



OPINION ARTICLE

From where to what: a neuroanatomically based evolutionary model of the emergence of speech in humans [version 1; referees: 3 approved with reservations]

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Abstract

In the brain of primates, the auditory cortex connects with the frontal lobe via the temporal pole (auditory ventral stream; AVS) and via the inferior parietal lobule (auditory dorsal stream; ADS). The AVS is responsible for sound recognition, and the ADS for sound-localization, voice detection and audio-visual integration. I propose that the primary role of the ADS in monkeys/apes is the perception and response to contact calls. These calls are exchanged between tribe members (e.g., mother-offspring) and are used for monitoring location. Perception of contact calls occurs by the ADS detecting a voice, localizing it, and verifying that the corresponding face is out of sight. The auditory cortex then projects to parieto-frontal visuospatial regions (visual dorsal stream) for searching the caller, and via a series of frontal lobe-brainstem connections, a contact call is produced in return. Because the human ADS processes also speech production and repetition, I further describe a course for the development of speech in humans. I propose that, due to duplication of a parietal region and its frontal projections, and strengthening of direct frontal-brainstem connections, the ADS converted auditory input directly to vocal regions in the frontal lobe, which endowed early *Hominans* with partial vocal control. This enabled offspring to modify their contact calls with intonations for signaling different distress levels to their mother. Vocal control could then enable question-answer conversations, by offspring emitting a low-level distress call for inquiring about the safety of objects, and mothers responding with high- or low-level distress calls. Gradually, the ADS and the direct frontal-brainstem connections became more robust and vocal control became more volitional. Eventually, individuals were capable of inventing new words and offspring were capable of inquiring about objects in their environment and learning their names via mimicry.

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1. Introduction

In the past five decades, gorillas, orangutans, chimpanzees and bonobos were shown capable of learning sign language (Blake, 2004; Gibson, 2011). An important cognitive distinction between the language used by humans and the language used by other apes is with the ability to ask questions. This was first noted by (Premack & Premack, 1984) who reported that, although their chimpanzee, Sarah, showed no difficulty answering questions or repeating questions before answering them, she never used the question signs for inquiring about her own environment. Jordania (2006), in his review of the literature, noted that other signing apes did not utilize questions and that their initiation of conversations was limited to commands (e.g., “me more eat”) and observational statements (e.g., “bird there”). This absence of a questioning mind is in direct contrast to human toddlers and children, who are renowned for their incessant use of questions. My interpretation of this human-ape distinction is that during human evolution, we transitioned from the display of curiosity toward items that are present in our environment (i.e., observational statements) to curiosity toward items that are absent in our environment (i.e., WH questions). Developing curiosity about out of sight events and objects could thus explain the rapid migration of humans across the globe. Furthermore, this curiosity toward the unknown is the driving force behind scientific exploration and technological development. One could hence argue that it is the ability to ask that separates us from other animals and makes the human species unique.

Although no non-human primate has been reported to ask questions, they were reported to exchange calls for monitoring location (i.e., contact calls). For example, when a mother and her infant are physically separated, each emits in turn a call to signal the other their location. This emission of contact calls could therefore be interpreted as akin in meaning to the question “where are you?” If human communication and contact calls are related, it suggests that the preliminary urge to learn about the unknown is derived from infants and mothers seeking to reunite. In the present paper, based on findings collected from brain research, genetics and paleoarcheology, I demonstrate that human speech and contact calls use the same brain structures, and consequently argue that human speech emerged from contact call exchange. I then argue that by modifying their contact calls with intonations, infants were capable of signaling their mothers whether they were under high- or low-level of distress. Given the turn taking nature of these calls, and as both mothers and infants were capable of modifying their calls with intonations, the ability to choose the call type eventuated with the first yes-no conversation structure. In this scenario infants were capable of inquiring about the safety of objects in their environment (i.e., with a low-level distress call) and mothers were capable of responding to that question with a high-level distress call to signal danger or a low-level distress call to signal safety. As the use of intonations became more prevalent, vocal control became more volitional. Eventually, individuals became capable of enunciating novel calls, and the question-answer conversation pattern further evolved for infants inquiring their mothers for the names of objects in their surrounding and then mimicking the mother’s vocal response.

2. Models of language processing in the brain and their relation to language evolution

Throughout the 20th century, our knowledge of language processing in the brain was dominated by the Wernicke-Lichtheim-Geschwind

model (Geschwind, 1965; Lichtheim, 1885; Wernicke & Tesak, 1974). This model is primarily based on research conducted on brain-damaged individuals who were reported to possess a variety of language related disorders. In accordance with this model, words are perceived via a specialized word reception center (Wernicke’s area) that is located in the left temporoparietal junction. This region then projects to a word production center (Broca’s area) that is located in the left ventrolateral prefrontal cortex. Because almost all language input was thought to funnel via Wernicke’s area and all language output to funnel via Broca’s area, it became extremely difficult to identify the basic properties of each region. This lack of clear definition for the contribution of Wernicke’s and Broca’s regions to human language rendered it extremely difficult to identify their homologues in other primates. (For one attempt, see Aboitiz & García, 1997). With the advent of the MRI and its application for lesion mappings, however, it was shown that this model is based on incorrect correlations between symptoms and lesions and is therefore flawed (Anderson *et al.*, 1999; Dronkers *et al.*, 1999; Dronkers, 2000; Dronkers *et al.*, 2004; Poeppel *et al.*, 2012; Rauschecker & Scott, 2009 - Supplemental Material; Vignolo *et al.*, 1986). The refutation of such an influential and dominant model opened the door to new models of language processing in the brain, and as will be presented below, to formulating a novel account of the evolutionary origins of human language from a neuroscientific perspective.

In the last two decades, significant advances occurred in our understanding of the neural processing of human auditory processing. In parallel to the refutation of the classical model, comparative studies reported on homologies between the auditory cortices of humans and other primates. Based on histological staining, functional imaging and recordings from the auditory cortex of several primate species, 3 auditory fields were identified in the primary auditory cortex, and 9 associative auditory fields were shown to surround them (Figure 1 top left; Bendor & Wang, 2006; Kaas & Hackett, 2000 - review; Petkov *et al.*, 2006; Rauschecker *et al.*, 1995). Anatomical tracing and lesion studies further indicated of a separation between the anterior and posterior auditory fields, with the anterior primary auditory fields (areas R-RT) projecting to the anterior associative auditory fields (areas AL-RTL), and the posterior primary auditory field (area A1) projecting to the posterior associative auditory fields (areas CL-CM; la Mothe *et al.*, 2006; Morel *et al.*, 1993; Rauschecker *et al.*, 1997). Recently, evidence accumulated that indicates homology between the human and monkey auditory fields. In humans, histological staining studies revealed two separate auditory fields in the primary auditory region of Heschl’s gyrus (Sweet *et al.*, 2005; Wallace *et al.*, 2002), and by mapping the tonotopic organization of the human primary auditory fields with high resolution fMRI and comparing it to the tonotopic organization of the monkey primary auditory fields, homology was established between the human anterior primary auditory field and monkey area R (denoted in humans as area hR) and the human posterior primary auditory field and the monkey area A1 (denoted in humans as area hA1; Da Costa *et al.*, 2011; Humphries *et al.*, 2010; Langers & van Dijk, 2012; Striem-Amit *et al.*, 2011; Woods *et al.*, 2010). Intracortical recordings from the human auditory cortex further demonstrated similar patterns of connectivity to the auditory cortex of the monkey. Recording from the surface of the auditory cortex (supratemporal plane) reported that the anterior Heschl’s gyrus (area hR) projects primarily to the middle-anterior superior temporal gyrus (mSTG-aSTG) and the posterior Heschl’s gyrus (area hA1)

projects primarily to the posterior superior temporal gyrus (pSTG) and the planum temporale (area PT; **Figure 1** top right; **Gourévitch et al., 2008; Guéguin et al., 2007**). This connectivity pattern is also corroborated by a study that recorded activation from the lateral surface of the auditory cortex and reported of simultaneous non-overlapping activation clusters in the pSTG and mSTG-aSTG while listening to sounds (**Chang et al., 2011**).

Downstream to the auditory cortex, anatomical tracing studies in monkeys delineated projections from the anterior associative auditory fields (areas AL-RTL) to the ventrolateral prefrontal cortex (VLPFC; **Munoz et al., 2009; Romanski et al., 1999**) and amygdala (**Kosmal et al., 1997**). Cortical recording and functional imaging studies in macaque monkeys further elaborated on this processing stream by showing that acoustic information flows from the anterior auditory cortex to the temporal pole (TP) and then to the VLPFC (**Perrodin et al., 2011; Petkov et al., 2008; Poremba**

et al., 2004; Romanski et al., 2004; Russ et al., 2007; Tsunada et al., 2011). This pathway is commonly referred to as the auditory ventral stream (AVS; **Figure 1**, bottom left-red arrows). In contrast to the anterior auditory fields, tracing studies reported that the posterior auditory fields (areas CL-CM) project primarily to the dorsolateral prefrontal cortex (although some projections do terminate in the VLPFC; **Cusick et al., 1995; Romanski et al., 1999**). Cortical recordings and anatomical tracing studies in monkeys further provided evidence that this processing stream flows from the posterior auditory fields to the prefrontal cortex via a relay station in the intra-parietal sulcus (IPS; **Cohen, 2004; Deacon, 1992; Lewis & Van Essen, 2000; Roberts et al., 2007; Schmahmann et al., 2007; Seltzer & Pandya, 1984**). This pathway is commonly referred to as the auditory dorsal stream (ADS; **Figure 1**, bottom left-blue arrows). Comparing the white matter pathways involved in communication in humans and monkeys with diffusion tensor imaging techniques indicates of similar connections of the AVS and ADS in the two species (Monkey: **Schmahmann et al., 2007; Human: Catani et al., 2004; Frey et al., 2008; Makris et al., 2009; Menjot de Champfleury et al., 2013; Saur et al., 2008; Turken & Dronkers, 2011**). In humans, the pSTG was shown to project to the parietal lobe (sylvian parietal-temporal junction-inferior parietal lobule; Spt-IPL), and from there to the dorsolateral prefrontal cortex (**Figure 1**, bottom right-blue arrows), and the aSTG was shown to project to the anterior temporal lobe (middle temporal gyrus-temporal pole; MTG-TP) and from there to the VLPFC (**Figure 1** bottom right-red arrows).

On the basis of converging evidence collected from monkeys and humans, it has been established that the AVS is responsible for the extraction of meaning from sounds (see **appendix A** for a review of the literature). Specifically, the anterior auditory cortex is ascribed with the perception of auditory objects, and downstream, the MTG and TP are thought to match the auditory objects with their corresponding audio-visual semantic representations (i.e., the semantic lexicon). This recognition of sounds in the AVS, although critical for intact communication, appears to contribute less to the uniqueness of human language than the ADS. This is demonstrated by the universality of sound recognition, as many mammalian species use it for localizing prey, predators or potential mates. As an example, dogs were reported capable of recognizing spoken words and extract their meaning (**Kaminski et al., 2004; Pilley & Reid, 2011**), and with fMRI this sound recognition ability was localized to the TP of the AVS (**Andics et al., 2014**). Studies also provided evidence that the sound recognition of non-human apes is equivalent in complexity to ours. Apes trained in human facilities were reported capable of learning human speech and comprehending its meaning (e.g., the bonobos, Kanzi and Panbanisha, were reported to recognize more than 3000 spoken English words; **Blake, 2004; Gibson, 2011**). Moreover, a study that compared humans and a chimpanzee in their recognition of acoustically distorted spoken words, reported no differences between chimpanzee and human performance (**Heimbauer et al., 2011**). Finally, a diffusion tensor imaging study that compared the white matter of humans and chimpanzees demonstrated significant strengthening of ADS connectivity, but not AVS connectivity (**Rilling et al., 2011**). This study thus indicates that it is the ADS, and not the AVS, that separates us from our apian relatives.

