The Neurobiology of Communication:

Comparative and Evolutionary Perspectives on Receptive Language

Workshop at the MRC Cognition and Brain Sciences Unit
15 Chaucer Road, Cambridge, CB2 2EF.

Wednesday 25th – Thursday 26th September 2002

Scientific Report

1. Neurophysiology and neuroanatomy of language perception - comparative studies

After welcoming remarks from **Dr Hui Wang** introducing the ESF and its research programs the opening session of the workshop started with four talks focussing on one of the core topics of the meeting: attempts to relate the function organisation of human vocal communication to the underlying neuroanatomy and neurophysiology, using evidence from single-cell recordings of responses to vocal sounds in old-world and new-world primates as well as anatomical and functional imaging data from humans.

The opening talk from **Troy Hackett** (Vanderbilt University) surveyed the relevant evidence regarding human and non-human primate auditory anatomy. Describing evidence for the multiple routes and multiple stages of auditory processing in the temporal lobe, Dr. Hackett persuasively argued that a well-developed understanding of the functional organisation of human language must ultimately be based on neuroanatomy and that clues from anatomical studies were already providing valuable constraints on the interpretation of research in a number of fields (functional imaging and neurophysiology) by suggesting a fundamental distinction between pathways involved in identifying or spatially localising auditory objects ("what" vs "where" pathways).

The theme of this opening talk was ably continued by **Xiaoqin Wang** (Johns Hopkins University School of Medicine) who has made substantial contributions to our understanding of the neural basis of vocal communication using single cell recording in awake marmosets (a highly vocal primate species, with a sizable repertoire of complex calls). Dr . Wang's analysis of the basic auditory features of marmoset calls spoke to acoustic-phonetic studies of human language, and showed that a number of basic features (perhaps as few as four or five) could adequately characterise this repertoire of calls. He also demonstrated that cells in marmoset auditory cortex showed tuning for both the identity of the call and the identity of the caller, illustrating the role that speaker identification can play in these highly social primates. This theme of vocal communication serving to identify speakers as well as messages is one that recurred in later talks.

The following talk from **Asif Ghazanfar** (Max-Planck Institute for Biological Cybernetics, Tubingen, Germany) also addressed the acoustic and neural bases of vocal communication in tamarinds and macaques. His talk was a valuable illustration of the role that comparative studies of old and new-world primates can play in showing the evolution of complex communication systems. In both species, Dr. Ghanzafar used a neuro-ethological approach, studying each species in a natural communication situation. By manipulating the acoustic structure of different types of call, it was possible to narrow down the set of auditory features that were used in identifying conspecific vocalisations. This work providing valuable clues for investigations of the tuning of cells that respond in a selective way to vocal signals, hypotheses that appeared to be confirmed in neurophysiological studies.

Following a short break, **Sophie Scott** (University College London) brought a close to this session by reporting a meta-analysis of a number of human functional imaging studies using Positron Emission Tomography (PET) and Functional Magnetic Resonance Imaging (fMRI). The results of an extensive series of studies in normal human adults confirmed many of the aspects of anatomical organisation that were identified in anatomical studies and in the aforementioned studies of non-human primates. For example, these studies provided convincing evidence of an anterior temporal processing stream dedicated to identifying and making sense of spoken language (corresponding to the "what" stream discussed by Hackett and others). Evidence for a posterior stream of processing was also presented. While the functional specialisation of this other stream remains a matter of debate it was clear that one candidate role was in mapping heard sounds on to the motor commands that could be used to generate these sounds.

The function and organisation of these multiple processing streams (hierarchical vs heterarchical) was discussed at length by commentators **Ingrid Johnsrude** (MRC-CBU, Cambridge) and **Josef Rauschecker** (George Washington University, Washington DC USA) and remained an important theme throughout the workshop.

2. The importance of gesture and imitation to language perception

Since communication relies not only the perception but also the production of vocal signals, an important theme of the workshop was a detailed consideration of the inter-dependence of these two processes, from both an evolutionary and a neurobiological perspective.

