ural learning environment for infants to facilitate linguistic processing. Audio, visual, and body movement data were collected simultaneously. The non-speech inputs of the learning system consisted of visual data, and head and hand positions in concert with eye gaze data. The possible meanings of spoken words were encoded in this nonlinguistic context, and the goal was to extract those meanings from raw sensory inputs. Our method first utilized eye and head movements as cues to estimate the speaker's focus of attention. At every attentional point in time, eye gaze was used as deictic reference (Ballard et al. 1997) to find the attentional object from all the objects in a scene, and each object was represented by a perceptual feature consisting of color, texture, and shape features. As a result, we obtained a temporal sequence of possible referents.

Next, a partitioning mechanism categorized spoken utterances represented by phoneme sequences into several meaning bins, and an expectation-maximization algorithm was employed to find the reliable associations of spoken words and their perceptually grounded meanings. Detailed descriptions of machine learning techniques can be obtained from Yu and Ballard (2004). The learning result is that this system can learn more than 85 percent of the correct word-meaning associations accurately, given that the word has been segmented. Considering that the system processes raw sensory data, and our learning method works in unsupervised mode without manually encoding any linguistic information, this level of performance is impressive.

Such results are very consistent with Arbib's proposal that these body constraints served to start language development on an evolutionary scale. However, this leaves unanswered the question of why *Homo sapiens evolved without language*. Arbib's argument seems to be that if a plausible sequence of steps is laid out, and the "height" or difficulty in transiting each step is small, then somehow evolution should have been compelled to follow this path. But our sequence of steps in the model of infant language learning also has small steps – recognize body movements, recognize intentions as communicated with body movements, recognize attentional objects in a scene, recognize the sounds that accompany these movements. These steps would be accessible for a variety of social species, and yet they were traversed only by humans.

Arbib makes special use of the hand representations, suggesting that perhaps humans had an edge in this category that provided the needed leverage. This is again very plausible, yet our studies show that you can get quite far just by hanging sounds on the end of the eye fixations and hand movements. From our point of view, any animal species that could communicate intention through body movement had the possibility of developing some kind of language. Hence, it is likely that some other constraints must be brought into play to account for the uniqueness of language in humans. Surprisingly, Arbib does not mention Miller's hypothesis that language is a product of sexual selection. Miller (2001) argues that the human brain must have been the kind of runaway process driven by sexual selection in a similar manner to Bower bird's nests and peacock's tails. Miller's arguments are extensively developed and show how *Homo sapiens* could have gotten a jump start on very similar species with very similar brain architectures.

Author's Response

The mirror system hypothesis stands but the framework is much enriched

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Abstract: Challenges for extending the mirror system hypothesis include mechanisms supporting planning, conversation, motivation, theory of mind, and prosody. Modeling remains relevant. Co-speech gestures show how manual gesture and speech intertwine, but more attention is needed to the auditory system and phonology. The holophrastic view of protolanguage is debated, along with semantics and the cultural basis of grammars. Anatomically separated regions may share an evolutionary history.

R1. Introduction

R1.1. The commentaries in perspective

The original mirror system hypothesis (MSH) states that:

> H1. The *parity requirement* for language in humans is met because Broca's area evolved atop the mirror system for grasping with its capacity to generate and recognize a set of actions.

The target article (TA) goes beyond MSH to distinguish a language-ready brain (equipping the child to learn a language) from a brain that "has" language (in the sense of, e.g., an innate "principles and parameters" universal grammar) and then to assert that:

> H2. Language readiness evolved as a multimodal manual/facial/vocal system with protosign providing the scaffolding for protospeech – these then co-evolved in an expanding spiral to provide "neural critical mass" for protolanguage

and further that:

> H3. Protolanguage was holophrastic – "protowords" were semantically more akin to phrases or sentences of modern language than words "as we know them."
>
> H4. Biological evolution gave humans a language-ready brain, but the emergence of human languages from protolanguage was a matter of history, not biology.
>
> H5. Whereas the original MSH focused on macaque F5 and Broca's area, F5 is part of a larger F5-PF-STS system in the macaque, and this "lifts" to a larger frontal-parietal-temporal language-ready system in the human brain.

Among them, H2 to H5 constitute an extended MSH. What needs stressing is that these four hypotheses are almost independent – and thus each must stand on its own. My response to the commentaries is grouped as follows:

Section R2 shows that complex imitation must be complemented by planning (R2.1) and viewed in developmental perspective (R2.2).

Section R3 generally endorses the role of the mirror sys-

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tem in evolution of the language-ready brain, but mechanisms supporting conversation (R3.1), motivation (R3.2), and theory of mind (R3.3) must also be taken into account.

Section R4 considers lessons from modeling biological neural networks (4.1) and evolving artificial networks (R4.2).

Section R5 reviews the debate over the claim (H2) that the path to protospeech was indirect. Discussion of co-speech gestures (R5.1) shows how strongly manual gesture and speech are intertwined. Future work must factor in new data on the auditory system (R5.2). Data on primate vocalization challenge H2 but do not topple it (R5.3). However, any claim that protosign had a large head start (if any) on protospeech in the expanding spiral is questionable. The challenge of evolving a phonological system remains (R5.4).

Section R6 discusses the transition from protolanguage to language with special attention to the debate on H3, the holophrastic view of language (R6.1). Issues on bringing semantics into MSH (R6.2) are followed by a brief discussion of H4, emphasizing the cultural basis of grammars (R6.3).

Section R7 revisits the overview in Figure 6 of the TA. Unfortunately, the figure was mentioned only in one commentary and then only in passing, but I discuss commentary relevant to the issues of whether anatomically separated regions may share an evolutionary history (R7.1) and how action planning supplements mirror systems in language evolution (R7.2).

In addition to the commentaries published here in this issue, I had the privilege of receiving equally fine commentaries from Yoonsuck Choe; Jean-Louis Dessalles & Laleh Ghadakpour; Peter Dominey; James Hurford; Masao Ito; David Kemmerer; Takaki Makino, Kotaro Hirayama & Kazuyuki Aihara (Makino et al.); Emese Nagy; Massimo Piattelli-Palmarini & Thomas Bever; Friedemann Pulvermüller; Andreas Rogalewski, Andreas Jansen, Ann-Freya Foerster, Stefan Knecht, & Caterina Breitenstein (Rogalewski et al.); Martin Ruchsow; Markus Werning; and Patricia Zukow-Goldring. These commentaries are posted on the BBSOnline Web site and have been given a fuller Author's Response. The supplemental commentaries with Author's Response are retrievable at the following URL: http://www.bbsonline.org/Preprints/Arbib-05012002/Supplemental/. I am particularly grateful to the many commentators whose correspondence allowed me to more fully understand the issues they raised. I cannot do justice to this "conversation" in 10,000 words here, but hope to develop many of the issues in *Beyond the Mirror: Biology and Culture in the Evolution of Brain and Language*, which I am currently preparing for publication by Oxford University Press.

I use **boldface** for commentators' names when responding to the present published commentaries and *italic* when discussing (more briefly) the supplemental ones. A commentator's name followed by the notation (p.c.) refers to the follow-up correspondence (personal communication), not the original commentary.

R1.2. Et cetera

A number of interesting points do not fit into the above framework:

R1.2.1. Birds and others. Pepperberg applies my criteria for language readiness to the behavior of the Grey parrot, Alex, that she has taught to communicate with humans using rudiments of English speech. Despite the lack of strong neural homologies between parrots, songbirds (Doupe & Kuhl 1999), and primates, we may still hope to model relevant circuitry (R4) to better understand what allows a neural network to achieve different language-related functions. **Fitch** notes that some species may have vocal but not bodily imitation, and vice versa. This is irrelevant to MSH, which asserts that humans had a particular history. This does not deny that comparative study of neural mechanisms underlying different forms of imitation may help us better understand the workings of the human brain – though the closer the homology, the more likely the payoff.

Pepperberg's assertion that little about my criteria for language readiness is unique to humans seems a blow to my claim to characterize what allows human children to learn "full language" where other species cannot. Perhaps there are differences of degree: for example, Alex does not meet my full criteria for "complex imitation." What enriches the discussion is that chimpanzees raised in a human environment can exhibit far more "protolanguage" than their wild cousins – observing animals in the wild does not define the limits of complexity of their behavior.

R1.2.2. Lateralization. Kaplan & Iacoboni show that motor activation to sight of an action is typically bilateral, whereas action sounds activate the motor cortex only in the left hemisphere. This may be related to evolutionary processes that lateralized language. Since lateralization has been debated extensively in *BBS* (Vol. 26, No. 2, Corballis 2003a), I will not comment here (but see R5.3) beyond the observation that, because children who receive a hemispherectomy early enough can gain fairly good command of language (though comprehension of syntax does show some left-hemisphere superiority [Dennis & Kohn 1975]), lateralization would seem to be not so much the genetic specification of different kinds of circuitry in the two hemispheres as a developmental bias which favors, but does not force, differential development of skills there.

R1.2.3. Sexual selection. Yu & Ballard cite the hypothesis that language is a product of sexual selection. I am unable to evaluate this hypothesis, but raise two questions: Does sexual selection function differently in early hominids and early great apes? Why does it not yield stronger dimorphism between male and female language use?

R1.2.4. Genetic underpinnings. Théoret & Fecteau note attempts to implicate the *FOXP2* gene in language. However, *FOXP2* is implicated in many systems, from the gut to the basal ganglia. It has been argued that because the gene changed only once from mouse to our common ancestor with the great apes but changed twice in the hominid line, it may hold the key to what distinguishes us from the great apes. However, the mutation of the gene seen in a number of members of the family KE does not reverse the two "recent" mutations to yield humans with a chimpanzee-like *FOXP2* gene. The KE language deficits seem more a function of motor problems than proving a causal relation between changes in *FOXP2* and the evolution of the language-ready brain (Corballis 2004). **Pepperberg**'s description of the use of expression of the *ZENK* gene to form a functional map of avian brains for behavior related both to auditory processing and vocal production and the coupling of this to

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neurophysiology, provides an encouraging model for future studies in macaques.

R2. Complex imitation

R2.1. Complex imitation and planning

I hypothesize that the mirror system for grasping evolved in two stages: first to provide feedback for dexterous manual control, then to underwrite the ability to act with other brain regions to make information available for interacting with others. *Makino, Hirayama & Aihara* (*Makino et al.*) observe that success in complex imitation requires the ability to recognize the goal of an action as the basis for mastering the action which achieves that goal. Indeed, Arbib and Rizzolatti (1997) gave the equation Action = Movement + Goal, and the mirror neurons system (MNS) model recognizes an action in terms of the goal of successful grasping of an affordance. Complex imitation takes us further. It rests on recognizing how different actions fit together to achieve various subgoals of the overall goal.

Bickerton and **Prudkov** assert that there cannot be imitation unless someone has first created something to imitate, and that mirror neurons offer no clue as to how totally novel sequences could have been created. Actually, new skills can emerge by trial and error. The problem is to preserve them. The data on chimpanzee cultures (Whiten et al. 2001) show how few skills chimpanzees acquire. I suggest that it is complex imitation that enables humans to move beyond such limited repertoires, cumulatively ratcheting up the available stock of novel skills.

Complex imitation presupposes a capacity for complex action analysis – the ability to analyze another's performance as a combination of actions (approximated by variants of) actions already in the repertoire. In modern humans, imitation undergirds the child's ability to acquire language, whereas complex action analysis is essential for the adult's ability to comprehend the novel assemblage of "articulatory gestures" that constitute each utterance of a language. However, the adult does not imitate this assemblage but rather factors it into the planning of his reply. I agree with **Bridgeman** that mirror systems must be supplemented by a planning capability to create, store, and execute plans for sequences of actions and communicatory acts. These apparent sequences are the expression of hierarchical structures. In Figure 5 of the TA, interpretation of actions of others is coupled to planning of one's own actions; Bridgeman stresses the need for the complementary evolution of these two capabilities. They underlie perception grammars and production grammars, mentioned in discussion of Figure 1 of the TA.

Bickerton observes that when someone addresses you, you do not just imitate what they said. True. The human mirror system creates a representation that can be used for feedback control, imitation (which monkeys do not exhibit), or generating some appropriate response while inhibiting mimicking. Only in pathology does this inhibition fail, yielding compulsive imitation (echopraxia; Podell et al. 2001).

R2.2. Imitation in developmental perspective

Zukow-Goldring sees affordances and effectivities (what the body can do; Shaw & Turvey 1981) as two sides of the mirror system. By directing the child's attention to its own effectivities in relation to affordances, the caregiver narrows the search space for learning, and thus enhances that learning (Zukow-Goldring 1996). These practices may pave the way to early word learning. The prolonged period of infant dependency in humans combines with caregiving to provide conditions for complex social learning.

Neonatal imitation is based on moving single effectors and thus differs from goal-directed imitation. (Studdert-Kennedy [2002] discusses data consistent with the view that the infant at first imitates sounds by moving one articulator and only later coordinates articulators.) Social reciprocity in neonatal imitation (R3.1) may be a necessary precursor for complex imitation, establishing that "I am like the other." Biological evolution may have selected for neonatal imitation as a basis for complex imitation.

Yu & Ballard found that body cues signaling intention can aid word learning in adults, suggesting the utility of such cues for children. Their computational model reliably associates spoken words and their perceptually grounded meanings. This model employs "small steps" which, they suggest, would be accessible by a variety of social species, and "yet they were only traversed by us." However, they seem accessible to parrots and bonobos as well as the 2-year-old child – which is why I emphasize complex imitation.

R3. Complementing complex imitation: Motivation and theory of mind

Conversation, motivation, and theory of mind – and prosody (R5.3) – must all be addressed in a satisfactory account of the language-ready brain. This requires expanding MSH rather than weakening it.

R3.1. Conversation

Kotchoubey emphasizes pragmatics, for example, what we say depends on the mental state (R3.3) of our "hearer." However, his claim that "We do not use language to transmit information, but to persuade and motivate" (R3.2) seems a false dichotomy. "Look at this beautiful flower" combines information – "This flower is beautiful" – and persuasion – "Look at this flower." Kotchoubey (personal communication) stresses that his starting point is cooperation between two or more humans, reinforcing the claims of MSH for relating praxic and communicative actions.

Nagy suggests an innate basis for conversation that precedes its pragmatic function – newborn infants communicate by using "imitation" right after birth (Nagy & Molnar 2004). She suggests that language develops from these early intersubjective "conversations" (Trevarthen 2001). The cycle of turn taking in "imitating" a small repertoire of "almost innate" gestures is crucial in establishing the social pattern of turn taking (R2.2). (Cf. "motherese"; R5.3.)

R3.2. Motivation

Prudkov downplays complex imitation, arguing that the complexity of languages builds on the ability of the human brain to construct diverse goals. He suggests that animals can form learned motivations only when basic drives are ac-

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tivated. However, animals can acquire secondary reinforcers, and so on. Chimpanzees have the ability to develop non-innate subgoals (e.g., cracking nuts). The mirror system is well linked to the motivational system in the macaque. The target article shows that the F5 mirror system for grasping is best understood within the larger F5-PF-STSa mirror system for manual and orofacial actions. Rizzolatti et al. (2001) observe that STSa is also part of a circuit that includes the amygdala and the orbitofrontal cortex and so may be involved in the elaboration of affective aspects of social behavior. Hence, Prudkov's transition to "non-innate motivation" may be less proximate for the evolution of the language-ready brain per se than complex imitation, which made possible the rapid acquisition of new skills.

R3.3. Theory of mind

Fabrega stresses that successful pantomime presupposes social cognition, awareness of self, and goal-setting – reversing the view of those who attribute self-consciousness to language (Macphail 2000). Fabrega (personal communication) also asks: "What are thoughts beyond internal use of language"? Arbib (2001a) suggests that there are forms of consciousness common to many mammals, but that mirror system developments help explain why humans also have forms of consciousness that build upon, rather than precede language. Development of increasing subtlety of language can feed back into the nonlanguage system to refine our perceptions and experience.

Fabrega says that I do not specify how much of the protosign/protospeech spiral is enough to support the cultural evolution of language, and he asks whether "protoculture" emerges as the expanding spiral gets underway. I suggest that chimpanzees have protoculture (Whiten et al. 2001), but that human culture is qualitatively different, and language makes it so.

Williams sees the greatest evolutionary advantage conferred by spoken language as its ability to communicate mentalistic concepts (theory of mind, ToM). Williams stresses selection pressure for social maneuvering where I have emphasized physical activities. Surely the two "domains of discourse" complement each other. Williams notes the possible role of the mirror neuron system in mentalizing (Gallese 2003; Meltzoff & Decety 2003). We need to investigate whether an account can be given of a shared evolution of "mirror systems" suiting both ToM and complex imitation. I hypothesize that the ancestral mirror system for manual praxis was distinct from the putative mirror system for facial expression of emotion. The former would support pantomime and thence on to multimodal symbols; and then the availability of symbols could enrich the latter to yield rudiments of ToM.

Indurkhya sees the key to language evolution in an ability to see and feels things from another perspective and stresses the role of metaphor. Projection restructures the target by creating a new ontology for it; generalization of responsiveness of a mirror neuron may provide a novel ontology for objects and actions that can newly yield this activity. The TA shows that pantomime must be supplemented by conventional gestures to yield protosign. Within language itself, metaphor broadens our language by extending (proto)words to new contexts. In some cases, context is enough to recapture the shade of meaning. In others, one must invent terms which can express shadings specific to the new domain.

