

Coevolution of Human Speech and Trade

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Abstract

We propose a novel coevolutionary explanation for the origin of speech in modern humans, and the lack thereof in other hominids. The coevolutionary process, in which trade facilitates speech and speech facilitates trade, gives rise to multiple stable trajectories. While a ‘trade-speech’ equilibrium is not an inevitable outcome for modern humans, we find it is a relatively likely scenario given our species evolved in Africa under climatic conditions supporting relatively high population densities. The origin of speech is not independent of the existence of economic institutions—the paleoeconomics of early human trade can help explain the physiological emergence of speech.

Keywords: evolution, language, coordination game, Homo sapiens, Neanderthals

1. Introduction

The emergence of human speech is one of the great mysteries of science. Human speech allows for superior communication, and is one of the foremost reasons why our species has been so successful. Scientists wonder over both *when* and *why* human speech developed (Holden 1998). Our focus in this paper is primarily on the *why* question; but since *why* is conditional on the answer to *when*, we begin the story there. 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, cultural interactions 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 “cultural explosion” about 40,000 years ago.¹ Lieberman (1998), however, 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 for why dating the origin of speech from the archaeological record is difficult).²

¹ 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 primitive *proto-language* as far back as 500,000 – 1.5 million years ago (Knight et al. 2000).

² 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).

The evolution-for-speech argument implies there is no single point in history when speech emerged – it was most likely a gradual process, in which morphological and behavioral changes happened hand in hand. While this provisionally settles the *when* question for now, the second fundamental question of *why* speech developed still remains unresolved. Since the primary evolutionary benefits of speech presumably 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 theories are based on altruistic or cooperative motives. One such theory argues 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 strategy for success, so that speech would fail to gain a foothold in the presence of evolutionary pressures (e.g., Knight et al. 2000).

Another cooperation theory is based on the observation that primates “groom” each other to help support relationships, which suggests 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 speech could have evolved along with social contracts (Deacon 1997; see

also Gifford 2004).³ 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 to perform an action 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. 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.

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.⁴ *Homo sapiens* evolved from *Homo heidelbergensis* and acquired human speech capabilities in the process—the only hominids to have acquired this capability (Lieberman 1998).⁵ For instance, like *Homo sapiens*, *Homo neanderthalensis* evolved (albeit somewhat

³ There is a substantial literature on the evolution of altruistic behaviors and social institutions. We do not attempt to cover all of it here; see Bowles et al. (2003) for a recent analysis.

⁴ 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.

⁵ Scientific classification of the hominid phylogeny (i.e., the hominid evolutionary tree) has changed in recent years

earlier) from *Homo heidelbergensis*, but did not acquire human speech capabilities (Lieberman 1998). Why not? Would not Neanderthals and other hominids also benefit 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, which fits into the rapidly growing literature on *paleoeconomics*, combines the trade-no trade insights 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.⁶ In general, economic models of trade exhibit multiple equilibria due to strategic complementarities—more trade by one agent increases the productivity of trade by 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

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.

⁶ 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 2005). While the list of topics is broad and varied, the common process of paleoeconomic models is to help unify underlying behavioral explanations through introducing formal economic modelling into research fields like anthropology and archaeology traditionally dominated by more descriptive approaches.

(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, arguing that Neanderthals went extinct due to inefficiencies caused by their lack of trade relative to humans (evidence of trading networks among early modern humans exists some 130,000 years ago; Holden 1998). Their trade-as-driver-of-evolution argument 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 forceful story to explain the origins of trade and our species' survival, and it formalizes Mellars' (2004) speculation that complex language was the key to human success over Neanderthals.

In the next section, we describe the physiological background behind the morphology of speech development in *Homo sapiens*. Section 3 begins our modeling process by developing a population growth model in which biological parameters depend on speech capabilities. Section 4 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 Lieberman (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 capacity and a greater risk of choking on food. 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 supralarynx (airway and vocal tract).⁷ 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

⁷ Human infants share this morphology, as animals tend to begin life with morphologies that more closely resemble

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.⁸ 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, one can recognize this change by many signs—a restructuring of the basicranium and a shortening of palate length are two good indicators of the change.

Some laryngeal descent probably occurred in *Homo erectus* and *Homo heidelbergensis*, without a 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

simpler forms of their ancestors and then grow into the more sophisticated morphologies characteristic of adults.
⁸ 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 200,000 years ago.

