31st Annual International Conference of the IEEE EMBS
Minneapolis, Minnesota, USA, September 2-6, 2009

Investigations of mammalian echolocation

D. S. Edwards, R. Allen, *Member, IEEE,* T. Papadopoulos, D. Rowan, S.Y. Kim, L. Wilmot-Brown

***Abstract*—Active echolocation is a sensory modality possessed by a variety of mammals and is used for the identification, classification and localization of objects. A multi stage model of the bat echolocation process has been used with recordings of rotated disks to plot frequency spectrums of the signals reaching each of the bats' ears. Recordings from objects made within the human audible frequency range have also been made for use in psychoacoustic experiments aimed at validating preliminary studies that have shown some human ability to localize objects using echolocation.**

I. INTRODUCTION

THE function of any echolocating system, be it a bat or human auditory system or man-made sonar, is to extract the acoustic signature of an object from the backscatter of the emitted signal (termed the echo). Short duration, low intensity signals must often be analyzed in the presence of much louder emitted signals and "clutter echoes" from objects of little interest to the system. Biological sonar systems make use of multiple spatially separated receivers, with the term binaural hearing referring to two ears. This increases loudness and can also be used to reduce masking in which the signal of interest is made more difficult to hear by noise. It also allows comparison of differences in time, phase and level between the ears, assisting in azimuth (horizontal) localization. Thus, the study of the binaural system can give clues as to what use is made of timing differences not just in quiet, but also with a low signal to noise ratio, SNR.

Mammalian species known to echolocate are:

- Many species of bats, *Chiroptera*, including all members of the group microchiroptera and at least one genus (*Rousettus* and possibly *Stenonycteris* [1] of the group *megachiropter.*
- Toothed whales (suborder *odontoceti* which includes dolphins, sperm whales, porpoises and orcas), though the signals used vary considerably.
- Two genera of North American shrew and tenrecs of Madagascar are the only terrestrial mammals known to echolocate [2]. They appear to use their ability to investigate their habitat rather than to locate food.

Additionally, some cave – dwelling birds employ a crude form of echolocation for navigation when nesting in dark caves.

Covey [3] argues that echolocating bats provide a good model for understanding neural mechanisms associated with temporal processing. Their ability to detect an echo with a very low SNR is also impressive and because they use the medium of air rather than water, their acoustic system is more easily compared with human ability. Research indicates that *Eptesicus fuscus*, the most commonly studied species, can detect signal modulations of 10 ns, implying the ability to detect changes in a range of around 2 μm [4]. This result has been met with skepticism [5] and has become a topic of research for both neuroscientists and those who wish to improve the design of sonar systems. However, our ability to understand such systems, let alone develop systems that match their performance is "still primitive" [6].

Engineers have used echolocation principles to create active sound navigation systems underwater (sound navigation and ranging, or sonar). Additionally, some visually impaired humans can echolocate. Charities such as World Access for the Blind [7] exist with aims that include training blind subjects to use echolocation abilities.

Humans use signals at lower frequencies than bats. The human auditory range is often considered to be in the region of 20 Hz to 20 kHz. Bat echolocation frequencies generally range from 25 kHz to 100 kHz, though some species are able to emit signals as high as 150 kHz [8]. A bat hunting a target 5 mm in length must emit pulses with a wavelength (λ) of no more than 5 mm to prevent the signals just bending around the target. If $\lambda = 5$ mm, $f = c/\lambda = 343/5\text{x}10^{-3} = 69$ kHz. This is well above the upper limit of human hearing and is thus termed ultrasound. The lower frequency cues accessible to humans and their larger head size also means that the right stimuli, they could potentially use time differences between the ears that bats would not have access to.

Though lower human frequency range and resolution capabilities prevent direct comparisons of ability between the species, it is conceivable that both bats and humans use the same or similar mechanisms for at least some echolocation tasks since bats, humans and other mammals share the same nuclei and cell types [8]. Research conducted at the Institute of Sound and Vibration Research (ISVR), Southampton and by its partners in the Biologically Inspired Acoustic Systems (BIAS) consortium is

---

Manuscript received April 7, 2009. This work was supported by RCUK through its Basic Technology Program for the Bioinspired Acoustics Systems project.

D. S. Edwards is with the Institute for Sound and Vibration Research, Southampton, SO171BJ, UK. (Corresponding author phone: +44(0)2380592689; fax: +44(0)2380593190 e-mail dse103@soton.ac.uk).

