Coevolutionary Investments in Human Speech and Trade

Richard D. Horan,[1] Erwin H. Bulte,[2] and Jason F. Shogren[3]

1: Department of Agricultural Economics, Michigan State University,
East Lansing, MI 48824-1039, USA
horan@msu.edu, ph: (517) 355-1301; fax: (517) 432-1800

2: Department of Economics, Tilburg University,
P.O. Box 90153, 5000 LE Tilburg, Netherlands, e.h.bulte@uvt.nl

3: Department of Economics and Finance, University of Wyoming,
Laramie, WY 82071-3985, USA, jramses@uwyo.edu

1

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Abstract: We propose a novel explanation for the emergence of language in modern humans, and the lack thereof in other hominids. A coevolutionary process, where trade facilitates speech and speech facilitates trade, driven by expectations and potentially influenced by geography, gives rise to multiple stable development trajectories. While the trade-speech equilibrium is not an inevitable outcome for modern humans, we do find that it is a relatively likely result given that our species evolved in Africa under climatic conditions supporting relatively high population densities.

1. Introduction

The emergence of human speech is one of the great mysteries of science. Scientists wonder over both *when* and *why* human speech developed (Holden 1998).[1] The question of *when* arises because of a 100,000+ year gap between the morphological development of speech (e.g., descent of the larynx; restructuring of the basicranium) and what many people consider to be unequivocal evidence of speech (e.g., art, symbols, and advanced tools that indicate sophisticated communication was taking place; see Holden 1998). Evidence suggests the necessary morphology appeared some 150,000-200,000 years ago; whereas clear evidence of spoken language does not exist until the Upper Paleolithic explosion about 40,000 years ago.[2] However,

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[1] In this paper, we focus primarily on *why*; but since *why* is conditional on the answer to *when*, we begin the story there.

[2] See for instance Holden (1998) and Lieberman (1984, 1998). While the morphology was in place 150,000-200,000 years ago, it did not appear over night. Aeillo and Dunbar (1993) point to other key developments in language evolution up to 250,000-400,000 years ago. And before that, *Homo erectus* could have been using

Lieberman (1998) argues this gap is a chimera—the morphology had to evolve for speech because it was simply too costly otherwise, e.g., it increased the risk of choking to death and reduced respiratory efficiency. Other experts agree that speech is a biological adaptation (Pinker and Bloom 1990), arguing that our present day inability to find convincing historical evidence better explains this 100,000+ year lag than any alternative theory (e.g., Holden, 1998, offers a variety of reasons).[3]

If one accepts this evolution-for-speech argument as provisionally settled for now, the second fundamental question of *why* speech developed still remains unresolved.[4] Since the primary evolutionary benefits of speech arise from social interactions (Knight et al. 2000), one can speculate that hominid behaviors provided the impetus. But which behaviors triggered speech? The challenge here is that detailed evidence of hominid behaviors is more difficult to unearth from the archaeological record than morphological changes, particularly prior to the Upper Paleolithic explosion. Several behavioral theories provide plausible explanations for *why* speech emerged. Most of these theories are based on altruistic or cooperative motives. Some argue the primary advantage of speech was to acquire secondary knowledge from an altruist willing to provide that information (Pinker and Bloom 1990). But others point out that free-riding, deception, and cheating could make reliance on second-hand information an unreliable

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primitive *proto-language* as far back as 500,000 – 1.5 million years ago (Knight et al. 2000). Finally, note the Upper Paleolithic explosion is a cultural explosion characterized by faster rates of innovation, more use of art and symbols, and cultural interactions (e.g., more advanced exchange networks). Also see Tattersall and Schwartz (2000) and Gamble (1999).

[3] Corballis (2002) suggests the morphology could have initially been used to produce songs useful in some sexual selection process, and that speech emerged later. He acknowledges (as do many others), however, that proto-language would have been used in conjunction with hand and facial gestures during this morphological evolution. Some experts believe speech would have evolved concurrently (e.g., Lieberman 1998).

[4] If Leiberman's hypothesis is incorrect, speech *capabilities* (via morphological developments) would have evolved separately from the *use of language*, in which case the benefits of language acquisition could have come at minimal cost since the morphology would have already existed. We might expect that language developed in response to the many social interactions in which it proved useful. See Hurford et al. (1998) for several theories of language evolution (as opposed to speech).

strategy (e.g., Knight et al. 2000).

Another cooperation strategy is based on the observation that primates "groom" each other to help support relationships, which suggests that language is a form of *vocal grooming* that could enable larger, more stable communities by allowing each individual to groom more people (Dunbar 1996). But again others counter that vocal grooming is "cheap" relative to physical grooming (or other forms of non-vocal signals) and may be unreliable (see Knight et al. 2000; Desalles 2000). They suggest costly rituals are required to improve the believability of signals (Knight 1998), and that speech could have evolved along with social contracts (Deacon 1997; see also Gifford 2004).[5] Others suggest evolutionary stable vocalization equilibria can arise when rules of kin selection or spatial selection are in place (Livingstone and Fyfe 2000), or that both costly and cheap (but honest) signals can emerge in a cooperative game in which a signaler tries to manipulate the receiver when it is in the receiver's best interest to be manipulated (see Noble 2000). Finally, some cooperative theories suggest speech emerged, but possibly after the morphology was in place, to free up hands otherwise used to communicate through gesture or to converse in the dark (e.g., Corballis 2004).

A few theories have been developed around competitive motives. Desalles (2000) suggests language could have evolved under conditions of political competitions between coalitions. Another idea is Ofek's (2001) theory of a *verbal arms race*. He argues speech and other brainpower investments were the result of runaway competition promulgated by trade, i.e., an arms race. He envisioned competition for trading partners, with better communicators gaining the relative advantage. The result is runaway selection – a Red Queen game, in which investments in speech capabilities run amok and no one gains a true competitive advantage.

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[5] There is a substantial literature on the evolution of altruistic behaviors and social institutions. We do not attempt to

The literature focuses on the conditions under which speech could emerge as an evolutionary stable equilibrium. But a convincing behavioral model should also explain why speech emerged in *Homo sapiens* and why other hominids did *not* develop human speech capabilities.[6] *Homo sapiens* evolved from *Homo heidelbergensis* (Smithsonian 2005a; Ward and Stringer 1997) and acquired human speech capabilities in the process—the only hominids to have acquired this capability (Lieberman 1998). For instance, like *Homo sapiens, Homo neanderthalensis* evolved (albeit somewhat earlier) from *Homo heidelbergensis* (Smithsonian 2005a; Ward and Stringer 1997), but did not acquire human speech capabilities (Lieberman 1998).[7] Why? Neanderthals and other hominids could have also benefited from unfettered hands, nighttime communication, improved knowledge, and an evolutionary speech investment trajectory.

Herein we develop a model of the coevolution of trade and speech that proposes a novel explanation for the question of *why* speech developed for *Homo sapiens* only. Our model combines the trade-no trade insight of Ofek (2001) and Horan et al. (2005) to consider a coordination game, in which the existence of multiple equilibria leads to an evolutionary split in the development of speech. In general, economic models of trade exhibit multiple equilibria due to strategic complementarities—more trade by one agent increases the productivity of trade by

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cover all of it here; see Bowles et al. (2003) for a recent analysis.

[6] Perhaps Livingstone and Fyfe's (2000) analysis comes close to this, as they describe how different spatial population structures may affect whether language evolves in a coevolutionary model of speech and physiology.

