FOCUS THEME - INVITED PAPER

The evolution of costly traits through selection and the importance of oral speech in e-collaboration

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Abstract Genes code for the expression of phenotypic traits, such as behavioral (e.g., aggressiveness) and morphological (e.g., opposing thumbs) traits. Costly traits are phenotypic traits that evolved in spite of imposing a fitness cost, often in the form of a survival handicap. In non-human animals, the classic example of costly trait is the peacock's train, used by males to signal good health to females. It is argued here that oral speech is a costly trait evolved by our human ancestors to enable effective knowledge communication. It is shown that, because it is a costly trait, oral speech should be a particularly strong determinant of knowledge communication performance; an effect that generally applies to e-collaborative tasks performed by modern humans. The effects of oral speech support in e-collaborative tasks are discussed based on empirical studies, and shown to be consistent with the notion that oral speech is a costly trait. Specifically, it is shown that the use of e-collaboration technologies that suppress the ability to employ oral speech, when knowledge communication is attempted, leads to the two following negative outcomes: (a) a dramatic decrease in communication fluency, and (b) a significant increase in communication ambiguity. These effects are particularly acute in e-collaborative tasks of short duration.

Keywords Human evolution · Costly traits · Handicap principle · Oral speech · Electronic communication · Electronic collaboration · Media naturalness · Compensatory adaptation

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Introduction

One phenomenon that has often puzzled computer science and information systems researchers over the years, particularly researchers interested in e-collaboration issues, is the high importance of having an audio channel for communication in the context of e-collaborative tasks (Graetz et al. 1998; Kock 2004; Kock and DeLuca 2007; Wainfan and Davis 2004). Whenever audio is available (e.g., teleconferencing, telephone conference calls, face-to-face meetings), tasks seem to be performed more easily and with fewer misunderstandings. Moreover, adding video to an already present audio channel typically adds little to the e-collaboration medium's ability to support group tasks (Burke and Aytes 2001). While this is not a universal phenomenon (see, e.g., Daly-Jones et al. 1998; Baker 2002), its frequent appearance in the empirical research literature merits a more robust theoretical analysis.

An evolutionary explanation of the importance of oral speech is proposed here, as a new theoretical contribution to the e-collaboration literature. It is argued that the high importance of oral speech is restricted to knowledge-intensive tasks. The reason for that, which is advanced in more detail in the subsequent sections, is that oral speech evolved among our hominid ancestors as a costly trait to enable efficient and effective knowledge communication. As a costly trait, oral speech is analogous to the large train used by male peacocks to attract mates (often incorrectly called the peacock's tail). That is, like the male peacock's train, oral speech is: (a) a survival handicap that only evolved because of its strong indirect effect on reproductive success, which counteracts its negative effect on survival; and (b) particularly important in the context of the task for which it evolved, namely communication of knowledge. Finally, it is argued

here that even in knowledge-intensive tasks, the negative effect caused by suppression of oral speech may be countered by compensatory adaptation, whereby individuals adapt their communicative behavior to overcome the limitations posed by the suppression of oral speech.

Costly and costless traits: survival costs, reproductive success, and the handicap principle

Costly traits are phenotypic traits that evolved in a species in spite of having a negative impact on survival performance (Gillespie 2004; Maynard Smith 1998; Rice 2004). Survival performance is the performance of an individual in the general task of survival, which can be measured by the age of the individual at the time of death. The older an individual of a species is, the more successful it is at surviving in spite of survival threats (e.g., disease, predators, and accidental falls).

Costly traits evolve because they have a positive impact on reproductive success (normally referred to as "fitness" by evolutionary biologists), generally measured as the number of surviving offspring or grand-offspring of an individual (Gillespie 2004; Hartl and Clark 2007). The positive impact on fitness results from the competing effects of a costly trait on: (a) survival performance, a negative effect; and (b) a task performance attribute, a positive effect. The net effect of these competing effects on fitness is positive, leading to an increase in the frequency of the genotype associated with the costly trait in the species.

One example of task performance attribute that could lead to such a positive net effect on fitness is the number of lifetime copulations an individual participates in, a performance attribute associated with the task of mating. A classic example of costly trait that evolved due to having increased the number of lifetime copulations individuals possessing the trait participated in, which in turn offset the survival cost of that trait, is the male peacock's train (Maynard Smith and Harper 2003; Zahavi and Zahavi 1997). The male peacock's train is frequently referred to, incorrectly, as the peacock's tail (Petrie et al. 1991; Zahavi and Zahavi 1997). Both males and females in the peacock species have tails, but only males have the tail appendages known as trains.

Costly traits may also exist that have competing effects on survival, and that are unrelated to mating, through intermediate effects on other variables that themselves directly affect survival. For example, propensity toward aggressive behavior among our ancestors might have increased their chances of being the target of violent behavior by other individuals, which contributed to a decrease in survival, but might also have increased their access to nutritious food obtained through hunting (for which aggressiveness is important), which in turn contributed to an increase in survival. In this sense, propensity toward aggressive behavior might have evolved as a costly trait, where the positive indirect effect on survival, mediated by increased access to nutritious food, was stronger than the negative indirect effect on survival from attracting violent behavior (Boaz and Almquist 2001; Dobzhansky et al. 1977).