The importance of this relation was nicely summarised by **Tecumseh Fitch** (Harvard University) who illustrated this point using the slogan "Perception can't be understood without consideration of production". This began an extremely interesting and entertaining presentation that discussed the role of the descended larynx in the evolution of communication in humans and a wide range of mammalian and reptilian species (including such diverse creatures as deer and alligators). Having introduced the human vocal apparatus in exquisite detail, Dr. Fitch provided a comparative perspective by describing a number of species in which a descended larynx (either permanent as in humans or temporary as in deer) has evolved. He argued persuasively that this descended

larynx evolved out of selective pressure to provide a vocal cue (in the harmonic spacing of vocal formants) that exaggerates the size of the speaker. A perceptual system to assess the size of speakers from their productions can be observed in many species (including humans) and illustrates a functional pressure that may have played an important role in driving vocal evolution.

The second talk from **Richard Wise** (Imperial College, London) provided a detailed tour of the anatomy of breath control both in modern humans and in early hominids. He described the need for precise control of the muscles of the diaphragm in order to produce the controlled, long-lasting vocalisations that are a near-unique feature of human language. Through analysis of spinal cord volumes, Ann MacLaren has provided convincing evidence that control of the inter-costal muscles used in producing speech was a feature with our recent hominid ancestors such as Neanderthals. Dr. Wise also provided a brief illustration of the neural systems involved in this control process, illustrating the role of both neo-cortical (M1, SMA, posterior STG) and other systems (thalamus, cerebellum, insula) in co-ordinating vocal production.

The systems identified by Dr. Wise also appear to play a role in the perception of spoken language. The third talk in this session by **Kate Watkins** (McGill University) provided an extremely valuable introduction to the mirror-neuron system identified by Rizzolatti and Arbib in monkeys and proposed to be crucial for vocal imitation and hence the evolution of human language. Dr. Watkins's work provided some extremely valuable evidence not only for the existence of this mirror neuron system in humans but also for its role in vocal perception. A Transcortical Magnetic Stimulation (TMS) study showed that perceiving speech or watching moving lips increased the excitability of motor cortex, suggesting an obligatory link between the perception and production of speech gestures. Furthermore in an elegant study that combined PET and TMS, Dr. Watkins showed that the systems involved in mediating this link were to be found in left inferior frontal regions, consistent with the hypothesised location of mirror neurons in Broca's Area.

The final talk of this session provided a wide-ranging critique of the exact role this mirror neuron system may play in language processing and evolution. **James Hurford** (University of Edinburgh) argued that the communication of arbitrary signs (in the Saussurean sense) provided a much more convincing core faculty for language evolution and questioned whether imitation itself was sufficient. Dr Hurford demonstrated that a number of other species were capable of impressive feats of imitation (a point also made by Tecumseh Fitch), suggesting that other cognitive and neural faculties should be invoked to explain the uniqueness of human language.

The central theme of this session, (links between perception and production), appears consistent with the evidence for multiple processing pathways hypothesised in the opening session. The suggestion that two of these pathways could involve the identification vs the imitation of spoken language was picked up by **Matt Davis** and **Karalyn Patterson** (MRC-CBU, Cambridge) in discussion, with neuropsychological evidence appearing to be broadly consistent with this anterior temporal vs posterior temporal/frontal division.

3. Perceptual components of communication

The third session of the workshop returned to the perception of spoken language, exploring evidence from different neuroimaging techniques (fMRI, EEG and MEG) for the anatomical and temporal organisation of the perception of spoken language.

The first talk of this session from **Kimmo Alho** (University of Helsinki) was concerned with human perception of spoken language, in particular early mechanisms of attentional selection and perceptual categorisation. Using a combination of electrophysiology (ERP, MEG) and haemodynamic measures (PET/fMRI) of human neural activity, Dr. Alho presented further evidence for rapid, language-specific perceptual categorisation of spoken input in temporal lobe systems (using the 'mismatch negativity').

Following on from this talk on early stages of perceptual processing involved in low-level phonemic categorisation and attentional selection, the next talk from **Riitta Salmelin** (Helsinki University of Technology) used MEG to localise (both spatially and temporally) the later stages of processing by which spoken information is lexically identified and mapped onto meaningful interpretations. An important technique used in these studies is to contrast the neural response to an expected sentence completion "The gambler had a streak of bad *luck*" with a response to an unexpected though plausible completion "*skin*" or to completions that were semantically anomalous ("*butter"*) or phonologically unexpected ("*luggage*"). Although it is widely assumed that the processes of spoken language comprehension proceed hierarchically from sound-based to meaning-based processes. The results of these studies point to a single component of the evoked response (the magnetic counterpart to the N400 response) that was affected by both a phonlogical and semantic manipulation. This challenge to traditional processing models of speech comprehension was much debated.