[7] Scientific classification of the hominid phylogeny (i.e., the hominid evolutionary tree) has changed in recent years due to new molecular findings (e.g., Ward and Stringer 1997). Lieberman (1998) refers to *Homo erectus* as the direct ancestor to both Neanderthals and *H. sapiens*, and Ofek (2001) refers to early *H. sapiens* as the immediate predecessor to both. According to the Smithsonian Institute (2005b), "For many years, scientists placed any problematic specimens displaying mixtures of "erectus-like" and "modern" traits into a confusing category: "Archaic" *Homo sapiens*...Recently, it has been proposed to separate these individuals into a distinct species. For this purpose,…the specimen name *Homo heidelbergensis* has seniority." Previously, *H. heidelbergensis* was the generic name given to the first hominids in Europe (Gamble 1999). Although *H. erectus* is now viewed on a different lineage than *H. sapiens and* Neanderthals (Smithsonian 2005a), many of the works cited here still make reference to *H. erectus* as the immediate ancestor to both species.

another agent. Multiple equilibria imply hominids must coordinate their decisions to capture the maximum gains provided from trade. Such coordination succeeds under the right bioeconomic circumstances and sufficient expectations for this outcome (Diamond 1982; Williamson and Wright 1993). Coordination failure, however, arises when these conditions and expectations exist but trade does not emerge (Cooper and John 1988). When we add coevolutionary processes to this class of coordination models, we find the potential for multiple behavioral and evolutionary equilibria, which we argue might explain the differences between the development of speech between early modern humans and Neanderthals.

Horan et al. (2005) addressed the issue of trade in the context of modern humans and Neanderthals, concluding that Neanderthals went extinct due to their lack of trade relative to humans (evidence of trading networks among early modern humans exists some 130,000 years ago; Holden 1998). But their finding begs the natural follow-up question that is at the heart of this paper: why do some species trade and others not? The coevolutionary story we develop in this paper provides a compelling story to explain the origins of trade and our species' survival, and it supports Mellars' (2004) speculation that complex language was the key to human success over Neanderthals.

A note before proceeding—our model fits into the rapidly growing literature on *paleoeconomics*. Within the scope of this field are fundamental scientific mysteries like the evolution of humans and human behaviour (Hansson and Stuart 1990; Galor and Moav 2002; Robson and Kaplan 2003; Rogers 1984), early human resource management and food procurement strategies (Smith 1975; Brander and Taylor 1998, Baker 2003; Bulte et al. 2006; Marceau and Myers 2005; Weisdorf 2005); the importance of biogeography (Olsson and Hibbs 2005); and the emergence of trade, early markets and property rights (Ofek 2001; Lagerlöf

6

2005). While the list of topics is broad and varied, the common process of paleoeconomic models is to help unify underlying behavioural explanations through introducing formal economic modelling into areas traditionally dominated by more descriptive approaches.

In the next section, we begin by describing the physiological background behind the morphology of speech development in Homo sapiens. Section 3 begins our modeling process by developing a population growth model where biological parameters depend on speech capabilities. Section 4 then develops a coevolutionary model based on trade and examines the role of strategic complementarities. Section 5 presents the results of a simulation. Finally, we offer conclusions in the last section.

2. Physiological background

Human speech requires several anatomical adaptations in addition to the associated cognitive abilities. These adaptations can be traced through the evolution of the upper respiratory system. The following discussion draws heavily from Lierberman (1984; 1998). The larynx originated in fish, allowing the swim bladder (the sac to which oxygen is passed from gills and which regulates depth) to become a primitive lung for some species. This is the *first functional branch point* (i.e., air breathing life vs. non-air breathing aquatic life) in the evolution of the upper respiratory system. A second branch point arose when fibers and cartilages were developed to pull the larynx open during breathing, to let in more air. A third branch point is where an elaboration of the larynx took place (vocal cords), allowing the larynx to act as a sound-generating device. Here phonetic ability began at the expense of aerobic activity. The fourth major branch point is the human supralaryngeal vocal tract, which we described below.

Primates and early hominids all exhibited a morphology between the third and fourth

branch points. *All* terrestrial mammals except for a subset of the *Homo* line share the same standard morphology of the surpralarynx (airway and vocal tract).[8] This morphology includes a raised larynx located behind the tongue and close to the roof of the nasopharynx, which leads into the nasal cavity. The result is that the larynx is locked into the nasopharynx during quiet respiration. This gives mammals the ability to drink and breathe (and also consume small amounts of food) simultaneously, without choking. The result also obligates nose breathing. For instance, infants only mouth-breathe when the nose is closed off and suffocation is imminent. Also relevant is that primate and early hominids have an elongated jaw, which creates some degree of a "snout". The snout lets air pass more directly (i.e., with only a slight curve) into the pharynx, and the greater surface area for teeth results in more efficient chewing. Also the longer snout can support stronger muscles for chewing (Lieberman 1984).

In modern adult humans, the larynx is much lower due to a recession of the jaws that causes the tongue to occupy not only the mouth but also part of the pharynx. In addition, the recession of the jaw results in the loss of a "snout", which causes the airway to turn at a 90 degree angle past the nasal cavity. The combination of these alterations, which creates the modern vocal tract and permits human speech, represents the fourth functional branch point.[9] The selection for this enhanced phonetic ability comes at the expense of efficiency of respiration, swallowing (leading to greater risk of choking), jaw opening and chewing (leading to a loss of nutrient intake), and also a mouth crowded with teeth (Lieberman 1984; 1998). From the perspective of comparative analysis of the fossil record, we can recognize this change by many

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[8] Human infants share this morphology, as animals tend to begin life with morphologies that more closely resemble simpler forms of their ancestors and then grow into the more sophisticated morphologies characteristic of adults.
[9] Speech capabilities, as provided by vocal tract morphologies, are necessary but not sufficient for language. Language also requires advanced cognitive abilities, which presumably co-evolved with the morphology. Klein (2003) notes the FOXP2 gene, which is involved in speech and language, achieved its current sequence less than

signs; in particular, a restructuring of the basicranium and a shortening of palate length are good indicators of the change.

Some laryngeal descent probably occurred in *Homo erectus* and *Homo heidelbergensis*, without significantly compromised curvature of the airway. This allowed for mouth breathing, which could have a selective value for physical activities since mouth breathing would let in more air. It could also have allowed for primitive linguistic ability but not human speech. This is not the branch point. The branch point probably came around the time of *H. heidelbergensis*, which branched off into Neanderthals and humans. Lieberman (1984) notes the branch point allowed for two possible pathways. One pathway was the development of modern speech, which humans accomplished. The other pathway involved increased muscular ability, which would have taken advantage of the more efficient respiration and chewing associated with a non-linguistic morphology. Neanderthals did not evolve the morphology required for modern speech, but they were more robust and stronger than modern humans (Klein 2003; Trinkhaus and Shipman 1993; Lovejoy and Trinkhaus 1980).[10]

To summarize, humans and Neanderthals had a common ancestor who had primitive linguistic abilities, but nowhere near the abilities of modern humans. These *H. heidelbergensis* were social creatures who undoubtedly worked together and communicated with each other, probably using a combination of primitive vocalization and gesturing. Primitive vocalization,

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200,000 years ago.

[10] There is indirect evidence that Neanderthals had primitive speech. Some signs of speech exist in that they cared for ill and the old, which suggests they developed human capital and passed it on (e.g., learning how to heal was not done each time by trial and error) (Lieberman 1984). They also had some complex culture (Gamble 1999). Neanderthal brains were also larger than those of modern humans (Corballis 2004), indicating the potential cognitive capacity for speech (Lieberman 1984; 1998). But their morphology suggests they had primitive speech at best. Lieberman (1984, 1998) finds that a Neanderthal skull could not have supported a human supralaryngeal vocal tract, and shows that trying to place a functioning human vocal tract in a Neanderthal skull would result in the larynx being positioned in the chest, which does not occur in any primate and is considered impossible.

however, would have been relatively inefficient. In addition, since sign languages generally

reflect the syntactic and cognitive base associated with a species' vocal capabilities, it is

reasonable to assume that gesturing was relatively inefficient too (Lieberman 1984). Moreover,

gesturing removes the hands from employment elsewhere, such as using tools, which reduces the

efficiency of production in a group setting.