Shipman 1993; Lovejoy and Trinkhaus 1980).⁹

To summarize, humans and Neanderthals had a common ancestor who had primitive linguistic abilities, but nowhere near the abilities of modern humans. *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, 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 relative to present sign languages (Lieberman 1984). Moreover, gesturing prevents one from using his or her hands 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. There would also have been evolutionary gains to investments in improved communication as a method 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?¹⁰

⁹ 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 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.

¹⁰ Indirectly, our model is a logical complement to the Robson and Kaplan (2003) story, which focuses 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 so as to increase longevity and reap the rewards of investing in a big brain. Their approach differs from our model, although we expect these investments could be related in that brain development allows for more sophisticated and clever communication, provided one also has the vocal ability to articulate these superior ideas. It is also evident that the payoffs from investing in muscles or communication depend on the longevity of individuals – something we treat as fixed in what

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

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

where d is the mortality rate, bF is the birth rate, F represents per capita consumption, and b is a 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 the geographic 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, $I \in [0,1]$.¹¹ Larger values of I represent a greater degree of vocalization and less strength, while smaller values of I represent less vocal ability and greater strength. 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). The birth rate parameter is decreasing in

follows. Extending the model to allow for endogenous longevity is left for future work.

¹¹ Our use of the scalar, I , to measure investments in both speech and strength is consistent with the notion that these investments were at odds. But it is also possible to develop a more complex model with two variables, one for each

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

Human choices may influence the proportional per capita population growth, G . The particular choice we consider now is whether an individual chooses to participate in exchange/trade. An individual may or may not produce all the food he or she 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 most other orders), and *market* exchange, which occurs between non-family members and which is unique to humans. In what follows we focus on market exchange, giving rise to efficiency gains through trade.

The exact nature of exchange in paleo times, and the exact emergence of market exchange in particular, is unknown (e.g., Isaac 1983, O’Connell 1999). Primates follow a “feed-as-you-go” strategy, consuming food where found, and they only engage in nepotistic exchange (Ofek 2001).¹² 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). It is evident that the transition from “feed-as-you-go” to the

investment, and also end up with diverging evolutionary trajectories as in the current simple model (see below).

organization structure founded on the “hub” occurred for some *Homo* lineages, but not for others. Neanderthals, for example, did not engage in trade to the same extent as modern humans (see Horan et al 2005 for a treatment of this issue).

For notational ease, we model trade implicitly through a “reduced-form approach” (see Horan et al. (2005) for an explicit model of paleo-trade).¹³ An individual’s economic decision is whether to produce and consume only his own output (nutrition), or to specialize 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 gross gains from trade relative to the no specialization/no trade scenario, and T represents transactions costs.¹⁴ The net gains from trade are endogenous in our model, even if the gross gains are a parameter, because population density enters the model through its attenuating effect on transaction costs (discussed below). An individual who specializes but is unable to find a trading partner consumes $\kappa Y(s)-T$, with $\kappa \in [0,1]$: while specialization increases the production of nutritional components for which he specializes, a 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, assume he finds a trading partner with certainty and attempts to trade with the first person he

¹² 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).

¹³ We can also derive our results from the implicit trading using a more notationally complex Ricardian trade model. Making gross gains endogenous unnecessarily complicates the model without affecting our primary results.

¹⁴ These exogenous gross gains could be modeled to be even greater when more people participate in the market, i.e., $Z=Z(\sigma N)$, with $Z'>0$. Again adding this feature unnecessarily complicates the model without affecting the primary results.

meets *only*; no additional searching occurs if a trade does not occur.¹⁵ 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 consumes nutrition of $Y+Z-T$ with probability (or belief) σ , and he consumes 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 the trading probability, ρ , is determined by taking the