Costless traits are defined here as phenotypic traits that have no negative impact on survival performance. Most costless traits are actually associated with enhanced survival performance, and may be observable indicators of unobservable underlying traits that enhance survival performance (Hamilton and Zuk 1982; Kokko et al. 2002). The ability of males of the fruit fly species *Drosophila subobscura* to engage in a rapid courtship dance with females is an example of trait that fits this definition (Maynard Smith and Harper 2003). Males increase their success at the task of mating by demonstrating to females that they possess the ability to dance vigorously in response to lead movements by the females. This trait is a costless trait because it has no negative impact on the survival success of males. In other words, the dance itself has no negative effect on the survival of males. The ability to dance is in fact positively correlated with survival performance, since it is an indicator of health.

The most widely cited theoretical framework in connection with the evolution of costly traits was proposed by Zahavi (1975), centered on what is known as the handicap principle (Walker 2008; Zahavi and Zahavi 1997). This framework is not only ingenious, but also intuitively appealing. These qualities have led to its becoming widely used in research not only by evolutionary biologists (Hausken and Hirshleifer 2008), but also by researchers in relatively new disciplines that build on evolutionary ideas, such as evolutionary psychology (Griskevicius et al. 2007; Walker 2008).

The handicap principle focuses on costly traits used for signaling; and is founded on the notion that those traits are honest indicators of the signalers' fitness. For example, the large train displayed by the males of the peacock species is a survival handicap, making them more vulnerable to predation (Maynard Smith and Harper 2003; Zahavi and Zahavi 1997). Thus males with large trains and who are still alive at the age of reproductive maturity also must possess other traits that make them particularly good at survival, such as vitality and speed. The tails are a reliable indicator of fitness, exactly because they are costly.

Three common characteristics of costly traits: rarity, late evolution, and strong effects

The discussion presented here expands on and refines the handicap principle to cover any costly trait, in connection

with the performance of any organism in any task that influences fitness, not only signaling tasks. Three key conclusions are reached, which are that costly traits should: be rare in nature, generally evolve late, and be costly not to use. While these conclusions are consistent with the handicap principle, they allow for predictions and explanations that go well beyond signaling tasks. As such, they provide the basis for the analysis of the evolution of oral speech and its importance in the task of knowledge communication.

Costly traits should be rare in nature The survival handicaps imposed by costly traits create obstacles for their evolution, eventually making those traits significantly rarer in nature than costless traits. These obstacles can be seen as "thresholds" for evolution of the traits, where the thresholds are proportional to the survival cost of the traits (Gillespie 2004; Hartl and Clark 2007; Maynard Smith and Harper 2003). Appendix A provides a mathematical elucidation of this evolutionary threshold notion.

New traits (e.g., high intelligence, long legs, and slow fat metabolism) usually appear in populations of organisms as a result of random genetic mutations; a general rule that applies to all organisms, including our hominid ancestors (Hartl and Clark 2007; Boaz and Almquist 2001; Mayr 1976). Therefore, the effects of new traits on fitness are also random, whether those traits are costly or costless. Evolution is not an engineering process; it is a wasteful process of continuous tinkering, where the vast majority of new traits are in fact detrimental to fitness (Hartl and Clark 2007; Wilson 2000). Traits that have a positive net effect on fitness are far and few in between (McElreath and Boyd 2007; Wilson 2000).

Given that costly traits must overcome obstacles, or thresholds, to evolve in a species, fewer costly traits than costless traits are likely to evolve. That is, the probability of evolution of costly traits in any species is generally lower than that of costless traits. Moreover, the higher the cost of the trait, the lower is its probability of evolution. Thus, costly traits should be rarer in nature than costless traits; the more costly, the rarer. Appendix B contains a mathematical formalization of this notion.

Costly traits should generally evolve late Lower probability events tend to take longer to happen than higher probability events. For example, let us assume that two people, PA and PB, randomly throw darts on two walls, WA and WB, each with a total area of 100 square feet. Both people throw one dart every minute, each time hitting a random spot on WA or WB. Either person receives an award if a dart falls within a target area of only 50 square feet, for WA, and 10 square feet, for WB. The target areas are hidden; that is, both PA and PB are unaware of where their target areas are. This

example is analogous to the evolution of new genetic traits, since genetic mutations are believed to appear largely at random in populations (Gillespie 2004; Hartl and Clark 2007).

Since the probability that PA will hit the target in each throw is 50%, which is higher than the 10% probability for PB, one can reasonably expect that PB will hit the target later than PA. Of course, it is possible that PB will hit the target in the first throw, but that is much less likely than PA hitting the target in the first throw. Analogously, since the probability of evolution of any costly trait is generally lower than that for a costless trait, with that probability decreasing with increases in the survival costs imposed by the costly trait, then it follows that costly traits should generally appear later in the evolutionary history of a species than costless traits.

Costly traits should be costly not to use Costly traits must have had a strong effect on the performance of the task for which they evolved in order to make up for the survival costs imposed by those traits. Today this would translate into a higher correlation between costly traits' measures and performance attributes for the task, than between costless traits' measures and the same task performance attributes. That is, not using a costly trait would be more costly, so to speak, than not using a costless trait in the context of the task for which the traits evolved.