There would have been evolutionary gains from investment in muscular ability to

increase productivity in light of the inefficient communication. There would also have been

evolutionary gains to investments in improved communication as a way to increase productivity.

But the physiologies of these investments are at odds since they involve different uses of the

upper respiratory system. The question is, given a common ancestor, why did some hominids

invest in communication while others in muscular ability?[11]

3. A model of hominid population dynamics

Consider a population of N individuals (or households) of hominids (*H. heidelbergensis*) living

on an area of size K. Following conventional models of population growth (e.g., McGehee and

Armstrong 1977; Dobson 2004), proportional per capita growth of a population (net per capita

fertility) at a point in time is given by

$$(1) \qquad \dot{N}/N = G = -d(v) + b(s,N)F(v,s)$$

where d is the mortality rate, bF is the birth rate, F represents per capita consumption, and b is a

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[11] In one sense our analysis is a logical complement of the Robson and Kaplan (2003) story, who focus on the brain development side of the equation. They look at a life-cycle model: during an individual's life, he may invest early energy flows into brain development and later energy flows into reducing mortality of the next generation (an intergenerational transfer) so as to increase longevity and reap the rewards of investing in a big brain. Our modeling approach differs, although we expect these investments could be related. Perhaps there is a clever way to make the connection.

density-dependent birth rate parameter (with $b_N<0$). Density-dependent growth implicitly

accounts for resource availability, which is likely to differ in different geographies (e.g., different

latitudes). We return to this issue in the numerical simulation of section 4.

The variables v and s in the growth equation (1) represent the physiological traits of

vocalization and strength. These traits are inversely related—the physiological changes needed

for increased vocalization reduces respiratory efficiency, resulting in reduced ability to provide

oxygen to muscle tissues. We model these two traits as a function of an underlying

physiological trait, which for simplicity we denote by the scalar, $I \in [0,1]$. Larger values of I

represent a greater degree of vocalization and less strength, while smaller values of I represent

greater strength and less vocal ability. Vocalization is given by the continuous function $v(I)$,

with $v_I > 0$. Denote strength by $s(I)$, which is decreasing in I ($s_I < 0$).

Mortality is increasing in vocalization ($d_v > 0$) because the associated drop in the larynx

leads to a greater risk of choking (Lieberman 1998).[12] The birth rate parameter is decreasing in

mass ($b_s < 0$). Larger animals tend to have lower birth rates, as more energy is required to

support greater mass, diverting energy flows away from reproductive activity. The per capita

consumption function F depends on both vocalization and strength. Equation (1) indicates the

population grows when nutrition is consumed at a rate greater than a subsistence level, defined as

$S=d(v)/b(s)$. Subsistence requirements are increasing in muscle mass and in vocalization, so that

greater vocalization ($I > 0$) has an ambiguous impact on subsistence requirements.

4. A simple exchange model with transactions costs

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[12] Vocalization may allow some people to talk their way out of trouble, which would reduce mortality. But we do not model conflict here.

Human choices may influence G, and the particular choice we consider is whether an individual participates in exchange/trade. An individual may or may not produce all the food he consumes. If not, the person engages in some form of exchange with others. Ofek (2001) identifies two types of exchange: *nepotistic* exchange, which occurs between family members and which is practiced by all mammals (and members of other orders), and *market* exchange, which occurs between non-family members and which is unique to humans. The exact nature of exchange in paleo times is not known. Primates follow a "feed-as-you-go" strategy, consuming food where found, and they only engage in nepotistic exchange (Ofek 2001).[13] In contrast, early modern humans followed the hunter-gatherer strategy of bringing food back to a central hub, where it could be reallocated among family and non-family members (Gamble 1999). There are conflicting views as to whether the hunter-gatherer model had been adopted by the time of *Homo erectus* (Isaac 1983; O'Connell 1999). Ofek (2001) makes a compelling case for nepotistic exchange and some limited market exchange.[14] We focus on market exchange. Along these lines, we believe it is useful to think of "individuals" in our model as being individual clans, so that trade occurs between non-related groups.

For notational ease, we model trade implicitly through a "reduced-form approach" (see

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[13] Primate mothers provide care for their young, while primate fathers may or may not be involved in this care, depending on the species (Ofek 2001).

[14] Nepotistic exchange, and even market exchange among hunter-gatherers, is assumed to occur in an egalitarian fashion (food sharing) (Baker 2005), but this is not necessarily an accurate depiction of what occurred in paleo times. While many modern hunter-gatherers such as the *!Kung* are considered food-sharers (Baker 2005; Gamble 1999), Gamble notes that the degree of equality in food sharing varies considerably among different (modern and paleo) human and primate groups. The specific behaviors that a group exhibits are correlated to the relative local abundance of food (Gamble). Dasgupta (1993) also notes inequality in food sharing among contemporary groups living close to subsistence, and provides an economic justification for this. Where food sharing is egalitarian, this does not necessarily imply a lack of exchange or efficiency. For instance, Kranich (1994) and Baker (2005) each discuss redistribution mechanisms that are both efficient and stable. Note that many other things could have been traded in addition to food, including tools, weapons, and resources (including fire provision). Ultimately, trade in tools and weapons used for food acquisition, or the resources used to produce tools and weapons, would affect food consumption and the magnitude of the potential gains from trade. Our reduced form approach can only implicitly capture these details.

Horan et al. (2005) for a model of explicit trade).[15]   An individual's economic decision is whether to produce and consume only his own output (nutrition), or to specialize to some degree and trade with others. An individual who neither specializes nor trades produces and consumes a nutrition level of $Y(s)$, with stronger individuals producing more nutrition ($Y_s > 0$). Someone who specializes and trades consumes $Y(s)+Z-T$, where Z represents the gains from trade relative to the no specialization/no trade scenario, and T represents transactions costs (discussed below).[16] An individual who specializes but is unable to find a trading partner consumes $\kappa Y(s)-T$, with $\kappa \in [0,1]$ since specialization increases the production of nutritional components for which he specializes, but lack of variety in the absence of trade generally decreases aggregate nutritional value.

Individuals who decide to trade must search for one trading partner. For simplicity, he attempts to trade with the first person he meets *only*; no additional searching occurs if a trade does not occur.[17] The transactions costs associated with searching for a potential trading partner and communicating about a trade are denoted $T(v,n)$, where $n=N/K$ represents hominid density. Assume $T_v < 0$ and $T_n < 0$: improved vocal ability reduces communication costs, and a denser population reduces search costs.

Whether a trade ultimately occurs depends on the other person's trading strategy. Denote $\sigma \in [0,1]$ to be the trading strategy adopted by others in the population, i.e., the likelihood that others will trade with the individual. A trader will consume nutrition of $Y+Z-T$ with probability

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(or belief) σ, and he will consume nutrition of $\kappa Y(s)-T$ with probability $1-\sigma$.