Indurkhya suggests that the ability to project one's self into other animals or objects might mark a crucial transition in hominid evolution. I think this notion is important. Much work on empathy emphasizes the similarities between self and other – but one must be able to maintain different models of other agents, adaptively going beyond what is held in common to imagine essential differences.

Williams and **Théoret & Fecteau** see autism as providing a window on the role of the mirror system in ToM and language. (Théoret & Fecteau add analysis of blindness.) Deficits in autism are prominent in speech associated with social communication, but praxic aspects of language are fairly well preserved. Perhaps what is affected is not so much language per se as the integration of this with affect and ToM. Interestingly, autistics may exhibit stereotypic mimicking (which monkeys do not have). Hence, it must be reiterated that a fully functional human mirror system inhibits mere repetition (echopraxia and echolalia) and instead relates the perception of perceived actions to the planning of an appropriate course of action.

R4. Lessons from modeling

R4.1. Biological neural networks

Horwitz, Husain, & Guenther (**Horwitz et al.**) note the importance of babbling in the development of spoken and sign languages. The Infant Learning to Grasp Model (ILGM; Oztop et al. 2004), mentioned briefly in the TA, is a theory of how "manual babbling" leads to an effective set of grasps. Arbib and Rizzolatti (1997) discussed the relevance of inverse and forward models to MSH, building on insights of Jordan and Rumelhart (1992) into vocal babbling. *Ito* and *Makino et al*. also stressed the importance of internal models; see Carr et al. (2003), Makino and Aihara (2003), Miall (2003), Wolpert et al. (2003), and Ito (2005).

Because *Piatelli-Palmarini & Bever* note the problem of determining similarity criteria for learning models, it is worth noting that the MNS and ILGM models have "innate" hand-related biases which enable them to acquire a range of grasps without having them built in. MNS input is the hand state relating the hand to the goal affordance of the object. ILGM acquires grasps whose visual manifestation MNS is to learn. ILGM has as its basis that the child reaches for a salient object, executes the grasp reflex if palmar contact is made, and builds a repertoire of grasps based on those which prove to be stable – stability supplies the reinforcement signal.

Dominey models the transformation between semantic structures and grammatical structures. He exploits the developmental analog of fractionation of holophrases to yield "words" which fill slots thus formed in the holophrase. Dominey et al. (2003) suggest that the resultant categorical distinction between function and content elements evolved first for sensory-motor function and then was exploited for phrasal-conceptual function. Dominey sees his modeling as consistent with Ullman's (2004) declarative/procedural model, in which the mental lexicon depends on temporal-lobe substrates of declarative memory, while mental grammar depends on a "procedural" network of frontal, basal-ganglia, parietal, and cerebellar structures supporting learning and execution of motor and cognitive skills.

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Horwitz et al. model how learning an auditory target for each native language sound may occur via a mirror neuron system. Guenther (p.c.) notes that in this modeling, the perceptual system organizes largely independently of the motor system, whereas motor development relies very heavily on the auditory perceptual system.

Horwitz et al. emphasize the importance of combining neural modeling with neurophysiological and brain imaging data. Horwitz and Tagamets (2003) and Arbib et al. (1994) developed techniques for using models of primate neurophysiological data to predict and analyze results of human brain imaging. Arbib et al. (2000) analyze imitation of motor skills, relating human brain imaging to data on the macaque mirror system.

R4.2. Evolving artificial networks

We turn to using "simulated evolution" to obtain versions of initially unstructured networks whose parameters fit them to better perform or learn a class of actions. (Cangelosi & Parisi [2002] and Briscoe [2002] include papers using artificial evolution to probe constraints on language, but almost all the papers are far removed from neurobiology.)

Parisi, Borghi, Di Ferdinando & Tsiotas (**Parisi et al.**) support MSH through computer simulations and behavioral experiments with humans which suggest that seeing objects or processing words referring to objects automatically activates canonical actions that we perform on them. Parisi et al. (p.c.) point out that because actions are the only inter-individually accessible aspect of behavior, interpreting meanings in terms of actions might explain how meanings can be shared.

Borenstein & Ruppin evolve networks in which evolution of imitation promotes emergence of neural mirroring. However, primate data suggest that neural mirroring preceded imitation in human evolution. Borenstein (p.c.) responds that the key point is that in their system only the evolution of imitation was solicited, yet a mirror system emerged – suggesting that the link between imitation and mirroring may be universal.

Pulvermüller opts for specifying the putative neural circuits of syntax and recursion first, and thinking about possible evolution later. In his model (Pulvermüller 2002), words are represented by distributed cell assemblies whose cortical topographies reflect aspects of word meaning; these assemblies are formed by correlation learning and anatomical constraints. Syntactic rules emerge from the interplay between sequence detectors and general principles of neuronal dynamics. My concern is that this approach is so focused on symbols that it is ill suited to grounding an evolutionary approach to neurolinguistics.

Fagg and Arbib (1992) modeled the surprising speed with which monkeys could learn to associate a visual pattern and a motor response. This led us to distinguish Stage I from Stage II learning. Stage I may take months of shaping for the monkey to learn a general task like "associate a new visual pattern on this screen with the correct pull on the lever in front of you and you will get a reward." In Stage II, the monkey knows the task, and then takes only seven or so trials to stabilize the correct response to a novel visual pattern (Mitz et al. 1991). My concern with models using small neural networks is that the search space is so restricted that Stage I is no longer necessary. As one approaches the more biological models of R4.1 one must constrain evolutionary models to provide insights that link to the anatomy and neurophysiology of real brains. A key challenge for MSH-related modeling is to understand how to "evolve" from a brain for which Stage I learning can never yield the ability to learn language, to a human brain in which perhaps 2.5 years of learning is required for Stage I to make possible the "word explosion" which distinguishes the human infant from the chimpanzee.

R5. The path to protospeech

Several commentaries concerned H2: protosign provides scaffolding for protospeech. Those who take a "speech only" approach ignore the fact that language is multimodal. However, future work on MSH needs greater attention to the auditory system.

R5.1. Co-speech gestures

McNeill, Bertenthal, Cole & Gallagher (**McNeill et al.**) show that speech and "gesticulations" form a single system – a "gesticulation" (Kendon 1988) is a motion that embodies a meaning relatable to the accompanying speech. About 90% of gesticulations synchronize with the speech segments with which they are co-expressive. I disagree with McNeill et al.'s claim that gesture and speech must convey the same idea unit. Kita and Özyürek (2003) compared speech-gesture coordination in Turkish, Japanese, and English descriptions of an animated cartoon. Gestures used to express motion events were influenced by how features of motion events were expressed in each language, but also by spatial information that was never verbalized. However, the key point is that gesticulation is truly part of language.

McNeill et al. reject the claim that language started as a gesture language that was supplanted by speech and stress the importance of a close coupling between manual and vocal action. However, they suggest that my concept of an expanding spiral of protosign and protospeech does not go far enough. They advocate the evolution of a speech-gesture system in which speech and gesture evolved in lockstep. This criticism may be mistaken. Gesticulations are part of language, not protolanguage. By contrast, protosign may indeed have had a pantomimic base, with protosign scaffolding protospeech.

In any case, **McNeill et al.** establish that protolanguage was multimodal and that gesture was not "turned off" in evolution. Relating this to brain function, McNeill et al. offer the telling example of a man who can control his limb movements only through arduous visually guided attentional control, yet can still gesticulate while speaking even when he cannot see his hands. Kemmerer describes a brain-damaged subject, with intact semantic and grammatical knowledge of motion events, whose ability to retrieve the phonological forms of concrete nouns, action verbs, and spatial prepositions was severely impaired but whose ability to produce gestures with language-typical information packaging was mostly preserved (Kemmerer et al., submitted).

Emmorey concedes that the existence of modern sign languages might seem to support my hypothesis that there was an early stage in the evolution of language in which communication was predominantly gestural. However, she rejects this view because "the only modern communities in which a signed language is dominant have deaf members."

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However, there are communities of hearing people using a signed language, albeit not their primary one (Kendon 1988). Emmorey suggests that sign languages can tentatively be traced back only 500 years, but such historical estimates are suspect. For example, http://www.ASLinfo.com/trivia.cfm says that by A.D. 530 Benedictine monks had invented signs to circumvent their vow of silence.

Emmorey asserts that "If communicative pantomime and protosign preceded protospeech, it is not clear why protosign simply did not evolve into sign language." **MacNeilage & Davis** suggest that I am "vulnerable" because I posit an open pantomimic protosign stage, whereas Hockett (1978) asserted that if manual communication had ever achieved openness, we would never have abandoned it for speech. However, I make no claim that protosign by itself realized the full potential of this openness. Emmorey further asserts: "A gestural-origins theory must explain why speech evolved at all, particularly when choking to death is a potential by-product of speech evolution." First, I do see slight advantages for speech over sign (agreeing with Corballis 2002) or, rather, for the early combination of protospeech with protosign over protosign alone, though this judgment is subjective. Second, Clegg and Aiello (2000) show that the risk of choking is highly overstated: "Mortality statistics for England & Wales . . . [show] that overall mortality from choking on food was very low averaging 0.6 per 100,000 head of population." Third, just as it is a matter of historical contingency that some tribes have both signed and spoken languages, it may well be that some tribes of early humans had languages dominated by speech and others had protolanguages dominated by sign. At a time of evolutionary bottleneck before humans left Africa 50,000 years ago, speech could have taken a dominant role. The counter-question to Emmorey is then: "If speech has primacy and sign is a modern innovation, how can one explain the ubiquity of co-speech gestures?"

R5.2. Taking the auditory system seriously

Bosman, López & Aboitiz (**Bosman et al.**), **Rauschecker**, and **Horwitz et al.** all make clear that future work on MSH must pay more attention to data on the auditory system than does the TA.

Bosman et al. (personal communication) argue that the biological principles that supported the evolution of mirror neurons for grasping may also have independently supported the evolution of auditory mirror neurons, but they agree that gesture may have helped establish certain semantic aspects of protolanguage by the use of pantomime. Their view is that protosign and protospeech coexisted and coevolved, and each contributed to the development of the other.

Bosman et al. discuss neurons in frontal areas of the monkey that respond strongly to vocalizations and thereby suggest that this domain may be the precursor of a vocalization mirror system similar to the mirror system for grasping. **Rauschecker** presents further relevant material on the macaque auditory system (R7).

Horwitz et al. note that a human may recognize 10^5 auditory objects, whereas the number of those that interest a monkey seems small. Moreover, monkeys seem far better in vision than audition in the use of long-term memory for objects. They thus argue that biological evolution gave hominids the ability to better discriminate and categorize auditory objects, retain them in memory, and relate them to articulatory gestures. I would agree, while noting that the success of speech has been linked to the ability to form an immense vocabulary from a small set of "phonemes" (the Particulate Principle; Studdert-Kennedy 2002).

R5.3. Primate vocalization

The issue is whether primate calls evolved directly to speech. **Seyfarth** argues that the parallels between primate same-different judgments for calls and children's perception of words cannot be ignored. However, such parallels suggest properties of auditory discrimination necessary for protospeech but do not help explain the crucial transition to production of an open-ended repertoire of symbols linked to an open semantics. Seyfarth faults me for characterizing primate vocalizations as "involuntary" signals but Note 6 of the TA addresses this explicitly. Seyfarth shows that I am wrong to deny that primate vocalizations are related to cortical regions, but his data primarily concern audition. **Bosman et al.** suggest that in the monkey there is overlap between area F5 and the cortical larynx representation, but **Gilissen** argues that monkey calls cannot be used as models for speech production because they are genetically determined in their acoustic structure. A number of brain structures crucial for the production of learned motor patterns such as speech production are dispensable for the production of monkey calls (Jürgens 1998).

I have been unable to consult Cheney and Seyfarth's (in press) paper which apparently asserts that primate social knowledge bears striking resemblances to the meanings we express in language, which are built up by combining discrete-valued entities in a structured, hierarchical, rule-governed, and open-ended manner. Though uninformed, I speculate that **Seyfarth** may be misled by our human ability to offer a language-like description of the primates' abilities. This is not to deny that prelinguistic knowledge of social relations is relevant to evolving the language-ready brain (R3.3).

Provine discusses contagious yawning and laughing. These seem analogous to the contagious alarm calls of nonhuman primates. He observes that laughter is a ritualization of the sound of labored breathing in rough-and-tumble play – but, presumably, we are talking of biological selection rather than the free symbol creation to which ritualization contributes at the phonological and morphosyntactic level in language (Bybee 2001). Laughter punctuates the speech stream, in contrast with the tight integration of gesticulation and speech (**McNeill et al.**).

Kotchoubey and **Fitch** note that my emphasis on cognitive-symbolic aspects of language ignores prosody. Kotchoubey notes that prosody subserves both affective prosody (emotional expression) and linguistic prosody (as in distinguishing between an assertion and a question) and that both forms of prosodic information are processed mainly in the right temporal lobe. In similar vein, **Gilissen** notes that human vocal behavior does resemble monkey calls in the emotional intonations superimposed on the verbal component. Kotchoubey (p.c.) observes that in many languages, intonation is the only distinction between question and declaration. He thus suggests that linguistic prosody is a part of the right hemisphere so closely controlled by the left that they cannot work without each other. This is reminiscent of the

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coupling of gesticulations to the syntax and semantics of a specific language.

Gilissen cites Falk's (2004a) evolutionary perspective on the hypothesis that, as human infants develop, a special form of infant-directed speech (motherese) provides a scaffold for their eventual acquisition of language. This enriches our discussion of the role of the caregiver in neonatal "conversation" (R3.1). Gilissen says that the special vocalizations of human motherese are in marked contrast to the relatively silent mother/infant interactions that characterize chimpanzees, yet suggests a possible link between monkey calls and motherese. This apparent contradiction suggests that the affective content of motherese (and protolanguage) builds upon the monkey vocalization system, but the information content of motherese (and protolanguage) has a complementary evolutionary history. **Kotchoubey** suggests that the left-hemispheric subsystem develops as described by MSH to subserve the cognitive-symbolic function, whereas the right-hemispheric subsystem is a direct successor of monkey vocalization mechanisms and gives language its intonational color. It is a long-standing observation (Hughlings Jackson 1878–79) that imprecations survive damage to the human brain that blocks normal speech. In Arbib (2002), I therefore suggested that the language-ready brain integrates action-oriented and affect-oriented systems in a pattern of cooperative computation.

Fitch adopts Darwin's hypothesis that our prelinguistic ancestors possessed an intermediate "protolanguage" that was musical and that music scaffolds the early structural and imitative aspects of language (prosody). He sees the semantic stage as coming later. However, even if we accept the importance of "musicality," it does not follow that the coevolution of vocal and manual gesture is tied more closely to music than to pantomime and linguistic communication – but it does encourage us to investigate how dance and music might enrich MSH.

R5.4. Evolving a phonological system

MacNeilage & Davis argue that my view that pantomime could be an open system disregards the view that for language to become an open system it must have a combinatorial phonology consisting of meaningless elements. However, I explicitly distinguish pantomime from protosign. But I do say too little about getting from a pantomimic repertoire to a speech repertoire. The following, adapted from Arbib (in press), may be helpful:

Signing exploits the signer's rich praxic repertoire of arm and hand movements, and builds up vocabulary by language-sanctioned variations on this multi-dimensional theme (move a hand shape along a trajectory to a particular position while making appropriate facial gestures). By contrast, speech has no rich behavioral repertoire of non-speech movements to build upon. Instead evolution took a particulate path, so that the word is built (to a first approximation) from a language-specific stock of phonemes (actions defined by the coordinated movement of several articulators, but with only the goal of sounding right rather than conveying meaning in themselves). On this analysis, a basic reach and grasp corresponds to a single word in signed language; whereas in speech, a basic reach and grasp is akin to a phoneme, with a word being one level up the hierarchy. In either case, the brain must provide a computational medium in which already available elements can be composed to form new ones, irrespective of the level at which these elements were themselves defined.

I characterized MacNeilage's frame/content theory as being about the evolution of syllabification but offering no clue as to what might have linked such a process to the expression of meaning. **MacNeilage & Davis** note that they now address this criticism by arguing that the first words may have been kinship terms based on baby talk (MacNeilage & Davis, in press b – I received the final version only after the TA was "set in concrete"). I do not deny that words like "mama" and "dada" may have been based on baby talk. But to suggest that this gives us insights into the emergence of protolanguage seems to me to conflate phylogeny and ontogeny – the prototalk of adult hunter-gatherers is unlikely to have been much like baby talk.

For **Fabrega**, the complexities of speech production seem in excess of what protosign/protospeech spiraling entails. I disagree. Even a protovocabulary of a few hundred protowords would already provide selective advantage for changes in the vocal apparatus which "full" language could exploit without further change. In any case, I insist that the appropriate framework must also explain co-speech gestures.