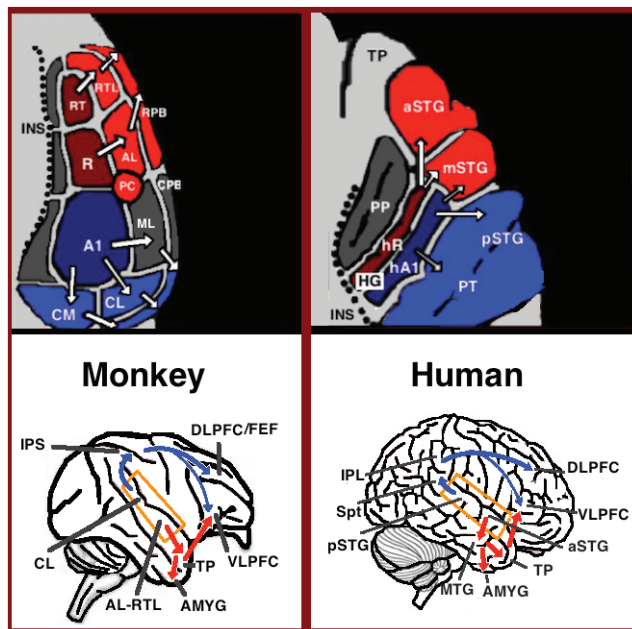


Figure 1. Dual stream connectivity between the auditory cortex and frontal lobe of monkeys and humans. Top: The auditory cortex of the monkey (left) and human (right) is schematically depicted on the supratemporal plane and observed from above (with the parieto-frontal operculi removed). Bottom: The brain of the monkey (left) and human (right) is schematically depicted and displayed from the side. Orange frames mark the region of the auditory cortex, which is displayed in the top sub-figures. Top and Bottom: Blue colors mark regions affiliated with the ADS, and red colors mark regions affiliated with the AVS (dark red and blue regions mark the primary auditory fields). Abbreviations: AMYG-amygdala, HG-Heschl's gyrus, FEF-frontal eye field, INS-insula, IPS-intra parietal sulcus, MTG-middle temporal gyrus, PC-pitch center, PP-planum polare, PT-planum temporale, TP-temporal pole, Spt-sylvian parietal-temporal, DLPFC/VLPFC- dorsolateral/ventrolateral prefrontal cortex, pSTG/mSTG/aSTG-posterior/middle/anterior superior temporal gyrus, CL/ML/AL/RTL-caudo-/middle-/antero-/rostrottemporal-lateral belt area, CPB/RPB-caudal/rostral parabelt fields.

In contrast to the AVS, the ADS has a diverse range of seemingly unrelated functions that process language. These functions, which will be detailed throughout this paper, include auditory localization, audio-visual integration, and voice detection in monkeys. In humans, the ADS has been further ascribed with speech articulation, speech repetition and perception, and production of linguistic prosody. In the present paper, I interpret the functional differences between the ADS of monkeys and humans as evidence of intermediate stages in the development of human speech.

3. The monkey ADS and its relationship with the visual dorsal stream

The most established role of the ADS is with audio-spatial processing. This is evidenced via studies that recorded neural activity from the auditory cortex of monkeys, and correlated the strongest selectivity to changes in sound location with the posterior auditory fields (areas CM-CL), intermediate selectivity with primary area A1, and very weak selectivity with the anterior auditory fields (Benson *et al.*, 1981; Miller & Recanzone, 2009; Rauschecker *et al.*, 1995; Woods *et al.*, 2006). In humans, behavioral studies of brain damaged patients (Clarke *et al.*, 2000; Griffiths *et al.*, 1996) and EEG recordings from healthy participants (Anourova *et al.*, 2001) demonstrated that sound localization is processed independently of sound recognition, and thus is likely independent of processing in the AVS. Consistently, a working memory study (Clarke *et al.*, 1998) reported two independent working memory storage spaces, one for acoustic properties and one for locations. Functional imaging studies that contrasted sound discrimination and sound localization reported a correlation between sound discrimination and activation in the mSTG-aSTG, and correlation between sound localization and activation in the pSTG and PT (Ahveninen *et al.*, 2006; Alain *et al.*, 2001; Barrett & Hall, 2006; De Santis *et al.*, 2006; Viceic *et al.*, 2006; Warren & Griffiths, 2003), with some studies further reporting of activation in the Spt-IPL region and frontal lobe (Hart *et al.*, 2004; Maeder *et al.*, 2001; Warren *et al.*, 2002). Some fMRI studies also reported that the activation in the pSTG and Spt-IPL regions increased when individuals perceived sounds in motion (Baumgart *et al.*, 1999; Krumbholz *et al.*, 2005; Pavani *et al.*, 2002). EEG studies using source-localization also identified the pSTG-Spt region of the ADS as the sound localization processing center (Tata *et al.*, 2005a; Tata *et al.*, 2005b). A combined fMRI and MEG study corroborated the role of the ADS with audio-spatial processing by demonstrating that changes in sound location results in activation spreading from Heschl's gyrus posteriorly along the pSTG and terminates in the IPL (Brunetti *et al.*, 2005). In another MEG study, the IPL and frontal lobe were shown active during maintenance of sound locations in working memory (Lutzenberger *et al.*, 2002).

In addition to localizing sounds, the ADS appears also to encode the sound location in memory, and to use this information for guiding eye movements. Evidence for the role of the ADS in encoding sounds into working memory is provided via studies that trained monkeys in a delayed matching to sample task, and reported of activation in areas CM-CL (Gottlieb *et al.*, 1989) and IPS (Linden *et al.*, 1999; Mazzoni *et al.*, 1996) during the delay phase. Influence of this spatial information on eye movements occurs via projections of the ADS into the frontal eye field (FEF; a premotor area that is responsible for guiding eye movements) located in the frontal lobe. This

is demonstrated with anatomical tracing studies that reported of connections between areas CM-CL-IPS and the FEF (Cusick *et al.*, 1995; Stricanne *et al.*, 1996), and electro-physiological recordings that reported neural activity in both the IPS (Linden *et al.*, 1999; Mazzoni *et al.*, 1996; Mullette-Gillman, 2005; Stricanne *et al.*, 1996) and the FEF (Russo & Bruce, 1994; Vaadia *et al.*, 1986) prior to conducting saccadic eye-movements toward auditory targets.

In the visual system, it is well established that the inferior temporal lobe processes the identity of visual objects (visual ventral stream; purple arrow in Figure 2), and that the IPS and FEF process visuospatial properties of objects and convert them into appropriate motor behaviors (visual dorsal stream; pink arrow in Figure 2; Goodale & Milner, 1992; Tanné-Gariépy *et al.*, 2002; Ungerleider & Haxby, 1994). Given the dual role of the IPS-FEF pathway in audiospatial and visuospatial processing, it is tempting to assume that spatial processing in both modalities occur in parallel. Cumulating evidence, however, suggests that audiospatial input is first converted into a visuospatial code and then processed via a visuospatial network. In monkeys, electrophysiological studies that recorded activity in the IPS reported that almost all the neurons in this area that are selective for auditory locations, are also selective to visual locations (Linden *et al.*, 1999; Mazzoni *et al.*, 1996). It was also shown that neurons in the IPS responded first to visual stimuli, and only after training do they become responsive to auditory stimuli (Grunewald *et al.*, 1999). Retrograde tracing from the IPS revealed that there were much less connections from the auditory cortex (primarily from areas CM-CL) than from the visual cortex (Lewis & Van Essen, 2000). The encoding of auditory information in visual working memory in the ADS is further demonstrated via a monkey fMRI study that correlated integration of auditory and visual stimuli with activation in the posterior, but not anterior, auditory cortex (Kayser *et al.*, 2009), and a behavioral working memory study of monkeys that demonstrated audio-visual integration to be susceptible to visual, but not auditory, interferences (Colombo & Graziano, 1994). Human studies also indicate that the ADS encodes sound locations in visual working memory. For example, an fMRI study that compared cortical activation during a visual motion discrimination task and an auditory motion discrimination task reported of overlapping activation in both modalities in the IPS (Lewis *et al.*, 2000). A subsequent cross-modal integration task then revealed heightened activation in the IPS that is selective to the combined auditory and visual stimuli. On this account, the researchers endowed the IPS with the role of audio-visual integration of spatial information. An fMRI study that compared the brain areas active during rehearsal of sound locations with rehearsal of visual locations in working memory reported that the IPS is the only region that is always active in both tasks (Martinkauppi *et al.*, 2000). An fMRI study that contrasted spatial orienting to sounds with spatial orienting to visual objects also reported of overlapping parietal and frontal activation in both tasks (Smith *et al.*, 2010b). Supporting the maintenance of sound locations in visual working memory in humans is also a study that reported of spatial bias in sound localization while wearing visuospatially distorting goggles (prism goggles; Zwiers *et al.*, 2003). Finally, a working memory study demonstrated that rehearsal of sound locations in working memory is more susceptible to visual interference than auditory interference (Clarke *et al.*, 1998). In contrast, rehearsal of

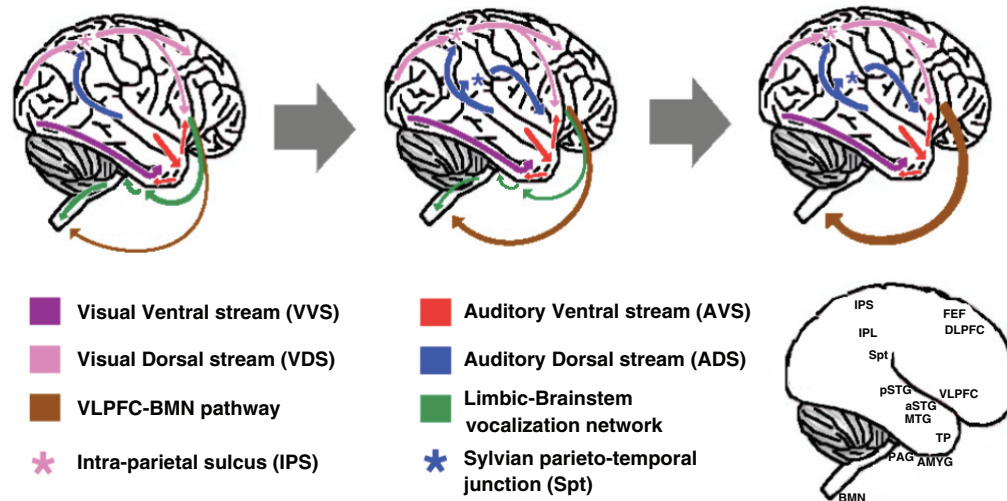


Figure 2. 'From Where to What' model - illustrated summary of brain development. The model depicts three stages in the early development of language, each characterized with its own neuroanatomical modifications (these changes are depicted here on schematized chimpanzee brains). Left: In extant monkeys/apes, sound recognition is processed via the auditory ventral stream (AVS; red arrows). Contact calls, however, are perceived in the pSTG. The pSTG then projects (blue arrow) to the IPS (pink asterisk), which is part of the visual dorsal stream (VDS, pink arrow). The IPS then projects to the VLPFC and FEF (pink arrow). The FEF guides saccadic eye-movements to the source of the call; the VLPFC initiates the vocal response by activating a cascading series of descending connections (green arrows). First, the VLPFC activates a network of limbic structures (e.g., amygdala; AMYG). The limbic network then projects to the midbrain periaqueductal grey (PAG), which in turn projects to the brainstem motor nuclei (BMN). Some elements of the vocal response are mediated via a direct VLPFC-BMN pathway (brown arrow). Middle: Approximately 2.5 million years ago, the *Homo* genus emerged as a result of duplication of the IPS (pink and blue asterisks) and subsequent duplication of its frontal projections (pink and blue arrows). Since the auditory cortex targeted the more proximal of these duplicated parietal regions (blue asterisk), a new pathway dedicated for auditory processing emerged (i.e., auditory dorsal stream; ADS-blue arrows). By strengthening pre-existing direct VLPFC-BMN connections (brown arrow), the ADS also acquired partial vocal control. This development of an audio-vocal pathway enabled individuals to modify contact calls with intonations for signaling high- and low-level distress calls. Right: Given that the ability to choose whether the emitted intonation signaled distress or safety was partially volitional, the modification of contact calls with intonations enabled question-answer conversations about other topics besides location. This use of intonations for more complex communication resulted with strengthening of the ADS and the descending VLPFC-BMN pathway (blue and brown arrows). Eventually, the ADS-VLPFC-BMN pathway acquired complete control over the vocal apparatus and speech became volitional.

simple tone sounds in working memory, which in the context of the present model is associated with processing in the AVS, is more susceptible to auditory interference than visual interference.

4. The ADS and the localization of con-specifics

In addition to processing the locations of sounds, evidence suggests that the ADS further integrates sound locations with auditory objects. Demonstrating this integration are electrophysiological recordings from the posterior auditory cortex (Recanzone, 2008; Tian *et al.*, 2001) and IPS (Gifford & Cohen, 2005), as well a PET study (Gil-da-Costa *et al.*, 2006), that reported neurons that are selective to monkey vocalizations. One of these studies (Tian *et al.*, 2001) further reported neurons in this region (CM-CL) that are characterized with dual selectivity for both a vocalization and a sound location. Consistent with the role of the pSTG-PT in the localization of specific auditory objects are also studies that demonstrate a role for this region in the isolation of specific sounds. For example, two functional imaging studies correlated circumscribed pSTG-PT activation with the spreading of sounds into an increasing number of locations (Smith *et al.*, 2010a-fMRI; Zatorre *et al.*, 2002-PET). Accordingly, an fMRI study correlated the perception of acoustic cues that are necessary for separating musical sounds (pitch chroma) with pSTG-PT activation (Warren *et al.*, 2003).