4.1 Hominid strategies and strategic complementarities in a one-shot game

We begin with a one-shot game to present some fundamental concepts that underlie the dynamic

model to follow. An individual hominid makes choices to maximize net fertility, which in our

model is consistent with maximizing nutrition. Each individual decides on a trading strategy,

denoted by $\rho \in [0,1]$, which represents the probability he searches for a trading partner. His

expected consumption is given by

$$(2) \quad F = \rho(\sigma[Y(s) + Z - T(v,n)] + [1-\sigma][\kappa Y(s) - T(v,n)]) + (1-\rho)Y(s)$$

In a one-shot game, the optimal choice of ρ is determined by taking the derivative of F with

respect to ρ

$$(3) \quad \frac{\partial F}{\partial \rho} = \sigma[Z + (1-\kappa)Y(s)] - T(v,n) - (1-\kappa)Y(s)$$

The right hand side (RHS) of (3) is the expected net gain from trading. If one decides to trade,

he incurs transactions costs and a loss of aggregate nutrition (assuming $\kappa < 1$ due to

specialization) with probability one, but he has a chance to recoup the nutritional losses and earn

an additional gain with probability σ. Note the expected net gain is increasing in κ: there is no

loss of nutrition when $\kappa = 1$.

If the RHS of (3) is negative, then $\rho = 0$. In a symmetric Nash equilibrium, $\rho = \sigma = 0$ and

there is no trade. This outcome always occurs when $T > Z$, and it may occur even when $Z > T$.

$Z > T$ is only a necessary (but not sufficient) condition for the RHS to be non-negative; the

possibility exists for some trading to occur. If the RHS is strictly positive, $\rho = 1$ and in a

symmetric Nash equilibrium everyone always trades ($\rho = \sigma = 1$). In this case, (3) reduces to Z-T>0.

If $Z>T$ and the RHS of (3) vanishes, then $\rho \in (0,1)$ and in a symmetric Nash equilibrium we have $\rho=\sigma=\hat{\sigma}=[T/Y+(1-\kappa)]/[Z/Y+(1-\kappa)]<1$. Assuming the necessary condition $Z>T$ is satisfied, the ultimate equilibrium depends on expectations of the individuals. A person wants to mimic the others in the group: trade if others trade; no trade if others do not trade; and randomize his trading behavior if others randomize.

Figure 1 illustrates the relation between an individual's trading strategy, ρ, and relative transactions costs, T/Z. For a given value of T/Z, each individual's expectations must lie on or above the $\hat{\sigma}$ curve for a trading equilibrium to emerge. As the relative transactions costs are increased, a trading equilibrium is less likely; it can only arise if there are sufficient expectations for trading. Finally, no trading occurs when relative transactions costs are sufficiently large, or $T/Z>1$. Any one of three equilibria could be realized as long as $Z>T$, and so exchange is not guaranteed. We focus on cases in which $Z>T$, such that all equilibria have a chance to emerge.

The interior equilibrium strategy, $\hat{\sigma}=[T/Y+(1-\kappa)]/[Z/Y+(1-\kappa)]$, is the ratio of costs to expected benefits. The ratio is reduced when κ is increased, indicating an increase in the relative benefits of trading. Reducing the equilibrium trading strategy when the relative benefits of trading are increased seems counter-intuitive in a static sense, but the intuition becomes clear when dynamic adjustments are considered. In a dynamic context, which we explore in the following section, $\hat{\sigma}$ represents a line of unstable equilibria as indicated by the phase arrows in Figure 1. If $\sigma>\hat{\sigma}$, the $\sigma=1$ equilibrium emerges; if $\sigma<\hat{\sigma}$, the $\sigma=0$ equilibrium arises. The impact of a larger κ in this case is to shift the $\hat{\sigma}$ curve downward (so that it crosses the origin when $\kappa=1$), resulting in a larger basin of attraction for trading equilibria.

Multiple equilibria arise due to the presence of strategic complementarities between the individual's strategy and the strategies of others (see Cooper and John; Kiyotaki and Wright;

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Williamson and Wright; Krugman). Strategies ρ and σ are strategic *behavioral* complements when the derivative

(4) $\partial^2 F /(\partial\rho\partial\sigma) = Z + (1-\kappa)Y$

is positive, which it always is: the marginal returns to one person's actions are increased when there is an increase in the others' actions (accordingly, this is a supermodular game; Levin 2003). We adopt the terminology of *strategic behavioral complements*, as opposed to the more standard term *strategic complements*, to distinguish between hominid strategies and evolutionary strategies, which we discuss below. Note the magnitude of the strategic complementarities are diminishing in κ, in accordance with the point that a larger κ increases the expected net benefits trading for any given value of σ. This implies the individual's strategy choice is less reliant on others' strategies, and an equilibrium involving at least some trading is more likely to emerge.

The notion of strategic complementarities can be carried over to the evolutionary scale, with hominid choices depending on the evolution of trait I and vice versa. Consider the impact of increased vocalization strategies on the benefits of trading strategies. Differentiating (3) we find that the derivative

(5) $\partial^2 F /(\partial\rho\partial I) = -T_v v_I - (1-\sigma)(1-\kappa)Y_s s_I$

is positive: vocalization increases the marginal benefits of trading, and so vocalization is a strategic *coevolutionary* complement to trading.[18] A larger value of κ reduces these strategic complementarities so for any value of I, we expect a larger basin of attraction for trading.

4.2 Replicator dynamics for the trading strategy

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[18] It is common in the evolutionary game theory literature to say that nature does strategize (Rice 2004), although technically this is not true. Rather, a selection process occurs within the natural system that makes it seem *as if* nature chooses a strategy to maximize fitness. If we take this more realistic view, it may be more appropriate to say that vocalization is a joint evolutionary complement to trading (as opposed to a strategic evolutionary complement).

Since the static model provides no intuition into how strategies evolve over time or whether

equilibrium strategies are stable (see Krugman), we reformulate the model as a dynamic one.

Population dynamics are again given by equation (1). Again we assume homogenous individuals

with a trading strategy σ. The replicator dynamics for the trading strategy take the form (Rice

2004; Bergstrom and Lachman 2003):

$$(6) \quad \dot{\sigma} = \alpha\big(\sigma[F_T^* - F^*] + (1-\sigma)\delta\big) = \alpha\big(\sigma(1-\sigma)[\sigma Z - T(v, n^*) - (1-\sigma)(1-\kappa)Y(s)] + (1-\sigma)\delta\big)$$

where F_T denotes expected consumption under trade (defined by (2) with $\rho=1$), F is mean

consumption in the population (which is also defined by (2) since people are homogeneous), and

δ is a strategy mutation term. The parameter $\alpha \in (0,1)$ indicates the speed of adjustment.

Without loss of generality, assume, cultural frictions slow changes in hominid strategies so these

evolve on a slower time scale than does N. We capture this friction by assuming N attains its

equilibrium value prior to adjustment: the superscript (*) denotes that N is evaluated at the steady

state value N^* (see Brock and Xepapadeas (2004) for a discussion of fast and slow time). This is

not a necessary assumption, but it helps us to focus on the tradeoffs between trading and

vocalization strategies.[19]

Equation (6) indicates individuals increase their trading strategy if doing so leaves them

better off on average (reflected by the term in brackets, $F_T - F$, which equals $\partial F/\partial \rho$ in (3)). We

also assume there is a constant but small rate δ of mutating one's strategy towards trading. This

mutation rate prevents the system from settling at the autarky corner (where $\sigma=0$): small efforts

to trade may be sustained as $\sigma \rightarrow 0$, although these efforts are insufficient to create a *snowball*

effect of run-away vocalization, holding the level of vocalization constant. Moreover, the effect

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[19] Moreover, if the gains from trade are not too large, as might be imagined for early hominids, then large changes in
trading or vocalization strategies may have little impact on the equilibrium value of N.

of the mutation term diminishes and ultimately vanishes as $\sigma \rightarrow 1$.[20]

Three evolutionarily stable strategies (ESS) arise from (6) when $Z>T$: (i) a *petite-trading* equilibrium supported by mutation, $\underline{\sigma} = [(\hat{Y}+T) - \sqrt{(\hat{Y}+T)^2 - 4\delta(\hat{Y}+Z)}]/[2(\hat{Y}+Z)]$ (where $\hat{Y} = (1-\kappa)Y(s)$), which is stable, (ii) an *unstable* equilibrium,

$\hat{\sigma} = [(\hat{Y}+T) + \sqrt{(\hat{Y}+T)^2 - 4\delta(\hat{Y}+Z)}]/[2(\hat{Y}+Z)]$, and (iii) a *trading* equilibrium, $\overline{\sigma} = 1$, which is stable. Note $\underline{\sigma} = 0$ and $\hat{\sigma} = (\hat{Y}+T)/(\hat{Y}+Z)$ (the line of interior equilibria in Figure 1) when $\delta = 0$.