Kaplan & Iacoboni argue that mirror neurons in premotor cortex that respond to the visual and auditory consequences of actions allow for a modality-independent and agent-independent coding of actions, which may have been important for the emergence of language. Kaplan and Iacoboni (in preparation) found that when subjects simultaneously saw and heard an action, there was greater activity in the premotor cortex compared with control conditions in which they only saw or only heard the action. *Rogalewski et al*. report the use of trans-cranial magnetic stimulation (TMS) to show that linguistic tasks, like speaking, covert reading, and listening to speech, activate the hand motor system bilaterally (Floel et al. 2003). Kaplan & Iacoboni argue that the role of audiovisual mirror neurons in the evolution of language deserves more attention. I agree, but suggest that the best framework for this is provided by the expanding spiral hypothesis. In discussing Kohler et al. (2002) and Ferrari et al. (2003), the TA argued that these data do not support the claim that protospeech mechanisms could have evolved from F5 without the scaffolding provided by protosign. This matter is further debated by Fogassi and Ferrari (in press), Arbib (2005), and MacNeilage & Davis (in press b).

R6. From protolanguage to language

R6.1. For and against holophrasis

The hypothesis that protolanguage was based on holophrases was offered as an alternative to the view of protolanguage utterances as strings of "words as we know them."

Fitch supports the holophrase theory of language origin but suggests that Baldwinian exaptations may underlie the first behavioral stages in the transition from holistic communication toward modern language. I accept that the development of an articulatory system adequate to the demands of (proto)language phonology may have involved a Baldwinian effect but doubt Fitch's claim that the transition to language must have been "strongly and consistently shaped by selection [. . .], given the communicative and

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conceptual advantages that a compositional, lexicalized language offers." Agriculture, writing, and living in cities provide evidence that being advantageous does not imply a genetic change. Because of this I took pains to make clear that one's account of the evolution of the human brain might be seen as having two very different results: "the language-ready brain" versus "the brain that 'has' language."

Bridgeman argues against holophrasis. He asserts that monkey calls can be paraphrased in one or two words, such as "leopard." However, the leopard call's meaning can be better approximated in English by the sentence: "There is a leopard nearby. Danger! Danger! Run up a tree to escape." To this he might respond, "It's only one word, because 'leopard' is enough to activate the whole thing." But once one moves to protolanguage, one may want to convey meanings like "There is a dead leopard. Let's feast upon it," and we clearly cannot use the alarm call as the word for leopard in this utterance. Bridgeman asserts that the generality of words is about the same in all languages and therefore constitutes a possibly biological "universal" of language. However, it is well known that a word in one language may require a phrase or more to translate into another language. I therefore maintain that the size of words is a result of a long history of building increasingly flexible languages.

Bickerton is so "language-centered" that he gives us little help in imaginatively recreating possible scenarios for a time when hominid protolanguage was at an early stage of development. He asserts that it is "questionable whether any species could isolate 'a situation' from the unbroken, ongoing stream of experience unless it already had a language with which to do so." But we know that biological evolution yielded a repertoire of primate calls each of which is akin to (but very different from) a "protoword" describing a "situation" in my sense, and I have tried to imagine how the brain could have so evolved that such protowords could be "invented" and disseminated in hominid communities. I suggest that early hominids very rarely created protowords for new situations. I require only a slow accretion of such nameable situations in each generation to build towards the critical mass that constituted protolanguage. Bickerton notes that those who play charades use "a large set of 'disambiguating signs' – stereotypic gestures for 'film title,' 'book title,' and so on." I concede that early hominids had no signs for these! But the crucial point is this: When I posit that there is a protoword for "The alpha male has killed a meat animal and now the tribe has a chance to feast together. Yum, yum!", I do not claim that (at first) there were protowords for all the variations, such as "The alpha male has killed a meat animal but it's too scrawny to eat. Woe is we." I think this point also addresses one half of **MacNeilage & Davis**'s dismissal of my supposed claim that hominids in the protospeech stage could have "dashed off complex semantic concepts with holistic phonetic utterances" (those are their words not mine). Bickerton cites Tallerman (2004), who argues that holophrasis was incompatible with contrastive phonology, but (as argued above) as the protovocabulary increased, the different protowords (whether signed, spoken, or both) would need to be readily generated and comprehended, and this could provide as much pressure for the particulate principle as does the anti-holophrase position.

Bickerton (p.c.) makes the telling point that I have offered no example of a hypothetical conversation consisting of representations of frequently occurring situations and that any model that will not do conversation (R3.1) is "worse than dubious." I have given too little thought to this, but suggest that protoconversations may have been like the interactions that we see in nonhuman primates, with a few protowords interspersed among actions, rather than taking – from the start – the form of a steady interchange of protowords.

I accept **Bickerton**'s argument that it is implausible that all "real words" are foreshadowed by widely distributed fragments of protowords. However, Kirby's (2000) computer simulation shows that statistical extraction of substrings whose meanings stabilize can yield surprisingly powerful results across many generations. I thus see the "Wray-Kirby mechanism" as part of the story of the protolanguage-language transition, but not the whole one. My sour fruit story, plus aspects of ritualization, provides other mechanisms whereby the virtues of a synthetic description might emerge – with the consequent demand for a protosyntax to disambiguate combinations once the combinatorics began to explode.

Wray notes that neurolinguistic and clinical evidence suggests that linguistic representation in the brain is mapped on the principle of functional motivation (Wray 2002a, Ch. 14). Wray (p.c.) expands on this as follows: When people lose language skills after a stroke, it is common for them to retain formulaic expressions such as "good morning" while they are unable to compose novel messages (cf. R5.3). She focuses on the functions of the material, and proposes that the functional locus supporting a class of lexical material – for example, names for people whose faces we recognize might be activated via the mechanisms that process visual face recognition, whereas expressions used for context-determined phatic interaction would be activated via, say, the right-hemisphere areas that handle context pragmatics – would be linked to the "language" areas of the left hemisphere. Damage to left-hemisphere language areas could block the ability to generate names and expressions on request, but spare the ability to use the words and expressions themselves, if activated as functional wholes.

Wray supports the holophrasis theory by focusing on the linguistic phenomenon of irregularity. She presents a number of "oddities" about language use that are readily explained if humans are predisposed to treat input and output holistically where they can, and to engage in linguistic analysis only to the extent demanded by expressive need. Her formulation bridges between "true wholes" (protolanguage holophrasis) and "apparent compounds" (formulas within a modern language) – supporting our view that the "protolexicon" had many such wholes, rather than combining "words as we know them." Wray shows that the "holophrastic impulse" remains part of modern language use, even though languages have long supplanted protolanguages in human society.

Bridgeman denies holophrasis, but then asks "How could the sorts of words that cannot be used alone get invented?" and looks for evidence to the development of language in children. He concedes that a child's first utterances are holophrases but "next comes a two-word slot grammar." But ontogeny does not equal phylogeny. The child "extracting statistics" from the adult word stream is a far cry from early hominids, for whom very few (proto)words already existed. In modeling the 2-year-old, Hill (1983; Arbib et al. 1987; cf. Peters 1983 for data) sees the child as extracting fragments of the adult's speech stream to provide a

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set of templates that describe situations. At first, "want milk" or "love Teddy" are unanalyzed wholes, but then words common to many templates crystallize out, and word categories follow as it is recognized that certain words can fill similar slots (recall *Dominey*'s modeling, R4.1). This supports the claim that "holophrasis" is prototypical but that modern communities provide a setting in which the "Wray-Kirby mechanism" can extract existing words in a few years rather than extending the protovocabulary over the course of many generations.

Piattelli-Palmarini & Bever note that although idioms like "he kicked the bucket" may be semantically non-compositional, they do obey strict syntactic constraints. However, it is a mistake to confuse Wray's observation of the role of formulas in modern language use with the idea that protowords were themselves formulas. We are trying to imagine hominids without syntax and understand how they did get syntax. *Hurford* asserts that a synthetic evolutionary route to compositional syntax is "simpler" than the analytic (Wray-Arbib) account. But by what measure? Once you have discovered the combinatorial power of using syntax to combine words, then words are simpler. But if you have not done so, then labeling significant events or constructs seems the simpler strategy – which is why I still support the holophrasis theory as a viable alternative to the synthetic account.

R6.2. Bringing in semantics

The issue of semantics was emphasized not only by **Indurkhya** (see sect. R3.1) but also by *Choe, Dessalles & Ghadakpour, Hurford, Pulvermüller, and Werning* (supplemental commentaries). Hurford caught me in an embarrassing lapse. When I disagreed with "Hurford's suggestion that there is a mirror system for all concepts," it turns out that I was disagreeing not with the ideas published in Hurford (2004) but with Hurford's preliminary ideas as expressed in early discussions before the paper was written. I am happy to report that we are now in essential agreement about the diversity of perceptual and motor schemas.

Choe cites a thought experiment of Choe and Bhamidipati (2004) to assert that voluntary action can provide meaning to one's internal perceptual state, and that maintained invariance in the internal perceptual state can serve as a criterion for learning the appropriate action sequence. **Parisi et al.** assert "If we interpret not only signs but also their meaning in terms of motor actions, we can understand how meanings can be shared between speakers and hearers. Motor actions are the only aspect of behavior which is inter-individually accessible." However, there is no "reddish action" as such. And we must be careful about jumping to the idea that every gesture mimics a direct action. Nonetheless, I welcome the discussion by Parisi et al. of evidence that language is grounded in action. Studies on the neural basis of cognition suggest that different areas are activated for manipulable and non-manipulable objects (Chao &Martin 2000); manual gestures may be automatically activated not only by visual stimuli but by words, too (Gentilucci 2003a; 2003b); and Borghi et al. (2004) found in a part verification task that responding by moving the arm in a direction incompatible with the part location was slow relative to responding in a direction compatible with the part location.

This could explain why *Ruchsow* argued that MSH is in good agreement with an externalistic account of semantics. The externalist denies that there is any fact about my mental or neural states that constitutes the meaning of my words (Kripke 1982; Wittgenstein 1958). For internalists, conversely, cognition is computation over (symbolic) representations (Kurthen 1992). Ruchsow rejects internalism because it lets us "throw the world away," allowing reason and thought to be focused on the inner model instead (Clark 1999). Ruchsow finds that many passages in the TA can be read in favor of externalism but sees "some sympathy for internalism" in references to fMRI and PET studies. Actually, I regard both externalism and internalism as incomplete and have sought a framework in which the partial truths of each can be integrated. Arbib and Hesse (1986) expanded my "internal" schema theory of "schemas in the head" to provide a complementary account of "external" schemas that reside in the statistics of social interaction and are thus the expression of socially shared (externalist) knowledge.

Werning confronts the "complex first" paradox: substance concepts are more frequently lexicalized across languages than attribute concepts, and their lexical expressions are ontogenetically acquired earlier. This is hard to reconcile with the view that prototypical substance concepts are semantically complex so that, for example, the substance concept [mango] is made up of the vector of attribute concepts <orange, oval, big, soft, sweet, edible, . . .>. My solution is to distinguish the distributed code for "orange" as a feature implicit in early visual processing from the neural representation of "orange" as a concept that can be put into words. Werning cites Fodor's (1995) view of mental representations to argue that it would be logically impossible to have two representations with the same content in one and the same brain. However, data reviewed in section 3.1 of the TA show that the size of an object may have different representations for grasping (dorsal) and "declaring" (ventral). Similarly, the color of an object may be salient in segmenting it from the background or distinguishing it from other objects, yet not enter consciousness. For the child, the redness of his truck is as indissoluble from the truck's identity as the fact that it has wheels – so the word "truck" may imply "redness" and "wheels" when the child does not have words or well-formed concepts for either.

Dessalles & Ghadakpour stress that an account of the evolutionary emergence of language should "explain why and how our ancestors got minds able to form predicative structures, and to express them through compositional languages." (See Hurford [2003] for a different approach to this problem.) They point to a crucial distinction between gaining the use of predicative structures to communicate some aspects of a situation and using predicates to "think new thoughts": "We can systematically express the negative version of a predicative structure, for example, 'Leo doesn't grasp the raisin,' whereas there is no perceptive meaning corresponding to the negation of a visual scene." I would agree, yet would suggest that one can imagine a series of "inventions" that would build more and more general power into such a capability. At first, the effort to apply certain recognition criteria failing to meet the threshold is what justifies the negation. This requires that context demands that only some tests, of all possible perceptual tests, be applied (cf. presuppositions). I would probably not say to you "There are no onions in my office" unless, for example, you knew I was in my office and had expressed your need of onions. Section 7 of the TA talks of language capabilities being extended by bricolage over a long period of time, and argues that "the language-ready brain" provided by the

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genome lacks much of what we now take for granted as parts of language. I view *and, not,* and *every* as human inventions augmenting language and thus reshaping thought.

R6.3. Concerning innate universal grammar

Kotchoubey questions my view that the development of language from protolanguage was social by noting that dissemination of "inventions" currently exploits such institutions as writing, hierarchical social organization, and mass media. I respond that it was because early humans did not have such institutions that their inventions would diffuse more slowly by protoword of mouth – and hand. That is why I think that the "cumulative bricolage" that led to the earliest "full" languages may have taken 100,000 years. Kotchoubey (p.c.) responds that the social mechanisms present from the very beginning, for example, socialization in tribes and education in families, are known to be very conservative and to brake progress rather to promote it. He thus argues that development of the first language rested on biological natural selection.

Kotchoubey notes that degrees of linguistic and genetic similarity between populations correlate, and that the transition from protolanguage to language may have covered 1,500 to 2,000 generations, and so he cannot understand why biological mechanisms should be denied during the evolution of the very first language. Yes, Cavalli-Sforza et al. (1996) attest that the length of isolation of a group yields correlated amounts of drift in both genetic structure and language structure, but there is no suggestion that the genetic changes are linked to the language changes. The counter to my hypothesis, then, would be to offer concrete proposals on how to shift the boundary from my set of criteria for protolanguage further into the language domain of syntax and compositional semantics. But how far? My firm conviction is that the genome does not specify a principles-and-parameters universal grammar, but I could accept that phonological expression of hierarchical structure might require a biological change not within my current criteria for language readiness. (Recall **Fitch** on Baldwinian exaptation, R6.1.)

Kemmerer supports the view that grammatical categories gradually emerged over hundreds of generations of historical language transmission and change. Linguists identify grammatical categories primarily by formal criteria, but the criteria used in some languages are either completely absent in others or are employed in ways that seem bizarre compared to English. For example, verbs are often marked for tense, aspect, mood, and transitivity, but some languages, such as Vietnamese, lack all such inflection; Makah, on the other hand, applies aspect and mood markers not only to words that are translated into English as verbs, but also to words that are translated into English as nouns or adjectives. Croft (e.g., 2001) addresses such quandaries by "construction grammar," seeking to identify the grammatical categories of individual languages according to the constructions unique to those languages. Of course, one may relate these to semantic and pragmatic prototypes: prototypical nouns specify objects and have referential functions, prototypical verbs specify actions and have predicative functions, and so on. Such considerations are very much consistent with the notion that languages (not Language-with-a-capital-L) evolved culturally through bricolage within many communities and diffusion across communities (Aikhenvald & Dixon 2002; Dixon 1997; Lass 1997; Ritt 2004).

R7. Towards a mirror-system based neurolinguistic model

Only one commentary touched on Figure 6 of the TA, but I gather here a number of comments relevant to the program it exemplified.

R7.1. Anatomically distinct regions may share an evolutionary history

Figure 6 of the TA offered a highly conceptual extension of the FARS model to include the mirror system for grasping and the language system evolved "atop" this. I see the various circuits as evolutionary cousins but do not require that the same circuitry subserves them. Given this, I am grateful for the review by **Barrett, Foundas & Heilman** (**Barrett et al.**) of functional and structural evidence supporting differential localization of the neuronal modules controlling limb praxis, speech and language, and emotional communication, but I am puzzled as to why they view these data as justifying rejection of an evolutionary relationship between the underlying mechanisms. Barrett et al. assert that the TA treats different forelimb gesture classes interchangeably, whereas, for example, it cites data from Corina et al. (1992a) which separate pantomime from signing.

There is no space here for a disquisition on mammalian brain evolution. Let me simply refer to Kaas (1993), Butler and Hodos (1996), Krubitzer (1998), and Striedter (2004) for support of the conclusion that increasing complexity of behavior is paralleled by increases in the overall size and number of functional subdivisions of neocortex and the complexity of internal organization of the subdivisions, and that reduplication of circuitry may form the basis for differential evolution of copies of a given system, with differing connectivities, and so on, to serve a variety of functions.

Barrett et al. usefully summarize data showing that in most humans, the left hemisphere may be dominant in the control of vocalization associated with propositional speech, but the right hemisphere often controls vocalization associated with emotional prosody, automatic speech, and singing. Moreover, **Kotchoubey** notes that although the right temporal lobe is critical for recognition of prosody (R5.3), prosodic aspects of language are also severely impaired in patients with lesions to orbitofrontal cortex (which has links to the mirror system, R3.2) and the corpus callosum. The latter, presumably, is related to integration between the two hemispheres.

Such data must be taken into account in building upon Figure 6 of the TA but do not contradict MSH at its current level of detail.