When elucidating the role of the primate ADS in the integration of a sound's location with calls, it remains to be determined what kind of information the ADS extracts from the calls. This information could be then used to make inferences about the function of the ADS. Studies from both monkeys and humans suggest that the posterior auditory cortex has a role in the detection of a new speaker. A monkey study that recorded electrophysiological activity from neurons in the posterior insula (near the pSTG) reported neurons that discriminate monkey calls based on the identity of the speaker (Remedios *et al.*, 2009a). Accordingly, human fMRI studies that instructed participants to discriminate voices reported an activation cluster in the pSTG (Andics *et al.*, 2010; Formisano *et al.*, 2008; Warren *et al.*, 2006). A study that recorded activity from the auditory cortex of an epileptic patient further reported that the pSTG, but not aSTG, was selective for the presence of a new speaker (Lachaux *et al.*, 2007-patient 1). The role of this posterior voice area, and the manner in which it differs from voice recognition in the AVS (Andics *et al.*, 2010; Belin & Zatorre, 2003; Nakamura *et al.*, 2001; Perrodin *et al.*, 2011; Petkov *et al.*, 2008), was further shown via electro-stimulation of another epileptic patient (Lachaux *et al.*, 2007-patient 2). This study reported that stimulation of the aSTG resulted in changes in the perceived pitch of voices (including the patient's own voice), whereas stimulation of the pSTG resulted in reports that her voice was "drifting away."

This report indicates a role for the pSTG in the integration of sound location with an individual voice. Consistent with this role of the ADS is a study that reported patients with AVS damage but spared ADS (surgical removal of the anterior STG/MTG) were no longer capable of isolating environmental sounds in the contralesional space, whereas their ability of isolating and discriminating human voices remained intact (Efron *et al.*, 1983). Preliminary evidence from the field of fetal cognition suggests that the ADS is capable of identifying voices in addition to discriminating them. By scanning fetuses of third trimester pregnant mothers with fMRI, the researchers reported of activation in area Spt when the hearing of voices was contrasted to pure tones (Jardri *et al.*, 2012). The researchers also reported that a sub-region of area Spt was more selective to maternal voice than unfamiliar female voices. Based on these findings, I suggest that the ADS has acquired a special role in primates for the localization of conspecifics.

5. The ADS role in the perception and response to contact calls

To summarize, I have argued that the monkey's ADS is equipped with the algorithms required for detecting a voice, isolating the voice from the background cacophony, determining its location, integrating the location of this voice into a visuospatial map of the area, and guiding eye movements for the origin of the call. An example of a behavior that utilizes all these functions is the exchange of contact calls, which are used by extant primates to monitor the location or proximity of conspecific tribe members (Biben *et al.*, 1986; Sugiura, 1998). The utilization of these ADS functions during the exchange of contact calls was demonstrated in studies of squirrel monkeys and vervet monkeys (Biben, 1992; Biben *et al.*, 1989; Cheney & Seyfarth, 1980; Symmes & Biben, 1985). In both species, mothers showed no difficulty in isolating their own infant's call, localizing it, and maintaining this location in their memory while approaching the source of the sound. A similar use of contact calls has been documented in our closest relatives, chimpanzees. The exchange of pant-hoot calls was documented between chimpanzees that were separated by great distances (Goodall, 1986; Marler & Hobbett, 1975) and was used for re-grouping (Mitani & Nishida, 1993). Because infants respond to their mother's pant-hoot call with

their own unique vocalization (staccato call; Matsuzawa, 2006), the contact call exchange appears also to play an important role in the ability of mothers to monitor the location of their infants. It is also worth noting that when a chimpanzee produced a pant-hoot call and heard no call in response, the chimpanzee was reported to carefully scan the forest before emitting a second call (Goodall, 1986). This behavior demonstrates the relationship between the perception of contact calls, the embedding of auditory locations in a map of the environment, and the guidance of the eyes for searching the origin of the call. Further corroborating the involvement of the ADS in the perception of contact calls are intra-cortical recordings from the posterior insula (near area CM-A1) of the macaque, which revealed stronger selectivity for a contact call (coo call) than a social call (threat call; Remedios *et al.*, 2009a). Contrasting this finding is a study that recorded neural activity from the anterior auditory cortex, and reported that the proportion of neurons dedicated to a contact call was similar to the proportions of neurons dedicated to other calls (Perrodin *et al.*, 2011).

Perceiving a contact call can be viewed as a three-step process. The individual is required to detect a voice, integrate it with its location and verify that no face is visible in that location (Figure 3). In the previous paragraphs, I provided evidence for the involvement of the ADS in the first two stages (voice detection and localization). Evidence for the role of the ADS in the integration of faces with their appropriate calls is provided by a study that recorded activity from the monkey auditory cortex (areas A1 and ML; Ghazanfar, 2005). The monkeys were presented with pictures of a monkey producing a call in parallel to hearing the appropriate call, or only saw the face or heard the call in isolation. Consistent with the prediction from the present model that visual perception of faces inhibits processing of contact calls, the face-call integration was much more enhanced for the social call (grunt call) than for the contact call (coo call). Associating this integration of faces with calls with processing in the ADS is consistent with the evidence presented earlier that ascribe the ADS with audio-visual integration (e.g., a monkey fMRI study correlated audio-visual integration with activation in the posterior, but not in the anterior, auditory fields; Kayser *et al.*, 2009).

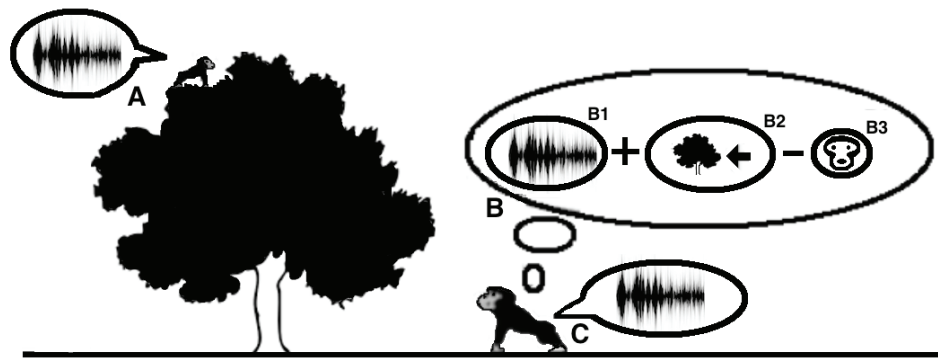


Figure 3. Discrete stages in contact call exchange. In accordance with the model, the original function of the ADS is for the localization of and the response to contact calls that are exchanged between mothers and their infants. When an infant emits a contact call (A), the mother perceives it (B) by integrating in the pSTG-IPS the identity of the speaker (B1) with the location of the call (B2) and maintains this information in visual working memory. Then, if the corresponding face is absent in that location (B3), the mother emits a contact call in return (C).

Hitherto, I have argued that the ADS is responsible for the perception of contact calls. However, as the perception of a contact call leads to producing a contact call in return, it is also desirable to suggest a pathway through which the ADS mediates vocal production. Monkey studies have demonstrated that the ADS doesn't directly process vocal production. This was shown through studies that damaged the temporoparietal and/or the VLPFC regions and reported that such lesions had no effect on spontaneous vocal production (Aitken, 1981; Sutton *et al.*, 1974). This conclusion is also consistent with comprehensive electro-stimulation mappings of the monkey's brain, which reported no spontaneous vocal production during stimulation of the temporal, occipital, parietal, or frontal lobes (Jürgens & Ploog, 1970; Robinson, 1967). These studies, however, reported emission of vocalizations after stimulating limbic and brainstem regions (amygdala, anterior cingulate cortex, basal forebrain, hypothalamus, mid-brain periaqueductal gray (PAG)). Moreover, based on a study that correlated chemical activation in the mid-brain PAG with vocal production, it was inferred that all the limbic regions project to central pattern generators in the PAG, which orchestrates the vocal production (Zhang *et al.*, 1994). In a series of tracing studies and electrophysiological recordings, it was also shown that the PAG projects to pre-motor brainstem areas (Hage & Jürgens, 2006; Hannig & Jürgens, 2005), which in turn project to brainstem motor nuclei (BMN; green arrows in Figure 2; Holstege, 1989; Holstege *et al.*, 1997; Lütke *et al.*, 2000; Vanderhorst *et al.*, 2001; Vanderhorst *et al.*, 2000). The BMN then activates the individual muscles of the vocal apparatus. Because documented calls of non-human primates (including chimpanzees) were shown with very little plasticity (Arcadi, 2000) and were observed only in highly emotional situations (Goodall, 1986), these limbic-brainstem generated calls are likely more akin to human laughter, sobbing, and screaming than to human speech. In relation to contact calls, a likely candidate for mediating the ADS with the limbic-brainstem vocal network is the VLPFC. This is because electrophysiological recordings (Cohen, 2004) and anatomical tracing (Deacon, 1992; Roberts *et al.*, 2007) studies in monkeys demonstrated this region to receive parietal afferents and to project to several limbic structures (Roberts *et al.*, 2007). Corroborating the role of the VLPFC in mediating vocal production of contact calls are studies that recorded neural activity from the VLPFC of macaques and reported neural discharge prior to cued or spontaneous contact call production (coo calls), but not prior to production of vocalizations-like facial movements (i.e., silent vocalizations; Coudé *et al.*, 2011; see also Gemba *et al.*, 1999 for similar results). Consistently, a study that sacrificed marmoset monkeys immediately after responding to contact calls (phee calls) measured highest neural activity (genomic expression of cFos protein) in the posterior auditory fields (CM-CL), and VLPFC (Miller *et al.*, 2010). Monkeys sacrificed after only hearing contact calls or only emitting them showed neural activity in the same regions but to a much smaller degree (See also Simões *et al.*, 2010 for similar results in a study using the protein Egr-1). Further supporting this ability of the VLPFC in regulating limbic-brainstem generated calls is the result of a tracing study that reported direct connections between the cortical motor area of the mouth and a brainstem motor nucleus that executes tongue movements (hypoglossal nucleus; Jürgens & Alipour, 2002). Hence, this study suggests that in addition to the VLPFC-AMYG-PAG-BMN pathway (green arrows in Figure 2), a second direct VLPFC-BMN pathway (brown arrow in Figure 2) has evolved in monkeys. The role

of this direct VLPFC-BMN pathway is not yet known, but its anatomical connectivity implies that it is capable of bypassing the limbic-brainstem vocal network, and therefore dominates vocal production.

6. Evolutionary origins of vocal control in humans

According to Falk's evolutionary hypothesis (2004), due to bipedal locomotion and the loss of hair in early *Hominins*, mothers were not capable of carrying their infants while foraging. As a result, the mothers maintained contact with their infant through a vocal exchange of calls that resemble contemporary "motherese" (the unique set of intonations that caregivers use when addressing infants). Following this model, Masataka (2009) provided evidence that macaque mothers are capable, to a limited extent, of modifying their contact calls to acoustically match those of their infants and further suggested that the human mother-infant prosodic vocal exchange evolved from the exchange of contact calls between our apian ancestors. Support for the use of prosody in contact calls are studies of squirrel monkeys and macaque monkeys that reported of small changes in the frequencies of contact calls, which resulted with the caller and responder emitting slightly different calls (Biben *et al.*, 1986; Sugiura, 1998). Evidence supporting the transition from contact call expression to volitional speech is provided by a study where macaque monkeys spontaneously learned to modify the vocal properties of their contact call for requesting different objects from the experimenter (Hihara *et al.*, 2003). Anecdotal reports of more generalized volitional vocal control, albeit rudimentary, in apes (Hayes & Hayes, 1952; Hopkins *et al.*, 2007; Kalan *et al.*, 2015; Koda *et al.*, 2007; Koda *et al.*, 2012; Lameira *et al.*, 2015; Tagliatela *et al.*, 2003; Wich *et al.*, 2008) further indicates that the ability to modify calls with intonations was enhanced prior to our divergence from our apian relatives.