R. Allen (e-mail ra@soton.ac.uk), T. Papadopoulos (e-mail tp@isvr.soton.ac.uk) and D. Rowan (e-mail dr@isvr.soton.ac.uk) and S.Y. Kim (e-mail syk@isvr.soton.ac.uk) are also with the ISVR.

L. Wilmot-Brown is with the Jamaica Association for the Deaf (e-mail llwb1v07@soton.ac.uk).

investigating the binaural cues available to bats and humans. Work has also been conducted within the ISVR on the design of a database for archiving and retrieval of key information on the acoustics of bat echolocation [9].

II. MODELLING ECHOLOCATION IN BATS

The physical quantities involved in bat echolocation processing are described in Fig.1. The bat emits an echolocation signal. An acoustic pressure disturbance p_{out} is measured at point $\boldsymbol{r}$ at distance r, azimuth (θ) and elevation (φ) relative to the centre of the bat's head. The disturbance propagates through the air until it is backscattered by the target creating a pressure disturbance p_{echo} back at point $\boldsymbol{r}$. This disturbance travels back towards the bat and reaches its two eardrums after having been diffracted by the pinnae and the head of the bat. The pressure signal reaching the bat's eardrum is denoted by p_{ear}.

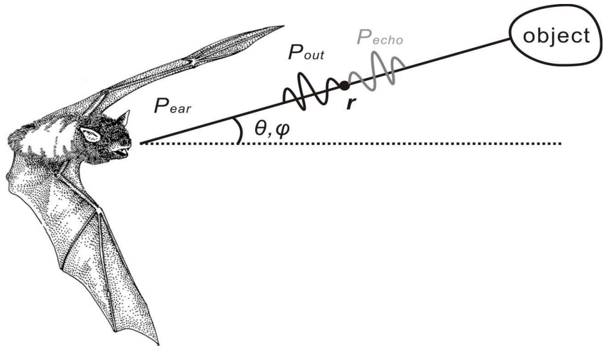

Fig. 1. Diagram of an echolocating system

To model echolocation in bats, it is useful to separate each stage of the process. Emission, reflection and reception are the basic components of the model [10].

Based on this model, the echolocation signal (p_{echo}) from a particular target that reaches the point before diffraction by the head can be predicted. This is achieved by convolution of the emitted signal (p_{out}) with the backscattering response of the object at a specified orientation (θ, φ) and distance (r). Convolution is a mathematical technique that expresses the amount of overlap between functions, effectively blending the emitted signal and backscatter response. The returning signal reaching the bat's ear (p_{ear}) can be predicted by convolution of the echolocation signal (p_{echo}) and the time-domain version of the head-related transfer function (HRTF) of the bat's head. The HRTF contains the information which describes the influence of the physical shape of the head and external ears in the frequency domain.

Directly recorded or artificially generated bat signals can be used to model the emission stage. To model the reflection stage, physical measurements of the backscattering impulse response from a target example have been made. Fig. 2 shows the response for a plastic disc. As the recording of raw data measured contains the influence of the microphone and speaker system, this effect was cancelled out using equalization (calibration). The 'emitted' label represents the signal generated from the speaker. The 'reflected' label represents the returning echo from the target disc. The reflection signature contains the target information such as size, shape and material.

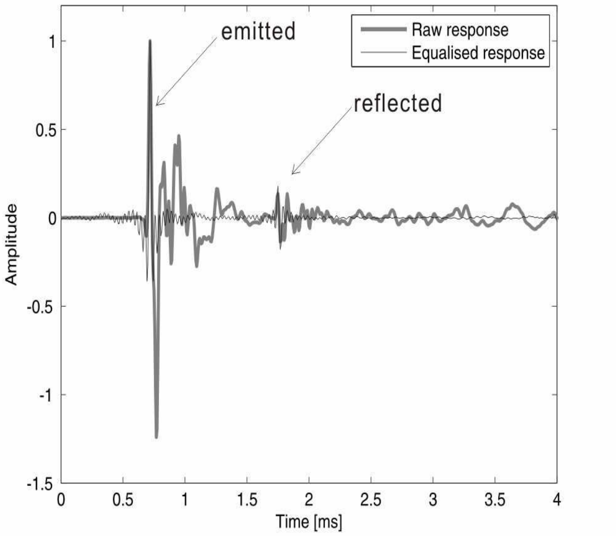

Fig. 2. Impulse response of a plastic disc (37 mm in diameter, 20 mm in thickness): Raw response and equalized response.