¹⁵ At the end of the period there is a limited window of opportunity to trade your output (or else it goes bad, or else it gets dark, etc.). Assume two people meet with certainty and this is the only opportunity to trade, but all the results spill over (again with more notational clutter) if instead we assume specialists can potentially meet Q people (as opposed to one). Mathematically, the assumption that two people meet with certainty amounts to frequency-dependent (or density-independent) contact between people, with a contact rate of $\beta=1$. The macro search theory literature also assumes frequency-dependent contacts, except they sometimes allow $\beta < 1$ (e.g., Williamson and Wright 1993; Kiyotaki and Wright 1993). Macro search models incorporate dynamic search processes, and so $\beta < 1$ means people spend more time searching. Herein we set $\beta=1$ to avoid this additional dynamic dimension (i.e., time spent searching versus the other dynamic processes of growth and mutation, etc.). Relaxing this restriction such that $\beta < 1$ would not change our basic findings. Note that we could have assumed density-dependent contacts as an alternative form. This contact function is usually written βN and represents the expected *number of contacts*, meaning you might contact many people. But then this raises the complicating question about who does any

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 the optimal decision is not to trade: $\rho = 0$. In a symmetric Nash equilibrium, $\rho = \sigma = 0$ and there is no trade. This outcome always occurs when transactions costs exceed the gains from trade, $T > Z$; and it may occur even when $Z > T$. $Z > T$ is 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 others: 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

particular individual trade with—the first person he or she meets? or the second? the third, and so on? This presumption again complicates the model without altering the basic coevolutionary insight which is our focus.

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 the 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 cost-benefit 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. Similarly and anticipating future results, the basin of attraction for trade increases as transaction costs fall (e.g., when population densities are higher or when geographical conditions for supporting human populations are more favorable).

Multiple equilibria arise due to the presence of strategic complementarities between the individual's strategy and the strategies of others (see Cooper and John 1988; Kiyotaki and Wright 1993; Williamson and Wright 1993; Krugman 1991). The trading strategies of the individual, ρ , and the others, σ , are strategic *behavioral* complements when the derivative

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

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 observation that a larger κ increases the expected net benefits from 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.

We now carry over the notion of strategic complementarities 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 see the derivative

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

is positive: vocalization increases the marginal benefits of trading, and so vocalization is a strategic *coevolutionary* complement to trading.¹⁶ 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

Since the static model provides no intuition into how strategies evolve over time or whether equilibrium strategies are stable, we reformulate the model as a dynamic one. Population dynamics are again given by equation (1). Again we assume homogenous individuals with a

¹⁶ In the evolutionary game theory literature, it is common to say that nature does strategize (e.g., Rice 2004), although technically this is inaccurate. 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 realistic view, it is more appropriate to say

trading strategy σ . The replicator dynamics for the trading strategy take the form (Rice 2004; Bergstrom and Lachman 2003):

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

where F_T denotes expected consumption under trade (defined by (2) with $\rho=1$), F is mean consumption in the population (defined by (2) with $\rho=\sigma$, 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 (e.g., induced by traditions, communication difficulties, or historic hostilities) 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 in dynamic models). While this is not a necessary assumption, it helps us highlight the tradeoffs between trading and vocalization strategies. Moreover, if the gains from trade are not too large, then large changes in trading or vocalization strategies may have little impact on the equilibrium value of N .

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 (see Foster and Young 1990; Rice 2004). 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 of the mutation term diminishes and ultimately

vocalization is a joint evolutionary complement to trading (as opposed to a strategic evolutionary complement).

vanishes as $\sigma \rightarrow 1$.¹⁷

Three evolutionarily stable strategies (ESS) arise from (6) when $Z > T$: (i) an *autarkic* equilibrium (with only nominal trade 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, $\bar{\sigma} = 1$, 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 there is no mutation, $\delta = 0$.

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 $\bar{\sigma}$ equilibrium arises whenever $\sigma_0 > \hat{\sigma}$.

The threshold level $\hat{\sigma}$ depends on the population density, n^* , through the impact of density on transaction costs. Specifically, $\hat{\sigma}'(n^*) < 0$; so trade is more likely to take off and establish itself in geographic regions that support denser populations. The establishment of trade depends on both environmental considerations (as some environments initially support greater densities) and initial expectations of individuals.

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, assume nature does strategize (Rice 2004), although technically this is inaccurate. Rather, a selection process occurs

¹⁷ 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, G . As we describe below, this choice of strategy depends on the level of trade. This section therefore defines the sufficient *level* of trade necessary to affect human evolution, and the sufficient *lack* of trade necessary to affect Neanderthal evolution.