The final talk of the session from **Keith Kluender** (University of Wisconsin, Madison) addressed the nature of the processing problem involved in perceptually categorising spoken input. Beginning with a description of the large number of possible phonemes that exist in the world's language, Dr. Kluender presented a compelling case for the phoneme as an important unit analysis in spoken language comprehension. Problems that had been associated with phoneme identification (essentially the high degree of variation in the input) could be addressed by consider the number of different acoustic features that can potentially convey any particular phonemic contrast. A modelling approach that uses covariation as a cue to the informativeness of input features was suggested.

Discussion of this session was provided by **Christophe Pallier** (INSERM, Orsay, France) and **Sarah Hawkins** (Department of Phonetics, Cambridge University) addressing, amongst other things, the validity of phonemes in linguistic description as well as the role of these units in speech perception. This discussion brought to an end the first day of the workshop.

4. Comparative, evolutionary and developmental perspectives on communication

The second day began with a wide-ranging session which addressed issues in human spoken language comprehension from diverse perspectives. Although there were few methodologies in common between talks, which covered behavioural investigation in a number of populations as well as a computational modelling, many common themes emerged from these presentations. These included the functional significance of perception-production links, the role of language-general and language-specific mechanisms in producing functional outcomes and the need to build explicit models in order to adequately specify and test formal theories.

The first talk of the session came from **Anne Cutler** (Max Planck Institute for Psycholinguistics, Nijmegen, Holland) who described a model of spoken word recognition, "Shortlist", which incorporated a mechanism, the "Possible Word Constraint" or PWC, to support the segmentation and identification of words in connected speech. A number of elegant, cross-linguistic investigations were dedicated to discovering whether the PWC was sensitive to the linguistic properties of words in various of the world's languages (including Sesotho, Portuguese and Japanese). The outcome of these studies suggested that despite language-specific constraints on the form of the minimal 'word' in these languages, the PWC nonetheless functioned in an identical fashion in each language. Suggesting that it provides a more-or-less universal mechanism for lexical segmentation of spoken input. Results of experiments in 12-month-old infants provide evidence for this mechanism functioning from an early stage of development.

The importance of developmental phenomena was advanced by the next speaker, **Marilyn Vihman** (University of Wales, Bangor) whose talk addressed the relationship between the production of specific phonemes during the babbling phase (between 6 and 12 months of age) and perceptual knowledge of those same phonemes in comprehension. Dr. Vihman argued for the role that production plays in tuning the perceptual system, and provided preliminary evidence for this relationship with a study showing a correlation between the phoemic inventory observed in babbling and infants listening preferences in perception. Interestingly, the form of this correlation was negative, such that infants preferred to listen to words containing sounds that they were unable to produce at that time, a novelty preference that might be consistent with models in which preferences are driven by the desire to learn as much from the input as possible.

The third talk in this session **Usha Goswami** (University College London) also addressed developmental issue, in particular the acquisition of written language in both normally developing and dyslexic individuals. Dr. Goswami described how learning to read an alphabetic script requires knowledge of the segmental content of spoken words, knowledge that develops at a progressively finer level of detail (from syllabic to subsyllabic to a phonemic level). Evidence was presented to suggest that dyslexia represents a specific failing of this phonological segmentation with consequences for the acquisition of literacy that depend on the nature of the relationship between the printed and spoken form of words. One novel piece of evidence presented was the demonstration that an auditory discrimination task, the p-centre task, was shown to predict the

segmentation and hence reading ability of dyslexic and normally developing readers. Possible mechanisms for the normal and disordered performance of this task was an important topic of debate following this talk.

The next three talks in this session covered computational models of the development and evolution of language in populations of artificial agents. These artificial simulations illustrate the link between those aspects of language that can be learned using simple, neurally inspired mechanisms and the role of cultural evolution in producing complex language. These artificial-life style simulations allow an escape from a long-held dogma concerning how neural mechanisms for processing complex language could evolve in the absence of the selective pressure provided by the need to communicate using a complex language. The first two talks illustrated the implications of these simulations for the emergence of complex phonological systems and syntactic classes respectively, and the third talk provided evidence of the relationship between the architecture and learning system proposed in these models and underlying neural mechanisms.