R7.2. Action planning complements mirror systems

I have already (in R2.1) applauded **Bridgeman**'s insistence that mirror systems must be supplemented by a planning capability to allow language to evolve. Interestingly, the design of Figure 6 of the TA was motivated in part by the work of Bridgeman. Recall the crucial role of inferotemporal cortex (IT) and prefrontal cortex (PFC) in modulating affordance selection in the FARS model. In the psychophysical experiments of Bridgeman et al. (1997; Bridgeman 1999), an observer sees a target in one of several possible positions, and a frame either centered before the observer or deviated

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left or right. Verbal judgments of the target position are altered by the background frame's position, but "jabbing" at the target never misses, regardless of the frame's position. The data demonstrate independent representations of visual space in the two systems, with the observer aware only of the spatial values in the cognitive (inferotemporal) system. The crucial point here is that communication must be based on the size estimate generated by IT, not that generated by posterior parietal cortex (PP). Thus, all three paths of Figure 6 of the TA are enriched by the prefrontal system, which combines current IT input with memory structures combining objects, actions, and relationships. (The figure just shows the path IT → DPLF as it may affect Wernicke's area.)

Bosman et al. disagree with the contrast (Arbib & Bota 2003) between the MSH theory presented in the TA as being "prospective" and the Aboitiz and García (1997) theory as being "retrospective." Our point was that Aboitiz and García focused on lexicon and syntax and looked at what might support them, without suggesting the intermediate stages that might have emerged through evolutionary pressures before language itself "appeared on the scene." As noted in the TA, these researchers emphasize working memory, whereas earlier work on MSH failed to do so. Hence the inclusion of working memories in Figure 6 of the TA. Further modeling must also take into account issues discussed in R4.1.

Figure 6 of the TA has auditory input only to area Tpt, whereas **Rauschecker** notes that auditory objects, including speech sounds, are identified in anterior superior temporal cortex (aST), which projects directly to inferior frontal regions and not along a posterior pathway, as classically assumed. He suggests that aST supports both the decoding of vocalizations in nonhuman primates and the decoding of human speech: "the conclusion is hard to escape that . . . nonhuman primate vocalizations are an evolutionary precursor to human speech sounds" (cf. discussion of **Seyfarth**, R5.3). However, brain imaging of users of sign language (Emmorey 2002) suggests that the brain regions constituting the perceptual and motor periphery differ between sign (parietal lobe in, manual-facial out) and speech (temporal lobe in; vocal-articulatory out), but that there are large overlap regions assumed to be responsible for syntactic and semantic processing at a level abstracted from the peripheral codes. This is the set of "new" regions which my theory begins to explain. Given this, I would not expect "protospeech" as it "spirally evolves" with "protosign" to invent a whole new periphery, but rather, to co-opt available resources. My impression would be that the auditory system of nonhuman primates is (almost) adequate for speech perception (note the restrictions reviewed by **Horwitz et al.**, R5.2) whereas (R5.4) the motor side needed immense changes to get separable control of vocal articulators to make the sounds of speech (as distinct from primate calls).

R8. Envoi

By way of conclusion, I simply invite the reader to return to section R1.1 of this response and assess my claim that, overall, the extended mirror system hypothesis is alive and well. I believe it has survived most of the criticism that would destroy its key claims, but that the commentaries provide many challenges for linking the evolving mirror system to other systems and for filling in many details that remain too sketchy or have not yet received due attention.

References

Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

Aboitiz, F. & García V. R. (1997) The evolutionary origin of the language areas in the human brain. A neuroanatomical perspective. *Brain Research Reviews* 25:381–96. [arMAA, CB]

Aboitiz, F., García, R., Brunetti, E. & Bosman, C. (in press) The origin of Broca's area and its connections from an ancestral working memory network. In: *Broca's area,* ed. K. Amunts & Y. Grodzinsky. Oxford University Press. [CB]

Acardi, A. C. (2003) Is gestural communication more sophisticated than vocal communication in wild chimpanzees? *Behavioral and Brain Sciences* 26:210–11. [CB]

Adolphs, R., Damasio, H. & Tranel, D. (2002) Neural systems for recognition of emotional prosody: A 3-D lesion study. *Emotion* 2:23–51. [BK]

Aikhenvald, A. Y. & Dixon, R. M. W. (2002) *Areal diffusion and genetic inheritance.* Oxford University Press. [rMAA]

Albert, M. L., Goodglass, H., Helm, N. A., Rubens, A. B. & Alexander, M. P. (1981) *Clinical aspects of dysphagia.* Springer-Verlag. [AMB]

Alissandrakis, A., Nehaniv, C. L. & Dautenhahn, K. (2002) Imitation with ALICE: Learning to imitate corresponding actions across dissimilar embodiments. *IEEE Transactions on Systems, Man, and Cybernetics, Part A* 32(4):482–96. [BI]

American Psychiatric Association (1994) *Diagnostic and statistical manual of mental disorders,* 4th edition. American Psychiatric Association. [HT]

Arbib, M. A. (1981) Perceptual structures and distributed motor control. In: *Handbook of physiology, section 2: The nervous system, vol. II: Motor control, part 1,* ed. V. B. Brooks, pp. 1449–80. American Physiological Society. [aMAA]

(2001a) Co-evolution of human consciousness and language. In: *Cajal and consciousness: Scientific approaches to consciousness on the centennial of Ramón y Cajal's textura*, ed. Pedro C. Marijuan. *Annals of the New York Academy of Sciences* 929:195–220. [arMAA]

(2001b) Computational models of monkey mechanisms for the control of grasping: Grounding the mirror system hypothesis for the evolution of the language-ready brain. In: *Simulating the evolution of language,* ed. A. Cangelosi & D. Parisi. Springer-Verlag. [aMAA]

(2002) The mirror system, imitation, and the evolution of language. In: *Imitation in animals and artifacts*, ed. C. Nehaniv & K. Dautenhahn, pp. 229–80. MIT Press. [aMAA]

(2003) Schema theory. In: *The handbook of brain theory and neural networks*, 2nd edition, ed. M. A. Arbib, pp. 993–98. A Bradford Book/MIT Press. [aMAA]

(2004) How far is language beyond our grasp? A response to Hurford. In: *Evolution of communication systems: A comparative approach*, ed. D. K. Oller & U. Griebel, pp. 315–21, MIT Press. [aMAA]

(2005) Interweaving protosign and protospeech: Further developments beyond the mirror. *Interaction Studies: Social Behaviour and Communication in Biological and Artificial Systems* 6:145–71. [arMAA, PFM]

(in press) A sentence is to speech as what is to action? [A Contribution to the Special Issue on Integrative Models of Brocas Area and the Ventral Premotor Cortex]. *Cortex: A Journal Devoted to the Study of the Nervous System and Behavior*. [rMAA]

Arbib, M. A. & Bota, M. (2003) Language evolution: Neural homologies and neuroinformatics. *Neural Networks* 16:1237–60. [arMAA, CB]

Arbib, M. A. & Hesse, M. B. (1986) *The construction of reality.* Cambridge University Press. [rMAA]

Arbib, M. A. & Rizzolatti, G. (1997) Neural expectations: A possible evolutionary path from manual skills to language. *Communication and Cognition* 29:393–423. [arMAA, PFM]

Arbib, M. A., Billard, A., Iacoboni, M. & Oztop, E. (2000) Synthetic brain imaging: Grasping, mirror neurons and imitation. *Neural Networks* 13:975–97. [rMAA]

Arbib, M. A., Bischoff, A., Fagg, A. H. & Grafton, S. T. (1994) Synthetic PET: Analyzing large-scale properties of neural networks. *Human Brain Mapping* 2:225–33. [rMAA]

Arbib, M. A., Caplan, D. & Marshall, J. C., eds. (1982) *Neural models of language processes.* Academic Press. [rMAA]

Arbib, M. A., Conklin, E. J. & Hill, J. C. (1987) *From schema theory to language.* Oxford University Press. [rMAA]

Arbib, M. A., Érdi, P. & Szentágothai, J. (1998) *Neural organization: Structure, function, and dynamics.* MIT Press. [rMAA]

https://doi.org/10.1017/S0140525X0547003X Published online by Cambridge University Press

Arbib, M. A., Fagg, A. H. & Grafton, S. T. (2003) Synthetic PET imaging for grasping: From primate neurophysiology to human behavior. In: *Exploratory analysis and data modeling in functional neuroimaging,* ed. F. T. Sommer & A. Wichert, pp. 232–50. MIT Press. [rMAA]

Arbib, M. A., Oztop, E. & Zukow-Goldring, P. (in press) Language and the mirrow system: A perception/action based approach to communicative development. *Cognitie Creier Comportament/Cognitive Brain Behavior* [aMAA]

Armstrong, D. F., Stokoe, W. C. & Wilcox, S. E. (1995) *Gesture and the nature of language*. Cambridge University Press. [aMAA, DM]

Atran, S. & Norenzayan, A. (2004) Religion's evolutionary landscape: Counterintuition, commitment, compassion, and communion. *Behavioral and Brain Sciences* 27(6):713–30. [HF]

Avikainen, S., Wohlschläger, A., Liuhanen, S., Hanninen R. & Hari, R. (2003) Impaired mirror-image imitation in Asperger and high-functioning autistic subjects. *Current Biology* 13:339–41. [HT]

Aziz-Zadeh, L., Iacoboni, M., Zaidel, E., Wilson, S. & Mazziotta, J. (2004) Left hemisphere motor facilitation in response to manual action sounds. *European Journal of Neuroscience* 19(9):2609–12. [JTK]

Aziz-Zadeh, L., Maeda, F., Zaidel, E., Mazziotta, J. & Iacoboni, M. (2002) Lateralization in motor facilitation during action observation: A TMS study. *Experimental Brain Research* 144(1):127–31. [JTK]

Baddeley, A. D. (1986) *Working memory.* Clarendon Press. [HF]

Ballard, D. H., Hayhoe, M. M., Pook, P. K. & Rao, R. P. N. (1997) Deictic codes for the embodiment of cognition. *Behavioral and Brain Sciences* 20:1311–28. [CY]

Barkow, J. H. (1989) *Darwin, sex and status: Biological approaches to mind and culture.* University of Toronto Press. [HF]

Baron-Cohen, S. (2002) I am loved, therefore I think. Book review of *The cradle of thought* by R. P. Hobson. *Nature* 416:791–92. [HT]

Barrett, A. M., Crucian, G. P., Raymer, A. M. & Heilman, K. M. (1999) Spared comprehension of emotional prosody in a patient with global aphasia. *Neuropsychiatry, Neuropsychology, and Behavioral Neurology* 12:117–20. [AMB]

Barrett, A. M., Dore, L. S., Hansell, K. A. & Heilman, K. M. (2002) Speaking while gesturing: The relationship between spontaneous speech and limb praxis. *Neurology* 58:499–500. [AMB]

Barrett, A. M., Schwartz, R. L., Raymer, A. L., Crucian, G. P., Rothi, L. J. G. & Heilman, K. M. (1998) Dyssynchronous apraxia: Failure to combine simultaneous preprogrammed movements. *Cognitive Neuropsychology* 15:685–703. [AMB]

Bass, A. H. & Baker, R. (1997) Phenotypic specification of hindbrain rhombomeres and the origins of rhythmic circuits in vertebrates. *Brain Behavior and Evolution* 50(Suppl.1):3–16. [EG]

Bass, A. H. & McKibben, J. R. (2003) Neural mechanisms and behaviors for acoustic communication in teleost fish. *Progress in Neurobiology* 69:1–26. [EG]

Bauer, G. & Johnson, C. M. (1994) Trained motor imitation by bottlenose dolphins (*Tursiops truncatus*). *Perceptual and Motor Skills* 79:1307–15. [BI]

Bergen, B. K. (2001) Nativization processes in L1 Esperanto. *Journal of Child Language* 28:575–95. [AW]

Bergman, T., Beehner, J., Cheney, D. L. & Seyfarth, R. M. (2003) Hierarchical classification by rank and kinship in baboons. *Science* 302:1234–36. [RMS]

Bickerton, D. (1990) *Language and species.* University of Chicago Press. [DB]

(1995) *Language and human behavior.* University of Washington Press. [aMAA, HF, WTF]

(1996) *Language and human behaviour, second edition.* University College London Press. [AW]

(2003) Symbol and structure: A comprehensive framework for language evolution. In: *Language evolution,* ed. M. H. Christiansen & S. Kirby, pp. 77–93. Oxford University Press. [DB, WTF]

Billard, A. (2000) Learning motor skills by imitation: A biologically inspired robotic model. *Cybernetics & Systems* 32:155–93. [EB]

Binder, J. R., Liebenthal, E., Possing, E. T., Medler, D. A. & Ward, B. D. (2004) Neural correlates of sensory and decision processes in auditory object identification. *Nature Neuroscience* 7:295–301. [JPR]

Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J. & Freund, H.-J. (1999) A parieto-premotor network for object manipulation: Evidence from neuroimaging. *Experimental Brain Research* 128:210–13. [aMAA]

Bischoff-Grethe, A., Crowley, M. G. & Arbib, M. A. (2003) Movement inhibition and next sensory state prediction in basal ganglia. In: *The basal ganglia, vol. VI*, ed. A. M. Graybiel, M. R. Delong, & S. T. Kitai, pp. 267–77. Kluwer/Plenum. [aMAA]

Blumenthal, A., ed. and trans. (1970) *Language and psychology: Historical aspects of psycholinguistics.* John Wiley. [DM]

Boesch, C. & Boesch, H. (1983) Optimization of nut-cracking with natural hammers by wild chimpanzees. *Behavior* 83:265–86. [arMAA]

Bookheimer, S. (2002) Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience* 25:151–88. [JPR]

Borenstein, E. & Ruppin, E. (2004) Evolving imitating agents and the emergence of a neural mirror system. In: *Artificial Life IX: Proceedings of the Ninth International Conference on the Simulation and Synthesis of Living Systems,* ed. J. Pollack, M. Bedau, P. Husbands, T. Ikegami & R. A. Watson. MIT Press. [EB]

(2005) The evolution of imitation and mirror neurons in adaptive agents. *Cognitive Systems Research (Special issue on Epigenetic Robotics)* 6(3):229–42. [EB]

Borghi, A. M., Di Ferdinando, A. & Parisi, D. (2002) The role of perception and action in object categorization. In: *Connectionist models of cognition and perception,* ed. J. A. Bullinaria & W. Lowe, pp. 40–50. World Scientific. [DP]

(submitted) Objects, spatial compatibility and affordances: A connectionist study. [DP]

Borghi, A. M., Glenberg, A. M. & Kaschak, M. P. (2004) Putting words in perspective. *Memory and Cognition* 32:863–73. [rMAA, DP]

Borghi, A. M., Parisi, D. & Di Ferdinando, A. (2005) Action and hierarchical level of categories: A connectionist perspective. *Cognitive Systems Research* 6:99–110. [DP]

Bosman, C., García, R. & Aboitiz, F. (2004) FOXP2 and the language working memory system. *Trends in Cognitive Sciences* 8:251–52. [CB]

Bostanov, V. & Kotchoubey, B. (2004) Recognition of affective prosody: Continuous wavelet measures of event-related brain potentials to emotional exclamations. *Psychophysiology* 41:259–68. [BK]

Boyer, P. (1994) *The naturalness of religious ideas: A cognitive theory of religion.* University of California Press. [HF]

Brauth, S. E., Liang, W. & Roberts, T. F. (2001) Projections of the oval nucleus of the hyperstriatum ventrale in the budgerigar: Relationships with the auditory system. *Journal of Comparative Neurology* 432:481–511. [IMP]

Breazeal, C., Buchsbaum, D., Gray, J., Gatenby, D. & Blumberg, B. (2005) Learning from and about others: Towards using imitation to bootstrap the social understanding of others by robots. *Artificial life* 11(1–2):31–62. [BI]

Bridgeman, B. (1992) On the evolution of consciousness and language. *Psycoloquy* 3(15) Consciousness (1). Refereed electronic journal, available at: http://www.cogsci.ecs.soton.ac.uk/cgi/psyc/newpsy?3.15. [BB]

(1999) Separate representations of visual space for perception and visually guided behavior. In: *Cognitive contributions to the perception of spatial and temporal events,* ed. G. Aschersleben, T. Bachmann & J. Müsseler, pp. 3–13. Elsevier Science. [rMAA]

(2003) *Psychology and evolution: The origins of mind.* Sage. [BB]

Bridgeman, B., Peery, S. & Anand, S. (1997) Interaction of cognitive and sensorimotor maps of visual space. *Perception & Psychophysics* 59:456–69. [rMAA]

Briscoe, T., ed. (2002) *Linguistic evolution through language acquisition: Formal and computational models.* Cambridge University Press. [rMAA]

Brown, R., Hobson, R. P., Lee, A. & Stevenson, J. (1997) Are there "autistic-like" features in congenitally blind children? *Journal of Child Psychology and Psychiatry* 38:693–703. [HT]

Burgess, N., Jeffery, K. F. & O'Keefe, J., eds. (1999) *The hippocampal and parietal foundations of spatial cognition.* Oxford University Press. [aMAA]

Butler, A. B. & Hodos, W. (1996) *Comparative vertebrate neuroanatomy: Evolution and adaptation.* Wiley. [rMAA]

Bybee, J. (2001) *Phonology and language use.* Cambridge University Press. [rMAA]

Byrne, R. W. (2003) Imitation as behaviour parsing. *Philosophical Transactions of the Royal Society of London. Series B* 358:529–36. [aMAA]

Byrne, R. W. & Russon, A. E. (1998) Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences* 21(5):667–84. [JHGW]

Byrne, R. W. & Whiten A. (1988) *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans.* Oxford University Press. [JHGW]