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

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

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

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

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 interpretation of parameter ϕ is analogous to that of the adjustment parameter α introduced in (6); 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, 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:

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

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).¹⁸ 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) has 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 ($\sigma \partial^3 F^*/(\partial I \partial \sigma \partial \rho) = \sigma(1 - \kappa)Y_s s_l < 0$). When σ is sufficiently small (i.e., when trade has only just emerged) or if κ is sufficiently large, then $\sigma(1 - \kappa)Y_s s_l$ 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

¹⁸ 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.

weighted by $(1-\kappa)$. 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.

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. In this case, an increase (decrease) in the trading strategy reinforces the incentives to increase (decrease) the vocalization strategy and vice versa. Sufficient levels of trade could therefore be a necessary condition for evolution into modern humans, while a sufficient lack of trade could lead to Neanderthal-style evolution.¹⁹

In contrast, if the individual's marginal benefits of trading are sufficiently negative, then $\partial^2 G^* / (\partial I \partial \sigma)$ may be negative. Trading would be a strategic coevolutionary substitute to vocalization in this case (that is, increasing the trading strategy reduces the benefits of vocalization), although vocalization remains a strategic coevolutionary complement to trading. The net result is that a hominid society could become trapped in an equilibrium involving low levels of trade and vocalization, as the investment incentives are not self-reinforcing.

5. Simulation

We will now show that there are two ways in which the trade-vocalization equilibrium can emerge. The equilibrium can emerge (1) due to favorable initial conditions in the presence of multiple equilibria caused by adverse geographic conditions supporting small population densities, or (2) as a globally optimal solution such as when geography supports “sufficiently”

¹⁹ 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).

large population densities. In the case of multiple equilibria, the key influence on the necessary initial conditions is the relative speed of adjustment of speech and trade. When the evolutionary speeds are asymmetric (i.e., $\alpha \neq \phi$), a Red King effect (defined shortly) kicks in for better or worse, depending on initial conditions.

5.1 Simulation: Geography and initial evolutionary conditions

Scenario A, illustrated in Figure 2, represents a situation in which both strategies, ρ and σ , evolve along an identical time scale, i.e., $\phi = \alpha$. Three equilibria emerge, two of which are locally stable: x is a locally stable, autarkic-strength equilibrium; y is a saddle-point equilibrium; and z is a locally stable, vocal-trade equilibrium. The saddle path is denoted by S .

All points above S are on trajectories leading to equilibrium z . The reason is that, in this region of the phase plane, vocalization and trade are bi-lateral strategic coevolutionary complements of sufficient magnitude as to overcome the hominid coordination failures. Vocalization and trading strategies strongly reinforce each other in this region, making z locally stable.

In contrast, all initial points below S follow trajectories to equilibrium x . The local stability of x in this region of the phase plane occurs because trade and vocalization are not strong strategic coevolutionary complements to one another. As a result, the reinforcing incentives are small. The increased trading incentives that come from increased vocalization are not enough to overcome the hominid coordination failures. Moreover, if people trade less then incentives for nature to invest in vocalization decline. The hominid society gets stuck in an autarkic-strength equilibrium.

Hominids (as a group) prefer equilibrium z to x , whereas nature is indifferent between these equilibria since $G^*=0$ holds at each equilibria. While the basin of attraction for z is large, getting there requires sufficient hominid coordination (i.e., a sufficiently large σ_0). The required value of σ_0 diminishes as vocalization (I_0) is increased, but some positive value of σ_0 is always required to enter the basin of attraction for equilibrium z .

Scenario B (Figure 3) captures the same situation as Scenario A except now there is asymmetric coevolution with the trading strategy evolving faster, i.e., $\phi < \alpha$. The effect is to rotate S clockwise, reducing the basin of attraction for equilibrium point z .²⁰ In our case, nature does not have a preference between x and z and so the effect is to *shrink* the basin of attraction for the hominids' preferred outcome, z . This change is like the *Red King* effect described by Bergstrom and Lachman (2003), in which the basin of attraction for the slower (faster) player's preferred outcome expands (shrinks). Intuitively, the smaller basin of attraction results because the faster player's effective "bargaining power" shrinks.²¹ In the current problem, the smaller basin of attraction occurs in the region where the trading strategy is diminishing over time (i.e., $\dot{\sigma} < 0$, located to the left of the $\dot{\sigma} = 0$ isocline). When the trading strategy declines relatively quickly it increases the downward pull toward equilibrium x —the greater speed enhances the

