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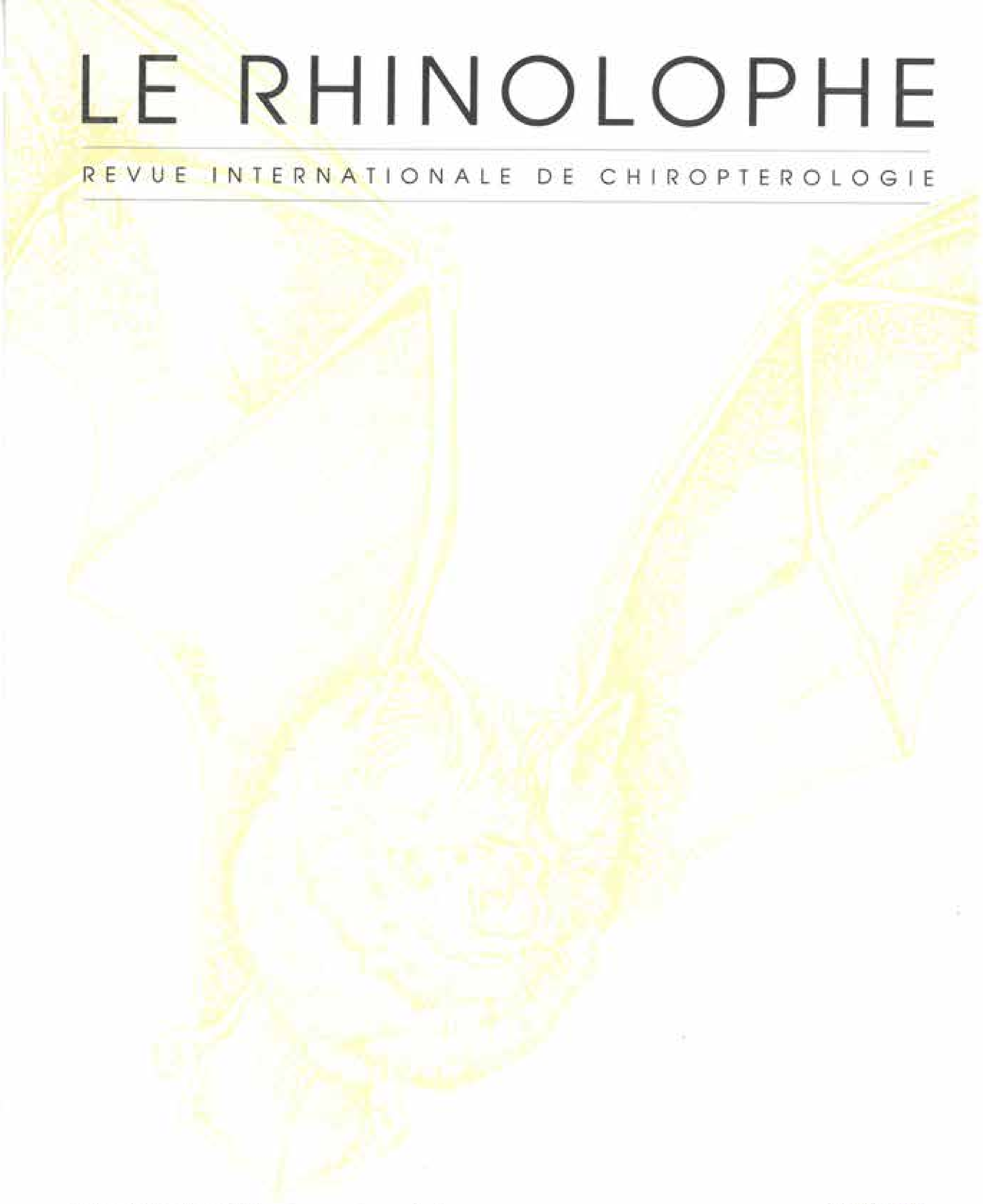

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Echolocation des chauves-souris - Genève, 18-20 novembre 1994

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Symposium Jurine
Echolocation des chauves-souris
Genève, Suisse, 18-20 novembre 1994

Le 20 février 1794, le chirurgien et naturaliste genevois Louis Jurine présenta à la Société de physique et des sciences naturelles de Genève son "Mémoire sur l'ouïe des chauves-souris" qui fut à la base de la découverte de l'échthe localisation des chiroptères. Ce symposium est organisé par le Muséum d'histoire naturelle de Genève et le Département de zoologie et de biologie animale de l'Université de Genève en commémoration de cette date importante.

The surgeon and naturalist Louis Jurine presented, on February 20, 1794, his "Mémoire sur l'ouïe des chauves-souris" to the members of the "Société de physique et des sciences naturelles" of Geneva. This paper initiated the study of echolocation of bats. In commemoration of this important date, the Museum of natural History of Geneva and the Department of zoology and animal biology of the University of Geneva organise this symposium.

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Sommaire

Présentation du symposium

Ce symposium commémore le bicentenaire des découvertes du naturaliste genevois Louis Jurine (1751-1819) sur l'écholocation des chauves-souris. Il permet à des chercheurs de divers horizons de se rassembler : historiens des sciences, physiciens, physiologistes et biologistes de laboratoire, ainsi qu'écologues et biologistes de terrain.

Les bases historiques

Les historiens des sciences (M. Buscaglia et R. Sigrist, du Séminaire d'histoire et philosophie des sciences de l'Université de Genève, et C. Violani, du Département de biologie animale de l'Université de Pavie) cernent l'environnement épistémologique dans lequel s'est développée, à la fin du XVIIIe siècle, l'hypothèse d'un "nouveau sens" chez les chauves-souris. R. Sigrist brosse un portrait de Jurine dans le contexte de son époque, alors que M. Buscaglia propose une analyse des constantes et des caractéristiques de la démarche scientifique adoptée par Jurine. C. Violani rappelle l'importance des travaux de Lazzaro Spallanzani, savant italien qui émit pour la première fois l'hypothèse d'un sens caché chez les chiroptères et communiqua ses premiers résultats à Jurine par l'intermédiaire de Jean Sénebier. Enfin, l'historien irlandais C.W.P. Mac Arthur apporte de nombreuses précisions sur Jurine.

On retiendra qu'un historique fouillé des découvertes de Jurine reste à faire : en effet, de nombreux documents ont été égarés ou demeurent lacunaires, de sorte que les historiens des sciences en sont le plus souvent réduits à émettre des hypothèses. Or certaines d'entre elles ne pourront être formulées qu'avec l'appui des spécialistes actuels de l'écholocation, par exemple pour l'identification des espèces étudiées par Jurine. De ce point de vue, le présent colloque doit permettre un premier échange d'informations extrêmement fructueux. Ces aspects historiques, rarement traités dans les colloques consacrés à l'écholocation, retiendront toute l'attention des biologistes, qui sont souvent conduits à présenter les développements de leurs disciplines respectives.

Avec les interventions de D.R. Griffin, de l'Université de Harvard, et de R. Galambos (San Diego), ce symposium connaît un impact exceptionnel. Ces deux chercheurs ont en effet marqué l'histoire contemporaine de la biologie en prouvant expérimentalement, dans les années 1940, l'existence de l'écholocation chez les chiroptères, validant ainsi les hypothèses émises par Jurine. Les communications qu'ils présentent ici permettent de donner un historique extrêmement précis de ces travaux, avec la présentation de documents et de films originaux. Ces auteurs introduisent également les thèmes centraux du colloque, à savoir les recherches actuelles sur l'écholocation des chiroptères et leurs perspectives d'avenir.