The talk from **Pierre-Yves Oudeyer** (Sony Computer Science Laboratory, Paris) presented the background and motivation for this modelling approach, as well as a demonstration that addressed an important issue concerning the emergence of phonological discreteness (i.e. phonemic units). Various hypotheses that have been proposed for the cause of this discreteness, including specific properties of the perceptual and motor systems were shown to be unnecessarily complex. A population of simple agents with artificial perceptual systems and vocal apparatus that participated in communication games/imitation converged on a system of shared, symbolic (i.e. phonemic) sounds. One elegant aspect of this work was the demonstration that the vowel inventories developed in different runs of the simulation showed approximately the same distribution as the vowel inventories in the world's languages providing an important validation of this technique.

The next modelling talk came from **Angelo Cangelosi** (University of Plymouth) who presented a number of simulations of physically and artificially embodied systems in which a 'mother' must communicate the status (edible/inedible, dangerous/safe) of objects in the world to a 'child'. These systems provide an example of a functional pressure that can give rise to genetic selection for communication abilities. One salient distinction in these simulations concerned the difference between objects in the world (represented by nouns in the emergent language) and verbs (represented by verbs in the emergent language). Each network in the population showed neural specialisation for these two classes of item, consistent with recent brain imaging data from humans. Though the analogy between these simple networks and complex brains may seem far-fetched it is at least suggestive.

The final talk of the session from **Gert Westermann** (Birkbeck College, University of London) returned more closely to the theme of exploring functional mechanisms underlying the acquisition of spoken language. The model that he presented simulated the development of perception-production links through a process of correlation learning between maps that represent either auditory input or motor output in a simulated vocal

tract. The model that he presented demonstrated a number of interesting phenomena that can emerge from this perception-production link: first, through babbling the network can learn to identify the sounds that it can produce from motor output. Second, through exposure to the sounds of a language in the environment, both the auditory and motor components of the network converge on the appropriate vowel inventory. Finally, a suggested extension to include visual input, provided a potential mechanism by which multi-modal, mirror neurons can emerge, providing a neural mechanism for the mirror system suggested by the results of **Watkins** and others on the first day.

The discussants for this session (**Jenni Rodd** and **James McQueen**) performed admirably in finding common threads in this group of diverse talks. The discussion focussed on the need to specify the computational mechanisms underlying the diverse phenomena presented in the session.

5. Perception of speech prosody

The final session of the meeting focussed on the perception of speech prosody, that is the rhythm and intonational contour that is an ever-present component of the speech signal. While some aspects of prosody support linguistic interpretation of the speech input (for instance, in guiding syntactic processing, or by supporting the segmentation of the speech stream into words), prosody also serves a number of extremely important communicative roles that are often excluded from traditional linguistic analysis, such as providing information on the emotional state of the speaker. The use of rhythm and intonation in musical expression provides the most powerful (and perhaps phylogenetically oldest) expression of this human capacity.

The first talk of this session came from **Carolyn Drake** (Université René Descartes, CNRS) who demonstrated a number of important characteristics of the perception and production of rhythm, for both musical and linguistic stimuli. The talk focussed on the use of tapping tasks as a means of eliciting the number of different levels of rhythmic analysis that are possible for a variety of stimuli. Results demonstrated a number of experientially determined properties of rhythmic analysis; familiarity with the rhythm of a language, or the structure of a culture's music allowed participants to analyse rhythmic signal at higher levels of structure (by tapping at longer intervals), illustrating the way in which rhythm constitutes an important form of knowledge of structured signals.

The second talk of the session from **Franck Ramus** (Lab. de Sciences Cognitives et Psycholinguistiques, CNRS) provided further support for the role that rhythmic plays in supporting the structural analysis of auditory input, by exploring the perception of linguistic rhythm in neonate humans and in non-human primates (cotton-top tamarinds). Using habituation paradigms, it was demonstrated that both populations had the capacity for discriminating the rhythm of different classes of spoken language (e.g. stress-timed languages like English compared to syllable-timed languages like French). The abilities of neonates provide support the role of rhythmic information in distinguishing (literally) the mother tongue from other language input. However, the striking capacity of non-

human primates provides evidence that this perceptual capacity need not reflect specialised, speech-specific mechanisms.