Supporting evidence for a role of the ADS in the transition from mediating contact calls into mediating human speech includes genetic studies that focused on mutation to the protein SRPX2 and its regulator protein FOXP2 (Roll *et al.*, 2010). In mice, blockage of SRPX2 or FOXP2 genes resulted in pups not emitting distress calls when separated from their mothers (Shu *et al.*, 2005; Sia *et al.*, 2013). In humans, however, individuals afflicted with a mutated SRPX2 or FOXP2 were reported with speech dyspraxia (Roll *et al.*, 2006; Watkins *et al.*, 2002). A PET imaging study of an individual with a mutated SRPX2 gene correlated this patient's disorder with abnormal activation (hyper-metabolism) along the ADS (pSTG-Spt-IPL; Roll *et al.*, 2006). Similarly, an MRI study that scanned individuals with mutated FOXP2 reported increased grey matter density in the pSTG-Spt and reduced density in the VLPFC, further demonstrating abnormality in ADS' structures (Belton *et al.*, 2003). A role for the ADS in mediating speech production in humans has also been demonstrated in studies that correlated a more severe variant of this disorder, apraxia of speech, with IPL and VLPFC lesions (Deutsch, 1984; Edmonds & Marquardt, 2004; Hillis *et al.*, 2004; Josephs, 2006; Kimura & Watson, 1989; Square *et al.*, 1997). The role of the ADS in speech production is also demonstrated via a series of studies that directly stimulated sub-cortical fibers during surgical operations (Duffau *et al.*, 2008-review), and reported that interference in the pSTG and IPL resulted in an increase in speech production errors, and interference in the VLPFC resulted in speech arrest (see also Acheson *et al.*, 2011; Stewart *et al.*, 2001 for similar results using magnetic interference in healthy individuals).

Further support for the transition from contact call exchange to human language are provided by studies of hemispheric lateralization (Petersen *et al.*, 1978). In one study, Japanese macaques and other old world monkeys were trained to discriminate contact calls of Japanese macaques, which were presented to the right or left ear. Although all the monkeys were capable of completing the task, only the Japanese macaques were noted with right ear advantage, thus indicating left hemispheric processing of contact calls. In a study replicating the same paradigm, Japanese macaques had an impaired ability to discriminate contact calls after suffering unilateral damage to the auditory cortex of the left, but not right, hemisphere (Heffner & Heffner, 1984). This leftward lateralization of contact call perception is similar to the long established role of the human left hemisphere in the processing human language (Geschwind, 1965).

Considering Falk's and Masataka's hypotheses, evidence also indicates that the ADS was involved in the transition of contact calls into human speech through a transitory prosodic phase. This view is consistent with an fMRI study that instructed participants to rehearse speech, and reported that perception of prosodic speech, when contrasted with flattened speech, results in a stronger activation of the PT-pSTG of both hemispheres (Meyer *et al.*, 2004). In congruence, an fMRI study that compared the perception of hummed speech to natural speech didn't identify any brain area that is specific to humming, and thus concluded that humming is processed in the speech network (Ischebeck *et al.*, 2007). fMRI studies that instructed participants to analyze the rhythm of speech also reported of ADS activation (Spt, IPL, VLPFC; Geiser *et al.*, 2008; Gelfand & Bookheimer, 2003). An fMRI study that compared speech perception and production to the perception and production of humming noises, reported in both conditions that the overlapping activation area for perception and production (i.e., the area responsible for sensory-motor conversion) was located in area Spt of the ADS (Hickok *et al.*, 2003). Supporting evidence for the role of the ADS in the production of prosody are also studies reporting that patients diagnosed with apraxia of speech are additionally diagnosed with expressive dysprosody (Odell *et al.*, 1991, Odell *et al.*, 2001; Shriberg *et al.*, 2006 - FOXP2 affected individuals). Finally, the evolutionary account proposed here from vocal exchange of calls to a prosodic-based language is similar to the recent development of whistling languages, since these languages were documented to evolve from exchanging simple calls used to report speakers' locations into a complex semantic system based on intonations (Meyer, 2008).

7. Neuroanatomical origins of vocal control

In section 3, I presented evidence that in monkeys audio-spatial input is integrated with visual stimuli in the IPS prior to guiding eye movements. However, human studies that explore the neuroanatomical correlates of inner and outer speeches report that these are processed in a purely auditory network. This was first shown by Conard (1962), who instructed participants to rehearse a sequence of letters and showed that, at recall, they tend to confuse letters that sound similar, but not letters that look similar. Following this discovery, in a series of studies Baddeley & Hitch (1974) demonstrated that simultaneous performance of visual and verbal working memory tasks was nearly as efficient as performance of the same visual or verbal tasks in isolation. In contrast, these researchers showed

that simultaneous performance of two separate verbal working memory tasks, or two visual working memory tasks, is less efficient than when performing each task in isolation (e.g., recitation of the alphabet, but not discrimination of faces, interferes with rehearsal of a sequence of digits in working memory). These findings led the researchers to propose the existence of two working memory systems, one for visuospatial material (i.e., the visuospatial sketchpad) and another for verbal material (i.e., the phonological loop). The neuroanatomical correlate of the phonological loop was identified in fMRI studies that compared the activation pattern of individuals when they listened to speech, and the pattern when they produced speech externally or internally (Buchsbaum *et al.*, 2001; Hickok *et al.*, 2003; Wise *et al.*, 2001). These studies reported that in both speech perception and production (covert or overt) area Spt became active, and thus associated this region with the conversion of auditory stimuli into appropriate articulations. The role of the ADS in verbal rehearsal is in accordance with other functional imaging studies that localized activation to the same region during speech repetition tasks (Giraud & Price, 2001; Graves *et al.*, 2008; Karbe *et al.*, 1998). An intra-cortical recording study that recorded activity throughout most of the temporal, parietal and frontal lobes also reported of activation during speech repetition in regions along the ADS (areas Spt, IPL and VLPFC; Towle *et al.*, 2008). The association of the ADS with rehearsal is also consistent with neuropsychological studies that correlated the lesion of individuals with speech repetition deficit, but intact auditory comprehension (i.e., conduction aphasia), to the temporoparietal junction (Axer *et al.*, 2001; Baldo *et al.*, 2008; Bartha & Benke, 2003; Buchsbaum *et al.*, 2011; Fridriksson *et al.*, 2010; Kimura & Watson, 1989; Leff *et al.*, 2009; Selnes *et al.*, 1985), and with studies that applied direct intra-cortical electro-stimulation to this same region and reported of a transient speech repetition deficit (Anderson *et al.*, 1999; Boatman *et al.*, 2000; Ojemann, 1983; Quigg & Fountain, 1999; Quigg *et al.*, 2006).

In a review discussing the role of the ADS in humans, Warren, Wise and Warren (2005) noted that there is similarity in function between the conversion of visual input into eye movements in the IPS, and the conversion of auditory input into articulations in area Spt. Given this dual role of the parietal lobe in sensory-motor transformation of both audio-spatial and verbal information, I propose that during *Hominin* evolution there was a cortical field duplication, with the IPS (pink asterisk in Figure 2) duplicating to form area Spt (blue asterisk in Figure 2). Such duplication is a common phenomenon in mammalian evolution and was reported in several cortical regions (Butler & Hodos, 2005). Consequently, because area Spt was closer to the auditory cortex than the IPS, area Spt received the majority of the auditory afferents. Moreover, because of the preexisting connections of the IPS with the VLPFC (Figure 2 pink arrow), I suggest that the duplication of the IPS resulted in further duplication of its projections to the VLPFC (Figure 2 blue arrow). The development of connections from the auditory cortex to area Spt, and from there to the VLPFC, thus resulted with a pathway dedicated for audio-vocal conversion. The cortical field duplication hypothesis is consistent with an fMRI study that reported visual and auditory working memory to activate neighboring regions in the VLPFC (Rämä & Courtney, 2005). Further support for the cortical field duplication comes from research of autism. This is because individuals with autism report that they think in pictures instead of

words (Grandin, 2008; Sahyoun *et al.*, 2009), which implies ADS impairment. This conclusion is also consistent with an fMRI study that reported weaker activation in the IPL and VLPFC of autistic patients than healthy participants (Just *et al.*, 2007).

Evidence for cortical duplication in the IPL also derives from the fossil record. A study that reconstructed the endocranium of early *Hominins* noted that *Homo habilis*, but not any of its *Australopith* ancestors, is characterized by a dramatic heightening (but not widening) of the IPL and less dramatic enlargement of the VLPFC, whereas the rest of the endocranium remains extremely similar to the endocranium of modern apes (Tobias, 1987). It is also worth reporting that the recently discovered *Australopithecus sediba* (Carlson *et al.*, 2011), which is the closest known relative to the *Australopith* predecessor of *Homo habilis*, also has a very ape-like parietal and frontal lobes (although some modifications of the orbitofrontal surface were noted). Based on these findings, I propose that the cortical field duplication in the IPL occurred 2.3–2.5 million years ago and resulted with the brain enlargement that characterizes the *Homo* genus (Kimbel *et al.*, 1996; Schrenk *et al.*, 1993; Wood & Baker, 2011). This development equipped early *Hominans* (i.e., members of the genus *Homo*; Wood & Richmond, 2000) with partial control of lip and jaw movements, and thus endowed them with sufficient vocal control for modifying innate calls with intonations.

8. Prosodic speech and the emergence of questions

In the opening paragraph of this paper, I described the inability of apes to ask questions, and proposed that the ability to ask questions emerged from contact calls. Because the ability to ask questions likely co-emerged with the ability to modify calls with prosodic intonations, I expand Falk's and Masataka's views regarding the prosodic origins of vocal language, and propose that the transition from contact calls to prosodic intonations could have emerged as a means of enabling infants to express different levels of distress (Figure 4). In such a scenario, the modification of a call with intonations designed to express a high level of distress is akin in meaning to the sentence “mommy, come here now!”. Hence, the modification

of calls with intonations could have served as a precursor for the development of prosody in contemporary vocal commands. On the other hand, the use of intonations for expressing a low-level of distress is akin in meaning to the sentence “mommy, where are you?”. Therefore, this use of prosody for asking the first question could have served as the precursor for pragmatically converting calls into questions by using prosody as well. This transition could be related to the ability of present-day infants of using intonations for changing the pragmatic utilization of a word from a statement to a command/demand (“mommy!”) or a question (“mommy?”). Evidence supporting a relationship between the ability to ask questions and the ADS is derived from the finding that patients with phonological dementia, who are known to suffer from degeneration along the ADS and show signs of ADS impairment (Gorno Tempini *et al.*, 2008; Rohrer *et al.*, 2010), were impaired in distinguishing whether a spoken word was a question or a statement (Rohrer *et al.*, 2012).

A possible route for the transition from emitting low-distress contact calls to asking questions is by individuals starting to utilize the former to signal interest about objects in their environment. Given that both contact call exchange and contemporary speech are characterized with turn taking, early *Hominans* could have responded to the low-level distress calls with either high or low level distress calls. For example, when an infant expressed a low-level distress call prior to eating berries, his/her mother could have responded with a high-level distress call that indicated the food is dangerous or a low-level distress call that indicated the food is safe (Figure 5). Eventually, the infant emitted the question call and waited for an appropriate answer from their mother before proceeding with their intended action. This conversation structure could be the precursor to present-day yes/no questions. As intonations became more prevalent and questions became more complex, the ADS and VLPFC-BMN pathways (blue and brown arrows in Figure 2) became more robust, and as a consequence individuals acquired more volitional control over the vocal apparatus. Consistent with the role of the ADS in speech repetition (see section 6),

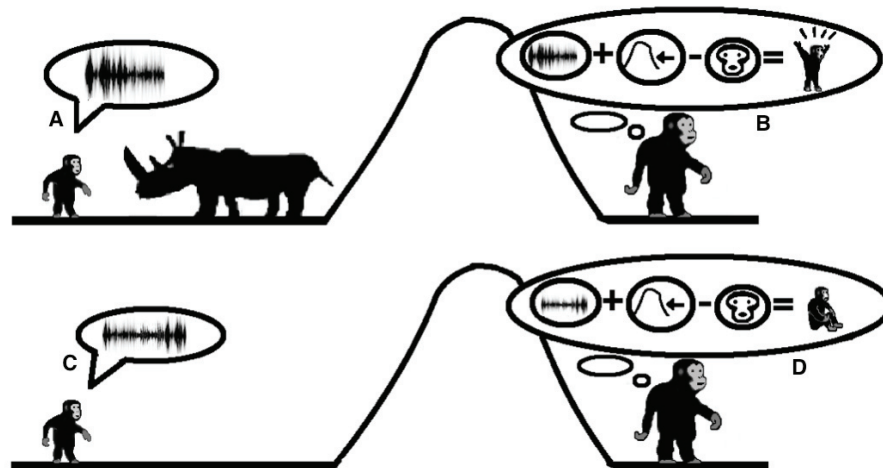


Figure 4. The use of prosody to signal levels of distress. In accordance with the model, vocal control began with the ADS modifying the rigid limbic-brainstem-generated vocalizations with intonations (prosody). This modification could have originated for the purpose of expressing different levels of distress. In this figure, we see a *Homo habilis* child using prosody to modify the contact call to express a high level of distress (A) or a low level of distress (C). The child's mother then registers the call by integrating his prosodic intonation and voice, the location, and the absence of his face to recognize whether her child requires immediate (B) or non-immediate (D) attention.