Essor de l'éco-éthologie

En éco-éthologie, les différents systèmes d'écholocation chez les chauves-souris en relation avec leur écologie sont mis en évidence par H.-U. Schnitzler, de l'Université de Tübingen. Il existe une relation étroite entre modes d'émission et niche écologique, de sorte que ces modes d'émission constituent un précieux auxiliaire dans la compréhension des guildes au sein des peuplements de chiroptères. Cette relation entre environnement et comportement doit notamment s'appuyer sur une description détaillée des cris des différentes espèces. A. Guillén, de la Station biologique de Doñana en Espagne, présente une description des sons émis par Molossops temminckii au Venezuela, révélant que cette chauve-souris se distingue nettement des autres Molossidés par ses cris, qui se rapprochent plus de ceux du genre Noctilio. K.-G. Heller, de l'Université d'Erlangen en Allemagne, a étudié en Malaisie *Cheiromeles torquatus*, la plus grande chauve-souris insectivore du monde. Il décrit les signaux émis en relation avec le comportement de l'animal, filmé avec une caméra vidéo. Quant aux Vespertilionidés, P.T. Andrews, de l'Université de Liverpool, offre d'intéressantes hypothèses sur l'évolution de l'écholocation des espèces chassant en milieu ouvert ou semi-ouvert, en fondant son analyse sur des modèles informatiques.

Lorsque les caractéristiques des cris ultrasoniques sont suffisamment connues, leur utilisation ouvre des perspectives intéressantes dans l'étude de l'éco-éthologie des espèces dans la nature. F. Matt, R. Aubauer et O. v. Helversen, des Universités d'Erlangen et de Darmstadt, ont ainsi développé un système d'enregistrement original des chiroptères sur le terrain, qui leur permet d'étudier le partage de l'espace et des ressources alimentaires de plusieurs espèces sympatriques en Allemagne. A.M. Boonman, H. Limpens et B. Verboom, de l'Institut forestier et d'environnement néerlandais, étudient également les relations entre structures paysagères et utilisation de l'espace par *Myotis dasycneme* aux Pays-Bas, par observation de cette chauve-souris au moyen d'appareils ultrasoniques. K. Zbinden, de Berne, fournit une excellente synthèse des développements actuels et futurs de la bioacoustique dans l'étude et la protection des chiroptères. La présence de spécialistes suisses dans ce domaine, collaborateurs réguliers du Centre de coordination pour l'étude et la protection des chauves-souris, mérite d'être soulignée. Enfin, G. Jones, de l'Université de Bristol, apporte une perspective différente : les enregistrements systématiques des cris émis par *Pipistrellus pipistrellus* en Grande-Bretagne révèlent l'existence de deux populations distinctes. On constate ici que les appareils ultrasoniques mis à la disposition des biologistes de terrain sont toujours plus performants, et qu'ils ouvriront des champs de recherche nouveaux, notamment dans la connaissance des chiroptères en relation avec la protection de l'environnement.

Progrès en physiologie

D'importants progrès ont été accomplis dans l'étude des systèmes auditifs périphériques et centraux. J. Butman, de l'Université de St-Louis (USA), nous dévoile les processus neuronaux de traitement des signaux sonores dans les régions spécialisées du cortex auditif. M. Wu et Ph.H.-S. Jen, de l'Université de Missouri, apportent des précisions sur le fonctionnement des neurones colliculaires inférieurs chez *Eptesicus fuscus*. Ph.H.-S. Jen en collaboration avec Y. Qian, de l'Université de Shanghai, explorent les centres d'activation de *Eptesicus fuscus* au moyen de traceurs immunocyto-chimiques. Enfin, A. Denzinger et H.-U. Schnitzler, de l'Université de Tübingen, ont testé en laboratoire le comportement d'*Eptesicus fuscus* en relation avec l'hypothèse du "Schalldruckpegel" (SPL) formulée en 1989 par Berkowitz et Suga.

Nouveaux outils mathématiques

Comme le montrent Y. Tupinier, N. Gache et P. Flandrin, du Laboratoire de physique de l'ENS de Lyon, le développement des outils mathématiques dans le domaine du traitement des signaux ultrasoniques (représentation de Wigner-Ville) se révéleront extrêmement utiles dans le domaine de la bioacoustique des chiroptères. Ces nouvelles approches devraient permettre de mieux analyser les signaux de faible puissance comme les harmoniques d'ordre élevé, trop souvent éliminées lors des analyses classiques effectuées au moyen de spectrogrammes.

Pascal Moeschler　　Louis de Roguin

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Louis Jurine, chirurgien et naturaliste (1751 - 1819)*

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Abstract. However a fundamental contributor to the discovery of bat echolocation, the surgeon and naturalist Louis Jurine (1751-1819) remains in some respects unknown. Among the reasons for that are the disappearance of his personal papers, the unpublished or posthumous nature of many of his works, or else his own humble origin. This paper should revive the complex and somewhat mysterious character of this Genevese, who mastered with rigour though as an amateur, as much medicine and experimental physiology as entomology, mineralogy and zoology, both descriptive and systematic. His story is that of a believer and pragmatic scholar, as that of a simple man in search of scientific and social recognition. It reveals a scientific circle in which, thirty years after Charles Bonnet and half a century after Linnaeus, natural history gains its full grandeur at last.

Aujourd'hui remis en lumière grâce à ses travaux pionniers sur l'ouïe des chauves-souris, le chirurgien et naturaliste genevois Louis Jurine (1751-1819) demeure une personnalité méconnue et quelque peu mystérieuse de notre passé scientifique. Véritable figure de la chirurgie du tout début du XIXe siècle, il s'illustra comme physiologiste aussi bien que comme naturaliste systématicien, et pratiqua à la fois l'entomologie, la zoologie, les sciences de la terre et même la botanique. L'oubli dans lequel il est tombé après sa mort tient à un ensemble de raisons, parmi lesquelles on peut avancer l'absence de disciples de haut parage, le fait qu'une grande partie de son oeuvre soit restée inédite, la disparition de ses papiers personnels, ainsi que sa volonté de ne faire l'objet d'aucun éloge après sa mort.

Comme praticien, le chirurgien Jurine bénéficia sa vie durant d'une extraordinaire réputation, qui lui valait de donner des consultations dans toute la région, et parfois même à Berne, Lausanne ou Yverdon. Il fut à plusieurs reprises appelé au chevet de célébrités, comme Mme de Staël, et se vit même offrir de devenir médecin consultant de la famille impériale à Paris. En tant que physiologiste, il fut l'auteur d'une vingtaine de publications et de nombreux travaux inédits, qui lui ont valu d'être correspondant des Sociétés de Médecine de Paris, Montpellier et Venise. Plusieurs de ses mémoires ont été couronnés, par la Société de Médecine de Paris ou par d'autres instances. Tel fut notamment le cas de son mémoire sur les gaz du corps humain, rédigé en 1787 pour «Déterminer quels avantages la médecine peut retirer des découvertes modernes sur l'art de connaître la pureté de l'air par les différents eudiomètres»[1], du *Mémoire sur le croup*, qui décrocha en 1812 la moitié du prix instauré par Napoléon sur ce sujet, ainsi que du *Mémoire sur l'angine de poitrine*, qui reçut en 1813 la médaille d'or de la Société de Médecine de Paris.