The above conclusions seem to be true when we look at the classical example of costly trait, the peacock species. Petrie et al. (1991) found that the costly ornamental train of the male peacock, and especially the number of eyespots on the train, are far more attractive traits for the peahens than other apparently costless traits. Costless ornamental traits are more numerous in the peacock species than costly ones, of which the only known one is the train, and their relative importance in the context of the mating task is dwarfed by the importance of the train. Examples of costless ornamental traits likely evolved for mating in the male of the peacock species are the crest atop the male's head, the brightly colored feathers on the male's chest, various color patterns around the eyes, various feather patterns occurring in different parts of the male's body, and the level of bilateral (i.e., left-right) symmetry of these ornamentations (Darwin 1871; Zahavi and Zahavi 1997).

The evolution of oral speech in humans: a costly trait associated with choking and illnesses

Modern oral speech was enabled by the evolution of a larynx located low in the neck (Laitman 1993; Lieberman 1998). The evolution of oral speech is one of the most

important landmarks in the evolution of the human species, having happened relatively recently in our evolutionary history (see Fig. 1). However, the new larynx design also significantly increased our ancestors' chances of death by choking during ingestion of food and liquids, and of suffering from various aerodigestive tract diseases such as gastroesophageal reflux (Laitman and Reidenberg 1997), among other survival-related problems. Oral speech must have been particularly important for effective communication in our evolutionary past, and effective communication must have been important for fitness enhancement (Pinker 2003), otherwise its survival cost would have prevented complex speech from evolving.

Oral speech seems to exhibit the three common characteristics of costly traits. Oral speech is a rare costly trait among human traits involved in the transfer of communicative stimuli. By all accounts, it is the only such trait that obviously imposed a survival cost as it evolved among our ancestors. In addition to increasing our ancestors' chances of death by choking, and of developing aerodigestive tract diseases, it also hampered our ancestors' ability to breathe while drinking water. Water sources are likely to have been a preferred site for predators to ambush prey (Boaz and Almquist 2001), as they are today, and the oxygen depletion caused by having to hold their breath while drinking created yet another survival cost for our ancestors. Other communication-related traits, such as the ability to use body language and facial expressions, do not seem to have imposed a similar survival handicap on our ancestors.

Oral speech also appeared late in the evolutionary history of hominids, in the last 100,000 years of that 3.5 million year history, or approximately the last 3% (Cartwright 2000; Laitman 1984; Lieberman 1998). This is consistent with it being a costly trait, since the evolution of a costly trait is a low probability event, and low probability events take more time to happen than high probability events. In fact, the evolution of oral speech coincides with the evolution of our species,

Homo sapiens, likely from another species within the genus Homo, namely Homo erectus (Boaz and Almquist 2001; Lieberman 1998). Many human evolution researchers believe that it was the evolution of oral speech, with the complexity of human interactions that it enabled, that made us truly human (Cartwright 2000; Dunbar 1993; Lieberman 1998).

Finally, empirical research on the effects of electronic communication media that suppress the ability to use oral speech suggests that it is very costly not to use oral speech in communicative interactions. This is reflected in as much as a tenfold reduction in communication fluency, coupled with a significant increase in communication ambiguity and perceived cognitive effort (Graetz et al. 1998; Kock 2005; Kock and DeLuca 2007; Kock et al. 2007; Simon 2006). Communication fluency is defined here as the number of ideas effectively conveyed per unit of time; and has been somewhat imprecisely measured as the number of words conveyed per unit of time (Kock 2005; Kock and DeLuca 2007). It seems that, when oral speech is removed from a communication medium, communication becomes rather cumbersome (Crowston et al. 2007; Graetz et al. 1998; Kock 2005). Table 1 summarizes the discussion so far regarding the relationship between oral speech and the three common characteristics of costly traits.

If the use of oral speech is enabled by an audio channel, adding a video channel typically has little impact on the effectiveness or ease with which communication takes place (Burke and Aytes 2001; Daly-Jones et al. 1998; Simon 2006). In this sense, oral speech could be seen to the communication task as analogous to what the peacock's train is to the mating task (Petrie et al. 1991); both are costly traits that have an effect that dwarfs the effects of other costless traits evolved in connection with the same task. There are exceptions to this general rule regarding the importance of a video channel (see, e.g., Daly-Jones et al. 1998), such as modern tasks in which shared and real-time visualization of an object or situation is important for the

Fig. 1 The evolution of oral speech in humans. (*Timeline*: period that goes from the evolution of the first hominids, the Australopithecines, until today. *Thick horizontal bars*: indicate the communication modes used in different hominid evolution stages)
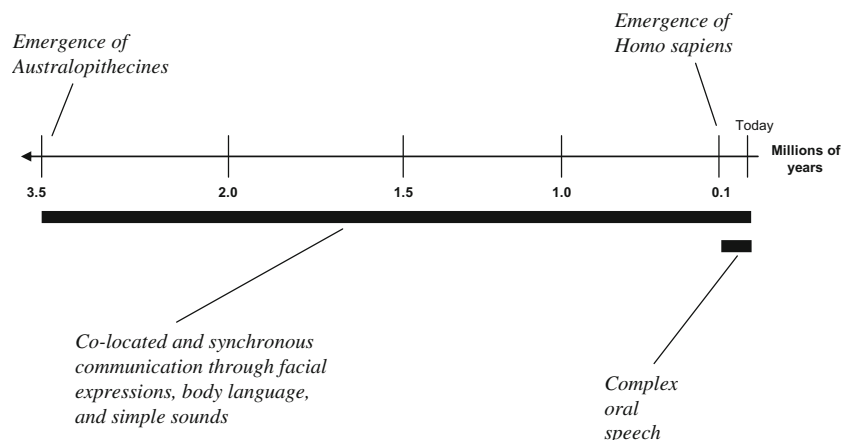
Table 1 Oral speech and the three common characteristics of costly traits