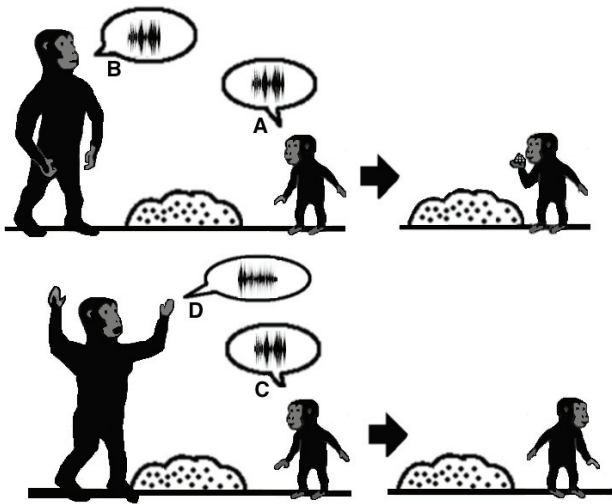


Figure 5. Prosody and the emergence of question-answer conversations. In accordance with the model, the modification of contact calls with intonations for reporting distress levels eventually transitioned into question-answer conversations about items in their environment. In this figure, a child is using low-level distress call (**A,C**) to ask permission to eat an unfamiliar food (berries). The mother can then respond with a high-level distress call (**D**) that signals danger or a low-level distress (**B**) that signals safety.

the increase in volitional vocal control could have then been used to invent new calls and teach them to offspring via vocal mimicry. This desire of offspring to learn about their environment by mimicking their mother's calls and then encoding the new words to long-term memory could have been the guiding force that sparked the curiosity to explore the unknown. Discussing the transition from exchanging low-level distress contact calls into complex vocal language, however, is beyond the scope of the present paper and a model for such transition is discussed in length in a sibling paper titled 'Vocal Mimicry as the Sculptor of the Human Mind. A Neuroanatomically based Evolutionary Model of The Emergence of Vocal Language' (Poliva, in preparation).

9. Comparisons of the 'From Where to What' model to previous language evolution models

Following in the footsteps of Dean Falk and Nobuo Masataka, the present model argues that human speech emerged from the exchange of contact calls via a transitory prosodic phase. Since the principle of natural selection was first acknowledged by the scientific community however, several other accounts of language evolution were proposed. Here, I'll present two schools of thought, and discuss their validity in the context of the present model.

The earliest model for language evolution was proposed by Charles Darwin. In his book, *The Descent of Man* (1871), Darwin equated speech exchange to bird song, and proposed that the perception and production of songs during mating rituals were the precursor to human language (singing ape hypothesis). Similar accounts suggesting music to participate in the evolutionary development of speech were also proposed by more recent researchers (Jordanaia, 2006; Masataka, 2009; Mithen, 2006). However, so far the idea of music as precursor to language has not taken hold in the scientific

community due to lack of substantiating evidence. In [appendix A](#), I cite evidence that the perception of melodies occurs in the aSTG of the AVS. Given the mounting evidence indicating that speech is processed primarily in the ADS, we would expect that precursors to speech would also be processed in the same pathway (although, see the review by [Stewart, 2006](#) who suggests roles also for other auditory fields in music perception). Since I hypothesize that singing-like calls were utilized for communication prior to complex vocal language, the idea of music perception and production isn't too different from the present model. However, arguing that music served as precursor to speech is different than arguing that music and speech emerged from a common proto-function. Investigating whether music served as a precursor to vocal language is problematic since such a model implies that music perception is a unique human trait. Therefore, in order to resolve the conundrum of music evolution and its level of contribution to the emergence of vocal language, future studies should first attempt to determine whether non-human primates can perceive music. (See [Remedios et al., 2009b](#) for preliminary findings).

A more recent school of thought argues that language with complex semantics and grammar was first communicated via the exchange of gestures and only recently became vocal (Gestural language model; [Arbib, 2008](#); [Corballis, 2010](#); [Donald, 2005](#); [Gentilucci & Corballis, 2006](#); [Hewes, 1973](#); [Studdert-Kennedy, 2005](#)). In accordance with this model, speech could have served for increasing communication distance and enabling communication under low visibility conditions (e.g., night, caves). This model is primarily based on the natural use of gestural communication between non-human primates, the ability of apes to learn sign language, and the natural development of sign languages in deaf communities. This model also received increased popularity since the discovery of mirror neurons, as these neurons are interpreted by proponents of the model as evidence of a mechanism dedicated to the imitation of gestures. From a neuroanatomical perspective it is plausible that vocal communication emerged from gestures. For instance, earlier I presented evidence that in monkeys the IPS encodes auditory stimuli into the visual dorsal stream. Given that the primary function of the visual dorsal stream is to convert visual stimuli into motor actions, it is possible that in addition to vocally responding to contact calls, this pathway served for converting visually observed gestures into producing gestures. This view is also consistent with an fMRI study that correlated hearing animal calls with bilateral activation in the mSTG-aSTG, whereas hearing tool sounds (e.g., hammer, saw) correlated with activation in the pSTG and IPL of the hemisphere contralateral to the dominant hand ([Lewis et al., 2006](#)). This recognition of tool sounds in the ADS instead of AVS is surprising because it could suggest that the teaching of tool use, which required gestures, was associated with speech production. Based on these findings I find the hypothesis that speech and gestures co-evolved compelling. However, given that my model delineates a course for the development of proto-conversations from calls that are used by extant primates, it is incongruent with the argument that a gestural language with complex grammar and semantics preceded vocal language.

10. 'From Where to What'- Future Research

In the present paper, I delineate a course for the early development of language by proposing five hypotheses: 1. In non-human primates, the ADS is responsible for perceiving and responding to

contact calls; 2. The ADS of non-human primates integrates auditory locations into the visual dorsal stream; 3. Duplication of the ape's IPS and its frontal projections (visual dorsal stream) resulted with a pathway (ADS) dedicated for converting auditory stimuli into articulations; 4. Mother-offspring vocal exchange was the predominant force that guided the emergence of speech in the ADS; 5. Speech emerged from modifying calls with intonations for signaling a low-level and high-level of distress, and these calls are the precursor to our use of intonations for converting words into questions and commands, respectively. Cumulative and converging evidence for the veracity of each of these hypotheses was provided throughout the paper. However, as the veracity of a model can only be measured by its ability to predict experimental results, I will present here outlines for 5 potential studies that can test each of these hypotheses.

In accordance with the first hypothesis, the ADS of non-human primates is responsible for the perception and vocal response to contact calls. A possible way of testing this hypothesis is by inducing bilateral lesions to the temporo-parietal junction of a monkey and then measuring whether the monkey no longer responds vocally to contact calls or responds less than before the lesion induction.

In accordance with the second hypothesis, audiospatial information is integrated in the IPS into visual regions and processed via the visual dorsal stream. This conclusion, although supported by many studies, is primarily derived from the study of [Grunewald *et al.* \(1999\)](#), who reported that, prior to training, neurons in the IPS responded only to visual stimuli and to auditory stimuli only after training. This study therefore needs to be replicated in more primate species to determine its veracity.

In accordance with the third hypothesis, the *Homo* genus emerged as a result of duplicating the IPS and its frontal projections. This duplication resulted with area Spt and its projections to the VLPFC. In contrast to the visual dorsal stream that processes audiovisual spatial properties, the human ADS processes inner and outer speech. I therefore predict that fMRI studies scanning participants while rehearsing auditory locations, visual locations and sentences, will find that the first two tasks activate a region more dorsal in the frontal lobe than the latter task.

In accordance with the fourth hypothesis, mother infant interaction was the guiding force that endowed the ADS with its role in speech. This hypothesis is primarily based on the finding that a sub-region of area Spt in human fetuses was shown selective to the voice of their mothers ([Jardri *et al.*, 2012](#)). Future studies should further explore whether this region remains active in the brain of infants and toddlers and whether mothers also possess a region in the ADS that is selective to the voice of their children.

In accordance with the fifth hypothesis, the ADS originally served for discriminating calls that signal different levels of distress by analyzing their intonations. At present day, this development is reflected in our ability to modify intonations for converting spoken words into questions and commands. A way of testing this hypothesis is by using fMRI to compare the brain regions active when participants discriminate spoken words into questions and commands, with the brain regions active when they discriminate these

words based on their emotional content (e.g., scared and happy). I predict that the former will activate the ADS whereas the latter the AVS.

Competing interests

No competing interests were disclosed.

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Appendix A: The auditory ventral stream and its role in sound recognition

Accumulative converging evidence indicates that the AVS is involved in recognizing auditory objects. At the level of the primary auditory cortex, recordings from monkeys showed higher percentage of neurons selective for learned melodic sequences in area R than area A1 ([Yin *et al.*, 2008](#)), and a study in humans demonstrated more selectivity for heard syllables in the anterior Heschl's gyrus (area hR) than posterior Heschl's gyrus (area hA1; [Steinschneider *et al.*, 2004](#)). In downstream associative auditory fields, studies from both monkeys and humans reported that the border between the anterior and posterior auditory fields ([Figure 1](#)-area PC in the monkey and mSTG in the human) processes pitch attributes that are necessary for the recognition of auditory objects ([Bendor & Wang, 2006](#)). The anterior auditory fields of monkeys were also demonstrated with selectivity for con-specific vocalizations with intracortical recordings ([Perrodin *et al.*, 2011](#); [Rauschecker *et al.*, 1995](#); [Russ *et al.*, 2007](#)) and functional imaging ([Joly *et al.*, 2012](#); [Petkov *et al.*, 2008](#); [Poremba *et al.*, 2004](#)). One fMRI monkey study further demonstrated a role of the aSTG in the recognition of individual voices ([Petkov *et al.*, 2008](#)). The role of the human mSTG-aSTG in sound recognition was demonstrated via functional imaging studies that correlated activity in this region with isolation of auditory objects from background noise ([Scheich *et al.*, 1998](#); [Zatorre *et al.*, 2004](#)) and with the recognition of spoken words ([Binder *et al.*, 2004](#); [Davis & Johnsrude, 2003](#); [Liebenthal, 2005](#); [Narain, 2003](#); [Obleser *et al.*, 2006a](#); [Obleser *et al.*, 2006b](#); [Scott *et al.*, 2000](#)), voices ([Belin & Zatorre, 2003](#)), melodies ([Benson *et al.*, 2001](#); [Leaver & Rauschecker, 2010](#)), environmental sounds ([Lewis *et al.*, 2006](#); [Maeder *et al.*, 2001](#); [Viceic *et al.*, 2006](#)), and non-speech communicative sounds ([Shultz *et al.*, 2012](#)). A study that recorded neural activity directly from the left pSTG and aSTG reported that the aSTG, but not pSTG, was more active when the patient listened to speech in her native language than unfamiliar foreign language ([Lachaux *et al.*, 2007](#)-patient 1). Consistently, electro stimulation

to the aSTG, but not pSTG, resulted in impaired speech perception (Lachaux *et al.*, 2007-patient 1; see also Matsumoto *et al.*, 2011 for similar finding). Intra-cortical recordings from the right and left aSTG of another patient further demonstrated that speech is processed laterally to music (Lachaux *et al.*, 2007-patient 2). Recordings from the anterior auditory cortex of monkeys while maintaining learned sounds in working memory (Tsunada *et al.*, 2011), and the debilitating effect of induced lesions to this region on working memory recall (Fritz *et al.*, 2005; Stepien *et al.*, 1960; Strominger *et al.*, 1980), further implicate the AVS in maintaining the perceived auditory objects in working memory. In humans, area mSTG-aSTG was also reported active during rehearsal of heard syllables with MEG (Kaiser *et al.*, 2003) and fMRI (Buchsbaum *et al.*, 2005). The latter study further demonstrated that working memory in the AVS is for the acoustic properties of spoken words and that it is independent to working memory in the ADS, which mediates inner speech.

In humans, downstream to the aSTG, the MTG and TP are thought to constitute the semantic lexicon, which is a long-term memory repository of audio-visual representations that are interconnected on the basis of semantic relationships. (See also the reviews by Hickok & Poeppel, 2007 and Gow, 2012, discussing this topic). The primary evidence for this role of the MTG-TP is that patients with damage to this region (e.g., patients with semantic dementia or herpes simplex virus encephalitis) are reported with an impaired ability to describe visual and auditory objects and a tendency to commit semantic errors when naming objects (i.e., semantic paraphasia; Noppeney *et al.*, 2006; Patterson *et al.*, 2007). Semantic paraphasias were also expressed

by aphasic patients with left MTG-TP damage (Dronkers *et al.*, 2004; Schwartz *et al.*, 2009) and were shown to occur in non-aphasic patients after electro-stimulation to this region (Hamberger *et al.*, 2007) or the underlying white matter pathway (Duffau *et al.*, 2008). Two meta-analyses of the fMRI literature also reported that the anterior MTG and TP were consistently active during semantic analysis of speech and text (Binder *et al.*, 2009; Vigneau *et al.*, 2006); and an intra-cortical recording study correlated neural discharge in the MTG with the comprehension of intelligible sentences (Creutzfeldt *et al.*, 1989).