Mais l'activité scientifique de Louis Jurine se développait également en histoire naturelle. Il publia en 1807 une *Nouvelle méthode de classer les Hyménoptères*, oeuvre taxonomique majeure pour ce grand ordre d'insectes, jusqu'alors peu étudié. Son *Histoire des monocles qui se trouvent aux environs de Genève* (1820), fait de lui un pionnier de l'hydrobiologie, tandis que son *Histoire abrégée des*

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* Cet article est le prélude d'un travail de plus grande ampleur à paraître dans la *Bibliothèque d'Histoire des Sciences*, n° 5, 1996.

poissons du lac Léman, éditée à titre posthume en 1825, a malheureusement été éclipsée par l'oeuvre ichtyologique de Cuvier, publiée peu après. Jurine fut aussi l'auteur d'une douzaine d'articles parus dans différentes revues, ainsi que de nombreux travaux inédits, ou qui n'ont fait l'objet que d'extraits plus ou moins sommaires. Tel fut notamment le cas des recherches sur les chauves-souris, dont Jean Peschier a donné une petite notice dans le *Journal de Physique* de 1798[2]. Ces différentes contributions ont fait de Jurine un correspondant de la "Société philomathique de Paris", puis de l'Institut de France (1799), de l'Académie des Sciences de Turin, et de plusieurs autres sociétés savantes, comme la "Societa Pontiana" de Naples, la "Gesellschaft Naturforschender Freunde" de Berlin, la "Société d'Histoire naturelle" de Paris, la "Société des Sciences et Arts de Lille", la "Wernerian Society" d'Edimbourg, ou encore la "Wetterauische Gesellschaft" de Hanau.

Pionnier en plusieurs domaines, Louis Jurine (Fig. 1) était aussi, à bien des égards, un parfait représentant de l'école genevoise des sciences naturelles. Il ne

Fig. 1 : Louis Jurine (1751-1819). La réputation dont il bénéficia, comme chirurgien, à l'époque du Consulat et de l'Empire, n'a d'égale que l'oubli dans lequel il est tombé après sa mort (gravure de Arlaud Jurine d'après Ch. Pradier).

faisait d'ailleurs pas mystère de sa filiation intellectuelle avec le savant et philosophe Charles Bonnet (1720-1793), dont il se voulait un simple disciple : «C'est toi qui m'as inspiré l'amour de l'étude de la nature; c'est la lecture de tes ouvrages qui m'a introduit dans cette intéressante carrière» écrira-t-il dans la Préface de son *Histoire des monocles*. Jurine entendait en effet inscrire son oeuvre scientifique, et notamment ses observations entomologiques, dans le prolongement de l'oeuvre de Bonnet, en particulier du *Traité d'Insectologie* (1745) et de la *Contemplation de la Nature* (1764). Situant ses observations et ses expériences dans le cadre de la philosophie de la nature, d'inspiration chrétienne, de son maître, partisan résolu de l'Echelle des Etres et de la continuité de la Nature, il ne manquait pas une occasion de défendre la théorie de la préformation des germes, pierre angulaire de la philosophie naturaliste de Bonnet.

Malgré cela, Jurine est tout le contraire d'un théoricien, ou d'un naturaliste en chambre. Ses connaissances physiologiques doivent en effet beaucoup à sa pratique chirurgicale, ce qui n'est d'ailleurs pas sans conséquence pour sa démarche expérimentale. Quant à sa passion pour la systématique, elle le rapproche davantage de Linné, ou d'entomologistes comme Fabricius et Latreille, que de l'histoire naturelle morale à la Bonnet, qu'il pratiquait également avec bonheur. La combinaison de ces deux qualités scientifiques, ou de ces deux types d'approches, si rarement réunies dans une même personne, celles du physiologiste expérimentateur et du naturaliste systématicien, fait de Louis Jurine un cas intéressant, sinon un personnage tout à fait à part.

Des origines modestes

Ce savant chirurgien, qui devait devenir, à partir des années 1790, l'une des gloires de Genève, eut des origines presque obscures. Contrairement aux Bonnet, Saussure, Pictet, Candolle et autres De la Rive, savants issus du patriciat, contrairement aussi à la plupart de ses futurs collègues, qui appartenaient à des familles bourgeoises, Jurine ne provenait pas d'un milieu particulièrement favorisé. Son père Sébastien (1722-1779), originaire de Lyon, n'était qu'un artisan assez modeste exerçant le métier de guimpier, c'est-à-dire de fabricant de galons et d'épaulettes, une activité traditionnelle à Genève. De ce fait, l'éducation du jeune Louis ne pouvait se comparer à celle des autres savants genevois, d'un niveau culturel et social plus élevé. Il suivit néanmoins une formation classique, fréquenta le Collège, puis l'Auditoire de Belles-Lettres de l'Académie, mais avec deux ans de retard sur la plupart de ses camarades. C'est sans doute pourquoi, déjà âgé de 18 ans, il n'entre pas à l'Auditoire de Philosophie, où Horace-Bénédict de Saussure, Louis Bertrand et François Mercier dispensaient les rudiments d'une formation scientifique aux futures élites de la ville, juristes et hommes politiques, pasteurs, professeurs, savants ou encore médecins. Jurine se met au contraire à travailler comme aide, pour ne pas dire comme serviteur, d'un chirurgien, dont nous n'avons pas retrouvé l'identité. Il demeurera dans cette situation pendant 4 ans[3], soit jusqu'en 1773, date à laquelle il passe avec succès les épreuves imposées par la "Faculté de médecine" de Genève pour devenir maître en chirurgie. Il a alors 22 ans. Fort de cette réussite, il convole l'année suivante avec Louise-Pernette Bonnet, fille richement dotée de feu Pierre Bonnet, un maître et marchand confiturier sans parenté directe avec le naturaliste Charles Bonnet. Ce mariage, qui lui procure une certaine aisance, lui permet d'aller étudier la chirurgie à Paris. Au terme d'une année d'études, il décroche le grade de Docteur en Chirurgie, décerné par la Faculté de la capitale (1775).

Peu après son retour, Jurine accède à la Bourgeoisie de Genève, moyennant le paiement de 2500 florins. En 1778, il acquiert le privilège de tenir boutique à la rue Neuve «pour la barbe et relativement à la profession de chirurgien»[4]. Dans ces mêmes années, Louis Jurine devient père de quatre enfants, qui naissent pratiquement coup sur coup : Christine (1776), Sébastien (1777), Adrienne (1778) et André (1780). L'aînée Christine, et le cadet André, montreront de véritables dispositions pour l'histoire naturelle, avant de connaître tous deux un destin tragique. Seul Sébastien fondera une famille et assurera une descendance.

Naissance d'une vocation scientifique

C'est vers la fin des années 1770 que Jurine commença à développer sa grande passion pour l'histoire naturelle, qu'il devait bientôt considérer comme «la vraie route pour se rendre heureux»[5]. Son ami Henri-Albert Gosse (1753-1816), libraire et futur pharmacien, l'initia d'abord à la botanique systématique, science alors peu pratiquée à Genève. Comme Sénebier l'a fait remarquer dans son *Histoire littéraire de Genève* (1786), ses concitoyens se préoccupaient alors avant tout de physico-mathématique, de physique expérimentale, de physiologie et même de géologie, mais bien peu d'histoire naturelle. Il faudra attendre la Révolution, et la grande vogue des idées de Rousseau, pour que la botanique commence à devenir une science à la mode.