²⁰ In the limit as $\phi \rightarrow 0$ (vocalization dynamics are extremely slow relative to trade dynamics), vertical movements seem to occur instantaneously relative to horizontal movements. In this case, the northwest separatrix S is defined by the northwest portion of the $\dot{\sigma} = 0$ isocline, and the southeast separatrix S becomes vertical and tangent to the $\dot{\sigma} = 0$ isocline at the point where the isocline bends backwards. Finally, note that S rotates counterclockwise relative to Figure 1 when hominid trade evolves more slowly than nature ($\alpha < \phi$). We do not investigate this case formally, but the results and intuition will be the opposite of that explained here.

²¹ The Red King effect emerges when two players are involved in a mutualism (a cooperative endeavor in which both players stand to gain) and one player's strategy evolves slower than another's. The intuition offered by Bergstrom and Lachman (2003) for the Red King effect is as follows. Each player involved in the mutualism prefers to be selfish, but as there are multiple equilibria the process of getting to one's preferred outcome is akin to bargaining for that outcome. In Schelling's (1960) early discussion of bargaining, a player stands to gain if his hands are tied by constraints originating from within his clan. This is the so-called Schelling conjecture, in which national negotiators can bargain harder in international agreements when they have domestic constraints they must satisfy. In evolutionary game theory models, a slower speed of adjustment effectively ties one's hands.

downward effect caused by coordination failures so that it overwhelms the counteracting upward effect caused by the complementary impact of greater vocalization. That is, the relatively larger value of α effectively reduces the strategic coevolutionary complementarities of vocalization on trade. Moreover, the faster reduction in trade reduces the incentives for vocalization. Together, these forces expand the basin of attraction for x .

In general, the idea of a shrinking basin of attraction leads Bergstrom and Lachman to conclude that the fastest player loses a Red King game; the opposite of the antagonistic coevolutionary Red Queen game in which the fastest player wins. But they recognize that this global result does not necessarily hold for each smaller region of the phase plane. While reducing the relative value of ϕ in our model reduces the overall basin of attraction for z , portions of this basin actually expand in regions where there has already been sufficient speech (or proto-speech) development – specifically, to the right of the right-hand arm of the saddle path S . That is, initial conditions matter. Since sufficient vocal abilities exist already in this region, less initial trade (possibly zero) is required to move to the vocalization-trade equilibrium. Moreover, the faster player wins in this region, similar to the Red Queen effect, but for a different reason. The intuition is the reverse of what we described earlier. The larger basin of attraction occurs in the region where the trading strategy is increasing over time (i.e., $\dot{\sigma} > 0$). Here, the relatively greater speed at which the trading strategy increases intensifies the upward pull acting on both strategies, effectively increasing the strategic coevolutionary complementarities and expanding the basin of attraction for z .

To sum up, when multiple equilibria exist and if trade evolves fast relative to vocalization, then (i) more initial trade is needed to get the coevolutionary process rolling towards z , at least when there is low initial vocalization, and (ii) less initial trade is needed to

move the system towards z when there is a sufficient initial level of vocalization (or proto-speech). One can only speculate as to what the initial conditions were prior to the fourth functional branch point, but we do know that some degree of proto-speech did exist. If this level were sufficient, trade could take hold even if initial rates were low or zero. But what level of proto-speech is sufficient? The answer depends on the underlying biological and environmental parameters. In particular, geography could have mattered, as better geographical conditions will shift the isoclines in ways that expand the basin of attraction for z . We now turn to a scenario in which geographical conditions are improved so much that the trade-vocalization equilibrium is globally stable.