After these talks on the perception of speech rhythm, the session then moved on to an investigation of the neural basis of the perception of linguistic prosody. **Kai Alter** (Max-Planck-Institut für neuropsychologische Forschung, Leipzig) gave a talk in which he demonstrated the use of Event-Related Potentials (ERPs) in establishing neural responses that are linked to the placement of major prosodic boundaries in linguistic stimuli. Through a series of well controlled studies, Dr. Alter demonstrated an ERP component, termed the "syntactic positivity shift" that provides a neurophysiological marker of processes involved in using speech prosody to assist syntactic analysis of spoken sentences.

The final two talks of this session took the discussion of speech prosody out of the linguistic domain and focussed instead on the role that prosody plays in communicating emotional information. Vocal signals of emotion are frequently overlooked in research, with prosody research often focussing on the communication of linguistic information, and research on emotion recognition most commonly focussing on facial rather than vocal signals. Nonetheless, as the example materials presented by **Sonja Kotz** (Max-Planck-Institut für neuropsychologische Forschung) made clear, there are readily identifiable vocal signals of emotion that can be identified independently of linguistic content. In measuring the neural response to positive, negative and neutral emotionally marked stimuli using fMRI, Dr. Kotz tested a long-standing hypothesis from neuropsychological studies that the perception and production of emotional prosody depends primarily on right hemisphere systems. While this neuroimaging data supports the role of temporal lobe and subcortical structures in the recognition of emotional prosody, evidence consistent with right-hemisphere lateralisation was not obtained.

Further evidence in support of the role of sub-cortical structures in the perception of emotional prosody came from **Marc Pell** (McGill University) who presented a detailed neuropsychological study of emotion recognition in a group of patients suffering from Parkinson's Disease (a neurodegenerative disorder affecting dopaminergic systems in the basal ganglia). The data contained instances of impaired recognition of vocal signals related to a number of emotions.

Discussion of the talks from this last session was provided by **Brechtje Post** and **Andrew Lawrence** who addressed issues relating to linguistic and emotional prosody respectively. In their discussion of these themes, both discussants emphasised the role that fine-grained distinctions (either in terms of the structural units proposed by linguistic analysis, or in contrasting emotional states such as fear and disgust) might play in explaining the neural basis of prosodic processing. An important concern for future research will be to consider how this more detailed set of cognitive distinctions may be neurally realised.

As detailed above, this meeting provided an important forum for the reunion of workers approaching the same phenomenon (language) but who have very different backgrounds, philosophies, and working methods. It provided a forum in which researchers could meet, often for the first time, other scientists whose work was different enough that they would not go to the same scientific meetings or even read the same journals. It is earnestly hoped that the delegates will extend this initial encounter, by forming collaborative links with others at the meeting.

European Science Foundation - EMRC Exploratory Workshop

NEUROBIOLOGY OF COMMUNICATION:
comparative and evolutionary perspectives on receptive language

Cambridge, United Kingdom, 25-26 September 2002

FINAL PROGRAMME

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Background and Objectives:

This workshop is intended to bring together workers who share an interest in the biological bases of perception of communicative acts, but who use different methodologies and have different theoretical perspectives. Work relevant to this issue is being pursued in multiple independent but complementary domains, from ethology and computational modelling to neuroanatomy. Functional neuroimaging provides a fresh source of information that can be integrated into a comparative, evolutionary, biological framework.

A synthesis of research in several disparate fields (functional neuroimaging, computational modelling, developmental psychology, anatomy, and comparative work; both across species and across languages) is required in order to advance our understanding of the biological bases of receptive language and to set the agenda for research programs in the future. This workshop is intended to bring workers at the forefront of these fields together, to discuss language perception, integrating perspectives across disciplines, in order to generate cognitively interesting, computationally parsimonious, and biologically plausible hypotheses that can then be tested using available techniques, including neuroimaging. Although all workshop participants share an interest in the biological underpinnings of communication, they approach the problem from different perspectives and may be unaware of parallel work at other levels of analysis or in other species. Research is becoming increasingly specialized, and research domains increasingly narrow, yet the neurobiology of language is a highly complex subject which can only be adequately tackled by combining insights from multiple perspectives. This workshop, with its specific research focus and interdisciplinary outlook, provides an opportunity for researchers to discover others with similar interests and research questions, allowing new ideas to develop.