A peine familiarisé avec les crucifères et les ombelles par la lecture de Crantz, puis avec les lichens en suivant Haller, Jurine se met à étudier les insectes avec Linné, puis découvre la géologie et la minéralogie à la suite de Jean-André Deluc. Il déclarera plus tard que la lecture de ses *Lettres sur l'Histoire de la Terre et de l'Homme, adressées à la reine de la Grande-Bretagne* (1779-80), fut le véritable point de départ de son propre goût dominant pour l'histoire naturelle en général. Cette passion se renforça ensuite à la lecture des oeuvres de Charles Bonnet, que Jurine considérera toujours comme son véritable maître. Mais contrairement à celui-ci, ou à Jean-André Deluc, il ne se sentira lui-même jamais la vocation d'un théoricien : confiant dans le cadre théorique et téléologique du «Philosophe Chrétien»[6], il se contentera d'étudier sereinement la nature par les voies de l'observation et de l'expérimentation, persuadé de contribuer ainsi à une meilleure connaissance des Oeuvres du Créateur. Pratiquement, Jurine aborda la science comme un collectionneur d'histoire naturelle, commençant par recueillir des plantes, puis des insectes et des minéraux, ainsi que des oiseaux. Cette dernière collection, la moins connue de toutes, comprendra un jour quelque 270 espèces, qui lui fourniront matière à une étude, demeurée inédite, des voies respiratoires chez les oiseaux. Il finira d'ailleurs par vendre cette collection, devenue trop encombrante, à son collègue Henri Boissier, afin qu'elle serve à l'instruction publique.

Sur le plan professionnel, Jurine cède, fin 1783, son privilège de barbier et sa boutique à un collègue, pour devenir l'un des trois chirurgiens de l'Hôpital de Genève. Ceci l'oblige à de fréquentes interventions, mais ne l'empêche pas de conserver sa clientèle privée. Des opérations difficiles et heureuses le mettent rapidement au niveau de la réputation, pourtant bien établie, de son prédécesseur Cabanis. Sans doute le succès des cours d'anatomie, qu'il donne à partir de 1787 dans le cadre de la Société des Arts, a-t-il également contribué à asseoir cette réputation[7].

Dans les années 1785-86, Jurine publie ses premiers articles scientifiques, mais aussi médicaux. Ce ne sont encore que des observations limitées, à l'exception de ses «Expériences et observations faites pour la guérison des plaies par le moyen du suc gastric», publiées dans un ouvrage de Sénebier. A cette époque, sa pratique de chirurgien conserve d'ailleurs une prééminence indiscutable sur ses recherches scientifiques, qui n'occupent que ses moments de loisirs.

Les années révolutionnaires n'apportent guère de bouleversements dans la vie bien ordonnée du chirurgien de l'Hôpital. Démocrate, membre et même président du Cercle politique des Droits de l'Homme, Jurine est de tempérament modéré et pragmatique : il demeure assez peu engagé politiquement, moins en tout cas que beaucoup de ses collègues, et préfère consacrer l'essentiel de son temps et de son énergie à ses patients, ainsi qu'à ses travaux scientifiques. C'est au cours de ces années 1790 en effet qu'il entreprend ses premières recherches d'envergure, notamment la mémoire sur l'eudiométrie appliquée à la médecine, déjà évoqué, et ses fameuses expériences sur les chauves-souris privées de la vue (1794). Il commence également à élaborer la *Nouvelle méthode de classer les Hyménoptères*, l'*Histoire des monocles*, suivis peu après du mémoire sur la respiration des oiseaux demeuré inédit. Ce redoublement d'activités scientifiques tient sans doute au fait que Jurine est désormais moins inquiet pour son avenir matériel immédiat, si bien que, comme le dira un jour Pictet : «Peu à peu la part de l'étude chérie s'accrut aux dépens de celle d'un art dont l'exercice a ses fatigues et ses malheurs»[8].

Une autre circonstance très favorable au développement de ses activités de recherche fut la création à Genève de sociétés savantes, et particulièrement la fondation, en août 1791, de la Société d'Histoire naturelle, devenue après 1798 la Société de Physique et d'Histoire naturelle (SPHN).

Jurine et les société savantes

Les sociétés savantes, genevoises et étrangères, ont en effet constitué un véritable tremplin pour les activités scientifiques de Louis Jurine. La Société de Physique et d'Histoire naturelle en particulier lui donna la possibilité de fréquenter régulièrement les membres de l'élite intellectuelle et sociale de Genève, ce que ses origines modestes ne lui avaient guère permis jusque-là. Cette instance de reconnaissance scientifique lui fournira une motivation supplémentaire, et sera un puissant stimulant pour ses recherches, notamment en histoire naturelle. A la SPHN, Jurine trouva en effet une tribune idéale pour communiquer ses travaux, pour échanger des points de vue, et pour se tenir au courant de l'actualité scientifique. Ce cadre institutionnel lui convenait d'autant mieux qu'il coïncidait parfaitement avec sa manière de concevoir la science, et en particulier l'histoire naturelle. La Société de Physique a en effet été fondée dans le but de procéder à une description plus ou moins systématique des environs de Genève, du point de vue de l'histoire naturelle. Et plus que tout autre, Jurine tenait à ce que cette société fonctionne comme une véritable académie scientifique, à ce qu'elle soit le foyer actif de la recherche à Genève. C'est pourquoi il veillera tout particulièrement à une application stricte des règlements, incitant inlassablement ses collègues à plus de régularité dans leurs communications et à plus d'assiduité dans leur participation aux séances.

Afin de favoriser le développement des collections, Jurine lègue dès 1791 son herbier de plantes alpines (comprenant 1300 espèces) à la Société; il accepte également d'en héberger provisoirement le cabinet de minéralogie, destiné à rassembler les pierres rares des environs, et notamment celles du Lac.

A partir d'avril 1803, la Société de Physique et d'Histoire naturelle, qui se réunit deux fois par mois, est encore complétée par une Société des Naturalistes Genevois, dont les réunions mensuelles permettent aux naturalistes locaux de disposer d'un cadre plus familier et plus spécialisé pour leurs travaux. Jurine en sera l'un des pilliers, avec le secrétaire Gosse, les géologues Guillaume-Antoine Deluc et Jean Tollet, et l'entomologiste François Huber.

C'est dans le cadre de ces deux sociétés que Jurine présentera la plupart de ses mémoires, sur des questions d'entomologie, de zoologie, de physiologie, de géologie, de minéralogie, de tératologie, ou encore de médecine. Ces dernières pouvaient également être traitées à la Société médico-chirurgicale, dont il fut membre dès sa fondation, en 1798. Seule une partie de ces travaux ont été publiés, ou intégrés à des ouvrages de plus grande ampleur.

Grâce à ces sociétés savantes, Jurine a également pu entrer en contact avec de nombreux naturalistes français, italiens, allemands ou helvétiques : c'est par exemple à la SPHN qu'il entendit parler pour la première fois, en janvier 1794, des recherches de Spallanzani sur les chauves-souris[9].

Un "notable" malgré lui

En février 1793, les citoyens genevois envoyèrent Jurine siéger à l'Assemblée nationale, où il se contenta d'un rôle fort modeste. Fin 1794, il fut néanmoins pressenti pour occuper l'une des magistratures suprêmes de Syndic, mais préféra se dérober aux sollicitations de ses amis. Nommé à la Grande cour de Justice criminelle, il n'y siégea que brièvement, et n'accepta pour toutes nouvelles fonctions publiques que celles de membre du Consistoire (1795) et de membre du Conseil législatif (1796). Jurine ne remplit pas même sa charge de professeur d'anatomie au Muséum d'Histoire naturelle, que les autorités révolutionnaires genevoises envisageaient de créer en 1794 : il jugea en effet préférable d'affecter au soulagement des pauvres de la République les sommes prévues pour l'équipement d'un cabinet d'anatomie humaine et comparée.

