from the presentations that quantitative assessments of risk for single species are often prevented by a lack of data. And, as David Andow stressed, the utility of risk assessment decreases as the level of taxonomic resolution decreases. Indeed, participants frequently remarked on the lack of data on the tempo and mode of biological invasions across all taxa and ecosystems considered. Disturbingly, the consensus was that, as bad a picture as recent reviews paint, the true numbers of invasive species, rates of invasion and ecological impacts are almost certainly much greater. Barring significant increases in effort, for most ecosystems we have little ability to detect changes in invasion rates that might follow from prevention and control efforts.

Acknowledgements

We would like to thank Gregory M. Ruiz (SERC) and James T. Carlton (Williams College, Mystic Seaport Maritime Studies Program, Mystic, CT, USA) for organizing this meeting.

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In Humboldt's footsteps

There are a few important transitions in evolution that seem to have occurred several times, whereas others appear to be unique. The former includes the emergence of multicellularity (plants, animals and fungi) and eusocial animals (hymenopterans, termites and naked mole rats); the latter category includes the origin of the genetic code, the appearance of eukaryotic sex (meiosis and syngamy) and, significantly for our topic, human language[1]. 'Unique' in this context means something specific: that all known lineages possessing the trait in question can be traced back to a common ancestor. Of course, this allows for the possibility that the trait did appear in other lineages, but these have all died out. Uniqueness of a transition might be a result of genuine difficulty (the required variation, or series of variations, is very rare), might be attributable to preemption (the first lineage to have 'made it' competitively prohibits a second trial) or might be caused by lack of sufficient time. Because the human language capacity originated sometime in the past five million years, the last option is oddly enough a valid possibility for language. Recently, several linguists and biologists set out to take stock of the status of our knowledge (or ignorance, if you are a pessimist) of the origins of language*.

*Origins of Language, Berlin, Germany, 16–18 December 1999.

Syntax and semantics

An important obstacle to our understanding of this problem is the poor characterization of the trait whose origin we wish to explain. The evolution of the eye is a relatively easy problem, because we know of several 'independent' origins of it – evolution has discovered approximately 40 ways of making an eye[2]. By contrast, even the phenomenological characterization of language by linguistic theories is far from agreed upon by linguists. Some would still speak about a monolithic universal grammar and, therefore, argue for the impossibility of evolution by natural selection (the Chomskyan line, as spelt out by Martin Bierwisch from the Working Group for Structural Grammar of the Max Planck Society in Berlin, Germany), whereas others argue that grammar must be broken down into multiple generative components (such as phonology, syntax and semantics)[3], each of which could have evolved in a mosaic manner (Ray Jackendoff, Institute for Advanced Study, Berlin, Germany).

The latter approach allows one to suggest a stepwise scenario for the origin of language, from simple symbols to symbols for abstract semantic relations, a system of grammatical relations and a system of inflections[4]. Although such a bold attempt venturing into an evolutionary realm is welcome, problems nonetheless abound. It remains entirely phenomenological without hints for the underlying neural computations and the selective forces. Moreover, a rigorous transition analysis[5] should be applied to such cases, requiring the formulation of a set of alternative evolutionary hypotheses from among which one can then choose on the basis of various plausibility criteria. We are far from such a scenario for language.

Another point of view is that many aspects of grammar might, in fact, be constrained by a 'special kind' of semantics (Daniel Dor, Tel-Aviv University, Israel; and Eva Jablonka, The Con Institute for the History and Philosophy of Science and Ideas, Tel-Aviv, Israel). Given such a setting, many grammatical features could have gone to fixation through a process of genetic assimilation (Baldwin effect)[6]. In a sense, this concept is the antithesis to the Chomskyan theory that syntax is independent from semantics ('colourless green ideas sleep furiously'). Although I suspect that the truth lies between the two extremes, I also endorse a clear formulation contrary to the common view, because it can be taken as a manifesto for a research programme. However, one must add a word of caution: there is some danger of circularity in the recourse to a 'special kind of semantics' underlying syntax. The other snag might be with demanding too much from genetic assimilation; the latter requires a rather universal (across individuals) and constant (across many generations) manifestation of the trait to be assimilated[7].