In contradiction to the Wernicke-Lichtheim-Geschwind model that implicates sound recognition to occur solely in the left hemisphere, studies that examined the properties of the right or left hemisphere in isolation via unilateral hemispheric anesthesia (i.e., the WADA procedure; Hickok *et al.*, 2008) or intra-cortical recordings from each hemisphere (Creutzfeldt *et al.*, 1989) provided evidence that sound recognition is processed bilaterally. Moreover, a study that instructed patients with disconnected hemispheres (i.e., split-brain patients) to match spoken words to written words presented to the right or left hemifields, reported vocabulary in the right hemisphere that almost matches in size with the left hemisphere (Zaidel, 1976). (The right hemisphere vocabulary was equivalent to the vocabulary of a healthy 11-years old child). This bilateral recognition of sounds is also consistent with the finding that unilateral lesion to the auditory cortex rarely results in deficit to auditory comprehension (i.e., auditory agnosia), whereas a second lesion to the remaining hemisphere (which could occur years later) does (Poeppel, 2012; Ulrich, 1978).

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I see this paper as a first draft of what could become an important contribution to neurally based approaches to the study of the evolution of the human brain's capacity for language. Its importance is three-fold:

1. It treats the ventral and dorsal streams for both the auditory and visual modalities.
2. It regards monkey calls not in terms of perception alone or production alone but rather in terms of their role in the interaction between two individuals in the context of their environment.
3. It places the ability to ask and answer questions at the heart of language use.

Below, I will offer several comments on how some shortcomings of the current version might be removed in future work by Poliva, but first a disclosure: I have emphasized the role of the two visual streams in relation to both the production and comprehension of language with an emphasis on the role of manual gesture and protosign in language evolution, and in terms of visual perception of what an utterance may be about (Arbib, 2013). By contrast, Bornkessel-Schlesewsky and Schlewsky (2013) offer hypotheses on the roles of the auditory streams in the perception of sentences of a spoken language, linking them to neurolinguistic data from their lab and others. I have attempted a preliminary synthesis of these approaches (Arbib, 2015). More recently, they have co-authored a review of relevant data on the auditory streams in both monkey and human with the claim that no major evolutionary innovations were required in these streams to make language possible (Bornkessel-Schlesewsky, Schlewsky, Small, & Rauschecker, 2015) – a claim with which I (and, I suspect, Poliva) would disagree. I hope to support the counter-claim in a forthcoming article in the *Journal of Neurolinguistics*. I believe Poliva's assessment of these articles would enrich his work, but now let me turn to other issues.

1. I endorse the key points of Amy Poremba's review: (i) The dorsal auditory stream was over-emphasized at the expense of assessing the role of the ventral stream and how these streams are integrated. (ii) Poremba notes the relevance of work from Mishkin's lab on auditory memory – see, e.g., Fritz, Mishkin, and Saunders (2005) which “raises the possibility that language is unique to humans not only because it depends on speech but also because it requires long-term auditory memory.” I would add that Aboitiz and his colleagues have emphasized the expansion of working memory capacity as a key element in evolving a language-ready brain (see Aboitiz, 2012, for a recent review of this approach). (iii) The leap from contact calls to “individuals ... capable of inventing new words and offspring ... capable of inquiring about objects in their environment and learning their names via mimicry” is essentially unbridged.
2. Since there are many monkey calls, it seems unclear why, if one is to use these calls as the core for evolving a brain with language, one should focus on contact calls alone. Including other calls might add more “evolutionary opportunities.” In this regard, note the argument of Seyfarth and

Cheney that one may see the structure of language prefigured in the “rules” monkeys develop for social cognition (Cheney & Seyfarth, 2005; Seyfarth & Cheney, 2014).

3. I suspect that further work in language evolution will reveal a “mosaic” of innovations, some of which are apparent in different monkey or ape species. One may hope that studies of the brains of different species will reveal diverse cues that illuminate, perhaps, the convergent evolution of different tiles of the language-supporting neural mosaic of the human brain. Consider, for example, the capability for turn taking in geladas (Gustison, le Roux, & Bergman, 2012; Richman, 1987) and marmosets (Miller, Thomas, Nummela, & de la Mothe, 2015; Takahashi, Narayanan, & Ghazanfar, 2013) as just one of the diverse components of language-ready brain that are differentially evident in different species of nonhuman primate.
4. Figure 1 shows dual stream connectivity between the auditory cortex and frontal lobe of monkeys and humans. What can be said about the intersection of the 2 streams in VLPFC? And what can be said about the interaction of DLPFC and VLPFC? Figure 2 depicts the “From Where to What model” via three stages of neuroanatomical modifications. It might be useful to first provide a diagram focusing on VVS and VDS (initial V for Visual) and discussing the relation in both anatomy and function of these paths with each other. It might also be helpful to present pieces of the model along with the exposition of the related data, postponing this integrative figure until the pieces are in place.
5. A valuable feature of Poliva’s model is its suggestion of how the response to an auditory call might initiate visual search as the basis for action (he emphasizes the mother emitting a call if the child is not seen; a related scenario would be movement toward the child if it were seen). This issue of integration of communication and action, which may (but need not) integrate audition with vision, is an important feature which too few studies take into account. My question is whether he unduly emphasizes cortical pathways involving the frontal eye fields and shortchanges subcortical interactions involving the superior colliculus (noting of course that these are open to cortical influences modulated by the basal ganglia).
6. In Figure 2, Poliva asserts: (i) “Approximately 2.5 million years ago, the *Homo* genus emerged as a result of [my italics] duplication of the IPS and subsequent duplication of its frontal projections” (a) Surely, many more changes led to the emergence of *Homo*. (b) At the end of Section 7, Poliva suggests the relevance of endocast data to this claim. Are there relevant data on apes that could help us assess this transition? (ii) “Since the auditory cortex targeted the more proximal of these duplicated parietal regions, a new pathway dedicated for auditory processing emerged (i.e., auditory dorsal stream; ADS.” But monkey data show an ADS, so what is the transition being suggested here? Picking up on the issue in (5), one needs to better understand the division of labor between ADS and subcortical mechanisms (as well as AVS, to reiterate Poremba’s point).
7. Poliva claims to review “evidence for a role of the ADS in the transition from mediating contact calls into mediating human speech” but simply cites data correlating ADS impairment with disorders like speech apraxia. Nothing in the data privileges contact calls over other vocal productions – and, anyway, clear articulation is a far cry [sic] from mechanisms supporting the role of syntax and semantics in language production and perception.
8. In relation to 6(i), Poliva notes the dual role of the parietal lobe in sensory-motor transformation of both audio-spatial and verbal information, and proposes that during *Hominin* evolution there was a cortical field duplication, of the IPS with further duplication of its projections to the VLPFC which

resulted in a pathway dedicated for audio-vocal conversion. How would this serve people who employ a signed language? (Of course, those who advocate a gestural origin of language must face the complementary question of how visuo-manual pathways came to support audio-vocal signals – which they must do because other primates lack vocal learning, let alone the use of syntax and semantics in either domain.)

9. Poliva stresses that the ability to ask and answer questions is an essential feature of language use. I agree. Future work on language evolution should pay more attention to the challenge of explaining how this evolved. However the focus on modifying contact calls with prosodic intonations seems to me too narrow (I may be wrong, but more argument would be needed) and (as Poremba observed) the account of the transition remains too sketchy. Poliva cites “the ability of present-day infants of using intonations for changing the pragmatic utilization of a word from a statement to a command/demand (“mommy!”) or a question (“mommy?”),” but one must be careful to distinguish these infant “communicative acts” from the ability to deploy grammar to formulate an open-ended repertoire of commands and questions using the structures of a language – let alone being able to marshal answers to questions of even modest complexity.
10. In any case, it seems mistaken to place exclusive emphasis on the role of ADS in the transition – one might thus assess the hypotheses of Bornkessel-Schlesewsky and Schlesewsky (2013) on the roles of both ADS and AVS (and frontal areas) in speech comprehension. However, a companion paper is promised: “Discussing the transition from exchanging low-level distress contact calls into complex vocal language, however, is beyond the scope of the present paper and a model for such transition is discussed [at] length in a sibling paper titled ‘Vocal Mimicry as the Sculptor of the Human Mind. A Neuroanatomically based Evolutionary Model of The Emergence of Vocal Language’ (Poliva, in preparation).” Perhaps it would be better if less were said about this topic in the present paper so that the implications of the evidence on ADS function and evolution could be better assessed for their merits irrespective of the contact call hypothesis.

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I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Competing Interests: No competing interests were disclosed.

Reader Comment 21 Jan 2016

Oren Poliva, Bangor University, UK

I want to thank the reviewer for his positive review and for his insightful and constructive comments. Below are my responses:

I endorse the key points of Amy Poremba's review: (i) The dorsal auditory stream was over-emphasized at the expense of assessing the role of the ventral stream and how these streams are integrated.

Response: I agree with the reviewer that the article focuses on the ADS, and pay little attention to the AVS. I also agree that the AVS partakes an important role in the perception and production of human language, and that it interacts with the ADS. However, as I also previously responded to Poremba, in the present paper I propose a model for the emergence of speech and not language, and speech appears to be primarily or solely a function of the ADS. A possible course for the transition from speech to language and the role the AVS in such functions is discussed in detail in the second paper (mentioned in the article).

Poremba notes the relevance of work from Mishkin's lab on auditory memory – see, e.g., Fritz, Mishkin, and Saunders (2005) which “raises the possibility that language is unique to humans not only because it depends on speech but also because it requires long-term auditory memory.” I would add that Aboitiz and his colleagues have emphasized the expansion of working memory capacity as a key element in evolving a language-ready brain (see Aboitiz, 2012, for a recent review of this approach).

Response: I agree with the reviewer that expansion of auditory memory (or its ability to sustain interferences as shown by Scott, Mishkin & Yin, 2012) took an important part in the evolution of language. However, as I previously responded to Poremba, this change likely occurred after *Hominins* acquired volitional control over the vocal apparatus, and thus is beyond the scope of the present paper. This issue is also discussed in detail in the second paper.

Scott BH, Mishkin M, Yin P. Monkeys have a limited form of short-term memory in audition. Proceedings of the National Academy of Sciences. 2012 Jul 24;109(30):12237–41.

The leap from contact calls to “individuals ... capable of inventing new words and offspring ... capable of inquiring about objects in their environment and learning their names via mimicry” is essentially unbridged.....

In any case, it seems mistaken to place exclusive emphasis on the role of ADS in the transition – one might thus assess the hypotheses of Bornkessel-Schlesewsky and Schlesewsky (2013) on the roles of both ADS and AVS (and frontal areas) in speech comprehension. However, a companion paper is promised: “Discussing the transition from exchanging low-level distress contact calls into complex vocal language, however, is beyond the scope of the present paper and a model for such transition is discussed [at] length in a sibling paper titled ‘Vocal Mimicry as the Sculptor of the Human Mind. A Neuroanatomically based Evolutionary Model of The Emergence of Vocal Language’ (Poliva, in preparation).” Perhaps it would be better if less were said about this topic in the present paper so that the implications of the evidence on ADS function and evolution could be better assessed for their merits irrespective of the contact call hypothesis.

Response: I agree with the reviewer that the article doesn’t delve enough into the transition from speech to vocal mimicry. As I responded to Poremba, and mentioned in the paper, this topic is discussed in detail in the second paper. As the primary concern of the present paper is the emergence of speech, I removed from the abstract and introduction any mentioning of the transition from speech to vocal mimicry based language, and limited its discussion to a short paragraph near the end of the paper.

Since there are many monkey calls, it seems unclear why, if one is to use these calls as the core for evolving a brain with language, one should focus on contact calls alone. Including other calls might add more “evolutionary opportunities.” In this regard, note the argument of Seyfarth and Cheney that one may see the structure of language prefigured in the “rules” monkeys develop for social cognition (Cheney & Seyfarth, 2005; Seyfarth & Cheney, 2014).