Caldwell, C.A. & Whiten, A. (2002) Evolutionary perspectives on imitation: Is a comparative psychology of social learning possible? *Animal Cognition* 5(4):193–208. [BI]

Cangelosi, A. & Parisi, D., eds. (2002) *Simulating the evolution of language.* Springer. [rMAA, DP]

Carey, D. P., Perrett, D. I. & Oram, M. W. (1997) Recognizing, understanding, and producing action. In: *Handbook of neuropsychology: Action and cognition, vol. 11,* ed. M. Jeannerod & J. Grafman, pp. 111–130. Elsevier. [aMAA]

Carr, L., Iacoboni, M., Dubeau, M.-C., Mazziotta, J. C. & Lenzi, G. L. (2003) Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences USA* 100(9):5497–502. [rMAA]

Carruthers, P. & Boucher, J. (1998) Introduction: Opening up options. In: *Language and thought: Interdisciplinary themes,* ed. P. Carruthers & J. Boucher, pp. 1–18. Cambridge University Press. [HF]

Casey, S. K. (2003) "Agreement" in gestures and signed languages: The use of

https://doi.org/10.1017/S0140525X0547003X Published online by Cambridge University Press

directionality to indicate referents involved in actions. Ph.D. Dissertation in Linguistics, University of California at San Diego. [aMAA]
Cavada, C. & Goldman-Rakic, P. S. (1989) Posterior parietal cortex in rhesus monkey: II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. *Journal of Comparative Neurology* 287:422–45. [aMAA]
Cavalli-Sforza, L. (1996) *Geni, popoli e lingue.* Adelphi. (German edition: *Gene, Völker und Sprachen*, trans. G. Memmert. Carl Hanser Verlag). [BK]
Cavalli-Sforza, L. & Feldman, M. (1981) *Cultural transmission and evolution.* Princeton University Press. [BK]
Cavalli-Sforza, L., Menozzi, P. & Piazza, A. (1996) *The history and geography of human genes.* (Abridged paperback edition). Princeton University Press. [rMAA]
Chao, L. L. & Martin, A. (2000) Representation of manipulable man-made objects in the dorsal stream. *Neuroimage* 12:478–84. [rMAA]
Cheney, D. L. & Seyfarth, R. M. (1982) How vervet monkeys perceive their grunts: Field playback experiments. *Animal Behaviour* 30:739–51. [RMS]
(1988) Assessment of meaning and the detection of unreliable signals in vervet monkeys. *Animal Behaviour* 36:477–86. [RMS]
(1990) *How monkeys see the world: Inside the mind of another species.* University of Chicago Press. [RMS]
(1998) Why monkeys don't have language. *The Tanner Lectures on Human Values* 19:175–219. [RMS]
(in press) Constraints and preadaptations in the earliest stages of language evolution. *Linguistic Review*. [rMAA, RMS]
Choe, Y. & Bhamidipati, S. K. (2004) Autonomous acquisition of the meaning of sensory states through sensory-invariance driven action. In: *Biologically inspired approaches to advanced information technology,* ed. A. J. Ijspeert & M. Murata. Springer. [rMAA]
Chomsky, C. (1969) *The acquisition of syntax in children from 5 to 10.* MIT Press. [aMAA]
Chomsky, N. (1965) *Aspects of the theory of syntax.* MIT Press. [AW]
Clark, A. (1999) An embodied cognitive science? *Trends in Cognitive Sciences* 3:345–51. [rMAA]
Clayton, N. S., Bussey, T. J. & Dickinson, A. (2003) Can animals recall the past and plan for the future? *Nature Reviews Neuroscience* 4:685–91. [IMP]
Clegg, M. & Aiello, L. C. (2000) Paying the price of speech? An analysis of mortality statistics for choking on food. *American Journal of Physical Anthropology* (Supplement) 30:126. [rMAA]
Cole, J., Gallagher, S. & McNeill, D. (2002) Gesture following deafferentation: A phenomenologically informed experimental study. *Phenomenology and the Cognitive Sciences* 1:49–67. [DM]
Corballis, M. C. (2002). *From hand to mouth: The origins of language.* Princeton University Press. [rMAA, KE, DM]
(2003a) From mouth to hand: Gesture, speech, and the evolution of right-handedness. *Behavioral and Brain Sciences* 26(2):199–260. [rMAA, CB, PFM]
(2003b) Laterality and human speciation. In: *Speciation of modern* Homo sapiens, ed. T. J. Crow. *Proceedings of the British Academy* 106:137–52. [aMAA]
(2004) FOXP2 and the mirror system. *Trends in Cognitive Sciences* 8:95–96. [rMAA, HT]
Corina, D. P., Poizner, H., Bellugi, U., Feinberg, T., Dowd, D. & O'Grady-Batch, L. (1992a) Dissociation between linguistic and nonlinguistic gestural systems: A case for compositionality. *Brain and Language* 43(3):414–47. [arMAA]
Corina, D. P., Vaid, J. & Bellugi, U. (1992b) The linguistic basis of left hemisphere specialization. *Science* 255:1258–60. [aMAA]
Corina, D. P., Jose-Robertson, L. S., Guillemin, A. High, J. & Braun, A. R. (2003) Language lateralization in a bimanual language. *Journal of Cognitive Neuroscience* 15(5):718–30. [aMAA]
Coulmas, F. (2003) *Writing systems: An introduction to their linguistic analysis.* Cambridge University Press. [aMAA]
Croft, W. (2001) *Radical construction grammar: Syntactic theory in typological perspective.* Oxford University Press. [rMAA]
Crow, T. J. (2002a) Sexual selection, timing and an X-Y homologous gene: Did *Homo sapiens* speciate on the Y chromosome? In: *The speciation of modern Homo sapiens*, ed. T. J. Crow, pp. 197–216. Oxford University Press. [aMAA]
(2002b) *The speciation of modern Homo sapiens.* Oxford University Press. [HF]
Culham, J. C., Danckert, S. L., DeSouza, J. F. X., Gati, J. S., Menon, R. S. & Goodale, M. A. (2003) Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research* 153:180–89. [aMAA]
Damasio, A. (1999) *The feeling of what happens: Body and emotion in the making of consciousness.* Harcourt Brace. [HF]
D'Andrade, R. D. (1987) A folk model of the mind. In: *Cultural models in language and thought,* ed. D. Holland & N. Quinn, pp. 112–48. Cambridge University Press. [HF]
Darwin, C. (1871) *The descent of man and selection in relation to sex.* John Murray. [WTF]
(1872/1965) *The expression of the emotions in man and animals*. University of Chicago Press. [aMAA]
Dave, A. S. & Margoliash, D. (2000) Song replay during sleep and computational rules for sensorimotor vocal learning. *Science* 290:812–16. [IMP]
Dawkins, R. (1996) *Climbing Mount Improbable.* Norton. [CB]
Deacon, T. W. (1989) The neural circuitry underlying primate calls and human language. *Human Evolution* 4:367–401. [EG]
(1997) *The symbolic species: The co-evolution of language and the brain.* W. W. Norton. [aMAA, DB, HF]
Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F. & Fazio, F. (1997) Brain activity during observation of actions: Influence of action content and subject's strategy. *Brain* 120:1763–77. [aMAA]
Demiris, Y. & Hayes, G. (2002) Imitation as a dual-route process featuring predictive and learning components: A biologically plausible computational model. In: *Imitation in animals and artifacts,* ed. K. Dautenhahn & C. Nehaniv. MIT Press. [EB]
Demiris, Y. & Johnson, M. (2003) Distributed, predictive perception of actions: A biologically inspired robotics architecture for imitation and learning. *Connection Science Journal* 15(4):231–43. [EB]
Di Ferdinando, A. & Parisi, D. (2004) Internal representations of sensory input reflect the motor output with which organisms respond to the input. In: *Seeing and thinking,* ed. A. Carsetti, pp. 115–41. Kluwer. [DP]
Dixon, R. M. W. (1997) *The rise and fall of languages*. Cambridge University Press. [arMAA]
Dominey, P. F., Arbib, M. A. & Joseph, J.-P. (1995) A model of corticostriatal plasticity for learning associations and sequences, *Journal of Cognitive Neuroscience* 7:311–36. [aMAA]
Dominey, P. F., Hoen, M., Lelekov, T. & Blanc, J. M. (2003) Neurological basis of language and sequential cognition: Evidence from simulation, aphasia and ERP studies. *Brain and Language* 86:207–25. [rMAA]
Donald, M. (1993) *Origins of the modern mind.* Harvard University Press. [WTF]
(1998) Mimesis and the executive suite: Missing links in language evolution. In: *Approaches to the evolution of language: Social and cognitive bases*, ed. J. R. Hurford, M. Studdert-Kennedy & C. Knight, pp. 44–67. Cambridge University Press. [aMAA]
Doupe, A. & Kuhl, P. (1999) Birdsong and human speech: Common themes and mechanisms. *Annual Review of Neuroscience* 22:567–631. [arMAA]
Ehrsson, H. H., Fagergren, A., Johansson, R. S. & Forssberg, H. (2003) Evidence for the involvement of the posterior parietal cortex in coordination of fingertip forces for grasp stability in manipulation. *Journal of Neurophysiology* 90:2978–86. [aMAA]
Ehrsson, H. H., Spence, C. & Passingham, R. E. (2004) That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science* 305:875–77. [BI]
Ellis, R. & Tucker, M. (2000) Micro-affordance: The potentiation of components of action by seen objects. *British Journal of Psychology* 91:451–71. [DP]
Emmorey, K. (2002) *Language, cognition, and the brain: Insights from sign language research.* Erlbaum. [arMAA, KE]
Evans, N. (2003) Culture, context and structuration in Australian languages. *Annual Review of Anthropology* 32:13–40. [aMAA]
Fabrega, H. (1997) *Evolution of sickness and healing.* University of California Press. [HF]
(2002) *Origins of psychopathology: Phylogenetic and cultural basis of mental illness.* Rutgers University Press. [HF]
(2004) Consciousness and emotions are minimized. *Behavioral and Brain Sciences* 27(6):736–37. [commentary on Atran, S. & Norenzayan, A. (2004) Religion's evolutionary landscape: Counterintuition, commitment, compassion, communion. *Behavioral and Brain Sciences* 27(6):713–30. [HF]
Fadiga, L., Craighero, L., Buccino, G. & Rizzolatti, G. (2002) Speech listening specifically modulates the excitability of tongue muscles: A TMS study. *European Journal of Neuroscience* 15:399–402. [aMAA]
Fagg, A. H. & Arbib, M. A. (1992) A model of primate visual-motor conditional learning. *Adaptive Behavior* 1:1–37. [rMAA]
(1998) Modeling parietal-premotor interactions in primate control of grasping. *Neural Networks* 11:1277–303. [aMAA]
Fairman, T. (2000) English pauper letters 1800–34, and the English language. In: *Letter writing as a social practice,* ed. D. Barton & N. Hall, pp. 63–82. John Benjamins. [AW]
Falk, D. (2004a) Prelinguistic evolution in early hominins: Whence motherese. *Behavioral and Brain Sciences* 27(4):491–503. [rMAA, EG, PFM]
(2004b) The roles of infant crying and motherese during prelinguistic evolution in early hominins. *American Journal of Physical Anthropology* (Suppl.) 38:93. [EG]
Ferguson, C. A. (1964) Baby talk in six languages. *American Anthropologist* 66:103–14. [PFM]
Ferrari, P. F., Gallese, V., Rizzolatti, G. & Fogassi, L. (2003) Mirror neurons

https://doi.org/10.1017/S0140525X0547003X Published online by Cambridge University Press

responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience* 17(8):1703–14. [arMAA]
Fichtel, C. & Hammerschmidt, K. (2002) Responses of red-fronted lemurs to experimentally-modified alarm calls: Evidence for urgency-based changes in call structure. *Ethology* 108:763–77. [RMS]
Fischer, J. (1998) Barbary macaques categorize shrill barks into two calls types. *Animal Behaviour* 55:799–807. [RMS]
Fischer, J. & Hammerschmidt, K. (2001) Functional referents and acoustic similarity revisited: The case of Barbary macaque alarm calls. *Animal Cognition* 4:29–35. [RMS]
Fischer, J., Hammerschmidt, K., Seyfarth, R. M. & Cheney, D. L. (2001a) Acoustic features of female chacma baboon barks. *Ethology* 107:33–54. [RMS]
Fischer, J., Metz, M., Cheney, D. L. & Seyfarth, R. M. (2001b) Baboon responses to graded bark variants. *Animal Behaviour* 61:925–31. [RMS]
Floel, A., Ellger, T., Breitenstein, C. & Knecht, S. (2003) Language perception activates the hand motor cortex: Implications for motor theories of speech perception. *European Journal of Neuroscience* 18(3):704–708. [arMAA]
Floreano, D. & Urzelai, J. (2000) Evolutionary robots with on-line self-organization and behavioral fitness. *Neural Networks* 13:431–43. [EB]
Fodor, J. A. (1995) *The language of thought.* Crowell. [rMAA]
Fogassi, L. & Ferrari, P. F. (in press) Mirror neurons, gestures and language evolution. *Interaction Studies: Social Behaviour and Communication in Biological and Artificial Systems*. [arMAA]
Fogassi, L., Gallese, V., Fadiga, L. & Rizzolatti, G. (1998) Neurons responding to the sight of goal directed hand/arm actions in the parietal area PF (7b) of the macaque monkey. *Social Neuroscience Abstracts* 24:257. [aMAA]
Foley, R. A. (2001) Evolutionary perspectives on the origins of human social institutions. In: *The origin of human social institutions,* ed. W. G. Runciman, pp. 177–96. Oxford University Press. [HF]
Foundas, A. L., Eure, K. F., Luevano, L. F. & Weinberger, D. R. (1998) MRI asymmetries of Broca's area: The pars triangularis and pars opercularis. *Brain and Language* 64(3):282–96. [AMB]
Friederici, A. D., Kotz, S. A., Steinhauer, K. & von Cramon, D. Y. (2003) The neural basis of the prosody-syntax interplay: The role of the corpus callosum. *Brain and Language* 87:133–34. [BK]
Fritz, J. B., Becker, D., Mishkin, M. & Saunders, R. C. (1999) A comparison of the effects of medial temporal and rhinal cortical lesions on auditory recognition memory in the rhesus monkey. *Society for Neuroscience Abstracts* 25:789. [BH]
Fuster, J. M. (2002) Physiology of executive functions: The perception-action cycle. In: *Principles of frontal lobe function,* ed. D. T. Stuss & R. T. Knight, pp. 96–108. Oxford University Press. [HF]
Galaburda, A. M. & Sanides, F. (1980) Cytoarchitectonic organization of the human auditory cortex. *Journal of Comparative Neurology* 190:597–610. [aMAA, JPR]
Gallese, V. (2003) The roots of empathy: The shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology* 36:171–80. [rMAA]
Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. (1996) Action recognition in the premotor cortex. *Brain* 119:593–609. [aMAA]
Gallese, V. & Goldman, A. (1998) Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences* 2:493–501. [JHGW]
Gamble, C. (1994) *Timewalkers: The prehistory of global colonization.* Harvard University Press. [aMAA]
Geertz, C. (1973) The growth of culture and the evolution of mind. In: *The interpretation of cultures,* ed. C. Geertz, pp. 55–83. Basic Books. [HF]
Gelfand, J. R. & Bookheimer, S. Y. (2003) Dissociating neural mechanisms of temporal sequencing and processing phonemes. *Neuron* 38(5):831–42. [aMAA]
Gemba, H., Miki, N. & Sasaki, K. (1997) Cortical field potentials preceding vocalization in monkeys. *Acta Otolaryngologica Supplemental* 532:96–98. [CB]
Gentilucci, M. (2003a) Grasp observation influences speech production. *European Journal of Neuroscience* 17(1):179–84. [arMAA]
(2003b) Object motor representation and language. *Experimental Brain Research* 153:260–65. [rMAA, DP]
Gerlach, C., Law, I. & Paulson, O. B. (2002) When action turns into words. Activation of motor-based knowledge during categorization of manipulable objects. *Journal of Cognitive Neuroscience* 14(8):1230–39. [aMAA]
Ghazanfar, A. & Hauser, M. D. (2001) The auditory behavior of primates: A neuroethological perspective. *Current Opinions in Neurobiology* 11:712–20. [RMS]
Ghazanfar, A. A., ed. (2003) *Primate audition: Ethology and neurobiology.* CRC Press. [aMAA]
Gibson, J. J. (1979) *The ecological approach to visual perception*. Houghton Mifflin. [aMAA]
Givon, T. (2004) Teaching grammar to apes. Final Project Report, NIH Grant No. 2P01 HD06016–29 SUB: 0015. [DB]
Glover, S. & Dixon, P. (2002) Semantics affect the planning but not control of grasping. *Experimental Brain Research* 146(3):383–87. [aMAA]
Glover, S., Rosenbaum, D. A., Graham, J. & Dixon, P. (2004) Grasping the meaning of words. *Experimental Brain Research* 154(1):103–108. [aMAA]
Goodale, M. A., Milner, A. D., Jakobson, L. S. & Carey, D. P. (1991) A neurological dissociation between perceiving objects and grasping them. *Nature* 349:154–56. [aMAA]
Goodson, J. L. & Bass, A. H. (2002) Vocal-acoustic circuitry and descending vocal pathways in teleost fish: Convergence with terrestrial vertebrates reveals conserved traits. *Journal of Comparative Neurology* 448:298–322. [EG]
Grace, G. (2002) Collateral damage from linguistics? 3: The role of culture-centrism. *Ethnolinguistic Notes* 4(23). Available at: http://www2.hawaii.edu/~grace/elniv23.html. (Online Journal). [AW]
Grafton, S. T., Arbib, M. A., Fadiga, L. & Rizzolatti, G. (1996) Localization of grasp representations in humans by PET: 2. Observation compared with imagination. *Experimental Brain Research* 112:103–11. [aMAA]
Greenfield, P. M. (1991) Language, tools and brain: The ontogeny and phylogeny of hierarchically organized behavior. *Behavioral and Brain Sciences* 14:531–95. [HF, IMP]
Grezes, J. & Decety, J. (2001) Functional anatomy of execution, mental simulation, observation and verb generation of actions: A meta-analysis. *Human Brain Mapping* 12:1–19. [aMAA]
(2002) Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia* 40:212–22. [aMAA]
Grezes, J., Armony, J. L., Rowe, J. & Passingham, R. E. (2003) Activations related to "mirror" and "canonical" neurones in the human brain: An fMRI study. *Neuroimage* 18(4):928–37. [aMAA]
Grezes, J., Costes, N. & Decety, J. (1998) Top-down effect of strategy on the perception of human biological motion: A PET investigation. *Cognitive Neuropsychology* 15:553–82. [aMAA]
Guenther, F. H. (1995) Speech sound acquisition, coarticulation and rate effects in a neural network model of speech production. *Psychological Review* 102:594–621. [BH]
Guenther, F. H. & Ghosh, S. S. (2003) A model of cortical and cerebellar function in speech. *Proceedings of the XVth International Congress of Phonetic Sciences,* ed. M. J. Sole, D. Recasens & J. Romero. pp. 169–73. Universitat Autonoma de Barcelona. [BH]
Guillaume, P. (1927/1973) First stages of sentence formation in children's speech. In: *Studies in child language development,* ed. C. A. Ferguson & D. I. Slobin, pp. 522–41. Holt, Rinehart & Winston. [AW]
Hallowell, A. I. (1960) Self, society, and culture in phylogenetic perspective. In: *The evolution of man: Mind, culture, and society, vol. 2, Evolution after Darwin,* ed. S. Tax, pp. 309–71. University of Chicago Press. [HF]
Hamzei, F., Rijntjes, M., Dettmers, C., Glauche, V., Weiller, C. & Buchel, C. (2003) The human action recognition system and its relationship to Broca's area: An fMRI study. *Neuroimage* 19(3):637–44. [aMAA]
Hanakawa, T., Honda, M., Sawamoto, N., Okada, T., Yonekura, Y., Fukuyama, H. & Shibasaki, H. (2002) The role of rostral Brodmann area 6 in mental-operation tasks: An integrative neuroimaging approach. *Cerebral Cortex* 12(11):1157–70. [aMAA]
Harris, R. (2002) Why words really do not stay still. *Times Literary Supplement* 26 July, 5182:30. [DM]
Hast, M. H., Fischer, J. M., Wetzel, A. B. & Thompson, V. E. (1974) Cortical motor representation of the laryngeal muscles in *Macaca mulatto. Brain Research* 73:229–40. [CB]
Hauser, M. D. (1996) *The evolution of communication.* MIT Press/Bradford Books. [aMAA, RMS]
(1998) Functional referents and acoustic similarity: Field playback experiments with rhesus monkeys. *Animal Behaviour* 55:1647–58. [RMS]
Hauser, M. D. & Anderson, K. (1994) Left hemisphere dominance for processing vocalizations in adult, but not infant, rhesus monkeys: Field experiments. *Proceedings of the National Academy of Sciences USA* 91:3946–48. [RMS]
Hauser, M. D., Chomsky, N. & Fitch, W. T. (2002) The faculty of language: What is it, who has it, and how did it evolve? *Science* 298:1569–79. [aMAA]
Heffner, H. E. & Heffner, R. S. (1984) Temporal lobe lesions and perception of species-specific vocalizations by macaques. *Science* 226:75–76. [RMS]
Heilman, K. M., Blonder, L. X., Bowers, D. & Crucian, G. P. (2000) Neurological disorders and emotional dysfunction. In: *The neuropsychology of emotion. Series in affective science,* ed. J. C. Borod. Oxford University Press. [AMB]
Heilman, K. M., Coyle, J. M., Gonyea, E. F. & Geschwind, N. (1973) Apraxia and agraphia in a left-hander. *Brain* 96:21–28. [AMB]
Heilman K. M. & Rothi L. J. G. (2003) Apraxia. In: *Clinical Neuropsychology,* 4th edition, ed. K. M. Heilman & E. Valenstein. Oxford University Press. [AMB]
Heine, B. (1997) *Cognitive foundations of grammar.* Oxford University Press. [aMAA]
Heiser, M., Iacoboni, M., Maeda, F., Marcus, J. & Mazziotta, J. C. (2003) The essential role of Broca's area in imitation. *European Journal of Neuroscience* 17:1981–86. [aMAA]