The equilibrium that ultimately arises depends on the initial strategy, defined by $\sigma(0) = \sigma_0$. The $\underline{\sigma}$ equilibrium emerges whenever $\sigma_0 < \hat{\sigma}$, and the $\overline{\sigma}$ equilibrium arises whenever $\sigma_0 > \hat{\sigma}$. The threshold level $\hat{\sigma}$ depends on the population density, n^*, with $\hat{\sigma}'(n^*) < 0$ so trade is more likely to take off (establish) in regions that support denser populations. The establishment of trade depends on both environmental considerations (as some environments initially support greater densities) and initial expectations.

4.3 Adaptive Dynamics for the Vocalization Strategy

Now consider the evolution of nature's vocalization strategy. Following the convention of the evolutionary game theory literature as applied to quantitative genetics, we assume nature does strategize (Rice 2004), although technically this is incorrect. Rather, a selection process occurs

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[20] We could also include a term for mutation away from trading (e.g., a small mutation rate of γ so that the term $\sigma\gamma$ is subtracted from equation (6)), but this would complicate the algebra without impacting on the dynamics when σ is small – the focus of our attention since this is the region where there exists the greatest uncertainty about the emergence of trading. The only significant impact of incorporating mutations away from trading would be to prevent the system from equilibrating at the full trade corner, $\sigma=1$.

within the natural system that makes it seem *as if* nature chooses a strategy to maximize fitness.

Mutations in *I* follow a process of adaptive dynamics (Brown and Vincent 1987; Rice 2004). A strategy for *I* is an evolutionary stable strategy (ESS) if

(7) $\quad \dfrac{\partial G^*}{\partial I} = 0$ and $\dfrac{\partial^2 G^*}{\partial I^2} < 0$

Following Diekmann and Law (1996), Lande (1979), and Krakauer and Jansen (2002), the evolution of the trait *I* is specified as follows:

(8) $\quad \dot{I} = \phi \mu N^* \dfrac{\partial G^*}{\partial I}$

where μ is the mutation rate of *I*, ϕ is the speed of adjustment, and using (2), G^* is given by

(9) $\quad G^* = -d(v) + b(s, N^*) F^*.$

The parameter ϕ is analogous to α; but if ϕ is sufficiently greater or smaller than α, the trading and mutation processes occur at different time scales. If ϕ is very small relative to α, trading dynamics are fast and mutation dynamics are slow; here the superscript (*) in (8) and (9) applies to both the trading strategy σ and the population *N*. If ϕ and α have similar magnitudes, the superscript (*) only applies to *N*. If ϕ is very large relative to α, trading dynamics are slow and mutation dynamics are fast. For now, we assume ϕ and α are of similar magnitudes; in our numerical simulation later in the paper we explore how changes in the relative magnitudes affect the dynamics.

From (8), trait *I* attains a steady state when $\partial G^* / \partial I = 0$, or when proportional net growth (G^*) is maximized (as is required by (7)). Otherwise, there are increases in vocalization (strength) when the marginal product of the trait on fitness is positive (negative). Investments in vocalization depend on the trading strategy. To see this, differentiate (9) to obtain:

$$(10) \quad \frac{\partial^2 G^*}{\partial I \partial \sigma} = b_s s_I \left[\frac{\partial F^*}{\partial \rho} + \sigma \frac{\partial^2 F^*}{\partial \rho \partial \sigma} \right] + b \left[\frac{\partial^2 F^*}{\partial I \partial \rho} + \sigma \frac{\partial^3 F^*}{\partial I \partial \sigma \partial \rho} \right] + \frac{\partial^2 G^*}{\partial I \partial N^*} \frac{\partial N^*}{\partial \sigma}$$

where $\partial F^*/\partial \rho$ is as defined in (3), $\partial^2 F^*/(\partial \rho \partial \sigma)$ is as defined in (4), and $\partial^2 F^*/(\partial I \partial \rho)$ is as defined in (5).[21] The first RHS term is of the same sign as the expression in brackets, which consists of the marginal impact of an individual's strategy on his own consumption ($\partial F^*/\partial \rho$, which may be positive or negative) plus the weighted (by σ) strategic behavioral complementarity effect of others' strategies on his consumption ($\sigma \partial^2 F^*/(\partial \rho \partial \sigma)$, which is positive). Assuming δ is sufficiently small, $\partial F^*/\partial \rho \geq 0$ when $\sigma \geq \hat{\sigma}$, in which case the first bracketed term is positive; the term can be negative if $\partial F^*/\partial \rho$ is sufficiently negative.

The second RHS term in (10) is of the same sign as the expression in brackets, which consists of the strategic coevolutionary complementarity effect of vocalization on trade ($\partial^2 F^*/(\partial I \partial \rho)$, which is positive) plus the weighted marginal impact of an individual's strategy on this complementarity ($\sigma \partial^3 F^*/(\partial I \partial \sigma \partial \rho) = \sigma(1 - \kappa) Y_s s_I < 0$). When σ is sufficiently small (i.e., when trade is only just emerging) or if or κ is sufficiently large, then $\sigma(1 - \kappa) Y_s s_I$ is small and the overall bracketed term is positive. Even when $\sigma=1$, the overall term is positive if increased vocalization has greater marginal impacts on transactions costs than on output weighted by (1-κ). Finally, the third RHS term in (10) reflects the impact of an increase in σ on the equilibrium population level N^*, which may be positive or negative but is presumably small if the net gains from trade are small.

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[21] The derivatives in expression (10) are taken prior to imposing the equilibrium condition $\rho=\sigma$. If the equilibrium condition was imposed first, then the expression in the first set of brackets would be written $\partial F^*/\partial \sigma$ and the expression in the second set of brackets would be written $\partial^2 F^*/(\partial \sigma \partial I)$. We have written the derivatives in the current form to highlight the role of strategic complementarities.

Assuming the final two terms in (10) are positive or negligible, trading is a strategic coevolutionary complement to vocalization ($\partial^2 G^* / (\partial I \partial \sigma) > 0$), provided the individual's marginal benefits of trading are positive or not too negative. If these marginal benefits are positive, we could have runaway selection for vocalization and trade—the investments made in each sector reinforce the incentives to invest in the other. In contrast, if the individual's marginal benefits of trading are sufficiently negative, $\partial^2 G^* / (\partial I \partial \sigma)$ may be negative. Trading is now a strategic coevolutionary substitute to vocalization, although vocalization remains a strategic coevolutionary complement to trading. The net result is that the hominid society could become trapped in an equilibrium involving low levels of trade and vocalization, as the investment incentives are not self-reinforcing. The upshot is that sufficient levels of trade could be a necessary condition for human evolution, while a sufficient lack of trade could lead to Neanderthal evolution.[22]

5. Simulation

We now explore the model numerically. Table 1 shows the functional forms and parameter values for three scenarios, and the associated phase diagrams are presented in Figures 2-4. In each case, the aggregate population N is held fixed for simplicity. If N was allowed to adjust, the only effect would be to shift the isoclines. As society moved away from (towards) trade, the equilibrium population would fall (rise), increasing (increasing) transactions costs and reducing (increasing) the basin of attraction for equilibrium z. The effect would be small, however, if the net gains from trade were also small.