Cette attitude réservée se maintiendra après l'annexion de Genève à la France, en avril 1798[10]. Aux yeux des autorités françaises, qui cherchaient à s'attacher la collaboration des notables ayant accepté les acquis de la Révolution, Jurine incarnait pourtant une élite du talent, appelée à prendre la relève des grandes familles patriciennes traditionnelles. Ainsi, il fut tout naturellement intégré au collège électoral du département du Léman, entité administrative nouvelle née de la réunion des anciens territoires genevois au Chablais savoyard et au pays de Gex. Jurine se vit ainsi sollicité pour certaines obligations protocolaires, comme celle de représenter Genève aux cérémonies du nouvel an républicain, à Paris. Mais jusqu'à la chute de l'Empire en 1814, ses activités politiques se limiteront pratiquement à des manifestations de ce genre, aussi factices qu'inévitables.

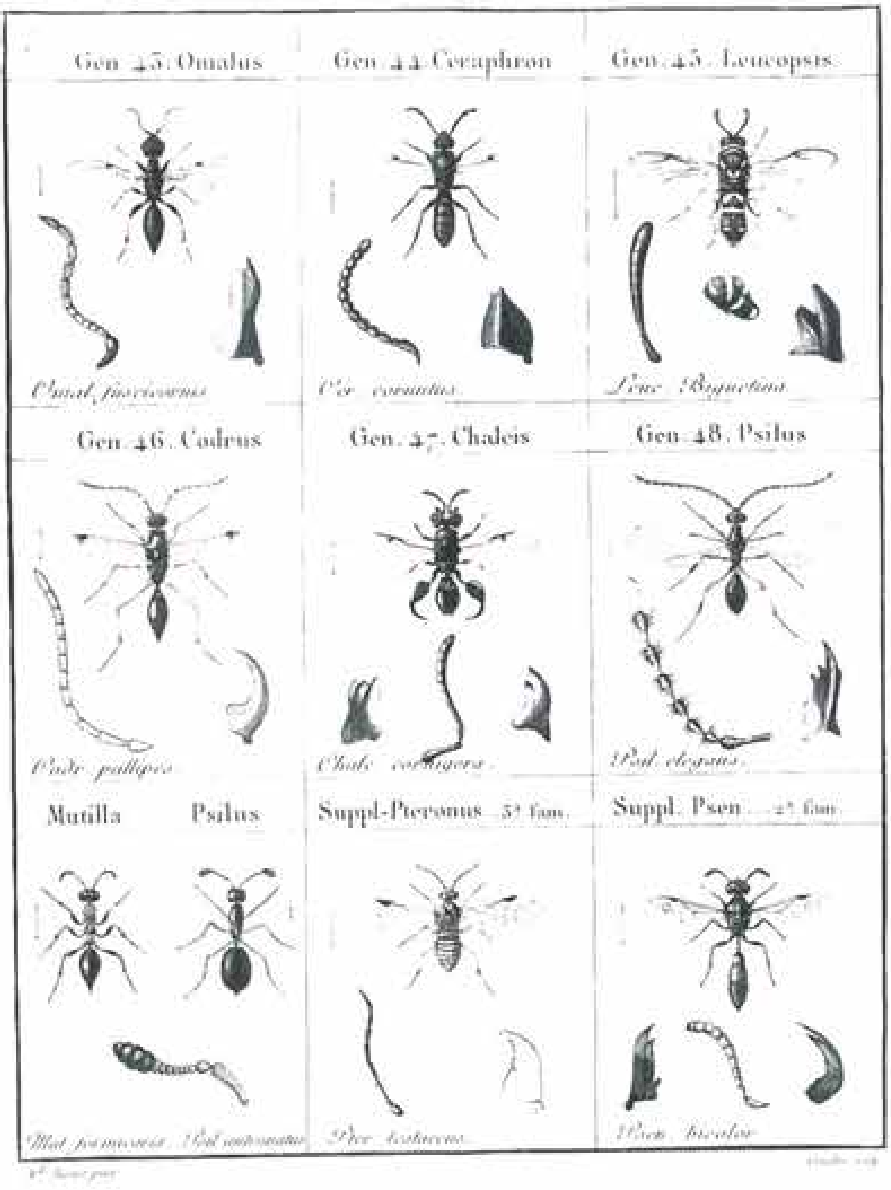
Au cours de cette période d'annexion, Genève, qui n'avait pu conserver ses magistrats et ses traditions politiques, tenta de se signaler à l'attention des étrangers comme un foyer de culture, fière de ses "gens de lettres", son Académie, ses pensionnats, ses périodiques "littéraires" ou encore ses sociétés savantes. Dans cette cité des Lumières, Jurine figure d'ailleurs en bonne place aux côtés des Marc-Auguste Pictet, Pierre Prevost, Jean Sénebier, Nicolas-Théodore de Saussure, Jean-Pierre Vaucher, Guillaume-Antoine Deluc et autres Odier ou Maunoir. Son cabinet de minéraux et d'insectes, qui passe pour l'un des plus riches et l'un des mieux ordonnés d'Europe, fait d'ailleurs l'admiration des visiteurs étrangers, notamment celle du Danois Bruun-Neergaard, de passage à Genève en 1801[11]. Aussi, lorsqu'il fut question, l'année suivante, de donner une nouvelle extension à l'Académie de Genève, par la création de huit chaires honoraires au sein de l'ancien Auditoire de Philosophie, Jurine se vit-il naturellement attribuer celle d'anatomie et de chirurgie. L'ancienne république reconnaissait ainsi le mérite d'un citoyen qui avait rendu de grands services à la collectivité comme chirurgien et comme démonstrateur d'anatomie. Jurine devait d'ailleurs justifier encore cette reconnaissance en s'occupant, en 1805, de la création d'une maternité à la rue des Barrières, et en donnant à plusieurs reprises un cours gratuit d'accouchement aux sages-femmes du département. Ce cours fut également pour lui l'occasion de rédiger un important «Mémoire sur l'allaitement artificiel», demeuré en partie inédit.

Reconnaissance scientifique et malheurs domestiques

A la reconnaissance obtenue comme praticien, Jurine chercha à ajouter le suffrage des savants, et notamment celui des académies étrangères. En 1807 parut enfin le premier volume, demeuré unique, de sa *Nouvelle méthode de classer les Hyménoptères et les Diptères*, sur laquelle il travaillait depuis plus de dix ans[12]. Dans cet ouvrage, qui portait sur un ordre d'insectes encore peu connu, même si Linné, Geoffroy et Fabricius avaient décrit nombre de genres et d'espèces, Jurine s'opposait à la classification artificielle de Fabricius, fondée notamment sur l'examen peu pratique des mandibules (système palpiforme). Il développait une systématique nouvelle mais d'inspiration linnéenne, basée sur l'examen des ailes des insectes, notamment sur la nervation, la forme et la connexion des cellules placées près du bord externe de l'aile, ainsi que sur les antennes et les mandibules. La plupart de ses genres et espèces devaient être repris par Latreille, dans le cadre de sa "méthode naturelle", puis par la plupart des entomologistes ultérieurs[13]. Les gravures de l'ouvrage, basées sur des dessins de sa fille Christine, apparaissent particulièrement remarquables pour l'époque (Fig. 2).