Common characteristic of costly traits	Evidence in connection with oral speech
Costly traits should be rare in nature	Oral speech is the only communication-related trait that clearly imposed a survival cost on our ancestors; conversely, various related costless traits seem to exist—e.g., the ability to use body language and facial expressions for communication.
Costly traits should generally evolve late	Oral speech evolved late among hominids, having appeared in the last 100,000 years of the 3.5 million years of hominid evolution—approximately the last 3% of that period.
Costly traits should be costly not to use	Suppressing oral speech in electronic communication media is costly, leading to as much as a tenfold reduction in communication fluency, coupled with a significant increase in communication ambiguity and perceived cognitive effort.

task completion. Examples would be a surgical intervention involving two or more geographically distributed doctors, and a real-time collaborative design of a car engine.

Oral speech and knowledge communication: the focused impact on fitness of this costly trait

The notion that oral speech is particularly important in modern human communication, as discussed so far, needs further theoretical elaboration and refinement. Simple observation of modern human communication practices suggests that oral speech is not equally important for all types of communication interactions. For example, if one person is trying to communicate his or her home or work address to another, to be used on a letter, then probably an e-mail will be just as effective as a phone call. Also, web-based social communication tools that enable human interaction through short text messages and provide no audio channel, such as Twitter, would probably not be as successful as they are if the theoretical framework put forth here applied to all types of communicative interactions.

This takes us back to a review of why oral speech evolved in the first place. More specifically, how did oral speech affect fitness among our ancestors? As discussed earlier, only if oral speech had a net positive impact on fitness, by enhancing the performance of a fitness-relevant task, it would have overcome the survival handicap associated with our customized vocal tract. The answer is that oral speech enabled the exchange of knowledge among our ancestors, which indirectly increased their reproductive success by allowing them to occupy what Pinker (2003) refers to as the "cognitive niche".

A common characteristic of the simple exchanges illustrated above (communication of a home or work address and interaction through short text messages) is that these types of exchanges involve little or no knowledge transfer. Therefore, if we assume that oral speech was evolved by our ancestors primarily to enable the communication of knowledge, its effect should not be particularly strong in communication interactions with little or no knowledge content. There are other factors that may induce modern humans to communicate electronically through text only, and with no audio—e.g., via e-mail without audio file attachments. Among those factors is the ease with which e-mail can be sent to many individuals at the same time. Video and audio blogs can be used for the same purpose, incorporating oral speech, but their use is still not as widespread and embedded in communication practices as is the use of e-mail.

Knowledge about "something" is defined here in a way analogous to how it is defined by many cognitive psychologists: as a set of mental schemas that allows one to predict the future, or find out more about a present situation, based on information about the present or the past (Gardner 1985; Kock 1999; Lee and Holyoak 2008; Waldmann et al. 1995). As noted by artificial intelligence researchers, with knowledge, one can build mental rules that can be expressed in the form of "if ... then ..." statements (Luger and Stubblefield 2008; Russel and Norvig 2002), or reworded as statements that contain linguistic elements that express causality such as "the reason for ... is ...", "this is ... because ...", and "the cause for ... is ..." (Kock 1999; Waldmann et al. 1995). For example, the statement "the temperature in room 118, where 100 people are attending a lecture, is now 78 degrees Fahrenheit" contains only information; whereas the following statement contains knowledge: "if the temperature in room 118 reaches 80 degrees Fahrenheit, most of the 100 people attending a lecture there will feel uncomfortable".

Our ancestors faced survival threats on a regular basis—exposure to pathogens, attacks by predators or territorial animals, encounters with venomous insects or snakes, and ingestion of toxins, among others. These events often occurred in specific contexts. For example, territorial animals would attack when their habitat was invaded by our ancestors, and venomous insects and snakes occur in higher quantities in certain areas (Hung 2004; Kock et al. 2008; Manipady et al. 2006). Without the ability to vicariously obtain knowledge linking contexts with survival

threats, our ancestors would have to experience the survival threats, or observe someone experiencing them at a close distance, in order to build that knowledge. Oral speech enabled vicarious knowledge acquisition regarding survival threats, and thus significantly increased our ancestors' chances of survival, easily overcoming the extra survival costs associated with our vocal tract.

Costly traits evolved by our human ancestors must have had a strong effect on the performance of the task for which they evolved, in order to make up for the survival costs imposed by those traits. In the case of oral speech, a strong candidate for the task in question in the knowledge communication task, where oral speech evolved in part to increase the performance with which knowledge about survival threats was communicated among our ancestors. Oral speech may also have influenced fitness in other ways, although avoidance of survival threats must have been an important element in the selection of this costly trait. For example, vicarious knowledge about survival-enhancing elements, such as seasonal availability of food, was likely also enabled by oral speech (Cartwright 2000; Dunbar 1999). So probably was the ability to build social relationships and court potential mates (Dunbar 1993; Miller 2000, 2002). This type of knowledge communication likely required reciprocal altruism to have evolved before, which mathematical formalizations and empirical evidence strongly suggest was the case in the human species (Fletcher and Zwick 2007; Henrich 2004; McElreath and Boyd 2007; Trivers 2002).

