\text{Syst}(B|O)$ (production). The matrix on the left shows the object-behaviour mappings from the same simulation run as Fig. 1. Here, production is more ambiguous than comprehension. The matrix on the right does not come from any of the simulations in this study, but is shown here for illustrative purposes. Here, both production and comprehension are highly systematic, as the associations between objects and behaviour approach one-to-one.

Figure 3. Mapping matrices from agents at the end of simulation runs in different condition combinations. Each of quadrants I, II, III and IV shows a
combination of imitation and pattern completion conditions. Each row within a quadrant corresponds to an environment structure condition. The two agents in each row are representative examples of the ten agents in one simulation run in the relevant condition combination. Each matrix shows the cooccurrence frequency counts of behaviours and objects in the agent’s experience over the 500 timesteps in the simulation. The social contact for these simulations was 0.6 in all cases. The average mapping coordination value $Coord$ as well as the systematicity of the mappings for production $Syst(B|O)$ and for comprehension $Syst(O|B)$ for all the agents in each run are shown below each matrix pair.

Figure 4. Mapping coordination in the agent population in the four combinations of imitation and pattern completion and the five levels of social contact (a) in the random environment, (b) in the frequency-structured environment and (c) in the dependency-structured environment. N=135 for each factor combination.

Figure 5. Systematicity of the mappings for production $Syst(B|O)$ in the four combinations of imitation and pattern completion and the five social contact conditions (a) in the random environment, (b) in the frequency-structured environment and (c) in the dependency-structured environment. N=135 for each factor combination.
Figure 6. Bimodal distribution of mapping systematicity for production $Syst(B|O)$ values with imitation and pattern completion in the dependency-structured environment at social contact level 0.6.

Figure 7. Systematicity of the mappings for comprehension $Syst(O|B)$ in the four combinations of imitation and pattern completion and the five levels of social contact (a) in the random environment, (b) in the frequency-structured environment and (c) in the dependency-structured environment. N=135 for each factor combination.

Figure 8. Bimodal distribution of mapping systematicity for comprehension $Syst(O|B)$ values with imitation and pattern completion in the dependency-structured environment at social contact level 0.6.

Figure 9. Mapping systematicity for comprehension $Syst(O|B)$ plotted against mapping systematicity for production $Syst(B|O)$ at social contact level 0.6, in the imitation and pattern completion conditions. The three environment structures are shown for comparison.
Figure 1.

<table>
<thead>
<tr>
<th>OBJECTS</th>
<th>BEHAVIOURS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>12 311 175 311</td>
</tr>
<tr>
<td>2</td>
<td>81 174 308 634</td>
</tr>
<tr>
<td>3</td>
<td>175 308 566 1114</td>
</tr>
<tr>
<td>4</td>
<td>311 634 1114 2260</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>BEHAV.</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>12</td>
<td>19</td>
<td>26</td>
<td>71</td>
</tr>
<tr>
<td>B</td>
<td>91</td>
<td>191</td>
<td>359</td>
<td>695</td>
</tr>
<tr>
<td>C</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>D</td>
<td>28</td>
<td>62</td>
<td>107</td>
<td>235</td>
</tr>
</tbody>
</table>
Figure 2.

| OBJS | BEHAVIOURS |  | Syst(B|O) | Syst(O|B) | Syst(B,O) |
|------|------------|---|---------|---------|----------|
|      | A | B | C | D |              |         |         |
| 1    | 12 | 91 | 1 | 28 | 0.43       | 0.14    | 0.27    |
| 2    | 19 | 191| 1 | 62 | 0.80       | 0.78    | 0.79    |
| 3    | 26 | 359| 3 | 107| 0.35       | 0.43    | 0.58    |
| 4    | 71 | 695| 3 | 235| 0.56       | 0.45    | 0.51    |