https://doi.org/10.1017/S0140525X0547003X Published online by Cambridge University Press

Herbert, M. R., Harris, G. J., Adrien, K. T., Ziegler, D. A., Makris, N., Kennedy, D. N., Lange, N. T., Chabris, C. F., Bakardjiev, A., Hodgson, J., Takeoka, M., Tager-Flusberg, H. & Caviness, V. S. (2002) Abnormal asymmetry in language association cortex in autism. *Annals of Neurology* 52:588–96. [HT]

Hewes, G. W. (1973) Primate communication and the gestural origin of language. *Current Anthropology* 14:5–24. [aMAA, PFM]

(1996) A history of the study of language origins and the gestural primacy hypothesis. In: *Handbook of human symbolic evolution,* ed. A. Lock & C. R. Peters. Oxford University Press. [PFM]

Hickok, G., Bellugi, U. & Klima, E. S. (1998) What's right about the neural organization of sign language? A perspective on recent neuroimaging results. *Trends in Cognitive Sciences* 12:465–68. [aMAA]

Hill, E. L. (2001) Non-specific nature of specific language impairment: A review of the literature with regard to concomitant motor impairments. *International Journal of Language and Communication Disorders* 36:149–71. [HT]

Hill, J. C. (1983) A computational model of language acquisition in the two-year-old. *Cognition and Brain Theory* 6:287–317. [rMAA]

Hobson, R. P. & Bishop, M. (2003) The pathogenesis of autism: Insights from congenital blindness. *Philosophical Transactions of the Royal Society of London B* 358:335–44. [HT]

Hockett, C. F. (1959) Animal "languages" and human language. *Human Biology* 31:32–39. [IMP]

(1978) In search of Jove's brow. *American Speech* 53:243–313. [rMAA, PFM]

Hofstadter, D. (1995) *Fluid concepts and creative analogies: Computer models of the fundamental mechanisms of thought.* Basic Books. [BI]

Holland, J. H. (1992) Genetic algorithms. *Scientific American* 267:66–72. [DP]

Holstein, B. I. (1970) *Use of metaphor to induce innovative thinking in fourth grade children.* Ph.D. thesis, School of Education, Boston University, Boston, MA. [BI]

Hornak, J., Bramham, J., Rolls, E. T., Morris, R. G., O'Doherty, J., Bullock, P. R. & Polkey, C. E. (2003) Changes in emotion after circumscribed surgical lesions of the orbitofrontal and cingulate cortices. *Brain* 126:1691–712. [BK]

Horwitz, B. (2005) Integrating neuroscientific data across spatiotemporal scales. *Comptes rendus Biologies* 328:109–18. [BH]

Horwitz, B., Amunts, K., Bhattacharyya, R., Patkin, D., Jeffries, K., Zilles, K. & Braun, A. R. (2003) Activation of Broca's area during the production of spoken and signed language: A combined cytoarchitectonic mapping and PET analysis. *Neuropsychologia* 41(14):1868–76. [aMAA]

Horwitz, B. & Tagamets, M.-A. (2003) Synthetic functional brain imaging. In: *The handbook of brain theory and neural networks,* 2nd edition, ed. M. A. Arbib. MIT Press. [rMAA]

Hunt, G. R. & Gray, R. D. (2002) Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society London. Series B* 270:867–74. [aMAA]

Hurford, J. R. (2003) The neural basis of predicate-argument structure. *Behavioral and Brain Sciences* 26(3):261–83. [rMAA]

(2004) Language beyond our grasp: What mirror neurons can, and cannot, do for language evolution. In: *Evolution of communication systems: A comparative approach,* ed. K. Oller, U. Griebel & K. Plunkett, pp. 297–313. MIT Press. [arMAA]

Husain, F. T., Tagamets, M.-A., Fromm, S. J., Braun, A. R. & Horwitz, B. (2004) Relating neuronal dynamics for auditory object processing to neuroimaging activity. *NeuroImage* 21:1701–20. [BH]

Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M. C., Mazziotta, J. C. & Rizzolatti, G. (2001) Reafferent copies of imitated actions in the right superior temporal cortex. *Proceedings of the National Academy of Science USA* 98:13995–99. [aMAA]

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C. & Rizzolatti, G. (1999) Cortical mechanisms of human imitation. *Science* 286(5449):2526–28. [aMAA, JHGW]

Indurkhya, B. (1992) *Metaphor and cognition.* Kluwer Academic Publishers. [BI]

(1994) The thesis "all knowledge is metaphorical" and meanings of "metaphor." *Metaphor and Symbolic Activity* 9(1):61–73. [BI]

(1998) On creation of features and change of representation. *Journal of Japanese Cognitive Science Society* 5(2):43–56. [BI]

Ingold, T. (1996) Language is the essence of culture. In: *Key debates in anthropology,* ed. T. Ingold, pp. 147–98. Routledge. [HF]

Ito, M. (2005) Bases and implications of learning in the cerebellum – adaptive control and internal model mechanism. *Progress in Brain Research* 148:95–109. [rMAA]

Izumi, A. & Kojima, S. (2004) Matching vocalizations to vocalizing faces in a chimpanzee (*Pan troglodytes*). *Animal Cognition* 7:179–84. [CB]

Jackendoff, R. (1983) *Semantics and cognition.* MIT Press. [HF]

(1999) Possible stages in the evolution of the language capacity. *Trends in Cognitive Sciences* 3(7):272–79. [WTF]

(2002) *Foundations of language: Brain, meaning, grammar, evolution.* Oxford University Press. [aMAA, PFM]

Jackson, J. H. (1878–79) On affections of speech from the disease of the brain. *Brain* 1:304–30; 2:203–22, 323–56. [rMAA]

Janis, I. L. (1982) *Groupthink: Psychological studies of policy decisions and fiascoes,* 2nd edition. Houghton Mifflin. [BK]

Janzen, T. & Shaffer, B. (2002) Gesture as the substrate in the process of ASL grammaticalization. In: *Modality and structure in signed and spoken languages,* ed. R. P. Meier, K. Cormier & D. Quinto-Pozos, pp. 199–223. Cambridge University Press. [KE]

Jarvis, E. D. & Mello, C. V. (2000) Molecular mapping of brain areas involved in parrot vocal communication. *Journal of Comparative Neurology* 419:1–31. [IMP]

Jeannerod, M., Decety, J. & Michel, F. (1994) Impairment of grasping movements. *Neuropsychologia* 32(4):369–80. [aMAA]

Jordan, M. I. & Rumelhart, D. E. (1992) Forward models: Supervised learning with a distal teacher. *Cognitive Science* 16:307–54. [rMAA]

Jürgens, U. (1997) Primate communication: Signaling, vocalization. In: *Encyclopedia of neuroscience,* 2nd edition. Elsevier. [aMAA]

(1998) Neuronal control of mammalian vocalization, with special reference to the squirrel monkey. *Naturwissenschaften* 85(8):376–88. [rMAA, WTF, EG]

(2002) Neural pathways underlying vocal control. *Neuroscience and Biobehavioral Reviews* 26:235–58. [EG]

(2003) From mouth to mouth and hand to hand: On language evolution. *Behavioral and Brain Sciences* 26(2):229–30. [CB]

Jürgens, U. & Alipour, M. (2002) A comparative study on the cortico-hypoglossal connections in primates, using biotine dextranamine. *Neuroscience Letters* 328:245–48. [CB]

Kaas, J. H. (1993) Evolution of multiple areas and modules within neocortex. *Perspectives on Developmental Neurobiology* 1:101–107. [rMAA]

Kanter, S. L., Day, A. L., Heilman, K. M. & Gonzalez Rothi, L. J. (1986) Pure word deafness: A possible explanation of transient deterioration following EC-IC bypass. *Neurosurgery* 18:186–89. [AMB]

Kaplan, J. T. & Iacoboni, M. (2005) Brain activations related to hearing and seeing an action. Presented at the Cognitive Neuroscience Society Annual Meeting, New York, April 2005. [JTK]

(in preparation) Multisensory coding of perceived actions in the motor system. [rMAA]

Kegl, J., Senghas, A. & Coppola, M. (1999) Creation through contact: Sign language emergence and sign language change in Nicaragua. In *Language creation and language change: Creolization, diachrony, and development,* ed. M. DeGraff, pp. 179–237. MIT Press. [KE]

Kemmerer, D., Chandrasekaran, B. & Tranel, D. (submitted) A case of impaired verbalization but preserved gesticulation of motion events: Investigating the language-specific representation of space from a neuropsychological perspective. [rMAA]

Kendon, A. (1988) *Sign languages of aboriginal Australia: Cultural, semiotic and communicative perspectives.* Cambridge University Press. [rMAA, DM]

Kertesz, A., Ferro, J. M. & Shewan, C. M. (1984) Apraxia and aphasia: The functional-anatomical basis for their dissociation. *Neurology* 34:40–47. [AMB]

Keysers, C., Kohler, E., Umilta, M. A., Nanetti, L., Fogassi, L. & Gallese, V. (2003) Audiovisual mirror neurons and action recognition. *Experimental Brain Research* 153(4):628–36. [JTK]

Kimura, D. (1993) *Neuromotor mechanisms in human communication* (Oxford Psychology Series No. 20). Oxford University Press/Clarendon Press. [aMAA]

Kirby, S. (2000) *Syntax without natural selection: How compositionality emerges from vocabulary in a population of learners.* In: *The evolutionary emergence of language*, ed. C. Knight, M. Studdert-Kennedy & J. R. Hurford. Cambridge University Press. [arMAA]

Kirzinger, A. & Jürgens, U. (1982) Cortical lesion effects and vocalization in the squirrel monkey. *Brain Research* 233:299–315. [CB]

Kita, S. & Özyürek, A. (2003). What does cross-linguistic variation in semantic coordination of speech and gesture reveal? Evidence for an interface representation of spatial thinking and speaking. *Journal of Memory and Language* 48(1):16–32. [rMAA]

Knight, C. (1991) *Blood relations: Menstruation and the origins of culture*. Yale University Press. [HF]

Kohler, E., Keysers, C., Umiltá, M. A., Fogassi, L., Gallese, V. & Rizzolatti, G. (2002) Hearing sounds, understanding actions: Action representation in mirror neurons. *Science* 297(5582):846–48. [arMAA, JTK, HT]

Kohler, W. (1917/1927) *The mentality of apes*, trans. E. Winter. Routledge & Kegan Paul. (Original work published 1917). [PNP]

Koski, L., Wohlschlager, A., Bekkering, H., Woods, R. P., Dubeau, M. C., Mazziotta, J. C. & Iacoboni, M. (2002) Modulation of motor and premotor activity during imitation of target-directed actions. *Cerebral Cortex* 12:847–55. [aMAA]

Kozima, H., Nakagawa, C. & Yano, H. (2003) Can a robot empathize with people? *Proceedings of the Eighth International Symposium on Artificial Life and Robotics (AROB 08)*, pp. 518–19. [BI]

https://doi.org/10.1017/S0140525X0547003X Published online by Cambridge University Press

Kripke, S. A. (1982) *Wittgenstein on rules and private language.* Harvard University Press. [rMAA]

Krubitzer, L. (1998) Constructing the neocortex: Influences on the pattern of organization in mammals. In: *Brain and mind: Evolutionary perspectives,* ed. M. S. Gazzaniga & J. S. Altman, pp. 19–34. Human Frontier Science Program. [rMAA]

Kubovy, M. & Van Valkenburg, D. (2001) Auditory and visual objects. *Cognition* 80:97–126. [BH]

Kuczaj, S. A., Gory, J. D. & Xitco, M. J. (1998) Using programs to solve problems: Imitation versus insight. *Behavioral and Brain Sciences* 21:695–96. [BI]

Kurthen, M. (1992) *Neurosemantik. Grundlagen einer praxiologischen kognitiven Neurowissenschaft.* Ferdinand Enke. [rMAA]

Lai, C. S., Fisher, S. E., Hurst, J. A., Vargha-Khadem, F. & Monaco, A. P. (2001) A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature* 413:519–23. [HT]

Langacker, R. (1987) *Foundations of cognitive grammar, vol. 1.* Stanford University Press. [aMAA]

(1991) *Foundations of cognitive grammar, vol. 2.* Stanford University Press. [aMAA]

Lass, R. (1997) *Historical linguistics and language change.* Cambridge University Press. [rMAA]