The reception stage depends on the HRTF of the species in question. A cast head model (kindly provided by Dr Dean Waters, University of Leeds, Biology) of an Egyptian fruit bat has been used to measure this. Contour plots of HRTFs measured in all azimuths provide several characteristics which explain the acoustical phenomenon around the bat-head cast. The measured data was examined in the frequency domain. Fig. 3 gives the details.

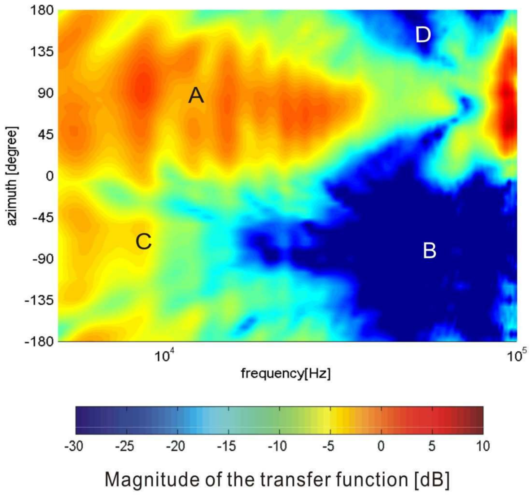

Fig. 3. HRTF of bat-head cast. Contour plot of the HRTF at left ear. Analysis is based on the previous study [11] and the details of the current analysis are described in a previous paper [12] A: High frequency doubling effect, B: Head shadowing effect, C: Acoustic bright spot, D: Extension of interference pattern to the ipsilateral hemisphere.

The HRTF was found to exhibit a change in the magnitude spectrum depending on azimuth. It is interesting to note that common features have been found in the contour plots of the measured HRTFs and those of human HRTFs from a previous study [11]. The same effect has been shown in the human HRTFs but the scale has been shifted up to the frequency region of 10 to 100 kHz in this study.

Comparing the HRTFs at the two ears provides information on the binaural cues available to the bat.

III. RESEARCH IN HUMANS

Few papers exist on human echolocation, especially with respect to azimuth localization. However, there is considerable literature on passive hearing localization which primarily makes use of interaural cues. Passive localization ability is poorest at near-threshold levels [13] and localization of sounds played just after a similar stimulus is biased towards the location of the initial stimulus in a series of effects known collectively as the precedence effect [14]. Listening tasks are also made more difficult when sounds not of interest, known as maskers are played at the same time (simultaneous masking) or just before (forward masking) or after the signal of interest. Active echolocation involves using cues from low intensity echoes which may overlap with the emitted signal which would act as a masker and initiate the precedence effect.

Early work by Rice [15] demonstrated that five blind subjects demonstrated some ability to localize a standard object in azimuth at a distance of 91 cm though full results are not given. Subjects used a signal of their choice (hiss or tongue click) and performed least well when the object was near 90˚. A study by Despres et al [16] reported ability to echolocate at above chance levels for a fairly acute (17.5˚) angle in a localization experiment at 90 cm of a 52 cm wide and 55 cm high board on a pole. Broadband signals were emitted from a speaker on a stand below the subjects' head. The signal used was white noise between 20 Hz and 20 kHz. Each burst of noise was 10 ms long and 10 bursts were presented in 10 seconds at a rate of 1 per second. When taking into account that it would take about 6 ms for the reflection of the 10 ms white noise to return from the board, the listener would be hearing both outgoing signal and echo together, experiencing a masking effect that makes the apparent ability to distinguish between left and right even more surprising.

Experiments conducted following a similar procedure at the ISVR supported these findings, with some inexperienced listeners able to do the task very well. These experiments also used a train of clicks spread over the same duration as the white noise. Measures were taken to prevent subjects from using cues other than those caused by echoes due to reflections of the intended stimulus from the board which pilot studies suggested were being used. This included playing a masking noise from speakers either side of the subject while moving the board, the inclusion of no sound control trials and using a method of statistical analysis designed to reduce the susceptibility of the results to bias and commonly used in psychoacoustic studies, d-prime. Figure 4 shows some of these results.