Syst(B|O) = 0.43
Syst(O|B) = 0.14
Syst(B,O) = 0.27

Syst(B|O) = 0.80
Syst(O|B) = 0.78
Syst(B,O) = 0.79
<table>
<thead>
<tr>
<th>(I)</th>
<th>NO Imitation, No Pattern Completion</th>
<th>(II)</th>
<th>NO Imitation, Pattern Completion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RANDOM ENVIRONMENT</td>
<td>RANDOM ENVIRONMENT</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Behaviours</td>
<td>Behaviours</td>
<td>Behaviours</td>
</tr>
<tr>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
</tr>
<tr>
<td>1</td>
<td>86</td>
<td>66</td>
<td>93</td>
</tr>
<tr>
<td>2</td>
<td>66</td>
<td>95</td>
<td>64</td>
</tr>
<tr>
<td>3</td>
<td>96</td>
<td>96</td>
<td>58</td>
</tr>
<tr>
<td>4</td>
<td>58</td>
<td>80</td>
<td>75</td>
</tr>
<tr>
<td>Coord=.04</td>
<td>Syst(B)O=.01</td>
<td>Syst(O)B=.00</td>
<td>Coord=.19</td>
</tr>
<tr>
<td></td>
<td>FREQUENCY-STRUCTURED ENVIRONMENT</td>
<td>FREQUENCY-STRUCTURED ENVIRONMENT</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Behaviours</td>
<td>Behaviours</td>
<td>Behaviours</td>
</tr>
<tr>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
</tr>
<tr>
<td>1</td>
<td>28</td>
<td>14</td>
<td>17</td>
</tr>
<tr>
<td>2</td>
<td>35</td>
<td>49</td>
<td>31</td>
</tr>
<tr>
<td>3</td>
<td>76</td>
<td>81</td>
<td>63</td>
</tr>
<tr>
<td>4</td>
<td>181</td>
<td>176</td>
<td>129</td>
</tr>
<tr>
<td>Coord=.91</td>
<td>Syst(B)O=.00</td>
<td>Syst(O)B=.18</td>
<td>Coord=.07</td>
</tr>
<tr>
<td></td>
<td>DEPENDENCY-STRUCTURED ENVIRONMENT</td>
<td>DEPENDENCY-STRUCTURED ENVIRONMENT</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Behaviours</td>
<td>Behaviours</td>
<td>Behaviours</td>
</tr>
<tr>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
</tr>
<tr>
<td>1</td>
<td>40</td>
<td>32</td>
<td>12</td>
</tr>
<tr>
<td>2</td>
<td>68</td>
<td>66</td>
<td>40</td>
</tr>
<tr>
<td>3</td>
<td>68</td>
<td>66</td>
<td>56</td>
</tr>
<tr>
<td>4</td>
<td>40</td>
<td>56</td>
<td>80</td>
</tr>
<tr>
<td>Coord=.53</td>
<td>Syst(B)O=.01</td>
<td>Syst(O)B=.04</td>
<td>Coord=.13</td>
</tr>
<tr>
<td></td>
<td>FREQUENCY-STRUCTURED ENVIRONMENT</td>
<td>FREQUENCY-STRUCTURED ENVIRONMENT</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Behaviours</td>
<td>Behaviours</td>
<td>Behaviours</td>
</tr>
<tr>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
</tr>
<tr>
<td>1</td>
<td>293</td>
<td>297</td>
<td>335</td>
</tr>
<tr>
<td>2</td>
<td>294</td>
<td>332</td>
<td>354</td>
</tr>
<tr>
<td>3</td>
<td>271</td>
<td>296</td>
<td>335</td>
</tr>
<tr>
<td>4</td>
<td>286</td>
<td>307</td>
<td>304</td>
</tr>
<tr>
<td>Coord=.15</td>
<td>Syst(B)O=.00</td>
<td>Syst(O)B=.00</td>
<td>Coord=.099</td>
</tr>
<tr>
<td></td>
<td>DEPENDENCY-STRUCTURED ENVIRONMENT</td>
<td>DEPENDENCY-STRUCTURED ENVIRONMENT</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Behaviours</td>
<td>Behaviours</td>
<td>Behaviours</td>
</tr>
<tr>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
</tr>
<tr>
<td>1</td>
<td>81</td>
<td>76</td>
<td>84</td>
</tr>
<tr>
<td>2</td>
<td>160</td>
<td>140</td>
<td>156</td>
</tr>
<tr>
<td>3</td>
<td>336</td>
<td>282</td>
<td>283</td>
</tr>
<tr>
<td>4</td>
<td>703</td>
<td>622</td>
<td>589</td>
</tr>
<tr>
<td>Coord=.98</td>
<td>Syst(B)O=.00</td>
<td>Syst(O)B=.18</td>
<td>Coord=.99</td>
</tr>
<tr>
<td></td>
<td>FREQUENCY-STRUCTURED ENVIRONMENT</td>
<td>FREQUENCY-STRUCTURED ENVIRONMENT</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Behaviours</td>
<td>Behaviours</td>
<td>Behaviours</td>
</tr>
<tr>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
</tr>
<tr>
<td>1</td>
<td>112</td>
<td>144</td>
<td>168</td>
</tr>
<tr>
<td>2</td>
<td>264</td>
<td>280</td>
<td>324</td>
</tr>
<tr>
<td>3</td>
<td>308</td>
<td>292</td>
<td>276</td>
</tr>
<tr>
<td>4</td>
<td>272</td>
<td>296</td>
<td>308</td>
</tr>
<tr>
<td>Coord=.88</td>
<td>Syst(B)O=.00</td>
<td>Syst(O)B=.03</td>
<td>Coord=.99</td>
</tr>
</tbody>
</table>

Figure 3.
Figure 4.

(a) Random environment

(b) Frequency-structured environment

(c) Dependency-structured environment
Figure 5.

(a) Random environment
(b) Frequency-structed environment
(c) Dependency-structured environment
Figure 6.
Figure 7.

(a) Random environment

(b) Frequency-structured environment

(c) Dependency-structured environment
Figure 8.
Figure 9.