Mais en novembre de cette année 1807, Jurine eut la

Fig. 2 : Planche (en couleurs) de la *Nouvelle méthode de classer les Hyménoptères* (1807), gravée par Gaisler d'après des dessins de Christine Jurine. La représentation des "cellules" des ailes, et celle, agrandie, des mandibules et des antennes, devaient faciliter au lecteur l'identification du genre, dont l'espèce représentée était souvent inédite.



douleur de perdre son fils cadet André, âgé de 27 ans seulement et qui annonçait un avenir des plus brillants comme anatomiste, comme médecin et comme naturaliste. Ce fut pour lui un coup extrêmement rude, que, selon le témoignage de son ami Gosse, même l'histoire naturelle et la religion eurent de la peine à atténuer. Le chirurgien cessa peu après d'opérer, réduisit sa pratique à des consultations médicales et se contenta du titre de chirurgien consultant de l'Hôpital. Sans doute à l'âge de 57 ans n'était-il pas mécontent d'abandonner un art «dont l'exercice a ses fatigues et ses malheurs» (Pictet dixit). Peut-être ne se sentait-il d'ailleurs plus la main aussi sûre que par le passé.

A partir de 1809, Jurine se met en tout cas à publier davantage d'articles de médecine et de chirurgie, et se lance dans de nouvelles recherches d'envergure. C'est ainsi qu'il décide de participer au concours, lancé en octobre de cette année, pour le meilleur *Mémoire sur l'angine de poitrine.* Son travail, qui décrit cette maladie, dont il devait lui-même mourir, comme résultant d'un état névralgique des principaux nerfs de la poitrine, recevra en 1813 la médaille d'or de la Société de Médecine de Paris. En 1810, Jurine décide de participer au concours instauré par Napoléon dans le but de récompenser le meilleur ouvrage sur le croup. Deux ans plus tard, il se voit attribuer la moitié des 12.000 francs du prix, assortis de la proposition, qu'il refusa, de devenir médecin consultant de la famille impériale.

Le chirurgien genevois n'aura en réalité guère le temps de savourer son succès. A la fin de cette même année 1812, il perd en effet coup sur coup sa femme, puis sa fille Christine, excellente observatrice qui l'aidait dans ses recherches, et qui réalisait les planches de ses ouvrages. Choqué, et même effondré, le malheureux père faillit sombrer dans la mélancolie, et renoncer du même coup à toute activité de recherche. De fait, il n'aura plus le courage d'achever sa *Nouvelle méthode de classer les Hyménoptères et les Diptères,* dont beaucoup de planches sont demeurées inédites, ni la force de terminer son Mémoire sur la respiration des oiseaux. Il aura également bien du mal à publier son *Histoire des monocles.*

C'est dans sa foi religieuse que Jurine puise les forces nécessaires à surmonter cette épreuve, et c'est en se lançant dans de nouvelles recherches d'histoire naturelle qu'il tente d'oublier les sombres pensées qui assaillaient son esprit. C'est ainsi qu'il se lance dans la collecte et l'étude des poissons du lac Léman et d'autres lacs alpins, préparant une monographie qui ne sera publiée qu'après sa mort, en 1825.

Les bouleversements européens de 1814, qui permettent la restauration de l'indépendance genevoise, puis l'entrée de la ci-devant République dans la Confédération, trouvent Jurine convalescent. Se souvenant d'avoir été transféré en 1809 de la chaire d'anatomie à celle de zoologie, il entreprend alors de préparer sérieusement le cours que l'on attendait de lui, et qu'il était, selon l'expression de Gosse «bien capable de rendre des plus intéressants, soit par la facilité de son élocution, soit par la grande généralité de ses connaissances»[14]. Ses talents pédagogiques s'étaient en effet principalement exercés jusque-là dans le cadre de la Société des Arts[15].

Elu en 1814 dans le nouveau Conseil Représentatif, Jurine combat aux côtés de Pictet et Boissier pour la transformation de l'Académie en Université, mais ce projet échouera devant l'opposition conjuguée des conservateurs et des pasteurs. En 1816, il obtient cependant, avec ses amis novateurs, la création d'une chaire d'histoire naturelle en faveur d'Augustin-Pyramus de Candolle. Cette chaire regroupera dans un même enseignement la botanique et la zoologie, dont Jurine avait été jusque-là le titulaire. L'année suivante, soit en 1817, il démissionne du Conseil Représentatif, suite au refus des conservateurs d'instaurer un jury en matière criminelle.

A défaut d'enseigner, le professeur d'anatomie, puis de zoologie aura su former quelques disciples de talent, tant en chirurgie qu'en histoire naturelle. Aux côtés du médecin Jean-François Berger (1779-1833), l'ami de son fils André, on peut mentionner le chirurgien Jean-François Mayor (1779-1854), le botaniste Stefano Moricand (1779-1854), le naturaliste Louis Perrot (1785-1865), le cristallographe Frédéric Soret (1795-1865) et le médecin Charles Coindet (1796-1876) sans oublier l'entomologiste Pierre Huber (1777-1840). Sous la Restauration, Jurine s'efforça de les faire entrer successivement à la Société des Naturalistes et à la Société de Physique, afin qu'ils jouent un rôle plus actif dans la vie scientifique locale. Lui-même participa à la fondation, en octobre 1815, de la Société helvétique des Sciences naturelles, et en 1816 à celle de la Société littéraire de Genève, dont il fut président honoraire. Souffrant d'infirmités croissantes, il s'efforça néanmoins de poursuivre ses recherches scientifiques, et de mettre un point final à son *Histoire des monocles,* qui devait faire de lui un pionnier de l'étude des crustacés inférieurs et de la biologie lacustre. Il disparut, victime d'une angine de poitrine, le 20 octobre 1819, soit peu avant la publication de cet ouvrage, et seulement cinq jours après sa dernière communication à la Société de Physique.

La mort de Louis Jurine fut d'autant plus durement ressentie par ses collègues que cette perte semblait irrémédiable. A Genève, on ne retrouvera en effet plus guère de naturaliste aussi expert que lui à la fois en physiologie et en systématique, et aussi versé dans les différentes branches de l'histoire naturelle. L'intégration à la SPHN de Sébastien Jurine (1777-1846), son unique enfant survivant, n'aura qu'une valeur d'exorcisme : le nouvel élu n'avait en effet guère manifesté jusque-là de vocation scientifique particulière. André-Louis (1803-1862), petit-fils du naturaliste, envisagea un temps d'achever l'ouvrage sur les poissons du lac, mais finit par y renoncer : il fera ultérieurement carrière dans la magistrature.

Quant aux disciples, que ce soit en chirurgie, en physiologie ou en histoire naturelle, aucun n'atteindra l'envergure du maître, hormis peut-être Pierre Huber. Jean-François Berger, le plus ancien, sombrera dans la mélancolie et la dépression. Frédéric Soret, le plus brillant sans doute, abandonnera pratiquement la recherche après 1822, pour entamer une brillante carrière politico-mondaine à la cour de Weimar, puis à Genève. Les autres deviendront d'honnêtes praticiens ou chercheurs, exerçant chacun dans un domaine particulier, selon les exigences d'une spécialisation croissante.