Knowledge communication performance refers to both the effectiveness and efficiency with which knowledge is communicated (Kock 1999; Russel and Norvig 2002; Waldmann et al. 1995). Effective knowledge communication between two individuals occurs when the knowledge possessed by one individual is comprehensively and unambiguously conveyed to the other individual. Efficient knowledge communication occurs when the knowledge possessed by one individual is quickly and effortlessly conveyed to the other individual.

The effects of oral speech in e-collaborative tasks: communication fluency and ambiguity

It follows from the theoretical discussion presented in the previous section that removing the ability to convey speech from an electronic communication medium is likely to impair communication performance much more strongly than removing the medium's ability to convey other communicative stimuli—e.g., facial expressions, body language, olfactory cues, and tactile stimuli. However, this effect is moderated by the extent the extent to which knowledge is being communicated. This conclusion is consistent with the results of various studies that compare the impact of various media on communication performance (Graetz et al. 1998; Kock 2004; Kock and DeLuca 2007).

Graetz et al. (1998) compared the performance in 4-person groups across three communication media conditions: face-to-face, telephone conferencing, and electronic chat. The experimental task required exchange of knowledge to be successfully accomplished, and the participants were given a limited amount of time (approximately 30 minutes) to review the information provided to them by the researchers and to discuss it with the other group members. Group outcome quality was about the same through the face-to-face and telephone conferencing media; slightly higher in the latter, a statistically insignificant difference. Group outcome quality was significantly lower through the electronic chat medium. Measures of perceived cognitive effort and frustration were about the same for the face-to-face and telephone conferencing media, and significantly higher for the electronic chat medium. In summary, the medium that did not enable oral speech was the least conducive to effortless and unambiguously knowledge communication. This is consistent with the view that oral speech is a costly trait that is "costly not to use" in the context of knowledge communication.

Particularly noteworthy is the finding by Kock and DeLuca (2007), in a study of individuals in two different countries, that the use of an electronic communication medium that suppressed the ability to convey speech (a version of e-mail) dramatically reduced communication fluency. In this study, communication fluency was measured as the number of words conveyed per unit of time, a surrogate measure. The reduction in fluency observed by Kock and DeLuca (2007) was estimated to have been more than tenfold; that is, e-mail users' fluency was less than 1/10 of their expected fluency communicating over the phone or face-to-face. This is too drastic a reduction to be explained by the known fact that typing is mechanically more cumbersome than speaking, which would normally lead to a twofold reduction in fluency (Kock 2004; McQueen et al. 1999). Again, it appears that our brain was designed by evolution to rely heavily on oral speech for effective and efficient knowledge communication, because oral speech was costly to evolve. As a result, it is costly not to use oral speech in modern human communication whenever a significant amount of knowledge must be exchanged.

Compensatory adaptation: counteracting the effects of oral speech suppression by e-collaboration technologies

A possible conclusion based on the arguments presented thus far is that a decrease in communication fluency and an

increase in ambiguity, caused by the suppression of oral speech in an electronic medium, may lead to a decrease in the quality of the outcomes accomplished by a group using the medium for most of its communication. Indeed, this seems to frequently be the case in short-duration tasks (Graetz et al. 1998; Kahai and Cooper 2003; Warkentin et al. 1997), but not necessarily in long duration tasks (Burke and Chidambaram 1999; Carlson 1995; DeLuca 2003; Kock 2005; Kock and DeLuca 2007). The reason is that, in long duration tasks, it is common to observe a phenomenon known as compensatory adaptation (Kock 2002). This phenomenon may counteract the problems associated with the suppression of oral speech (Kock 2005; Kock et al. 2007).

Compensatory adaptation seems to be one of the reasons why groups performing knowledge-intensive tasks over a relatively long period of time (e.g., days, weeks, or months), using an e-collaboration medium that suppresses oral speech, often have the same or even better performance than groups where oral interaction is not suppressed (Kock 2005). As long as there is motivation among group members to expend additional compensatory effort, which may be strongly influenced by social factors (Bandura 1986; Fulk 1993), group members are likely to adapt their communicative behavior in order to compensate for the obstacles posed by the e-collaboration medium's suppression of oral speech (Short et al. 1976; Ulijn et al. 2001).

Compensatory adaptation can be understood as a moderating effect. That is, the effects of oral speech suppression on communication fluency and ambiguity are moderated by compensatory adaptation, whose moderating effect is in turn positively correlated with e-collaborative task duration. In short duration tasks, the negative effects of oral speech suppression on communication fluency and ambiguity are likely to be particularly acute, as there is no time for compensatory adaptation to take place. In long duration tasks, the e-collaborators may adapt their behavior to compensate for the cognitive obstacles caused by the suppression of oral speech. This phenomenon has been referred to as compensatory adaptation to e-collaboration media of low naturalness (Kock 2004).

Discussion and conclusion

The arguments presented in the previous sections can be summarized into three main predictions. The first refers to the effects of oral speech suppression on communication fluency and ambiguity in the context of e-collaboration. The second refers to the moderating effect that the amount of knowledge communicated is likely to have on these effects. The third prediction refers to the moderating effect that compensatory adaptation is likely to have on the effects of oral speech suppression on communication fluency and ambiguity. Compensatory adaptation itself is correlated with task duration, and may take place even when a large amount of knowledge is being communicated. These predictions are outlined below, and followed by recommendations for the use of e-collaboration tools in organizations.