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[22] Eventually, a lack of trade could lead to Neanderthal extinction, after humans and Neanderthals begin competing on the same territory (see Horan et al. 2005). Note herein we implicitly consider geography in our model, which occurs via the carrying capacity via the density-dependent growth, and we capture the joint determination associated with coevolution. Here in our model trade facilitates speech, speech facilitates trade.

Scenario A, illustrated in Figure 2, represents a situation in which both strategies evolve along an identical time scale (i.e., $\phi=\alpha$). There are three equilibria: x is a locally stable, strength equilibria; y is a saddle-point equilibria; and z is a locally stable, vocal-trade equilibria. The saddle path is denoted by S. All initial points below S will follow trajectories to equilibrium x. All initial points above S will follow trajectories to equilibrium z. While the basin of attraction for z is large, getting there requires sufficient coordination (i.e., a sufficiently large σ_0) in the absence of sufficient vocalization. The required value of σ_0 diminishes as vocalization is increased, but some positive value of σ_0 is always required to enter the basin of attraction for equilibrium z.

Figure 3 represents the same situation as Figure 2 except that the trading strategy evolves faster in this case. The effect is to reduce the slope of S, increasing the basin of attraction for equilibrium point z. This is like the *Red King* effect described by Bergstrom and Lachman (2003). The Red King effect emerges when two players are involved in a mutualism – a cooperative endeavor in which both players stand to gain. As in bargaining models, a player stands to gain if his hands are tied (Schelling 1960).

This is what happens when one player's strategy evolves slower than another's – the basin of attraction for the slower player's preferred outcome expands. Bergstrom and Lachman (2003) call this the Red King effect—the slower player wins the game; the opposite of the (antagonistic evolutionary) Red Queen game in which the fastest player wins. In the present case, hominids (as a group) and nature both gain if they cooperate on the choices of trading and speech. When nature moves slower than hominids, the basin of attraction around nature's preferred outcome, z (trade and vocalization), increases. In the limit as $\phi \rightarrow 0$ (so that vocalization dynamics are extremely slow relative to trade dynamics), vertical movements seem

22

to occur instantaneously relative to horizontal movements. The northwest separatrix S is defined by the northwest portion of the $\dot{\sigma} = 0$ isocline in this case, and the southeast separatrix S becomes vertical and tangent to the $\dot{\sigma} = 0$ isocline at the point where the isocline bends backwards. If σ_0 is to the right of S, then all hominids trade before any vocalization mutations occur. If the phase arrows are as in Figure 3, such that vocalization increases when $\sigma = 1$, the system eventually settles at equilibrium z. If σ_0 is to the left of S, the system immediately moves to the lower section of the $\dot{\sigma} = 0$ isocline. From there, it moves slowly towards the equilibrium point x.

The Red King effect does not arise when hominids move slower than nature. For instance, in the limit as $\alpha \to 0$ (so that trade dynamics are extremely slow relative to vocalization dynamics), horizontal movements seem to occur instantaneously relative to vertical movements. In that case, S becomes a horizontal line through y, reducing the basin of attraction around the preferred outcome for hominids, equilibrium z (vocalization and trade). The basin of attraction is reduced in this case because the change in time scale does nothing to prevent the coordination failures that arise within the hominid group when σ_0 is small.

Finally, figure 4 represents a region that supports a twenty percent larger equilibrium population density (all other parameter values are identical to those in Figure 2). The outcome is lower transactions costs than in Figure 2 due to the larger population density. We find no interior equilibrium. Rather, the vocalization-trade equilibrium z is globally stable.

The differences between Figures 2 and 3, or between Figures 2 and 4 can help explain the evolutionary outcome of Neanderthals (strong, non-traders with limited vocal abilities) versus humans (traders with advanced vocal abilities). In Figures 2 and 3, trade is one of two equilibria that could emerge. Trade could have emerged for more favorable initial expectations about trading, or it could have emerged in regions where cultural changes (i.e., adoption of trade)

23

occurred more rapidly such that initial expectations did not matter as much (as in Figure 3). In Figure 4, initial expectations do not matter; only environmental conditions matter. Trade could have also emerged in regions supporting greater hominid densities. Note once trade and vocalization take sufficient hold of the population so the system begins to close in on z, then migration into regions that support smaller population densities (e.g., Figure 2) will not send the population back to equilibrium x. This raises the possibility that humans crossed into Europe without losing any of these abilities.

6. Discussion and conclusion

The origins of human speech are among the most prominent *paleo puzzles* of modern science. It is virtually impossible to overstate the importance of abstract language for the cultural evolution of our species. Yet, because archaeological evidence is scant, key issues with respect to the humble beginnings of vocalization are far from settled. While there are several theories that try to shed light on the origins of speech, they appear incomplete as it is sometimes unclear why they do not apply to other hominids or, indeed, other primates. What is so unique about the evolution of our species that we developed this extraordinary capacity that comes at a significant personal cost?

We propose an explanation based on strategic complementarities that result in multiple stable development trajectories – one giving rise to modern humans and another one to a muscular Neanderthal-like species with limited capacities for speech. Key elements in our model are that (i) one's decision to trade (or not) affects the returns to similar decisions taken by other agents, (ii) transaction costs are influenced by vocalization abilities, and that (iii) trading decisions in turn affect the morphological evolution of humans – favoring investments in muscles or vocalization. While it is not inevitable that early humans started on one trajectory

24

and Neanderthals on another, we do believe that the geography of the species' stomping grounds could have increased the likelihood of the outcome. The picture that emerges is one where nature and human behaviors are jointly determined, with cooperation among humans not being the sole driving force. Rather cooperation between humans and between humans and nature increased our odds of survival relative to other hominoids.

References

Aiello, L.C. and R.I.M. Dunbar, "Neocortex Size, Group Size, and the Evolution of Language", *Current Anthropology* 34(1993): 184-193.

Baker, M.J., "Technological Process, Population Growth, Property Rights, and the Transition to Agriculture", Working Paper 2005-09, Department of Economics, United States Naval Academy, 2005.

Baker, M. "An Equilibrium Conflict Model of Land Tenure in Hunter-Gatherer Societies", *Journal of Political Economy* 111(2003): 124-173.

Bergstrom, C.T. and M. Lachman, "The Red King Effect: When the Slowest Runner Wins the Coevolutionary Race", *Proceedings of the National Academy of Sciences* 100(2003):593-598.

Bowles, S., J.-K. Choi, and A. Hopfensitz, "The Co-Evolution of Individual Behaviors and Social Institutions", *Journal of Theoretical Biology* 223(2003): 135-147.

Bulte, E.H., R.D. Horan, and J.F. Shogren, "The Economics of Pleistocene Megafauna Extinction: Early Humans and the Overkill Hypothesis" *Journal of Economic Behavior and Organization*, 59(2006): 297-323.

Brander, J. A. and M.S. Taylor, 1998. The Simple Economics of Easter Island: A Ricardo-Malthus Model of Renewable Resource Use. *American Economic Review* 88: 119-138.