Leavens, D. A. (2003) Integration of visual and vocal communication: Evidence for Miocene origins. *Behavioral and Brain Sciences* 26:232–33. [CB]

Liberman, A. M., Cooper, F. S., Shankweiler, D. P. & Studdert-Kennedy, M. (1967) Perception of the speech code. *Psychological Review* 74(6):431–61. [JTK, JPR]

Lieberman, P. (2002) On the nature and evolution of the neural bases of human language. *Yearbook of Physical Anthropology* 45:36–62. [aMAA]

Liepmann, H. (1905) Die linke Hemisphäre und das Handeln. *Münchener Medizinische Wochenshrift* 49:2322–26, 2375–78. [AMB]

(1920) Apraxia. *Ergebnisse der Gesamten Medizin* 1:516–43. [AMB]

Linnankoski, I., Laakso, M.-L., Aulanko, R. & Leinonen, L. (1994) Recognition of emotions in macaque vocalizations by children and adults. *Language & Communication* 14:183–92. [BK]

Locke, J. L. (1993) *The child's path to spoken language.* Harvard University Press. [PFM]

Lord, C., Risi, S., Lambrecht, L., Cook, E. H., Jr., Leventhal, B. L., DiLavore, P. C., Pickles, A. & Rutter, M. (2000) The autism diagnostic observation schedule-generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders* 30:205–23. [JHGW]

MacNeilage, P. F. (1998) The frame/content theory of evolution of speech production. *Behavioral and Brain Sciences* 21:499–546. [aMAA, HF, PFM]

(2003) Mouth to hand and back again? Could language have made those journeys? *Behavioral and Brain Sciences* 26(2):233–34. [rMAA, PFM]

MacNeilage, P. F. & Davis, B. L. (1990) Acquisition of speech: Frames, then content. In: *Attention and Performance XIII*, ed. M Jeannerod. Erlbaum. [PFM]

(2000) Origin of the internal structure of word forms. *Science* 288:527–31. [PFM]

(2004) Baby talk and the origin of the word. Paper presented at the Fifth International Conference on the Evolution of Language, Leipzig, Germany, April 2004. [PFM]

(in press a) Baby talk and the emergence of first words. *Behavioral and Brain Sciences*. [PFM]

(in press b) The frame/content theory of evolution of speech: Comparison with a gestural origins theory. *Interaction Studies: Social Behavior and Communication in Biological and Artificial Systems.* [arMAA, PFM]

Macphail, E. M. (2000) The search for a mental Rubicon. In: *The evolution of cognition,* ed. C. Heyes & L. Huber, pp. 253–72. MIT Press. [rMAA, HF]

Makino, T. & Aihara, K. (2003) Self-observation principle for estimating the other's internal state: A new computational theory of communication. *Mathematical Engineering Technical Reports* METR 2003–36, Department of Mathematical Informatics, Graduate School of Information Science and Technology, University of Tokyo. [rMAA]

Manthey, S., Schubotz, R. I. & von Cramon, D. Y. (2003) Premotor cortex in observing erroneous action: An fMRI study. *Cognitive Brain Research* 15(3):296–307. [aMAA]

Marino, L. (2002) Convergence of complex cognitive abilities in cetaceans and primates. *Brain, Behavior and Evolution* 59:21–32. [EG]

Marom, Y., Maistros, G. & Hayes, G. (2002) Toward a mirror system for the development of socially-mediated skills. In: *Proceedings of the Second International Workshop on Epigenetic Robotics: Modeling Cognitive Development in Robotic Systems, Edinburgh, Scotland,* vol. 94, ed. C. Prince, Y. Demiris, Y. Marom, H. Kozima & C. Balkenius. Lund University Cognitive Studies. [EB]

Matelli, M., Camarda, R., Glickstein, M. & Rizzolatti, G. (1986) Afferent and efferent projections of the inferior area 6 in the macaque monkey. *Journal of Comparative Neurology* 251:281–98. [aMAA]

McNeill, D. (1992) *Hand and mind: What gestures reveal about thought.* University of Chicago Press. [DM]

(2000) Introduction. In: *Language and gesture,* ed. D. McNeill, pp. 1–10. Cambridge University Press. [DM]

Meltzoff, A. N. & Decety, J. (2003) What imitation tells us about social cognition: A rapprochement between developmental psychology and cognitive neuroscience. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 358(1431):491–500. [rMAA, JHGW]

Meltzoff, A. N. & Prinz, W. (2002) The imitative mind: Development, evolution and brain bases. In: *Cambridge studies in cognitive development,* ed. K. W. Fischer & G. Hatano. Cambridge University Press. [JHGW]

Miall, R. C. (2003) Connecting mirror neurons and forward models. *NeuroReport* 14:2135–37. [rMAA]

Miller, G. F. (2001) *The mating mind: How sexual choice shaped the evolution of human nature.* Anchor Books. [CY]

Minter, M. E., Hobson, R. P. & Bishop, M. (1998) Congenital visual impairment and "theory of mind." *British Journal of Developmental Psychology* 16:183–96. [HT]

Mitz, A. R., Godshalk, M. & Wise, S. P. (1991) Learning-dependent neuronal activity in the premotor cortex: Activity during the acquisition of conditional motor associations. *Journal of Neuroscience* 11(6):1855–72. [rMAA]

Moore, B. R. (1992) Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning. *Behaviour* 12:231–63. [WTF, BI]

Murdock, G. P. (1959) Cross-language parallels in parental kin terms. *Anthropological Linguistics* 1:1–5. [rMAA, PFM]

Myowa-Yamakoshi, M. & Matsuzawa, T. (1999) Factors influencing imitation of manipulatory actions in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 113:128–36. [aMAA]

Nagy, E. & Molnar, P. (2004) Homo imitans or homo provocans? The phenomenon of neonatal initiation. *Infant Behavior and Development* 27:57–63. [rMAA]

Newbury, D. F., Bonora, E., Lamb, J. A., Fisher, S. E., Lai, C. S., Baird, G., Jannoun, L., Slonims, V., Stott, C. M., Merricks, M. J., Bolton, P. F., Bailey, A. J., Monaco, A. P., (International Molecular Genetic Study of Autism Consortium) (2002) FOXP2 is not a major susceptibility gene for autism or specific language impairment. *American Journal of Human Genetics* 70:1318–27. [HT]

Nishitani, N., Avikainen, S. & Hari, R. (2004) Abnormal imitation-related cortical activation sequences in Asperger's syndrome. *Annals of Neurology* 55:558–62. [HT]

Noble, W. & Davidson, I. (1996) *Human evolution, language, and mind: A psychological and archeological inquiry.* Cambridge University Press. [HF]

Nowak, M. A., Plotkin, J. B. & Jansen, V. A. A. (2000) The evolution of syntactic communication. *Nature* 404:495–98. [aMAA]

Ochipa, C., Rothi, L. J. G. & Heilman, K. M. (1994) Conduction apraxia. *Journal of Neurology, Neurosurgery and Psychiatry* 57:1241–44. [AMB]

Owren, M. J., Hopp, S. L. & Seyfarth, R. M. (1992) Categorical vocal signaling in nonhuman primates. In: *Nonverbal vocal communication: Comparative and developmental approaches,* ed. H. Papousek, U. Jürgens & M. Papousek. Cambridge University Press. [RMS]

Owren, M. J., Seyfarth, R. M. & Cheney, D. L. (1997) The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cynocephalus ursinus*). *Journal of the Acoustical Society of America* 101:2951–63. [RMS]

Oztop, E. & Arbib, M. A. (2002) Schema design and implementation of the grasp-related mirror neuron system. *Biological Cybernetics* 87:116–40. [aMAA, EB]

Oztop, E., Bradley, N. S. & Arbib, M. A. (2004) Infant grasp learning: A computational model. *Experimental Brain Research* 158:480–503. [aMAA]

Papagno, C., della Sala, S. & Basso, A. (1993) Ideomotor apraxia without aphasia and aphasia without apraxia: The anatomical support for a double dissociation. *Journal of Neurology, Neurosurgery and Psychiatry* 56:286–89. [AMB]

Passingham, R. (1993) *The frontal lobes and voluntary action.* Oxford University Press. [aMAA]

Patterson, D. K. & Pepperberg, I. M. (1994) A comparative study of human and parrot phonation: Acoustic and articulatory correlates of vowels. *Journal of the Acoustical Society of America* 96:634–48. [IMP]

(1998) Acoustic and articulatory correlates of stop consonants in a parrot and a human subject. *Journal of the Acoustical Society of America* 106:491–505. [IMP]

Paulesu, E., Goldacre, B., Scifo, P., Cappa, S. F., Gilardi, M. C., Castigllioni, I., Perani, D. & Fazio, F. (1997) Functional heterogeneity of left inferior frontal cortex as revealed by MRI. *Neuroreport* 8:2011–17. [AMB]

Payne, K. & Payne, R. (1985) Large scale changes over 19 years in songs of humpback whales in Bermuda. *Zeitschrift für Tierpsychologie* 68:89–114. [EG]

Peirce, A. (1985) A review of attempts to condition operantly alloprimate vocalizations. *Primates* 26:202–13. [RMS]

Pepperberg, I. M. (1992) Proficient performance of a conjunctive, recursive task

https://doi.org/10.1017/S0140525X0547003X Published online by Cambridge University Press

by an African Grey parrot (*Psittacus erithacus*). *Journal of Comparative Psychology* 106:295–305. [IMP]
(1999) *The Alex studies: Cognitive and communicative abilities of Grey parrots.* Harvard University Press. [IMP]
(2005a) Grey parrots do not always "parrot": Phonological awareness and creation of new labels from existing vocalizations. In: *Proceedings of the Third International Symposium on Imitation in Animals and Artifacts, 2005 Artificial Intelligence and the Simulation of Behavior Convention.* pp. 97–104. [IMP]
(2005b) Insights into imitation in Grey parrots (*Psittacus erithacus*). In: *Perspectives on imitation: From neuroscience to social science,* ed. S. L. Hurley & N. Chader, pp. 243–62. MIT Press. [IMP]
Pepperberg, I. M., Brese, K. J. & Harris, B. J. (1991) Solitary sound play during acquisition of English vocalizations by an African Grey Parrot (*Psittacus erithacus*): Possible parallels with children's monologue speech. *Applied Psycholinguistics* 12:151–78. [IMP]
Pepperberg, I. M. & Brezinsky, M. V. (1991) Acquisition of a relative class concept by an African Grey Parrot (*Psittacus erithacus*): Discriminations based on relative size. *Journal of Comparative Psychology* 105:286–94. [IMP]
Pepperberg, I. M. & Gordon, J. D. (2005) Number comprehension by an African grey parrot (*Psittacus erithacus*), including a zero-like concept. *Journal of Comparative Psychology* 119:197–209. [IMP]
Pepperberg, I. M. & Shive, H. A. (2001) Simultaneous development of vocal and physical object combinations by a Grey Parrot (*Psittacus erithacus*): Bottle caps, lids, and labels. *Journal of Comparative Psychology* 115:376–84. [IMP]
Perrett, D. I., Mistlin, A. J., Harries, M. H. & Chitty, A. J. (1990) Understanding the visual appearance and consequence of hand actions. In: *Vision and action: The control of grasping,* ed. M. A. Goodale, pp. 163–342. Ablex. [aMAA]
Perrett, D., Rolls, E. T. & Cann, W. (1982) Visual neurons responsive to faces in the monkey temporal cortex. *Experimental Brain Research* 47:329–42. [DB]
Perrett, D., Smith, P. A. J., Mistlin, A. J., Chitty, A. J, Head, A. S., Potter, D. D, Broenniman, R., Milner, A. P. & Jeeves, M. A. (1985) Visual analysis of body movements by neurones in the temporal cortex of the macaque monkey. *Behavior and Brain Research* 16(2–3):153–70. [DB]
Peters, A. M. (1983) *Units of language acquisition.* Cambridge University Press. [rMAA, AW]
Petersen, M. R., Beecher, M. D., Zoloth, S. L., Moody, D. B. & Stebbins, W. C. (1978) Neural lateralization of species-specific vocalizations by Japanese macaques. *Science* 202:324–27. [RMS]
Petitto, L. A. & Marentette, P. F. (1991) Babbling in the manual mode: Evidence for the ontogeny of language. *Science* 251:1493–96. [BH]
Petrides, M. & Pandya, D. N. (1984) Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *Journal of Comparative Neurology* 228:105–16. [aMAA]
Pfeiffer, J. E. (1982) *The creative explosion. An inquiry into the origins of art and religion.* Cornell University Press. [HF]
Pinker, S. (1995) *The language instinct: How the mind creates language.* Harper Perennial. [CB]
Ploog, D. (1988) Neurobiology and pathology of subhuman vocal communication and human speech. In: *Primate vocal communication,* ed. D. Todt, P. Goedeking & D. Symmes. Springer Verlag. [EG]
Plumer, T. K. & Striedter, G. F. (1997) Auditory and vocalization related activity in the vocal control system of budgerigars. *Society for Neuroscience Abstracts* 100:10. [IMP]
(2000) Auditory responses in the vocal motor system of budgerigars. *Journal of Neurobiology* 42:79–94. [IMP]
Podell, K., Wisniewski, K. & Lovell, M. R. (2001) The assessment of echopraxia as a component of executive control deficit in traumatic brain injury. *Brain and Cognition* 47(1–2):349–53. [rMAA]
Poremba, A., Malloy, M., Saunders, R. C., Carson, R. E., Herscovitch, P. & Mishkin, M. (2004) Species-specific calls evoke asymmetric activity in the monkey's temporal poles. *Nature* 427:448–51. [RMS]
Prell, C. G., Hauser, M. D. & Moody, D. B. (2002) Discrete or graded variation within rhesus monkey screams? Psychophysical experiment on classification. *Animal Behaviour* 63:47–62. [RMS]
Provine, R. R. (1986) Yawning as a stereotyped action pattern and releasing stimulus. *Ethology* 72:109–22. [RRP]
(1989) Faces as releasers of contagious yawning: An approach to face detection using normal human subjects. *Bulletin of the Psychonomic Society* 27:211–14. [RRP]
(1993) Laughter punctuates speech: Linguistic, social and gender contexts of laughter. *Ethology* 95:291–98. [RRP]
(1996) Laughter. *American Scientist* 84:38–45. [RRP]
(2000) *Laughter: A scientific investigation*. Viking. [RRP]
Prudkov, P. N. (1999a) Human evolution expanded brains to increase motivational ability, not expertise capacity. *Psycoloquy* 10(012). Available at: http://www.cogsci.soton.ac.uk/cgi/psyc/newpsy?10.012. (Online Journal). [PNP]
(1999b) Origin of culture: Evolution applied another mechanism. *Psycoloquy* 10 (037). Available at: http://www.cogsci.soton.ac.uk/cgi/psyc/newpsy?10.037. (Online Journal.) [PNP]
(1999c) The role of motivation in the origin of language. *Psycoloquy* 10(069). Available at: http://www.cogsci.soton.ac.uk/cgi/psyc/newpsy?10.069. (Online Journal.) [PNP]
Prudkov, P. N. & Rodina, O. N. (1999) Synthesis of purposeful processes. *Psycoloquy* 10(070). Available at: http://www.cogsci.soton.ac.uk/cgi/psyc/newpsy?10.070. (Online Journal.) [PNP]
Pulvermüller, F. (2002) A brain perspective on language mechanisms: From discrete neuronal ensembles to serial order. *Progress in Neurobiology* 67(2):85–111. [rMAA]
Quine, W. V. (1960) *Word and object.* MIT Press. [CY]
Rauschecker, J. P. (1998) Cortical processing of complex sounds. *Current Opinion in Neurobiology* 8:516–21. [JPR]
Rauschecker, J. P. & Tian, B. (2000) Mechanisms and streams for processing of "what" and "where" in auditory cortex. *Proceedings of the National Academy of Sciences of the United States of America* 97:11800–806. [JPR]
Raymer, A. M. & Ochipa, C. (1997) Conceptual praxis. In: *Apraxia: The neuropsychology of action,* ed. L. J. G. Rothi & K. M. Heilman. Psychology Press. [AMB]
Reiss, D. & McCowan, B. (1993) Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence for vocal learning. *Journal of Comparative Psychology* 107:301–12. [WTF]
Rendall, D. (2003) Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. *Journal of the Acoustical Society of America* 113:3390–402. [RMS]
Rendall, D., Seyfarth, R. M., Cheney, D. L. & Owren, M. J. (1999) The meaning and function of grunt variants in baboons. *Animal Behaviour* 57:583–92. [RMS]
Ribeiro, S., Cecchi, G. A., Magnasco, M. O. & Mello, C. (1998) Toward a song code: Evidence for a syllabic representation in the canary brain. *Neuron* 21:359–71. [IMP]
Richards, D. G., Wolz, J. P. & Herman, L. M. (1984) Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus. Journal of Comparative Psychology* 98:10–28. [WTF]
Ritt, N. (2004) *Selfish sounds and linguistic evolution*. Cambridge University Press. [rMAA]
Rizzolatti, G. & Arbib, M. A. (1998) Language within our grasp. *Trends in Neurosciences*. 21(5):188–94. [aMAA, CB, JPR]
Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G. & Matelli, M. (1988) Functional organization of inferior area 6 in the macaque monkey II. Area F5 and the control of distal movements. *Experimental Brain Research* 71:491–507. [aMAA]
Rizzolatti, G. & Craighero, L. (2004) The mirror-neuron system. *Annual Review of Neuroscience* 27:169–92. [HT]
Rizzolatti, G., Fadiga L., Gallese, V. & Fogassi, L. (1996a) Premotor cortex and the recognition of motor actions. *Cognitive Brain Research* 3:131–41. [aMAA]
Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Perani, D. & Fazio, F. (1996b) Localization of grasp representations in humans by positron emission tomography: 1. Observation versus execution. *Experimental Brain Research* 111:246–52. [aMAA]
Rizzolatti, R., Fogassi, L. & Gallese, V. (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience* 2:661–70. [arMAA]
Rizzolatti G. & Luppino G. (2001) The cortical motor system. *Neuron* 31:889–901. [aMAA]
(2003) Grasping movements: Visuomotor transformations. In: *The handbook of brain theory and neural networks,* 2nd edition, ed. M. A. Arbib, pp. 501–504. MIT Press. [aMAA]
Rizzolatti, G., Luppino, G. & Matelli M. (1998) The organization of the cortical motor system: New concepts. *Electroencephalography and Clinical Neurophysiology* 106:283–96. [aMAA]
Rolls, E. T. & Arbib, M. A. (2003) Visual scene perception. In: *The handbook of brain theory and neural networks*, 2nd edition, ed. M. A. Arbib. MIT Press. [aMAA]
Romanski, L. M. & Goldman-Rakic, P. S. (2002) An auditory domain in primate prefrontal cortex. *Nature Neuroscience* 5:15–16. [CB, JPR]
Ross, E. D. (1981) The aprosodias. Functional-anatomic organization of the affective components of language in the right hemisphere. *Archives of Neurology* 38(9):561–69. [AMB, BK]
Rothi, L. J. G., Raade, A. S. & Heilman, K. M. (1994) Localization of lesions in limb and buccofacial apraxia. In: *Localization and neuroimaging in neuropsychology,* ed. A. Kertesz. Academic Press. [AMB]
Ruppin, E. (2002) Evolutionary autonomous agents: A neuroscience perspective. *Nature Reviews Neuroscience* 3(2):132–41. [EB]
Saunders, R. C., Fritz, J. B. & Mishkin, M. (1998) The effects of rhinal cortical