Response: The reviewer presents an interesting question when he suggests that contact calls might not be special. The paper he cites suggests that rule based alarm calls could serve as a potential precursor to human language. In my opinion, contact calls are a more likely candidate precursor to present day vocal conversation than alarm calls. Like present day vocal conversations, contact call are characterized with turn taking and require interaction between (at least) two participants. The content of contact calls is also similar to present day question answer dialogue (as if similar to the question ‘where are you?’ and the answer ‘I’m here, Where are you?’). Alarm calls in contrast, although context dependent and thus likely under cortical influence, do not require vocal response and thus don’t resemble conversation. Moreover, as I present in the paper, converging evidence suggests that both human speech and contact call exchange in non-human primates are processed in the ADS. As far as I’m aware of, no study provided evidence that alarm calls are processed in the ADS. (Given its dependence on observing emotive stimuli, I would assume that expressing alarm calls occurs through processing in the visual ventral stream and amygdala, and response to alarm calls occurs through the auditory ventral stream and amygdala.)

I suspect that further work in language evolution will reveal a “mosaic” of innovations, some of

which are apparent in different monkey or ape species. One may hope that studies of the brains of different species will reveal diverse cues that illuminate, perhaps, the convergent evolution of different tiles of the language-supporting neural mosaic of the human brain. Consider, for example, the capability for turn taking in geladas (Gustison, le Roux, & Bergman, 2012; Richman, 1987) and marmosets (Miller, Thomas, Nummela, & de la Mothe, 2015; Takahashi, Narayanan, & Ghazanfar, 2013) as just one of the diverse components of language-ready brain that are differentially evident in different species of nonhuman primate.

Response: I admit I got confused from the reviewer's comment. The reviewer argues that turn taking occurs in gelada monkeys. The studies he cite however don't mention such behavior. The reviewer then proceed to cite turn taking vocal behavior in marmoset monkeys, as an alternative explanation to how humans developed turn taking in conversations. The reviewer, however, cite studies that explore turn taking in the exchange of contact calls, which further support the discussed model.

Figure 1 shows dual stream connectivity between the auditory cortex and frontal lobe of monkeys and humans. What can be said about the intersection of the 2 streams in VLPFC? And what can be said about the interaction of DLPFC and VLPFC?

Response: In the paper I describe two pathways connecting the auditory cortex with the prefrontal cortex. The prefrontal cortex is primarily ascribed with planning and problem solving. When detecting and responding to contact calls, the prefrontal cortex likely mediates high level processing, such as determining the best way to overcome an obstacle in order to reach the caller. In the present model, I attempt to demonstrate that the detection and production of contact calls occur in the same pathway as speech in humans, and on that account attribute a relationship between them. The role of the prefrontal cortex in such high level processing is not necessary for establishing this relationship and is thus beyond the scope of the present paper.

Figure 2 depicts the "From Where to What model" via three stages of neuroanatomical modifications. It might be useful to first provide a diagram focusing on VVS and VDS (initial V for Visual) and discussing the relation in both anatomy and function of these paths with each other. It might also be helpful to present pieces of the model along with the exposition of the related data, postponing this integrative figure until the pieces are in place.....

In Figure 2, Poliva asserts: (i) "Approximately 2.5 million years ago, the *Homo* genus emerged as a *result of* [my italics] duplication of the IPS and subsequent duplication of its frontal projections" (a) Surely, many more changes led to the emergence of *Homo*. (b) At the end of Section 7, Poliva suggests the relevance of endocast data to this claim. Are there relevant data on apes that could help us assess this transition? (ii) "Since the auditory cortex targeted the more proximal of these duplicated parietal regions, a new pathway dedicated for auditory processing emerged (i.e., auditory dorsal stream; ADS." But monkey data show an ADS, so what is the transition being suggested here? Picking up on the issue in (5), one needs to better understand the division of labor between ADS and subcortical mechanisms (as well as AVS, to reiterate Poremba's point).... In relation to 6(i), Poliva notes the dual role of the parietal lobe in sensory-motor transformation of both audio-spatial and verbal information, and proposes that during *Hominin* evolution there was a cortical field duplication, of the IPS with further duplication of its projections to the VLPFC which resulted in a pathway dedicated for audio-vocal conversion. How would this serve people who employ a signed language? (Of course, those who advocate a gestural origin of language must face the complementary question of how visuo-manual pathways came to support audio-vocal

signals – which they must do because other primates lack vocal learning, let alone the use of syntax and semantics in either domain.)

Response: I agree with the reviewer that in depth description of the visual streams and addition of evidence for the parietal duplication hypothesis could add more depth to the paper. However, reviewer 2 (Josef Rauschecker) argued that the section of the paper discussing the relationship between the auditory and visual streams is problematic, and overall disagreed with the parietal duplication hypothesis. Although I don't entirely agree with his perspective, given that the paper is already rich in hypotheses and evidence, I chose to remove the sections discussing this topic from the paper. Possibly, the parietal duplication hypothesis will be presented in the future in its own paper.

A valuable feature of Poliva's model is its suggestion of how the response to an auditory call might initiate visual search as the basis for action (he emphasizes the mother emitting a call if the child is not seen; a related scenario would be movement toward the child if it were seen). This issue of integration of communication and action, which may (but need not) integrate audition with vision, is an important feature which too few studies take into account. My question is whether he unduly emphasizes cortical pathways involving the frontal eye fields and shortchanges subcortical interactions involving the superior colliculus (noting of course that these are open to cortical influences modulated by the basal ganglia)

Response: I agree with the reviewer that area LIP in the intraparietal sulcus likely guides eye movements via projections to the frontal eye field and the superior colliculi. Such connections from the area LIP to the superior colliculi were described in tracing studies (Lynch et al., 1985). However, to the best of my knowledge no study so far demonstrated that this parieto-collicular pathway carries auditory information. It would also be very difficult to demonstrate that auditory influence on the superior colliculus occurs via connections from area LIP and not via ascending connections from the inferior colliculi. Given the lack of evidence of an auditory parieto-collicular pathway I chose at this point not to include it in the revised paper.

Lynch, J. C., AMs Graybiel, and L. J. Lobeck. "The differential projection of two cytoarchitectonic subregions of the inferior parietal lobule of macaque upon the deep layers of the superior colliculus." *Journal of Comparative Neurology* 235.2 (1985): 241-254.

Poliva claims to review "evidence for a role of the ADS in the transition from mediating contact calls into mediating human speech" but simply cites data correlating ADS impairment with disorders like speech apraxia.

Response: In addition to the paragraph discussing the role of the ADS in speech production, I present throughout the paper many other studies that indirectly show a role of the human ADS in speech production, such as fMRI studies that compare speech production to the production of melodies (Hickok et al., 2003) and many studies that ascribe the ADS with a role in speech repetition (Hickok et al., 2007).

Nothing in the data privileges contact calls over other vocal productions

Response: Many studies have shown that the ADS (associated in human with speech

production) has a special role in the detection and production of contact calls. For example:

“Further corroborating the involvement of the ADS in the perception of contact calls are intra-cortical recordings from the posterior insula (near area CM-A1) of the macaque, which revealed stronger selectivity for a contact call (coo call) than a social call (threat call; Remedios *et al.*, 2009a). Contrasting this finding is a study that recorded neural activity from the anterior auditory cortex, and reported that the proportion of neurons dedicated to a contact call was similar to the proportions of neurons dedicated to other calls (Perrodin *et al.*, 2011).”

Also:

“Consistently, a study that sacrificed marmoset monkeys immediately after responding to contact calls (phee calls) measured highest neural activity (genomic expression of cFos protein) in the posterior auditory fields (CM-CL), and VLPFC (Miller *et al.*, 2010). Monkeys sacrificed after only hearing contact calls or only emitting them showed neural activity in the same regions but to a much smaller degree (See also Simões *et al.*, 2010 for similar results in a study using the protein Egr-1).”

– and, anyway, clear articulation is a far cry [sic] from mechanisms supporting the role of syntax and semantics in language production and perception.

Response: I agree with the reviewer that arguing that the ADS processes speech does not necessitate that the ADS process more complex linguistic functions such as semantics and syntax. This is why in the paper I only present a model for the emergence of speech. More complex linguistic functions and possible evolutionary course will be discussed in the second paper.

Poliva stresses that the ability to ask and answer questions is an essential feature of language use. I agree. Future work on language evolution should pay more attention to the challenge of explaining how this evolved. However the focus on modifying contact calls with prosodic intonations seems to me too narrow (I may be wrong, but more argument would be needed) and (as Poremba observed) the account of the transition remains too sketchy. Poliva cites “the ability of present-day infants of using intonations for changing the pragmatic utilization of a word from a statement to a command/demand (“mommy!”) or a question (“mommy?”),” but one must be careful to distinguish these infant “communicative acts” from the ability to deploy grammar to formulate an open-ended repertoire of commands and questions using the structures of a language – let alone being able to marshal answers to questions of even modest complexity.

Response: I agree with the reviewer that adults often use complex syntax to ask questions. However, given that children (and occasionally adults) can express a question with a single word using intonations, suggests, in my opinion, that such question asking method could have preceded syntax, and thus indicate of an intermediate stage in the evolution of language. A transition from a single word question to syntax likely occurred at later evolutionary stages, and is thus beyond the scope of the present paper.

Competing Interests: No competing interests were disclosed.

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Josef Rauschecker

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This is an interesting contribution to the literature on language evolution. The first two sections ('Introduction' and 'Models of Language Processing in the Brain...') are a joy to read. Later sections are more controversial and contain serious flaws that have to be brought up to speed with the current literature. These concerns are summarized here:

1) The terminology is quite fuzzy. For instance, when the author refers to 'perception' he seems to mean 'detection' or 'processing'. In most people's minds, and in most extant models of perception and action, perception is specifically tied to the ventral stream. Therefore, it can, almost by definition, not also be a property of the dorsal stream. This is best exemplified in the Abstract: The author states: '*I propose that the primary role of the auditory dorsal stream (ADS) in monkeys/apes is the perception and response to contact calls.*' This misstatement can be fixed by replacing 'perception' with 'detection'. Similarly, in a later sentence ('Perception of contact calls occurs by the ADS detecting a voice...'), 'Perception' can be substituted by 'Processing'. Thirdly, in the Abstract's second paragraph, the following sentence does not make any sense: 'Because the human ADS processes also speech production and repetition...'. Here, 'processes' needs to be replaced with 'performs'.

2) In the third section, the author first makes a strong case for a role of the ADS in auditory spatial processing, for encoding of sound location in memory and for use of this information in guiding eye movements. The published literature is well represented, though a key reference is missing here ([Tian et al., Science, 2001](#)). Then, in a surprising turnaround, the author suddenly concludes that 'audiospatial input is first converted into a visuospatial code and then processed via a visuospatial network'. The evidence cited stems from 15-year old studies of monkey area LIP, which is part of a visuospatial network; auditory signals, however, are relayed to a different part of IPS (area VIP; [Lewis & VanEssen, 2000](#)), for which corresponding studies have not been performed. Figure 2, which pertains to this section, reflects this misinterpretation: While the version on the left is neuroanatomically acceptable (with the only difference that parietal cortex is not just a visuospatial but a multisensory or amodal network, the versions in the center and on the right are incorrect on multiple grounds, most notably by postulating the 'duplication of the IPS [pivoting around an imaginary blue asterisk] and subsequent duplication of its frontal projections'. The assumptions about anatomical connections of the IPL with ventrolateral prefrontal cortex (VLPFC) are largely unsubstantiated and the characterization of VLPFC as a motor representation is plain wrong. I assume what the author may be referring to is ventral premotor cortex (PMv), which is indeed the terminal point of the auditory dorsal stream and is closely interfacing with Broca's area.

3) According to a third hypothesis put forward by the author, "*the Homo genus emerged as a result of duplicating the IPS and its frontal projections. This duplication resulted with area Spt and its projections to the VLPFC. In contrast to the visual dorsal stream that processes audiovisual spatial properties, the human ADS processes inner and outer speech.*" This hypothesis is seriously flawed, because both ADS and VDS process spatial properties and both process sensorimotor signals. In fact, they may be one and the same structure. Thus, there is no fundamental difference between visual and auditory processing that would require duplication of IPS or its projections or special evolution of speech (see [Bornkessel et al., 2015](#)).