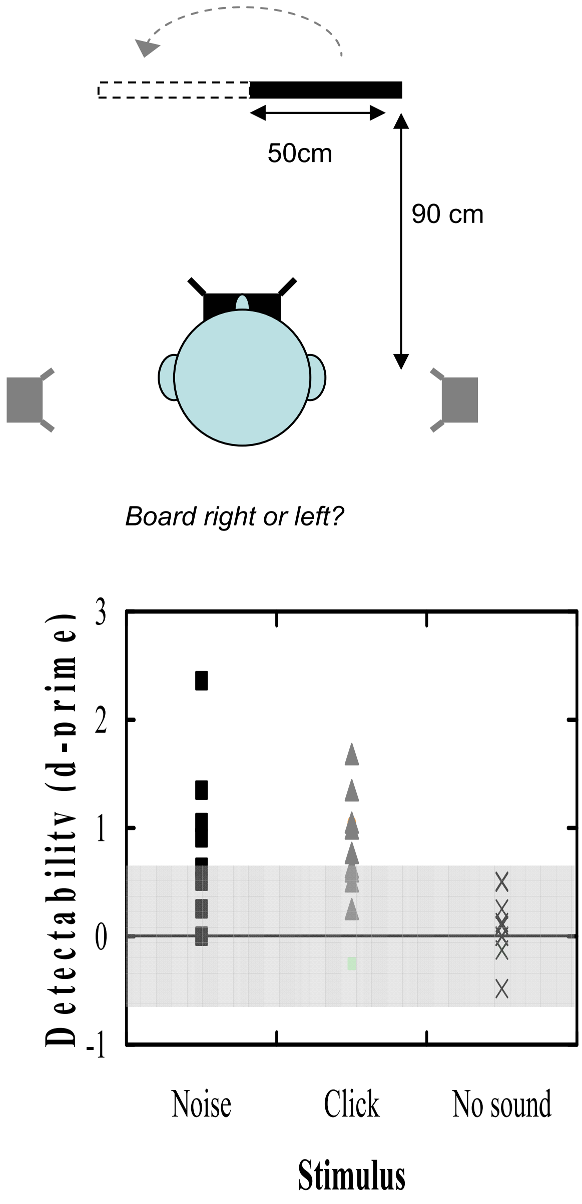

Fig. 4. *Upper panel:* illustration of human experiment inspired by [16]. Stimulus (60 dB SPL) is produced from the speaker (dark) directly below subject's chin rest. Subject is blindfolded and broadband noise is produced by two lateral speakers (grey) during board movement to mask any sounds. Subjects report whether board is to the left or right. *Lower panel:* results of one experiment using 12 inexperienced normal-hearing and normal-sighted subjects. A measure of detectability for board position, d-prime (related to % correct; zero is chance; 4 is close to perfect ability to detect given the number of trials used in the analysis) is given for each subject separately for three stimulus conditions: 10-s-long series of bursts broadband noise and clicks and no sound. The grey area illustrates a range of individual values of d' that were not statistically significantly better than chance.

A question that could be asked is whether visually impaired subjects outperform those without impairment. For instance, neural plasticity can allow redeployment of visual cortical areas to other modalities and blind subjects are likely to have more experience of using echo cues. The Despres et al study found that subjects with various degrees of optical impairment outperformed those with near perfect vision, though ISVR pilot studies have been unable to verify this.

Other important questions include the role of experience and training, the effects of which have not (quite) been shown to be statistically significant so far in the present study. Results indicate that even some inexperienced subjects can perform the task very well, with a huge level of inter-subject variability. Another question of interest is the effect of distance on ability to localize an object. As a board is moved away from the speaker, simultaneous and forward masking effects should be reduced as the delay time of the echo increases, but the intensity of the echo will be reduced. The effect of noise on the ability to localize objects should also be investigated.

In order to gather much more data for use in answering such questions, an experimental technique has been devised in which recordings are taken within an anechoic chamber of reflections from objects positioned at different degrees of azimuth. Impulse responses are being measured using the Maximum Length Sequence (MLS) technique. These recordings can be used to simulate the effect of any emitted signal being directed at the object through convolution. Such signals will be used in psychoacoustic experiments, both with and without the outgoing signal present, in which the exact acoustic characteristics of the echolocation signal reaching each ear are known to the researchers.