Communication fluency and ambiguity A key prediction based on the discussion put forth here is that removing the ability to convey speech from an e-collaboration medium used by modern humans is likely to decrease communication fluency and increase communication ambiguity much more strongly than removing the medium's ability to convey other communicative stimuli such as facial expressions and body language. The reason is that the ability to use speech for communication evolved at a much higher survival cost among our human ancestors than the ability to use any other communicative stimulus.

The moderating effect of knowledge communication The negative effects of oral speech suppression on communication fluency and ambiguity are moderated by the amount of knowledge communication taking place in an e-collaborative task. Due to the context in which oral speech evolved among our ancestors, oral speech is not equally important for all types of communication interactions among modern humans; it is particularly important in knowledge-intensive communication. Communicating one's home address to another person, for example, can be easily and effectively accomplished through e-mail. Conversely, if one engineer wants to communicate knowledge about how to design a new car engine to a production manager, then the suppression of oral speech may make the communication much slower and ambiguous.

The moderating effect of compensatory adaptation Another moderating effect, similar to but of a different kind than knowledge communication, is compensatory adaptation. Compensatory adaptation, or the degree to which individuals adapt to a communication medium that is unnatural (e.g., one that suppresses oral speech), seems to moderate the negative effects of oral speech suppression on communication fluency and ambiguity. Compensatory adaptation to media that suppress oral speech typically happens over time (e.g., days, weeks or months), as individuals modify their communicative behavior to make up for the shortcomings of the medium. This may be one of the reasons why compensatory adaptation is not normally observed in short duration tasks requiring intense knowledge exchange. For example, groups performing knowledge-intensive tasks through text-based e-collaboration technologies, and where the tasks last from a few minutes to a few hours, generally

tend to produce task outcomes of inferior quality. These groups would be better off either: (a) performing the task face-to-face or using an e-collaboration technology that provides an audio channel; or (b) performing the task using a text-based e-collaboration technology, but over a long time period (e.g., a few days) so that compensatory adaptation can take place.

The increasingly distributed nature of organizational processes (e.g., sets of activities that are repeated over and over again) and projects (e.g., sets of activities that are carried out once or a few times) requires tasks to be accomplished by groups of individuals who are not only geographically distributed, but also distributed across multiple time zones. Given this, it is impractical to try to ensure that all activities in a process or project are performed face-to-face, or even through e-collaboration involving synchronous oral speech interactions. Sometimes ubiquitous text-based asynchronous communication such as e-mail must be used for part of the process or project, due to cost constraints. It is also possible that asynchronous oral speech interactions will be used (e.g., voice messaging or e-mail with attached audio messages) for part of the process or project, due to group members having to work from different time zones.

A more practical piece of advice to managers, which follows from the theoretical discussion, is the following: (a) break organizational processes and projects into component collaborative activities; (b) rank those activities in terms of the perceived amount of knowledge exchange involved; (c) make sure that highly knowledge-intensive activities are performed through media that incorporate synchronous oral speech (e.g., face-to-face or teleconferencing interaction), which may mean that certain group members will have to make special accommodations to participate in group discussions (e.g., attend a meeting at 3a.m., local time); (d) make sure that moderately knowledge-intensive activities are performed through media that incorporate some form of oral speech, even if asynchronous (e.g., voice messaging or e-mail with attached audio messages); and (e) encourage the use of text-based e-collaboration media for activities that involve little or no knowledge exchange among participants, as this is likely to be the cheapest and most widely available organizational communication medium.

Appendix A: The threshold for evolution of costly traits

One of the most fundamental contributions to mathematical evolutionary thinking was made by Price (1970). He showed that for any trait to evolve through selection, in any population or subpopulation of individuals of the same species, the trait must satisfy Eq. (1), whose main element

is a covariance term. The fitness of an individual that possesses the trait (e.g., number of surviving offspring) is measured through W, and Z is a measure of the manifestation of the trait in the individual (e.g., $Z=1$ if the trait is present, and $Z=0$ if it is absent). The trait in question can be any morphological, physiological or behavioral trait; examples could be opposing thumbs, aggressiveness, or a large train (tail appendage) with many eyespots.

$$Cov(W, Z) > 0 \tag{1}$$

Equation (1) can be re-written as Eq. (2) in terms of the standardized measures of W and Z, referred to as w and z. This allows for its use in the context of path analysis (Wright 1934, 1960), which in turn greatly simplifies (as it will be shown below) theoretical reasoning based on comparative analyses of evolution of traits through selection.

$$Cov(w \cdot Sw + \overline{W}, z \cdot Sz + \overline{Z}) = Cov(w \cdot Sw, z \cdot Sz)$$
$$= Sw \cdot Sz \cdot Cov(w, z) > 0 \Rightarrow Cov(w, z) > 0 \tag{2}$$