Brock, W. and A. Xepapadeas, "Ecosystem Management in Models of Antagonistic Species Coevolution", Working paper, University of Crete, 2004.

Brown, J.S. and T.L. Vincent, "Coevolution as an Evolutionary Game" *Evolution* 41(1987):66-79.

Cooper, R. and A. John, "Coordinating Coordination Failures in Keynesian Models", *The Quarterly Journal of Economics* CIII(1988): 441-463.

Dasgupta, P., *An Inquiry into Well-Being and Destitution*. Oxford: Oxford University Press, 1993.

Deacon, T.W., *The Symbolic Species*, New York: Norton, 1997.

Dessalles, J.-L., "Language and Hominid Politics", in *The Evolutionary Emergence of Language: Social Function and the Origins of Linguistic Form*, C. Knight, M. Studdert-Kennedy, and J.R. Hurford, eds., Cambridge: Cambridge University Press, 2000.

Diamond, P., "Aggregate Demand Management in Search Equilibrium", *Journal of Political Economy* 90(1982): 881-894.

Diekmann, O. and R. Law, "The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Process", *Journal of Mathematical Biology* 34(1996): 579-612.

Dobson, A. "Population Dynamics of Pathogens with Multiple Host Species", *The American Naturalist* 164(2004): S64-S78.

Dunbar, R.I.M., *Grooming Gossip and the Evolution of Language*, London: Faber and Faber, 1996.

Galor, O., and O. Moav, "Natural Selection and the Origin of Economic Growth", *Quarterly Journal of Economics* 117(2002): 1133-1191.

Gamble, C., *The Paleolithic Societies of Europe*, Cambridge: Cambridge University Press, 1999.

Gifford, A. Jr., "The Evolution of the Social Contract", *Constitutional Political Economy* 13(2002): 361-379.

Hansson, I. and C. Stuart, "Malthusian Selection of Preferences", *American Economic Review* 80(1990): 529-544.

Horan, R.D., E.H. Bulte, and J.F. Shogren, "How Trade Saved Humanity from Biological Exclusion: An Economic Theory of Neanderthal Extinction", *Journal of Economic Behavior and Organization*, 58(2005): 1-29.

Holden, C., "No Last Word on Human Origins", *Science* 282(1998): 1455.

Kiyotaki, N. and R. Wright, "A Search-Theoretic Approach to Monetary Economics" *American Economic Review* 83(1993):63-77.

Klein, R.G., "Whither the Neanderthals?", *Science* 299(2003): 1525-1526.

Knight, C., "Ritual/Speech Coevolution: A Solution to the Problem of Deception", in *Approaches to the Evolution of Language: Social and Cognitive Bases*, J.R. Hurford, M. Studdert-Kennedy, and C. Knight, eds., Cambridge: Cambridge University Press, 1998.

Knight, C., M. Studdert-Kennedy, and J.R. Hurford, "Language: A Darwinian Adaptation?", in *The Evolutionary Emergence of Language: Social Function and the Origins of Linguistic Form*, C. Knight, M. Studdert-Kennedy, and J.R. Hurford, eds., Cambridge: Cambridge University Press, 2000.

Krakauer, D.C. and V.A.A. Jansen, "Red Queen Dynamics of Protein Translation", *Journal of Theoretical Biology* 218(2002): 97-109.

Kremer, M., 1993. Population Growth and Technical Change: One Million B.C. to 1990, *Quarterly Journal of Economics* CVIII: 681-716

Krugman, P. "History Versus Expectations" *The Quarterly Journal of Economics* 106(1991):651-667.

Lagerlöf, N.P., 2005. "Slavery and other property rights", York University Mimeo

Lande, R. "Quantitative Genetic-Analysis of Multivariate Evolution, Applied to Brain-Body Size Allometry" *Evolution* 33(1979):402-416.

Levin, J. "Supermodular Games", Lecture notes, Department of Economics, Stanford University, 2003.

Lieberman, P. *Eve Spoke*, New York: W.W. Norton and Co., 1998.

Lieberman, P. *The Biology and Evolution of Language*, Cambridge: Harvard University Press, 1984.

Livingstone, D. and C. Fyfe, "Modelling Language-Physiology Coevolution", in *The Evolutionary Emergence of Language: Social Function and the Origins of Linguistic Form*, C. Knight, M. Studdert-Kennedy, and J.R. Hurford, eds., Cambridge: Cambridge University Press, 2000.

Lovejoy, C.O. and E. Trinkhaus, "Strength and Robusticity of the Neandertal Tibia", *American Journal of Physical Anthropology* 53(1980): 465-470.

Marceau, N. and G.M. Myers, "On the Early Holocene: Foraging to Early Agriculture", *Economic Journal* (in press), 2005

McGehee, R. and R. Armstrong. "Some Mathematical Problems Concerning the Ecological Principle of Competitive Exclusion", *Journal of Differential Equations* 23(1977):30-52.

Mellars, P., "Neanderthals and the Modern Human Colonization of Europe", *Nature* 432(2004): 461-465.

Noble, J., "Cooperation, Competition and the Evolution of Prelinguistic Communication", in *The Evolutionary Emergence of Language: Social Function and the Origins of Linguistic Form*, C. Knight, M. Studdert-Kennedy, and J.R. Hurford, eds., Cambridge: Cambridge University Press, 2000.

Ofek, H., *Second Nature: Economic Origins of Human Evolution*, Cambridge: Cambridge University Press, 2001.

Olsson, O. and D. Hibbs, "Biogeography and Long-Run Economic Development", *European Economic Review* 49, pp. 909-938, 2005

Pinker, S. and P. Bloom, "Natural Language and Natural Selection", *Behavioral and Brain*

Sciences 13(1990): 707-784.

Rice, S.H., *Evolutionary Theory: Mathematical and Conceptual Foundations*, Sunderland, MD: Sinauer, 2004.

Robson, A.J. and H.S. Kaplan, "The Evolution of Human Life Expectancy and Intelligence in Hunter-Gatherer Economies", *American Economic Review* 93(2003): 150-169

Schelling, T., *The Strategy of Conflict*. Cambridge: Harvard University Press, 1960.

Smith, V.L. The Primitive Hunter Culture, Pleistocene Extinction and the Rise of Agriculture, *Journal of Political Economy* 83(1975): 717-755.

Smithsonian Institution, "Early Human Phylogeny" http://www.mnh.si.edu/anthro/humanorigins/ha/a_tree.html (accessed August 30, 2005a).

Smithsonian Institution, "*Homo heidelbergensis*" http://www.mnh.si.edu/anthro/humanorigins/ha/heid.htm (accessed August 30, 2005b).

Tattersall, I., Schwartz, J.H., 2000. Extinct Humans. New York: Westview Press.

Ward, R. and C. Stringer, "A Molecular Handle on the Neanderthals", *Nature* 388(1997): 225-226.

Trinkhaus, E. and P. Shipman, *The Neandertals: Changing the Image of Mankind*, New York: Knopf, 1993.

Weisdorf, J.L., 2005. "From Foraging to Farming: Explaining the Neolithic Revolution", *Journal of Economic Surveys*, 19:4, p. 561-586

Williamson, S. and R. Wright, "Barter and Monetary Exchange Under Private Information" *American Economic Review* 84(1993):104-123.