Quant au remarquable cabinet Jurine, il ne servira guère jusqu'en 1846, date à laquelle les minéraux furent vendus à Paris, tandis que les insectes étaient légués au Muséum de Genève. Enfin, les papiers personnels de Louis Jurine, qui comprenaient tant de travaux inédits ont fini par disparaître, ce qui nous interdit à jamais de reconstituer l'ensemble de l'oeuvre de ce savant méconnu. Mais les fragments qui subsistent ne laissent guère de doutes quant aux talents de leur auteur.

Notes

1. Intitulé du concours lancé en 1787 par l'Académie royale de chirurgie. Par suite des circonstances politiques, le mémoire de Jurine n'a été publié qu'en 1798.
2. «Extrait des expériences de Jurine sur les chauves-souris qu'on a privées de la vue» par Peschier, in *Journal de Physique*, t. 46, févr. 1798, pp. 145-148.
3. Quatre années séparent en effet la sortie de l'Auditoire de Belles-Lettres de l'obtention de la maîtrise en chirurgie. En 1814 en tout cas, Jurine parlera à son neveu Aimé Martin «d'une expérience antique, fondée sur 45 [et non 40] ans de pratique» (BPU : Ms suppl. 140, f° 71-72), ce qui paraît confirmer cette hypothèse de l'apprentissage.
4. Archives d'Etat de Genève : Notaire R.G. Prevost, vol. 3, p. 103, 3 août 1778.
5. Terme tiré d'une lettre à Gosse du 6 mai 1779 (BPU : Ms fr 2617, envel. 4).
6. Surnom donné à Charles Bonnet.
7. Pictet le laisse d'ailleurs clairement entendre dans son *Discours d'ouverture*..., p. 12.
8. *Discours d'ouverture* ..., p. 13.
9. Le mémoire de Spallanzani sur la question avait été adressé à Sénebier pour être communiqué aux Genevois, et notamment à H.-B. de Saussure.
10. Jurine n'assista pas à la chute de l'ancienne république genevoise, puisqu'il se trouvait alors à Berne (sept. 1797 - sept. 1798).
11. cf T.C. Bruun-Neergaard, *Journal de mon voyage avec le citoyen Dolomieu*, Paris, 1802, pp. 114-118.
12. En réalité, cet ouvrage était pratiquement terminé depuis 1799.
13. Jurine, qui avait établi près d'une centaine de genres, craignait de les avoir trop multipliés. Il était pourtant encore loin des milliers de genres recensés aujourd'hui !
14. Lettre à Wyttenbach, 6 oct. 1814 (BBB : Mss h.h. XIV, 150, 6, n° 752).
15. A signaler toutefois un petit cours d'entomologie, donné en 1797 au jardin botanique de la SPHN et un cours d'anatomie donné en 1802 à l'Académie.

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The lost papers of Louis Jurine : A note

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Mr C.W.P. Mac Arthur, whose memoir on Louis Jurine's lost papers on the hearing and the parasites of bats is awaiting publication*, was invited to address the symposium. Speaking *ex tempore* he said that the story of Jurine had been exposed by Dijkgraaf, Galambos and Griffin, then expanded by Théodoridès, who had revealed that Mangili, Spallanzani's successor at Pavia, had accepted the hearing theory of his predecessor, first advanced by Jurine. It was difficult, however, to find this valuable paper in natural history libraries, as it had been published in the proceedings of an historical conference on Italian neurology and it was marred for those reliant on its English summary by a mistranslation of the French text, which made Jurine achieve his results by *cutting off*, instead of *blocking* the ears of his subjects. Following Théodoridès, much research had brought new information on the subject : Castellani's publication of Spallanzani's memoir of October, 1793, addressed to the Geneva Society of Natural History, had been followed by the same scholar's edition of Spallanzani's notebooks; the correspondence, outward and inward, of Spallanzani had appeared in full, in twelve volumes, edited by Di Pietro; research into the Société Philomathique of Paris by Mandelbaum had brought to light that Jurine, in 1798, had read to the Society his papers of 1794, at a meeting attended by Duméril, though not by Cuvier, the first for three months from which the latter had absented himself. The speaker himself had clarified the role of Jean Peschier and had discovered Jurine's unpublished reply to Cuvier's dismissal of his declaration that bats directed themselves by their hearing. The speaker also referred to his unsuccessful search among Jurine's descendants at Bordeaux for his papers and his daughter's accompanying anatomical drawings of bats and of their parasites; he suggested that success might attend enquiry among descendants of Jurine in the Vincens-Saint-Laurent line.

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* Mac Arthur, C.W.P., «Louis Jurine's papers on the hearing of Bats and on their parasites : a retrospect with new information», *in* R. SIGRIST, V. BARRAS & M. RATCLIFF (Ed.), *Louis Jurine, chirurgien et naturaliste (1751-1819)* [à paraître, 1997]

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The Magic Well of bat echolocation

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Abstract. Jurine's conclusion that bats use their ears to avoid obstacles was validated by 1940 measurements using the then-new method of recording electrical activity generated by the cochlea when sounds move the ear drum. Bat cochleas were shown to respond to sound frequencies far above those audible to man, cats and guinea pigs. Silent motion pictures will be presented showing the behavior of flying bats before and after their eyes were covered or their ears were plugged, experiments of the sort Jurine must have performed in 1794, along with sound motion pictures that showed for the first time that bats emit ultrasonic sounds whose repetition rate increased greatly just before obstacles were avoided. Recent discoveries of the use of echolocation to capture moving prey, and the adaptations of echolocation to the varying lifestyles of different groups of bats and cave dwelling birds will also be reviewed.

Karl von Frisch called the behavior of honeybees a Magic Well, because the more he learned about their communication and orientation the more surprising and significant discoveries came to light. Louis Jurine and his successors opened up a comparable Magic Well, because the more we learn about what bats learn from the echoes of their orientation sounds, the more surprising echolocation becomes. So many developments have occurred since the 1940s that I can only supplement Dr. Galambos' account of his physiological experiments by reviewing what strikes me as the principal surprises since 1941, emphasizing how unexpected these discoveries were at the time they were achieved. More complete reviews are available by MOSS & SCHNITZLER (1994) and in the volumes edited by BUSNEL (1967), BUSNEL & FISH (1980), and NACHTIGALL & MOORE (1988).

First and in many ways foremost were the quiet and perceptive observations and experiments conducted by Sven Dijkgraaf under difficult wartime conditions. He noticed the audible component of bats' ultrasonic orientation sounds and showed by experiments quite similar to ours that these were closely linked to obstacle avoidance. This demonstrated, among other things, that careful and thoughtful observations can often suffice to solve important scientific problems without what we often assume to be essential instrumentation. As we wrestle with some of the more intricate problems raised by later investigations of echolocation it is constructively sobering to recall how much Dijkgraaf learned without any high tech apparatus (DIJKGRAAF, 1943, 1946). It is remarkable that none of the many students of bats and their orientation had previously noticed the audible components of the orientation sounds and recognized that they helped to explain how bats avoid obstacles in the dark.

G.W. Pierce did not have a cathode ray oscilloscope, but by 1945 these instruments were readily available from wartime applied research projects, and their use revealed how short was the duration of the ultrasonic sounds we had discovered in the late 1930s. Equally important, oscilloscope displays showed that the orientation sounds of vespertilionid bats were not noise bursts but frequency modulated chirps in which the frequency drops by about one octave in one or two milliseconds (GRIFFIN, 1946).