Scenario C (Figure 4) represents a geographic region that supports more individuals; in this case we consider a twenty percent larger population carrying capacity k (all other parameter values are identical to those in Scenario A). The larger densities reduce transactions costs of trading relative to Scenario A, increasing individuals' marginal benefits of trading. For lower levels of vocalization, the autarkic equilibrium strategy, $\underline{\sigma}$, is increased relative to Scenario A and the unstable equilibrium strategy, $\hat{\sigma}$, is reduced. For greater levels of vocalization, both of these equilibria disappear (the discriminant of $\underline{\sigma}$ and $\hat{\sigma}$ becomes negative) so that only the trading equilibrium $\bar{\sigma} = 1$ remains. The overall effect is to shift the $\hat{\sigma} = 0$ isocline to the left. The larger marginal benefits of trade also increase the marginal benefits of vocalization, although the effect on the $\dot{I} = 0$ isocline is small. The net result is that a bifurcation results relative to Scenario A, as the isoclines no longer intersect and the vocalization-trade equilibrium z becomes globally stable. Given our parameters, the bifurcation occurs with about a 25 percent increase in k from the baseline. While this value is simulated, it does suggest the follow pattern—if either environmental or cultural conditions or both improve to support greater densities of humans, a

threshold is crossed such that speech via trade emerges as a stable global equilibrium.

5.2 Discussion: The role of geography

The differences between Scenarios A and B, and between A and C may help explain the distinct evolutionary outcomes of Neanderthals (strong, non-traders with limited vocal abilities) versus humans (traders with advanced vocal abilities). Earlier we established that lowering the transaction costs of trade increases the basin of attraction for the speech-trade equilibrium. This is confirmed in the numerical analysis – we find that for some parameter values the speech-trade outcome is inevitable. 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) occurred more rapidly such that initial expectations did not matter as much (as in Figure 3). In Scenario C, however, initial expectations do not matter—only environmental conditions as created by the geographic region matter. *Better* geographic conditions support greater human densities, and as a consequence, the system settles at z .

Our model predicts that the speech-trade equilibrium of modern humans is more likely to be the outcome for species with high population densities (due to favorable geography). Were densities of the direct ancestors of *Homo sapiens* in Africa actually greater than densities of the direct ancestors of European Neanderthals? While knowledge about prehistoric population densities is scant, there is reason to believe this was the case. Humans evolved in Africa, in a relatively warm and stable climate. In contrast Neanderthals eked out an existence under much more brutal circumstances – making a living in Eurasia in the grip of an ice age. Binford (2001), for instance, estimated populations of hunter-gatherers by ecological zone during the Mesolithic (admittedly a more recent period), based on gradients of diminishing prey availability and

growing season as one moves away from the tropics, and the pattern of his findings is consistent with the notion that hominid densities would have been greater in Africa. Keeley (1988) also finds that population density in hunter-gatherer societies is negatively correlated with latitude. Firming up the linkage between speech and trade, Keeley notes only societies with high population densities develop complicated culture characterized by, among other things, “standard valuables or currency” which would enable trade to operate efficiently (p.405).²²

We close this section with two speculative observations. First, it is conceivable that our analysis of the *why* of the origin of speech also sheds light on the *when* question. If the co-evolutionary process involving trade is responsible for the development of speech, it is possible the emergence of speech coincides with (or shortly follows) a sudden increase in pre-human population densities in Paleolithic times. This would not be unprecedented. For example, Stiner et al. (1999, p.190) conclude “human population densities increased abruptly during the late Middle Paleolithic and again during the Upper and Epi-Paleolithic periods.” The model predicts that such growth pulses are conducive to the evolution of speech – population shocks, induced by climate or custom, could cast the system into the basin of attraction of the speech-trade equilibrium.

Second, 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., represented by a shift in the isoclines that alters the system from Scenario C [Figure 4] to Scenario A [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.

²² Keeley (1998) uses the term “complex” in reference to the particular type of culture being described here, but for consistency we stick with Gamble’s (1999) use of the term “complicated”. Gamble uses “complicated” to describe human cultures and “complex” to describe the less-sophisticated Neanderthal cultures.

6. Discussion and conclusion

The origin of human speech is among the most prominent *paleo puzzles* of modern science. It is impossible to overstate the importance of abstract language for the cultural evolution of our species. But because archaeological evidence is scant, key issues about the beginnings of vocalization remain unsettled. While several theories exist to shed light on the origin of speech, they appear incomplete as it is unclear why they do not apply to other hominids or other primates. What is so unique about the evolution of our species that we developed this extraordinary capacity—one that comes at a significant personal cost?