https://doi.org/10.1017/S0140525X0547003X Published online by Cambridge University Press

lesions on auditory short-term memory (STM) in the rhesus monkey. *Society for Neuroscience Abstracts* 24:1907. [BH]
Scherer, K. R. (1986) Vocal affect expression: A review and a model for future research. *Psychological Bulletin* 99:143–65. [BK]
Schubotz, R. I. & von Cramon, D. Y. (2003) Functional-anatomical concepts of human premotor cortex: Evidence from fMRI and PET studies. *NeuroImage* 20 (Suppl. 1):S120–31. [JTK]
Scott, S. K., Blank, C. C., Rosen, S. & Wise, R. J. (2000) Identification of a pathway for intelligible speech in the left temporal lobe. *Brain* 123 (Pt 12):2400–406. [JPR]
Seddoh, S. A. (2002) How discrete or independent are "affective prosody" and "linguistic prosody"? *Aphasiology* 16(7):683–92. [BK]
Seltzer, B. & Pandya, D. N. (1994) Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: A retrograde tracer study. *Journal of Comparative Neurology* 15:445–63. [aMAA]
Seyfarth, R. M. & Cheney, D. L. (2003a) Meaning and emotion in animal vocalizations. *Annals of the New York Academy of Sciences* 1000:32–55. [CB]
(2003b) Signalers and receivers in animal communication. *Annual Review of Psychology* 54:145–73. [RMS]
Seyfarth, R. M., Cheney, D. L. & Marler, P. (1980) Monkey responses to three different alarm calls: Evidence for predator classification and semantic communication. *Science* 210:801–803. [RMS]
Shallice, T. (1988) *From neuropsychology to mental structure.* Cambridge University Press. [HF]
Shaw, R. & Turvey, M. (1981) Coalitions as models of ecosystems: A realist perspective on perceptual organization. In: *Perceptual organization,* ed. M. Kubovy & J. R. Pomerantz, pp. 343–415. Erlbaum. [rMAA]
Simner, M. L. (1971) Newborn's response to the cry of another infant. *Developmental Psychology* 5:136–50. [RRP]
Skelly, M., Schinsky, L., Smith, R. W. & Fust, R. S. (1974) American Indian Sign (Amerind) as a facilitator of verbalization for the oral verbal apraxic. *Journal of Speech and Hearing Disorders* 39:445–56. [AMB]
Smith, E. E. & Jonides, J. (1998) Neuroimaging analyses of human working memory. *Proceedings of the National Academy of Sciences U.S.A.* 95:12061–68. [CB]
Snowdon, C. T. (1989) Vocal communication in New World monkeys. *Journal of Human Evolution* 18:611–33. [EG]
(1990) Language capacities of nonhuman animals. *Yearbook of Physical Anthropology* 33:215–43. [RMS]
Snowdon, C. T., French, J. A. & Cleveland, J. (1986) Ontogeny of primate vocalizations: Models from birdsong and human speech. In: *Current perspectives in primate social behavior,* ed. D. Taub & F. E. King. Van Nostrand Rheinhold. [RMS]
Speedie, L. J., Wertman, E., Tair, J. & Heilman, K. M. (1993) Disruption of automatic speech following a right basal ganglia lesion. *Neurology* 43:1768–74. [AMB]
Stoel-Gammon, C. & Otomo, K. (1986) Babbling development of hearing-impaired and normally hearing subjects. *Journal of Speech and Hearing Disorders* 51:33–41. [BH]
Stokoe, W. C. (2001) *Language in hand: Why sign came before speech.* Gallaudet University Press. [aMAA]
Striedter, G. (1994) The vocal control pathways in budgerigars differ from those in songbirds. *Journal of Comparative Neurology* 343:35–56. [IMP]
(2004) *Principles of brain evolution.* Sinauer Associates. [rMAA]
Studdert-Kennedy, M. (2002) Mirror neurons, vocal imitation and the evolution of particulate speech. In: *Mirror neurons and the evolution of brain and language,* ed. M. Stamenov & V. Gallese, pp. 207–27. John Benjamins. [rMAA]
Studdert-Kennedy, M. G. & Lane, H. (1980) Clues from the differences between signed and spoken languages. In: *Signed and spoken language: Biological constraints on linguistic form,* ed. U. Bellugi & M. Studdert-Kennedy. Verlag Chemie. [PFM]
Suddendorf, T. (1999) The rise of the metamind. In: *The descent of mind: Psychological perspectives on hominid evolution,* ed. M. C. Corballis & S. E. G. Lea, pp. 218–60. Oxford University Press. [HF]
Suddendorf, T. & Corballis, M. C. (1997) Mental time travel and the evolution of the human mind. *Genetic, Social, and General Psychology Monographs* 123(2):133–67. [HF, PNP]
Suddendorf, T. & Whiten, A. (2001) Mental evolution and development: Evidence for secondary representation in children, great apes, and other animals. *Psychological Bulletin* 127:629–50. [JHGW]
Supalla, T. (1986) The classifier system in American Sign Language. In: *Noun classes and categorization, vol. 7 of Typological studies in language,* ed. C. Craig. John Benjamins. [aMAA]
Supalla, T. & Newport, E. (1978) How many seats in a chair? The derivation of nouns and verbs in American sign language. In: *Understanding language through sign language research*, ed. P. Siple. Academic Press. [aMAA]
Sutton, D. & Jürgens, U. (1988) Neural control of vocalization. In: *Comparative primate biology, vol. 4, Neurosciences.* Alan R. Liss. [EG]
Tager-Flusberg, H. (1997) The role of theory of mind in language acquisition: Contributions from the study of autism. In: *Research on communication and language disorders: Contributions to theories of language development,* ed. L. Adamson & M. A. Romski. Paul Brookes. [HT]
Taira, M., Mine, S., Georgopoulos, A. P., Murata, A. & Sakata, H. (1990) Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Experimental Brain Research* 83:29–36. [aMAA]
Tallerman, M. (2004) Analyzing the analytic: Problems with holistic theories of protolanguage. Paper presented at the Fifth Biennial Conference on the Evolution of Language, Leipzig, Germany, April 2004. [rMAA, DB]
Talmy, L. (2000) *Towards a cognitive semantics,* 2 vols. MIT Press. [aMAA]
Théoret, H., Halligan, E., Kobayashi, M., Fregni, F., Tager-Flusberg, H. & Pascual-Leone, A. (2005) Impaired motor facilitation during action observation in individuals with autism spectrum disorder. *Current Biology* 15(3):R84–85. [HT]
Tian, B., Reser, D., Durham, A., Kustov, A. & Rauschecker, J. P. (2001) Functional specialization in rhesus monkey auditory cortex. *Science* 292:290–93. [JPR]
Tomasello, M. (1999a) *The cultural origins of human cognition.* Harvard University Press. [HF]
(1999b) The human adaptation for culture. *Annual Review of Anthropology* 28:509–29. [aMAA]
Tomasello, M. & Call, J. (1997) *Primate cognition.* Oxford University Press. [aMAA]
Tonkonogy, J. & Goodglass, H. (1981) Language function, foot of the third frontal gyrus, and rolandic operculum. *Archives of Neurology* 38:486–90. [AMB]
Tononi, G. & Edelman, G. M. (1998) Consciousness and complexity. *Science* 282:1846–51. [HF]
Trevarthen, C. (2001) The neurobiology of early communication: Intersubjective regulations in human brain development. In: *Handbook on brain and behavior in human development,* ed. A. F. Kalverboer & A. Gramsbergen, pp. 841–82. Kluwer. [rMAA]
Tsiotas, G., Borghi, A. & Parisi, D. (in press) Objects and affordances: An Artificial Life simulation. *Proceeding of the XVII Annual Meeting of the Cognitive Science Society.* [DP]
Tucker, D. M., Watson, R. T. & Heilman, K. M. (1977) Affective discrimination and evocation in patients with right parietal disease. *Neurology* 17:947–50. [AMB]
Tucker, M. & Ellis, R. (1998) On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology: Human Perception and Performance* 24(3):830–46. [DP]
(2004) Action priming by briefly presented objects. *Acta Psychologica* 116:185–203. [DP]
Ullman, M. (2004) Contributions of memory circuits to language: The declarative procedural model. *Cognition* 92:231–70. [rMAA]
Umiltá, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C. & Rizzolatti, G. (2001) I know what you are doing. A neurophysiological study. *Neuron* 31:155–65. [aMAA]
Ungerleider, L. G. & Mishkin, M. (1982) Two cortical visual systems. In: *Analysis of visual behaviour,* ed. D. J. Ingle, M. A. Goodale & R. J. W. Mansfield, pp. 549–86. MIT Press. [JPR]
Vaccari, O. & Vaccari, E. E. (1961) *Pictorial Chinese-Japanese characters*, 4th edition. Charles E. Tuttle. [aMAA]
Valenstein, E. & Heilman, K. M. (1979) Apraxic agraphia with neglect-induced paragraphia. *Archives of Neurology* 36:506–508. [AMB]
Ventner A., Lord, C. & Schopler, E. (1992) A follow-up study of high-functioning autistic children. *Journal of Child Psychology and Psychiatry* 33:489–507. [HT]
Visalberghi, E. & Fragaszy, D. (2002) "Do monkeys ape?" Ten years after. In: *Imitation in animals and artifacts*, ed. C. Nehaniv & K. Dautenhahn. MIT Press [aMAA]
Voelkl, B. & Huber, L. (2000) True imitation in marmosets? *Animal Behaviour* 60:195–20. [aMAA]
Wang, X., Merzenich, M. M., Beitel, R. & Schreiner, C. E. (1995) Representation of species-specific vocalization in the primary auditory cortex of the common marmoset: Temporal and spectral characteristics. *Journal of Neurophysiology* 74:2685–706. [RMS]
Watson, R. T., Fleet, W. S., Gonzalez-Rothi, L. & Heilman, K. M. (1986) Apraxia and the supplementary motor area. *Archives of Neurology* 43:787–92. [AMB]
Weydemeyer, W. (1930) An unusual case of mimicry by a catbird. *Condor* 32:124–25. [WTF]
Wheeler, M. A., Stuss, D. T. & Tulving, E. (1997) Toward a theory of episodic memory: The frontal lobes and autonoetic consciousness. *Psychological Bulletin* 121(3):331–54. [HF]
Whiten A. & Byrne, R. W. (1997) *Machiavellian intelligence II.: Evaluations and extensions.* Cambridge University Press. [JHGW]

https://doi.org/10.1017/S0140525X0547003X Published online by Cambridge University Press

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. (2001) Charting cultural variation in chimpanzees. *Behaviour* 138:1481–516. [arMAA]

Whiten, A., Horner, V., Litchfield, C. & Marshall-Pescini, S. (2004) How do apes ape? *Learning and Behaviour* 32:36–52. [JHGW]

Wierzbicka, A. (1992) *Semantics, culture, and cognition: Universal human concepts in culture-specific configurations.* Oxford University Press. [HF]

(1993) A conceptual basis for cultural psychology. *Ethos* 21(2):205–31. [HF]

Wildgruber, D., Ackermann, H., Klose, U., Kardatzki, B. & Grodd, W. (1996) Functional lateralization of speech production at primary motor cortex: A fMRI study. *NeuroReport* 7:2791–95. [AMB]

Wilkins, W. K. & Wakefield, J. (1995) Brain evolution and neurolinguistic preconditions. *Behavioral and Brain Sciences* 18:161–226. [HF]

Williams, H. (1989) Multiple representations and auditory-motor interactions in the avian song system. *Annals of the New York Academy of Sciences* 563:148–64. [IMP]

Williams, J. H. G., Whiten, A., Suddendorf, T. & Perrett, D. I. (2001) Imitation, mirror neurons and autism. *Neuroscience and Biobehavioral Reviews* 25:287–95. [HT, JHGW]

Wilson, S. M., Saygin, A. P., Sereno, M. I. & Iacoboni, M. (2004) Listening to speech activates motor areas involved in speech production. *Nature Neuroscience* 7(7):701–702. [CB, JTK]

Wittgenstein, L. (1958) *Philosophical investigations.* Blackwell. [rMAA]

Wolpert, D. M., Doya, K. & Kawato, M. (2003) A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 358:593–602. [rMAA]

Worden, R. (1998) The evolution of language from social intelligence. In: *Approaches to the evolution of language,* ed. J. R. Hurford, M. Studdert-Kennedy & C. Knight. Cambridge University Press. [RMS]

Wray, A. (1998) Protolanguage as a holistic system for social interaction. *Language & Communication* 18:47–67. [aMAA, DB, HF, AW]

(2000) Holistic utterances in protolanguage: The link from primates to humans. In: *The evolutionary emergence of language: Social function and the origins of linguistic form,* ed. C. Knight, M. Studdert-Kennedy & J. Hurford, pp. 285–302. Cambridge University Press. [aMAA, DB, HF, AW]

(2002a) *Formulaic language and the lexicon.* Cambridge University Press. [rMAA, WTF, AW]

(2002b) Dual processing in protolanguage: Performance without competence. In: *The transition to language,* ed. A. Wray, pp. 113–37. Oxford University Press. [AW]

(2004) "Here's one I prepared earlier": Formulaic language learning on television. In: *The acquisition and use of formulaic sequences,* ed. N. Schmitt, pp. 249–68. John Benjamins. [AW]

Yu, C. & Ballard, D. H. (2004) A multimodal learning interface for grounding spoken language in sensory perceptions. *ACM Transactions on Applied Perception* 1:57–80. [CY]

Yu, C., Ballard, D. H. & Aslin, R. N. (2003) The role of embodied intention in early lexical acquisition. In: *Proceedings of the 25th Annual Conference of the Cognitive Science Society*, pp. 1293–98, ed. R. Alterman & D. Kirsh. Erlbaum. A long version is submitted to *Journal of Cognitive Science.* [CY]

Zatorre, R. J., Bouffard, M. & Belin, P. (2004) Sensitivity to auditory object features in human temporal neocortex. *Journal of Neuroscience* 24:3637–42. [JPR]

Zentall, T. & Akins, C. (2001) Imitation in animals: Evidence, function, and mechanisms. In: *Avian visual cognition,* ed. R. G. Cook. Available online at: http://www.pigeon.psy.tufts.edu/avc/zentall/. [BI]

Zeshan, U. (2003) Aspects of Turk Isaret Dili (Turkish Sign Language). *Sign Language & Linguistics* 6(1):43–75. [KE]

Zoloth, S. R., Petersen, M. R., Beecher, M. D., Green, S., Marler, P., Moody, D. B. & Stebbins, W. C. (1979) Species-specific perceptual processing of vocal sounds by monkeys. *Science* 204:870–72. [RMS]

Zuberbuhler, K. (2003) Referential signaling in nonhuman primates: Cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior* 33:265–307. [RMS]

Zuberbuhler, K., Cheney, D. L. & Seyfarth, R. M. (1999) Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology* 113:33–42. [RMS]

Zukow-Goldring, P. (1996) Sensitive caregivers foster the comprehension of speech: When gestures speak louder than words. *Early Development and Parenting* 5(4):195–211. [rMAA]

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