Nature and nurture

It is still an open question how much of our linguistic capacity is truly innate. When we think of the neural basis for language we used to think of the neocortex (such as the classic Broca and Wernicke areas), but, in fact, more ancient brain areas, including the basal ganglia, might have partly been recruited for linguistic processing (Philip Lieberman, Brown University, Providence, Rhode Island, USA). And there is enormous epigenetic complexity in the brain; therefore, the amount of hard wiring that goes

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to our language faculty must be limited. The 'biologization' of the origin of language might be possible by the neural decomposition of this trait, requiring a wealth of data from comparative neuroanatomy and neurophysiology. One crucial factor seems to have been the liberation of the brain from visceral tasks, primarily through the dramatic increase in size of the prefrontal cortex (Terrence Deacon, Boston University, MA, USA).

The minimum necessary amount of linguistic input for normal language development is an empirical, but controversial, issue. The fact that such input is necessary at all is by no means argument against an innately predisposed, neurally manifest faculty. Proper eyesight in many animals does not develop without visual input, and a crucial period for normal acquisition is also a common element shared by language and vision[8]. One view, supported by evidence from pidgin and creole languages, holds that an initial lexicon and social interaction might suffice (Bernard Comrie, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany).

Whatever one thinks about the origin of the language faculty, one can independently enquire about the origins of languages. Biologists will find it, in strange contrast to many linguists, fascinating to learn about the 'macrotaxonomy' and 'macroevolution' of languages. Once one claims to have a clear view of the analogy to mutation in the linguistic realm, one can attempt, with the appropriate methodology, to construct large-scale phylogenies of languages. Old views are partially modified in the course of this research; for example, one finds that the previously erected category of Nostratic languages is probably paraphyletic and has to be replaced by the Euroasiatic group. Even if 80% of the current views are discarded later, it is an immensely interesting field[9]. Sadly, it will not shed much light on the origin of language as such – the latter is too far back in time.

Prospects

At the beginning of the new millennium, one is safe to bet that a vigorously growing field of research will be evolutionary neurolinguistics. Indeed, we badly need more relevant information from brain studies. It is remarkable that production of the past tense for regular and irregular English verbs seems to reside in different brain areas[10]. However, it is discouraging for a simple-minded modular concept of the mind that the genetic disorder called Williams syndrome seems more complex than previously thought: patients are good at numeracy but poor at language in infancy, while in adulthood it is the other way round[11]. It is only through a multidisciplinary approach that one can hope for a convincing reconstruction of how our species began to talk and why others did not, and why, perhaps, they might be unlikely to do so in the future.

Acknowledgements

I would like to thank Jürgen Trabant (Academy of Berlin–Brandenburg, Germany) for organizing this meeting.

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How learning mechanisms might affect evolutionary processes

That there are mechanisms that allow the inheritance of acquired characters is no longer a taboo in evolutionary biology. That such mechanisms might lead to evolutionary changes not envisaged in traditional neodarwinian thinking is gradually being realized[1]. Nevertheless, nothing is more convincing than a compelling example. New work by Payne *et al.*[2,3] on the mechanisms underlying the speciation in brood-parasitic indigobirds (*Vidua chalybeata*) provides such an example. It demonstrates how early learning can produce offspring that behave dramatically differently from their parents. The sudden, saltatorial changes can give rise to a new, reproductively isolated branch to the species from one generation to the next. This might drive subsequent speciation.

Radiation and speciation by colonization?

Avian brood parasites lay their eggs in the nests of other species (the host), thus exploiting the other species' parental care to their own reproductive benefit. Some parasitic species are generalists, such as the brown-headed cowbird (*Molothrus ater*), laying their eggs in the nests of several host species. Others are closely linked to one particular host. Most of the brood-parasitic viduid finches (indigobirds and whydahs – Estrildae) belong to the latter category. Viduid finches parasitize estrildid finch species. The young of various viduid finches show an astonishing similarity to young of the host species in mouth markings (which stimulate parental feeding behaviour) and plumage characteristics[4]. In addition, male parasites sing a species-specific song that resembles the song of the host. Female parasites are attracted to that particular songtype over others. The song of the host species stimulates ovarian development and attracts females to the nest of the host. The morphological similarities in the offspring of the two species and the host-oriented behaviour of the parasites suggest a long history of coevolution. Indeed, Nicolai[4] suggested that viduid finches cospeciated with their hosts. However, recent mtDNA studies make this unlikely. They showed not only that the most likely branching patterns of the parasite species do not match with those of their hosts, but also that speciation of the parasites occurred more recently[5]. These observations support the 'colonization' model, in which a parasitic lineage switches from one host species to a new one, leading to subsequent adaptation to the new host. But, although one can imagine that a female parasite might lay her egg in the nest of a species that previously was not a host, this still seems a long way off from founding a new branch of the parasite species tree. How is it possible that parasites that are adapted to their

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