Acoustic modeling techniques such as auditory filter banks can be used to compare binaural acoustic cues available to bats and humans at different stages of their auditory systems.

IV. FUTURE WORK AND APPLICATIONS

The aim of this research is to gain a better understanding of the mammalian binaural hearing system. Current work is aimed at fundamental understanding, knowledge that may be applied to both engineering and hearing problems. For example, understanding the limits of, training involved and most useful signal for human echolocation will be useful in guiding organizations aiming to teach blind participants to echolocate and may provide insights into how humans perceive echoes and the workings of the precedence effect. Increased knowledge of binaural processing will be of use when trying to coordinate two or more receivers such as hearing aids, cochlear implants, especially where directional information is of importance. Other benefits of coordinating receivers can be envisaged in sonar systems and with cooperative unmanned robotic vehicles. Improvements in sonar systems can also be of benefit to medical scanning, geological investigation and remote sensing.

ACKNOWLEDGMENT

The authors acknowledge the Bioinspired Acoustics Systems project Consortium partners for their input.

REFERENCES

[1] G. Neuweiler "The Biology of Bats" Oxford University Press, New York, 2000.

[2] T. E. Tomsai "Echolocation by the short-tailed shrew *Blarinava brevicaud,*" Journal of Mammalogy, vol 60, no 4, pp. 751-759, 1979.

[3] E. Covey, "Brainstem mechanisms for analyzing temporal patterns of echolocation sounds: a model for understanding early stages of speech processing," *Journal of Neurophysiology*, vol 66, no. 3, pp. 1080-1094, 1991.

[4] J.A Simmons. M. J. Ferragamo, C. F. Moss, S. B. Stevenson, and R. Altes, "Discrimination of jittered sonar echoes by the echolocating bat, *Eptesicus fuscus*: the shape of target images in echolocation", *Journal of Comparative Physiology A*, vol. 167, no. 5, pp. 589-616, 1990.

[5] K. Beedholm, "The transfer function of a target limits the jitter detection threshold with signals of echolocating FM – bats," *Journal of Comparative Physiology A*, vol. 192, no. 5, pp. 461-468, 2006.

[6] 7 J. G. Rees, R. A., Allen, J, Busby and P. Jackson, "Learning from how animals use sound: Developing biologically inspired acoustic systems", In *Proc. of Biological Approaches fir Engineering* March, 2008. University of Southampton, March 2008, pp. 62-65.

[7] D. Kish, "World access for the blind" website. http://www.waftb.org/recent_events.htm

[8] A. D. Grinell "Hearing in bats: An overview" in Hearing in Bats, A.N. Popper and R R. Fay, Ed. Springer-Verlag, pp 1-36, 1995.

[9] D. Edwards, T. Papadopoulos, R. Allen, D. Rowan, "Bat echolocation database tool" in Proc. 5th International Conference on Bio-Acoustics, Loughborough, 2009, pp. 175-178.

[10] T. Papadpoulos and R. Allen. "Experimental method for the acoustical modeling of the echolocation process in bats," *Proc. Inst. Acoust.* 29(3), 2007.

[11] D. S. Brungart and W. M. Rabinowitz. Auditory localization of nearby sources. Head related transfer functions. *J. Acoust. Soc. Am.* 106(3): pp. 1465-1479, 1999.

[12] S. Y. Kim, T. Papadopoulos, R. Allen, D. Rowan, "Measurement of the head-related transfer function of a bat-head cast" in Proc. 5th International Conference on Bio-Acoustics, Loughborough, 2009, pp. 167-174.

[13] A.T. Sabin, E. A. Macpherson and J. C. Middlebrooks "Human sound localization at near-threshold levels," *Hearing Research*, vol. 199, pp124-134, 2005.

[14] R. Y. Litovsky, H. S., Colburn, W. A. Yost, and S. J. Guzman, "The precedence effect," *Journal of the Acoustical Society of America*, vol. 106, no. 4, pp. 1633-1654, 1999.

[15] C.E. Rice, "Human Echo Perception," *Science*, vol. 155, no. 3763, pp. 656-664, 1967.

[16] O. Despres, V. Candas, and A. Dufour, "Auditory compensation in myopic monaural, or humans: Involvement of binaural, echo cues?" *Brain Research*, vol. 1041, no. 1, pp. 56-65, 2005.