Table 1. Simulation model equations and parameter values

| Biological Process	Equations	Parameter values	Notes
Vocalization	$v=v_0(1+v_1I)$	$v_0 = 0.5$ $v_2 = 1$	
Strength	$s=s_0(1-s_1I)$	$s_0 = 1$ $s_2 = 0.75$	
Mortality	$d=d_0(1+d_1v)$	$d_0 = 0.07$ $d_1 = 0.15$	
Birth	$b=b_0(1-b_1s) - b_2N$	$b_0 = 0.35$ $b_1 = 1.2$ $b_2 = (b_0y(s(0.5))-d_0)/(y_0k)$ $k = 0.75$ for Scenarios A and B; $k = 1.0$ for Scenario C	b_2 is the density-dependent fertility term, calibrated at an initial equilibrium (i.e, where $G=0$) with mid-range level of strength, $I=0.5$, so that initial output at this point is $y(s(0.5))$, k is the carrying capacity, expressed as a density
Output	$Y=Y_0s$	$Y_0 = 0.5$	
Transactions cost	$T=T_0(1-v)/n$	$T_0 = 1$	
Gains from Trade		Z	0.75
Mutation rate		$\mu=1$	The impact of μ cannot be separated from that of ϕ, as the effective speed of adjustment is $\mu\phi$.
Speed of adjustment		$\alpha = 0.0002$ in Scenario A; $\alpha = 0.02$ in Scenario B $\phi = 0.0002$	Our discussion of the speed of adjustment is centered around the separatrices, which do not exist in Scenario C
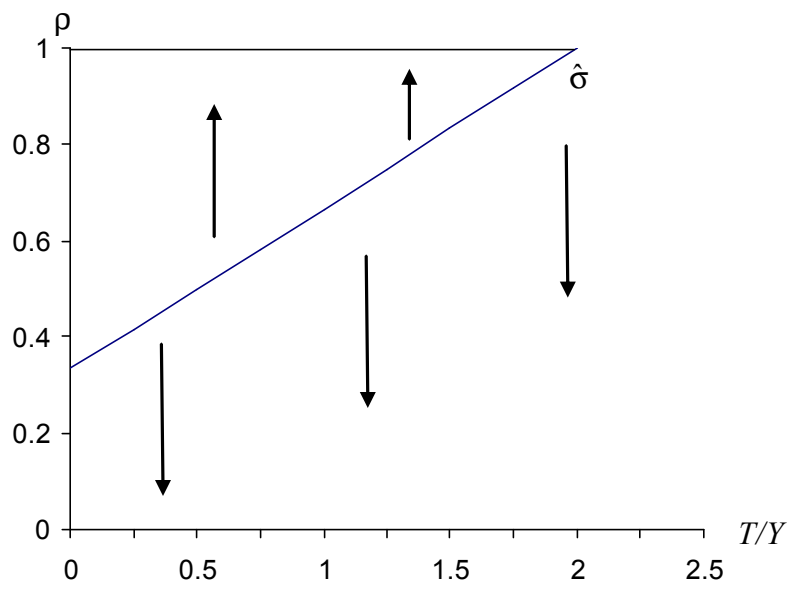
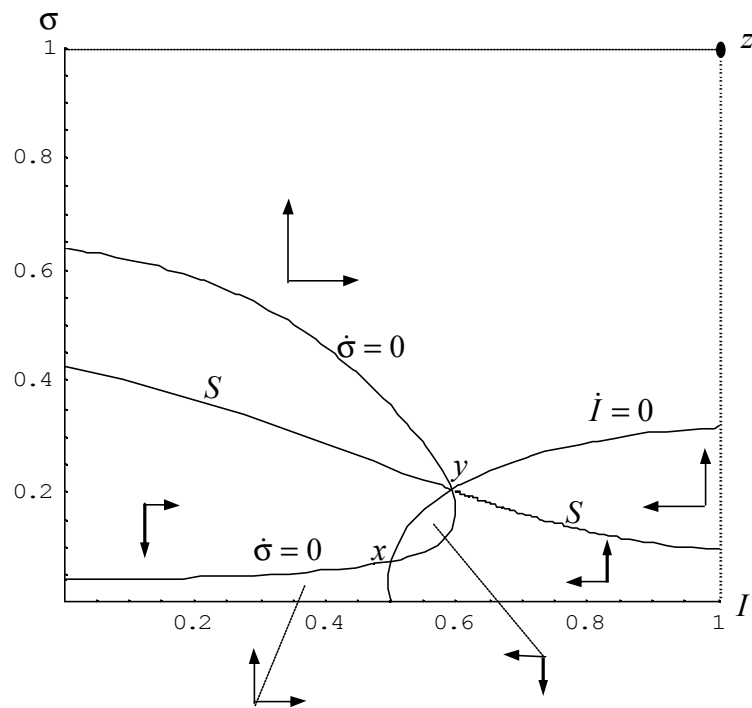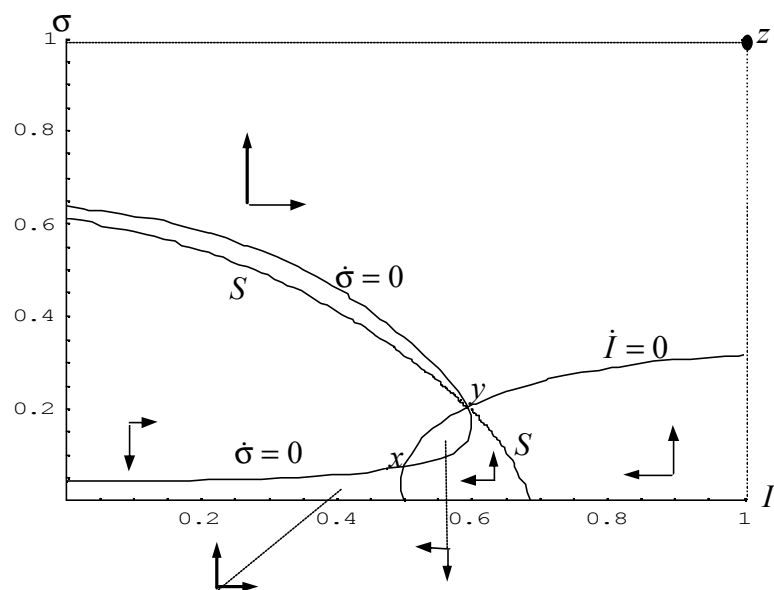Figure 1. Interior equilibria of the static model (with phase arrows drawn in to indicate the need to consider dynamics).
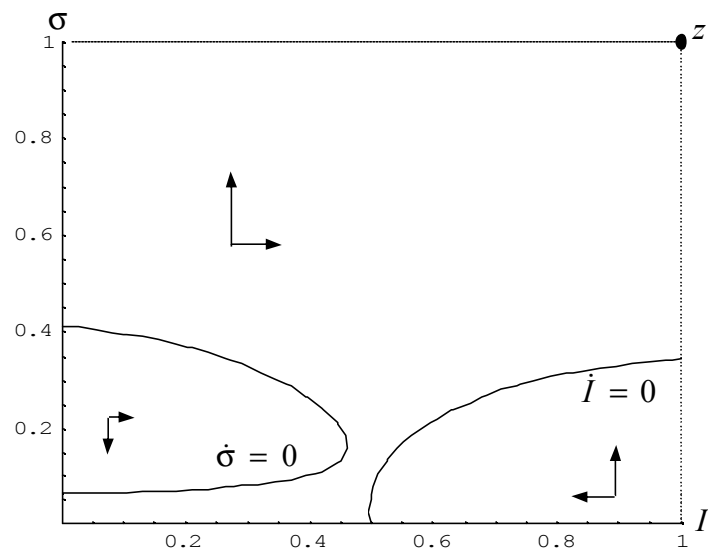
Figure 2. Scenario A

Figure 3. Scenario B

Figure 4. Scenario C