Talks: 30 minutes + 5 minutes for questions
Discussions: 20 minutes

Wednesday 25th September 2002

08.45-09.00 *Tea/Coffee*

Neurophysiology and neuroanatomy of language perception - comparative studies

9.00 - 9.10 **Welcoming remarks / Introduction to the European Science Foundation**

Ingrid JOHNSRUDE (MRC-CBU) / Hui WANG (ESF)

9.10 - 9.45 **Streams of processing in the auditory system**

Troy HACKETT (Vanderbilt University)

9.45 -10.20 **Neural mechanisms for vocal communication in non-human primates**

Xiaoqin WANG (Johns Hopkins University School of Medicine)

10.20 - 10.55) **Acoustic and neural bases for primate vocal communication**

Asif GHAZANFAR (Max-Planck Institute for Biological Cybernetics

10:55 - 11.10 Tea/Coffee

11.10 - 11:45 **Neuroanatomical and functional organization of speech perception**

Sophie SCOTT (University College London)

11.45 - 12:05 **Discussion:** Josef Rauschecker, Ingrid Johnsrude

The importance of gesture and imitation to language perception

12.05 - 12.40 **The evolution of speech: A comparative perspective**

Tecumseh Fitch

12.40 - 13.15 **The neural control and evolution of breath control in humans**
Richard Wise

13.15 - 14.00 *Lunch*

14.00 - 14.35 **Modulation of motor excitability by visual and auditory stimuli**
Kate Watkins

14.35 - 15.10 **Language beyond our grasp: what mirror neurons can, and cannot, do for language evolution**
James Hurford

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Wednesday 25th September (continued)

15.10 - 15.30 **Discussion:** Karalyn Patterson, Matt Davis

15.30 - 15.45 *Tea/Coffee*

Perceptual components of communication

15.45 - 16.20 **Speech processing, attention and brain activity**
Kimmo Alho

16.20 - 16.55 **Cortical dynamics of speech comprehension**
Riitta Salmelin

16.55 - 17.45 **One empiricist view of speech perception**
Keith R. Kluender

17.45 - 18.05 **Discussion:** Christophe Pallier, Sarah Hawkins

19.00 *Dinner - Le Gros Franck, Cambridge*

Thursday 26th September 2002

08.45-09.00 *Tea/Coffee*

Comparative, evolutionary and developmental perspectives on communication

09.00 - 09.35 **Universal processes and language-conditioned processes in the recognition of continuous speech**
Anne Cutler

09.35 - 10.10 **The role of production patterns in infant perception**
Marilyn Vihman

10.10 - 10.45 **Phonology, Reading, P-Centres and Dyslexia**
Usha Goswami

10.45 - 11.00 *Tea/Coffee*

11.00 - 11.35 **The origins of the sensory-motor organisation of speech sounds**
Pierre-Yves Oudeyer

11.35 - 12.40 **Modelling Language Evolution with Neural Networks: Interaction between Comprehension, Production and Cognitive Abilities**
Angelo Cangelosi

12.40 - 13.25 *Lunch*

13.25 - 14.00 **Sensorimotor Integration in a Neural Network Model of the Babbling Phase**
Gert Westermann

14.00 - 14.20 **Discussion:** Jenni Rodd, James McQueen

Perception of speech prosody

14.20 - 14.55 **Temporal processing of sound sequences**
Carolyn Drake

14.55 - 15.30 **Domain- and species-specificity of prosody perception**
Franck Ramus

15.30 - 15.45 Tea/Coffee

15.45 - 16.20 **The processing of linguistic prosody: Evidence from ERPs and fMRI**
Kai Alter

16.20 -16.55 **On the lateralization of emotional prosody: ERP and fMRI evidence**
Sonja Kotz

16.55 - 17.30 **Subcortical contributions to socio-emotive judgements of prosody**
Marc Pell

17.30 - 17.50 **Discussion:** Brechtje Post, Andrew Lawrence

17.50 *Close of workshop*

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