Figure 2 shows a path model where a costly trait measured by y is represented. All the measures are standardized, which is why they are indicated with lowercase letters. The measure y has a positive causal relationship with a task performance attribute a. For example, a could be number of lifetime copulations of an individual, a performance attribute associated with the mating task, in the case of a trait used for mate choice. The measure y has a negative causal relationship with s, a measure of survival performance. For example, s could be age of an individual at the time of death. Since any individual must be alive to perform any task, s also has a positive causal relationship with a. Both a and s have positive causal relationships with fitness (w). The magnitudes of these relationships are given by the path coefficients p_{ay}, p_{sy} etc. All path coefficients are positive except for p_{sy}, which is negative since it refers to the survival cost of trait y. (For simplicity, a trait measured by y is also called trait y.)
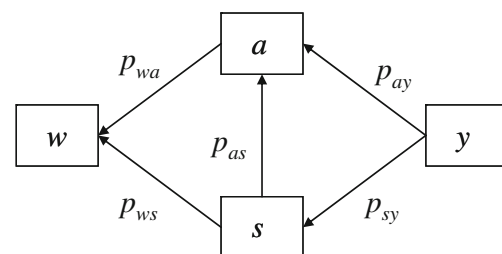

Fig. 2 Path model showing a costly trait and its relationship with fitness. (y: measure of a costly trait; e.g., $y=1$ if the costly trait is present, and $y=0$ if the trait is absent. a: task performance attribute measure. s: survival success measure; e.g., age at the time of death. w: fitness, measured as number of surviving offspring. p_{ay}, p_{sy} etc.: path coefficients, or standardized partial regression coefficients)

In path analysis the covariance between any pair of variables is given by the sum of the products of the path coefficients in all paths connecting the two variables (Wright 1934, 1960). Thus, combining Eq. (2) with Fig. 2 leads to Eq. (3), which must be satisfied for any costly trait y to evolve through selection.

$$p_{wa} \cdot p_{ay} + p_{ws} \cdot p_{sy} + p_{wa} \cdot p_{as} \cdot p_{sy} > 0 \Rightarrow p_{wa} \cdot p_{ay}$$
$$> -p_{sy} \cdot (p_{ws} + p_{wa} \cdot p_{as}) \Rightarrow$$
$$p_{ay} > -p_{sy} \cdot \left(\frac{p_{ws}}{p_{wa}} + p_{as} \right) \tag{3}$$

For a costless trait x, a trait with no negative effect on survival, Eq. (3) is reduced to Eq. (4) because p_{sy} equals zero. What this equation tells us is that a costless trait x will always evolve as long as it has a positive causal relationship with a task performance attribute a, assuming that a has a positive causal relationship with fitness (w).

$$p_{ax} > 0 \tag{4}$$

In the task of mating for example, any costless trait x that increases mating success (measured by a) would evolve through selection, with trait frequency growth subject to the constraints posed by chance events unrelated to the trait. That is, the trait would evolve to the point of becoming widespread in a population only if it is not eliminated by chance from the population at its early stages of evolution; e.g., the only individual that initially possesses the trait is killed by a lightning strike before reaching reproductive maturity (Gillespie 2004; Graur and Wen-Hsiung 2000). A costly trait y (e.g., the male peacock's train), on the other hand, would have to meet a more stringent requirement for evolution. It would only evolve through selection if the trait's positive effect on a surpassed the threshold given by the right side of Eq. (3).

Appendix B: Probability of evolution of costly traits

Let us assume that the appearance of a new costly trait y in a population will lead to a variation in p_{ay} and $-p_{sy}$ that will be given by random numbers going from 0 to D. Let us also represent T as in Eq. (5):

$$T = \left(\frac{p_{ws}}{p_{wa}} + p_{as} \right) \tag{5}$$

The value of T is assumed here to be largely population specific, in a relatively stable environment, and thus should remain relatively constant as new costly or costless traits appear in a population and either evolve or disappear in response to selection pressures. This can be illustrated for the task of mating, where a can be the number of lifetime copulations a male of a species engages in. In this case, the effect of a on fitness (w), the effect of survival performance (s) on w, and the effect of s on a are relatively constant for the males of the species.

In a relatively stable environment this can be shown to hold for any task whose performance is measured by a. This conclusion also follows from the assumption that those effects can be represented through stable regression coefficients; an assumption that is routinely used in mathematical population genetics models (Gillespie 2004; Rice 2004).

On the other hand, the effects that new traits x or y have on a and/or s can vary widely, since those traits appear in the population as a result of stochastic processes. Those effects will in turn ultimately dictate whether those traits will evolve or disappear in the species. For species that live today in environments similar to those in which most of their traits evolved, the value of T can be easily estimated empirically since the path coefficients are standardized partial regression coefficients.

Given the above assumptions, the probability of evolution of a new costly trait y in a population will be given by Eq. (6), assuming that T is equal to or greater than one. This equation reflects the intersection spaces of variation of D and DT, and can easily be verified through simple Monte Carlo simulations.

$$P(Evo(y)) = \frac{D}{D \cdot T} \cdot \frac{1}{2} \Rightarrow$$
$$P(Evo(y)) = \frac{1}{(2 \cdot T)} \tag{6}$$

T is assumed to be equal to or greater than one because it is difficult to conceive of a species population or subpopulation for which the performance of a task is more important for fitness than survival, even for the all-important task of mating. Let us consider, for example, spider species where the males are routinely cannibalized by their large and aggressive female mates during or after copulation (see, e.g., Wilder and Rypstra 2008). In these species, the male spiders must still successfully survive up to the moment of copulation. Therefore, when looked at as a subpopulation of the species to which they belong, those male spiders will likely have a ratio p_{ws} / p_{wa} that is greater than 1 (and thus a T greater than 1) for the task of mating, regardless of the fact that they contribute little more than their sperm to the survival of their offspring (and thus to their own fitness).