Our proposed explanation is based on the idea of *strategic complementarities* that result in multiple stable development trajectories – one path gives rise to modern humans, the other gives rise to a muscular Neanderthal-like species with limited capacities for speech. Key elements in our model are (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 (iii) trading decisions affect the morphological evolution of humans – favoring investments in muscles or vocalization. Taken together these three elements create conditions favorable for speech to emerge as a complement to trading, which served humanity by increasing our fertility and as a consequence, population.

While it is not inevitable that early humans started on one trajectory and Neanderthals on another, we believe this separation could have been triggered by expectations or the geography of the species’ territory. In particular, better geography leading to greater population densities could have increased the likelihood of the speech-trading outcome. The story that emerges is one in which nature and human behaviors are jointly determined, with cooperation among humans not being the sole driving force. Rather cooperation between (i) humans themselves

through economic institutions (e.g., trade) and (ii) between humans and nature through more gains from better vocalization increased the odds for speech to emerge, and consequently increase our odds of survival relative to other hominoids. In our story, the origin of speech is not independent of the existence of economic institutions—the paleoeconomics of trade can help explain the physiological origins of speech.

Finally, the reader should note our model says nothing about the volume of trading (e.g., numbers and types of goods being traded). This means that the outcome of $\sigma=1$ in our model is a bit ambiguous – it could mean that everyone trades but they only exchange two goods. That does not capture a large amount of trade, and it is probably close to reality for the time period in question. A more complete model would include *who* is trading *what*. Future research might look into this question, possibly through the use of agent-based modeling (in which thousands of hominids are specified over space and allowed to interact). One could then examine the conditions under which money arises and trading opportunities really explode, perhaps explaining the Paleolithic revolution of 40,000 - 35,000 B.P.

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Table 1. Simulation model equations and parameter values

Biological Process	Equations	Parameter values	Notes
Vocalization	$v=v_0(1+v_1I)$	$v_0 = 0.5$ $v_1 = 1$	
Strength	$s=s_0(1-s_1I)$	$s_0 = 1$ $s_1 = 0.75$	
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	$T=T_0(1-v)/(N/K)$	$T_0 = 1$ $K=1$	
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

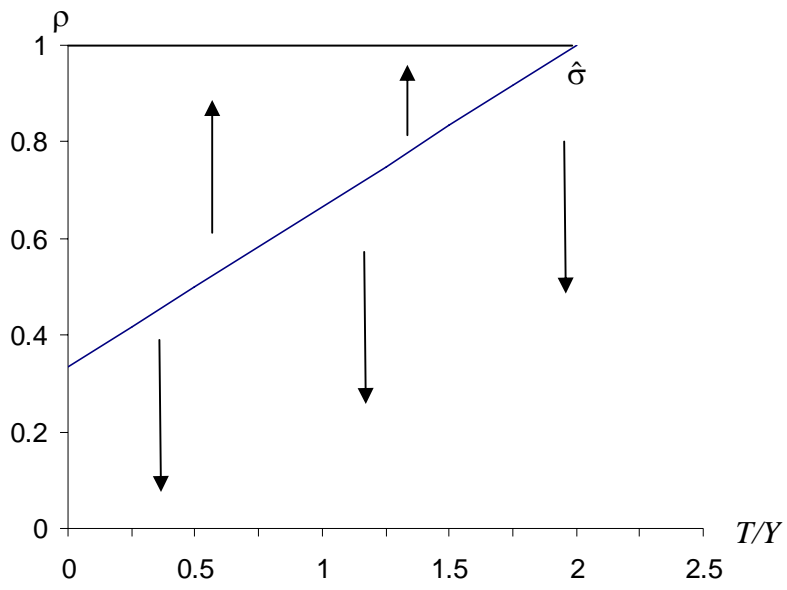


Figure 1. Interior equilibria of the static model (with phase arrows drawn in to indicate the need to consider dynamics).