4) Additional citations that the author should add:

DeWitt and Rauschecker, 2012 ¹

DeWitt and Rauschecker, 2013 ²

Bornkessel-Schlesewsky, *et al.*, 2015 ³

Mesulam, *et al.*, 2015 ⁴

Roux, *et al.*, 2015 ⁵

References

1. DeWitt I, Rauschecker JP: Phoneme and word recognition in the auditory ventral stream. *Proc Natl Acad Sci U S A*. 2012; **109** (8): E505-14 [PubMed Abstract](#) | [Publisher Full Text](#)
2. DeWitt I, Rauschecker J: Wernicke's area revisited: Parallel streams and word processing. *Brain and Language*. 2013; **127** (2): 181-191 [Publisher Full Text](#)
3. Bornkessel-Schlesewsky I, Schlesewsky M, Small SL, Rauschecker JP: Neurobiological roots of language in primate audition: common computational properties. *Trends Cogn Sci*. 2015; **19** (3): 142-50 [PubMed Abstract](#) | [Publisher Full Text](#)
4. Mesulam MM, Thompson CK, Weintraub S, Rogalski EJ: The Wernicke conundrum and the anatomy of language comprehension in primary progressive aphasia. *Brain*. 2015; **138** (Pt 8): 2423-37 [PubMed Abstract](#) | [Publisher Full Text](#)
5. Roux FE, Miskin K, Durand JB, Sacko O, Réhault E, Tanova R, Démonet JF: Electrostimulation mapping of comprehension of auditory and visual words. *Cortex*. 2015; **71**: 398-408 [PubMed Abstract](#) | [Publisher Full Text](#)

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Competing Interests: No competing interests were disclosed.

Author Response 05 Jan 2016

Oren Poliva, Bangor University, UK

This is an interesting contribution to the literature on language evolution. The first two sections ('Introduction' and 'Models of Language Processing in the Brain...') are a joy to read. Later sections are more controversial and contain serious flaws that have to be brought up to speed with the current literature. These concerns are summarized here:

1) The terminology is quite fuzzy. For instance, when the author refers to 'perception' he seems to mean 'detection' or 'processing'. In most people's minds, and in most extant models of perception and action, perception is specifically tied to the ventral stream. Therefore, it can, almost by definition, not also be a property of the dorsal stream. This is best exemplified in the Abstract: The author states: '*I propose that the primary role of the auditory dorsal stream (ADS) in monkeys/apes is the perception and response to contact calls.*' This misstatement can be fixed by replacing 'perception' with 'detection'. Similarly, in a later sentence ('Perception of contact calls occurs by the ADS detecting a voice...'), 'Perception' can be substituted by 'Processing'. Thirdly, in the Abstract's second paragraph, the following sentence does not make any sense: 'Because the human ADS

processes also speech production and repetition...'. Here, 'processes' needs to be replaced with 'performs'.

Response: As far as I understand it, perception refers to all elements of the external world that reach our awareness. In accordance with this definition, through the AVS we perceive the identity of sounds and through the ADS we perceive the location of sounds. As human speech production is also processed in the ADS, I would expect that we also perceive elements of speech preparation through the ADS. A good example is a study that reported of patients who were electrically stimulated in the left inferior parietal lobule and consequently believed they produced sounds, when in fact they didn't (Desmurget et al., 2009). This study can be argued to demonstrate perception of speech preparation in the ADS. Nonetheless, considering that different researchers might have different definitions for perception, I replaced instances that describe perception with detection wherever it was applicable.

Desmurget M, Reilly KT, Richard N, Szathmari A, Mottolese C, Sirigu A. Movement intention after parietal cortex stimulation in humans. Science. 2009 May 8;324(5928):811–3.

2) In the third section, the author first makes a strong case for a role of the ADS in auditory spatial processing, for encoding of sound location in memory and for use of this information in guiding eye movements. The published literature is well represented, though a key reference is missing here ([Tian et al., Science, 2001](#)). Then, in a surprising turnaround, the author suddenly concludes that 'audiospatial input is first converted into a visuospatial code and then processed via a visuospatial network'. The evidence cited stems from 15-year old studies of monkey area LIP, which is part of a visuospatial network; auditory signals, however, are relayed to a different part of IPS (area VIP; [Lewis & VanEssen, 2000](#)), for which corresponding studies have not been performed. Figure 2, which pertains to this section, reflects this misinterpretation: While the version on the left is neuroanatomically acceptable (with the only difference that parietal cortex is not just a visuospatial but a multisensory or amodal network, the versions in the center and on the right are incorrect on multiple grounds, most notably by postulating the 'duplication of the IPS [pivoting around an imaginary blue asterisk] and subsequent duplication of its frontal projections'. According to a third hypothesis put forward by the author, "*the Homo genus emerged as a result of duplicating the IPS and its frontal projections. This duplication resulted with area Spt and its projections to the VLPFC. In contrast to the visual dorsal stream that processes audiovisual spatial properties, the human ADS processes inner and outer speech.*" This hypothesis is seriously flawed, because both ADS and VDS process spatial properties and both process sensorimotor signals. In fact, they may be one and the same structure. Thus, there is no fundamental difference between visual and auditory processing that would require duplication of IPS or its projections or special evolution of speech (see Bornkessel et al., 2015).

Response: Although I don't entirely agree with the reviewer's perspective in this regard, given that the paper is already rich in evidence and hypotheses, I removed the sections (last paragraph of section 3 and section 7) discussing these hypotheses in the revised version. Also, I removed figure 2 from the revised version, and accordingly modified the manuscript to accommodate this change.

3) ...I assume what the author may be referring to is ventral premotor cortex (PMv), which is indeed the terminal point of the auditory dorsal stream and is closely interfacing with Broca's area.

Response: Thinking back, I agree with the reviewer that referring to this region as the ‘ventral premotor cortex’ is more accurate. The reason I referred to this region as the ventrolateral prefrontal cortex is to be consistent with previous papers (e.g., Romansky et al., 1999). As it possible that the area most often referred to as Broca’s area encompasses both parts of the ventrolateral prefrontal cortex and ventral premotor cortex, in the revised manuscript I replaced the term ‘ventrolateral prefrontal cortex’ with its anatomical equivalent, the ‘inferior frontal gyrus’.

Romanski LM, Bates JF, Goldman-Rakic PS. Auditory belt and parabelt projections to the prefrontal cortex in the rhesus monkey. *J Comp Neurol.* 1999 Jan 11;403(2):141–57.

As a final note, I want to thank the reviewer for his time and effort, and hope he finds the revised version even more enjoyable to read.

Competing Interests: No competing interests were disclosed.

Referee Report 17 July 2015

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Amy Poremba

Department of Psychology, University of Iowa, Iowa City, IA, USA

This contribution is a wide-ranging theory of how speech evolved in humans, which incorporates the dorsal and ventral auditory processing streams, but primarily focused on the auditory dorsal stream.

There are several large leaps in the proposed trajectory for language evolution such as, “eventually, individuals were capable of inventing new words and offspring were capable of inquiring about objects in their environment and learning their names via mimicry.” While the first part of the overall proposed theory is well supported, these latter stages are under-supported by current knowledge, particularly when moving to discussing individuals that became capable of enunciating novel calls (e.g., last paragraph of introduction); (some publications that may be helpful, comment by [Meguerditchian et al., 2014](#); original article, [Ackermann et al., 2014](#)). The steps proposed for inventing new words and inquiring about objects are likely to require a large number of processes and the theory does not specify what those steps might be. Overall, Poliva’s theory as set forth does generate some interesting, testable, hypotheses as demonstrated in section 9, and the leaps in the logical flow do not negate these as the hypotheses are more closely related to the current knowledge base.

As this is a theory of “From where to what,” missing for me was a better description of how the dorsal and ventral streams might interact in this theory. Calls still need to be “recognized” as auditory objects and imaging and recording studies have indicated the ventral stream does process this type of information. The ventral stream was given much less prominence and described in the appendix. It would be nice to include a paragraph or two on how the two systems may work together or how the ventral stream object identification comes to participate or interact with word formation and questions about objects.

In the first paragraph of the introduction, curiosity toward the unknown may be related to non-human primates’ tendency to pick novel objects from known objects. This is also true in many lower animals. The

development of curiosity of objects that are absent from our environment as Poliva suggests must also be related to memory development. One must be able to remember that objects exist and have detailed memories in order to determine if an object is indeed missing. There are aspects of work by Mishkin and colleagues suggesting that the lack of robust, or expansive, long-term auditory memory may relate to the absence of complex communication systems in non-human primates, such as rhesus macaques. Clearly, visual memory is much more extensive and robust than auditory memory and the sign language that other non-human primates have demonstrated may be related to the robust nature of visual memory. The issue of memory mechanisms necessary for identifying that auditory objects are indeed missing from the environment, and how these may differ and interact between auditory and visual systems, should at least be mentioned in passing.

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Competing Interests: No competing interests were disclosed.

Author Response 05 Jan 2016

Oren Poliva, Bangor University, UK

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There are several large leaps in the proposed trajectory for language evolution such as, “eventually, individuals were capable of inventing new words and offspring were capable of inquiring about objects in their environment and learning their names via mimicry.” While the first part of the overall proposed theory is well supported, these latter stages are under-supported by current knowledge, particularly when moving to discussing individuals that became capable of enunciating novel calls (e.g., last paragraph of introduction); (some publications that may be helpful, comment by [Meguerditchian et al., 2014](#); original article, [Ackermann et al., 2014](#)). The steps proposed for inventing new words and inquiring about objects are likely to require a large number of processes and the theory does not specify what those steps might be. Overall, Poliva’s theory as set forth does generate some interesting, testable, hypotheses as demonstrated in section 9, and the leaps in the logical flow do not negate these as the hypotheses are more closely related to the current knowledge base.

Response: I agree with the reviewer that the final evolutionary stages show a leap and are not strongly substantiated with evidence. As mentioned in the paper, in depth discussion of these stages is presented in a sibling paper, which is currently in writing. Nonetheless, in the revised manuscript, I made more effort to describe possible transition to mimicry. Moreover, I removed discussing this issue from the abstract and introduction, as it is not the primary concern of the present paper.

As this is a theory of “From where to what,” missing for me was a better description of how the dorsal and ventral streams might interact in this theory. Calls still need to be “recognized” as auditory objects and imaging and recording studies have indicated the ventral stream does process this type of information. The ventral stream was given much less prominence and described in the appendix. It would be nice to include a paragraph or two on how the two systems

may work together or how the ventral stream object identification comes to participate or interact with word formation and questions about objects.

Response: As mentioned above, in the revised manuscript I downplayed the role of the ADS in object naming and mimicry, and limited the discussion to speech. In depth discussion into the role of the AVS in these functions will be presented in the sibling paper. There was simply too many hypotheses and topics to cover, which made it impossible to include them all in a single paper.

In the first paragraph of the introduction, curiosity toward the unknown may be related to non-human primates' tendency to pick novel objects from known objects. This is also true in many lower animals.

Response: The hypothesis that curiosity to novel objects prompted our curiosity to the unknown is an interesting alternative hypothesis. Humans, however, since the beginning of written history, were also documented with another curiosity: desire to explore unknown places. In the present paper, I present evidence that the primary drive for the emergence of speech was by lost infants and mothers seeking to reunite. This model seems to explain both the emergence of speech and our unique curiosity for the unknown and is thus parsimonious. Presenting an alternative explanation would entail evidence for a different evolutionary course, and is thus beyond the scope of the present paper. Saying that, I'll be very interested to read about evidence for an evolutionary course that explains the curiosity to the unknown from this perspective. In the present model, I argue that the first question ever asked was "where are you". It leaves me wondering that if the curiosity to the unknown was prompted by curiosity to novel objects, then what could have been the first question?

The development of curiosity of objects that are absent from our environment as Poliva suggests must also be related to memory development. One must be able to remember that objects exist and have detailed memories in order to determine if an object is indeed missing. There are aspects of work by Mishkin and colleagues suggesting that the lack of robust, or expansive, long-term auditory memory may relate to the absence of complex communication systems in non-human primates, such as rhesus macaques. Clearly, visual memory is much more extensive and robust than auditory memory and the sign language that other non-human primates have demonstrated may be related to the robust nature of visual memory. The issue of memory mechanisms necessary for identifying that auditory objects are indeed missing from the environment, and how these may differ and interact between auditory and visual systems, should at least be mentioned in passing.

Response: The hypothesis that expansion of auditory memory contributed to the development of language is very interesting and I do appreciate that the reviewer brought this research to my attention. However, in the present paper I only describe an evolutionary course up to the advent of the first conversation. Enhancement of auditory memory likely occurred in later stages of language development, and is thus beyond the scope of the present paper.

As a final note, I want to thank the reviewer for her insightful comments and opinions, and hope that she enjoys the revised version of the paper.

Competing Interests: No competing interests were disclosed.

Discuss this Article

Version 1

Author Response 26 Aug 2015

Oren Poliva, Bangor University, UK

Thank you for your comment. Why do you think the model presented in this book is relevant to the present speech evolution model?

Competing Interests: No competing interests were disclosed.

Reader Comment 15 Aug 2015

Andrew Freinkel, Stanford University School of Medicine (Emeritus), USA

It's striking to me that the author made no mention of the spectacularly important work of Julian Jaynes in his book "The Origin of Consciousness In the Breakdown of the Bicameral Mind." If Dr. Poliva is unaware of Jaynes's work, he may find it of interest.

Competing Interests: No competing interests were disclosed.