Equation (6) can be depicted in a graph, as shown in Fig. 3. The graph shows the variation of the probability of evolution of a new costly trait y in a population (vertical axis) based on values of T ranging from 1 to 10 (horizontal axis).

As can be inferred from Fig. 3, costly traits will always have a lower probability of evolution than costless traits, because the value of T for the latter traits is always zero. This suggests that costly traits should be rarer in nature than costless ones, regardless of the task for which they were evolved; e.g., mating, communication, fighting.

Moreover, costly traits should be particularly rare in species where the value of T is high. This would be the case in species where the number of offspring born to females was small; and in species where the offspring relied heavily on their parents for survival in their early years of life, when most deaths occur. (In these species, the effect of survival on fitness would have been much higher than the effect of mating on fitness.) These are characteristics of the human species, and likely of the hominid ancestors in the human lineage (Boaz and Almquist 2001; Cartwright (2000). Thus, T values should have been high for our hominid ancestors, making the evolution of costly traits difficult.

Of course, in order to evolve, costly and costless traits also have to satisfy the condition that their covariance with fitness is greater than zero (i.e., that they have a positive net impact on fitness), which rarely is the case for new genetic mutations. Most new genetic mutations have either a negative or neutral effect on fitness; in the latter case they may evolve by chance, through a process known as genetic drift (Gillespie 2004; Hartl and Clark 2007; Maynard Smith 1998). Costly traits, unlike costless ones, have another condition to satisfy: they must overcome the survival costs that they impose.
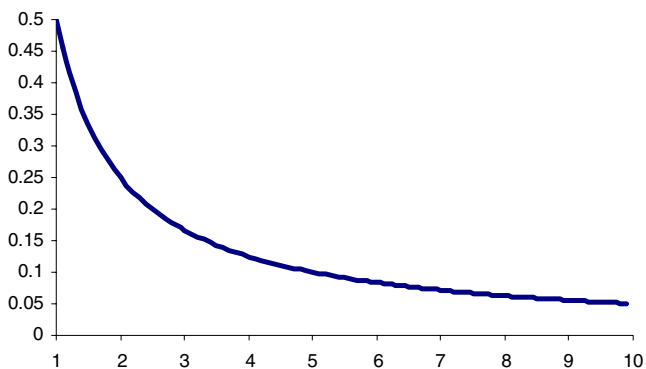

Fig. 3 Probability of evolution of a new costly trait. (*Vertical axis*: Probability of evolution of a new costly trait y in a population. *Horizontal axis*: T values ranging from 1 to 10)
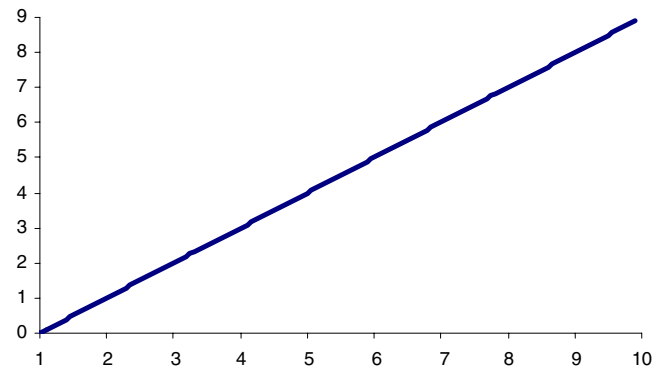

Fig. 4 Variation of the expected ratio between p_{ay} and p_{ax}. (*Vertical axis*: Expected ratio between p_{ay} and p_{ax}. *Horizontal axis*: T values ranging from 0 to 10.)

Appendix C: Different effects of costly and costless traits

Let us also assume that the appearance of costly and costless traits in a population will lead to random values of p_{ax} and—p_{sy} in the range from 0 to D. The expected value of p_{ax} for costless traits that evolve will then be given by D divided by 2. The expected value of p_{ay}, on the other hand, will be given by $(DT-D)/2$, assuming that T is equal to or greater than 1. Therefore, the expected ratios between p_{ay} and p_{ax} will be given by Eq. (7).

$$E\left(p_{ay}/p_{ax}\right) = \frac{(D \cdot T - D)/2}{D/2} \Rightarrow$$
$$E\left(p_{ay}/p_{ax}\right) = T - 1 \qquad (7)$$

The graph in Fig. 4 shows the variation of the expected ratio between p_{ay} and p_{ax} (vertical axis) based on values of T ranging from 1 to 10 (horizontal axis). The ratio grows proportionally with T, and is a measure of how strong the expected effect of a costly trait y on the task performance attribute a is, compared with the expected effect of a costless trait x. For simplicity, it is assumed here that both types of traits are either independent from each other, or spread to fixation in a species at different points in time. For dependent traits or traits that evolve at the same time, the mathematical analysis becomes more complex, but the results are qualitatively the same.

An expected ratio between p_{ay} and p_{ax} of 1.3, for example, means that the standardized effect of any costly trait on a given task performance attribute a is on average 30% stronger than the effect of any costless trait on the same task performance attribute. A ratio of 8 means that the costly trait is on average 800% stronger (e.g., $p_{ay}=.4$ and $p_{ax}=.05$). Standardized effects are expressed in terms of standard deviations of the variables to which they refer. For example, a $p_{ay}=.4$ means that a 1 standard

deviation variation in y causes a .4 standard deviation variation in a.

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