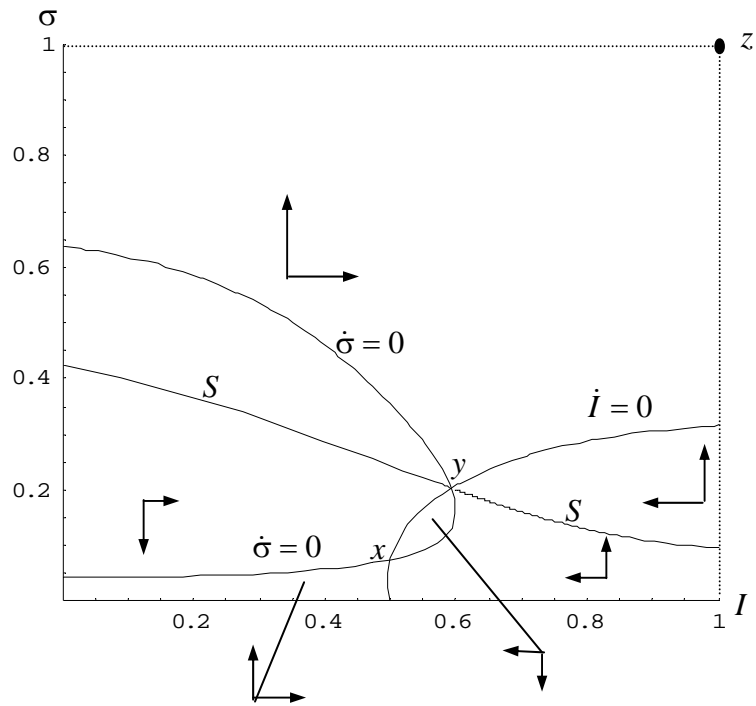


Figure 2. Scenario A—symmetric evolutionary dynamics

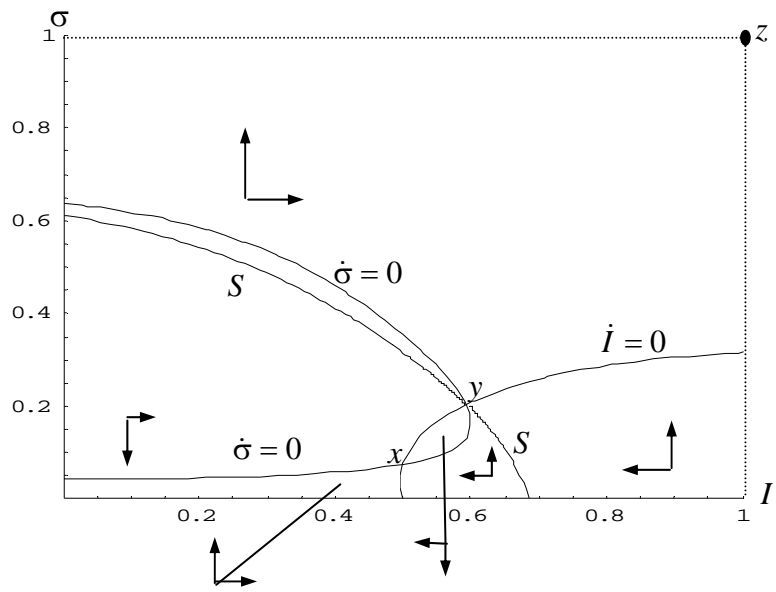


Figure 3. Scenario B—asymmetric evolutionary dynamics

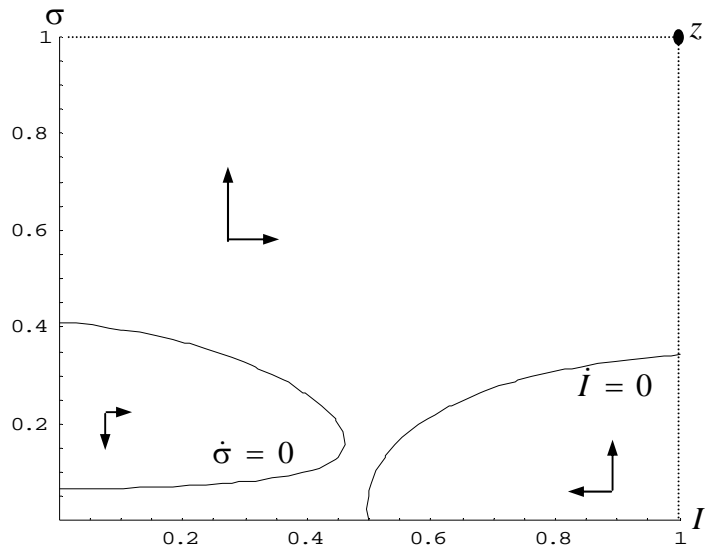


Figure 4. Scenario C—Better Geographic conditions