It is difficult, but important, to remind ourselves that for many years bat echolocation was viewed almost solely as a collision warning system. All biologists knew that bats in temperate latitudes feed on flying insects, but in the early 1950s the notion that they might use echolocation to detect small flying insects and to guide their complex interception maneuvers seemed quite incredible. Serious consideration of this possibility required studying the orientation sounds of bats out-of-doors where they were pursuing their normal insect prey. But such an enterprise seemed truly outrageous because we could only study the ultrasonic sounds of bats with expensive laboratory apparatus that required AC power. To anyone familiar with modern apparatus it seems ludicrous how much effort was necessary in 1951 for the first acoustic studies of insect pursuit under natural conditions, as I have described in detail on pp. 174-202 of *Listening in the Dark* (GRIFFIN, 1958).

Overcoming inhibitions about taking our best apparatus into the field led to the discovery that *Eptesicus fuscus* and *Myotis lucifugus* increase the repetition rate of their ultrasonic pulses to a much greater extent than when they dodge small obstacles in the laboratory, and furthermore that the frequency pattern of the individual pulses are also adapted to the changing requirements of insect detection, pursuit and capture (GRIFFIN, 1953). But this did not suffice to convince everyone that bats really used echolocation to capture small flying insects. One commentator remarked that when his dog chased a rabbit it also increased the repetition frequency of its yelps, without anyone maintaining that the chase was guided by echolocation.

A few years later in collaboration with Frederic Webster and several students, we learned how to induce reasonably normal insect catching in a laboratory flight room, something I had repeatedly tried but failed to accomplish in earlier years. This enabled us to demonstrate conclusively that at least under some conditions *Myotis lucifugus* rely exclusively on echolocation to intercept fruit flies at rates of several per minute (GRIFFIN, WEBSTER & MICHAEL, 1960). Prey capture by echolocation has since been studied extensively in a variety of species, and it turns out to be variable with specific adaptations for several types of hunting, as reviewed by SCHNITZLER & HENSON (1980).

Another series of surprises stemmed from comparative studies of the many and diverse groups of bats. F.P. MOEHRES (1953) opened this door by finding that the orientation sounds of the horseshoe bats of genus *Rhinolophus* had much longer durations - up to 100 milliseconds, and that the frequency was very nearly constant. Previously it had seemed that "a bat is a bat", and that the odd looking faces in no way justified the notion that their echolocation might be significantly different from the bats of the family Vespertilionidae. This was followed by KULZER (1958) who found that bats of the suborder Megachiroptera do not use echolocation, except for the genus *Rousettus* which guide their flight in dark caves and similar man made tunnels by clicks audible to human ears. Moehres' discovery of the constant frequency signals of *Rhinolophus ferrumequinum* was followed up by Schnitzler's demonstration of Doppler shift compensation by which these bats vary the frequency of their emitted signals so that Doppler shifted echoes fall in a narrow region of high auditory sensitivity. Remarkably enough one species of the neotropical genus *Pteronotus*, but not other species of this genus, have evolved a similar system of long duration, constant frequency signals as well as Doppler shift compensation (SCHNITZLER, 1973).

The lack of interest in comparative studies was so strong that in the early 1950s I was advised by outstanding experts that it would be a foolish waste of time and money to take my bulky and delicate apparatus to Panama for a first look at the rich variety of neotropical bats. When I nevertheless did so, one of the first surprises was to find that the abundant *Carollia perspicillata* avoided small obstacles with agility comparable to my familiar *Myotis lucifugus*, but without emitting any detectible sounds. I was back with Spallanzani and Jurine. Plugging the ears disoriented *Carollia*, and I thought I could hear faint signals from a crude bat detector that translated high frequency sounds into audible signals. But when I later developed two dozen reels of film depicting cathode ray oscillograph traces there was nothing clearly rising above the background noise. The human auditory system could reach down into the noise and detect the faint translated pulses, but I had no objective proof that *Carollia* emitted any orientation sounds at all.

The problem was one of microphone sensitivity, and shortly afterwards plastic diaphram electrostatic microphones became available and revealed that *Carollia* and other fruit eating bats of the neotropics orient their flight by means of low intensity orientation sounds. They do not pursue flying insects, and apparently these faint sounds suffice for obstacle avoidance. For these "whispering bats" it seems that echolocation really is only a collison warning system (GRIFFIN & NOVICK, 1955). Other investigations have shown that some species of bats detect their insect prey by passive listening, and some use vision to a much greater extent than seemed likely in 1940 as Galambos and I watched deafened *Myotis lucifugus* blunder into the walls of our flight room.

Other important developments have included the neurophysiology of bat echolocation, beginning with GRINNELL (1963), extended by Suga beginning in the 1960s, and ramifying to the refined experiments of Suga and many other investigators in later years, as reviewed by SUGA (1994) and several chapters in POPPER & FAY (1994). Then Asher Treat and Kenneth Roeder discovered that some insects have evolved countermeasures against predation by echolocating bats (reviewed by ROEDER, 1967). The most common of these countermeasures is auditory sensitivity to the orientation sounds of bats and evasive maneuvers that often allow the insect to escape capture. But a few species of insects that can hear approaching bats emit brief ultrasonic clicks that reduce the effectiveness of the bat's interception maneuvers. These clicks may interfere with echolocation, or in some cases they may serve as warning signals conveying the information that this is a bad tasting or even poisonous insect, as reviewed by SURLYKKE & MILLER (1985).

Another major advance has been the development by Simmons of training methods by which bats can be asked what they can and cannot detect by echolocation, and the extent to which they can discriminate between targets on the basis of their echoes. This technique has opened up whole new vistas in our understanding of bat echolocation. For instance it allowed Simmons to confirm that bats, like artificial radar and sonar systems, determine range to a target by the time delay between emission of an orientation signals and the return of its echo (SIMMONS, 1973). Similar experiments are being applied to a problem posed, but not solved, by some experiments that I and my colleagues carried out in the early 1960s.

We had inquired to what extent bats could discriminate between similar small targets. This problem is critical for bats hunting insects by echolocation, because almost all insects are on the order of a wavelength in size, so that they generate echoes that vary enormously with angle of view and with the orientation of the insect's body and wings relative to the direction from which sounds impinge. We first trained *Myotis lucifugus* to catch mealworms tossed up as they flew past in a large flight room. When they were catching almost every tossed mealworm we randomly interspersed plastic disks of roughly the same size. After several days of practice the bats were catching almost all the mealworms but rejecting most of the disks, even though the echoes of both types of target varied by a hundred fold or more depending on their orientation. The spectral intensity of the echoes from the edible and inedible targets overlapped almost totally (GRIFFIN, FRIEND & WEBSTER, 1965). Simmons and his colleagues have employed much more refined methods of analyzing echoes from mealworms and disks than were available 30 years earlier and found that fine details of the timing of glints or peaks in echo amplitude differ significantly between target shapes. This may explain how bats distinguish between different species of insects by echolocation (reviewed by SIMMONS, 1989).

In other experiments Simmons and his colleagues have attempted to measure the smallest time differences that bats can distinguish. They developed apparatus that returns alternate echoes at slightly different time delays. These echoes simulate what a bat would receive from a target that jitters in range between successive emission of orientation sounds. The results of these jitter experiments indicate that *Eptesicus fuscus* can detect differences in echo return time as small as 10 nanoseconds (SIMMONS *et al.*, 1990). This is much smaller than any other known time discrimination achieved by animal or human brains. For instance, the time differences that we employ in binaural directional discrimination are on the order of a microsecond, about 100 times greater than these thresholds of jitter detection. It is not at all surprising that these experiments have been severely challenged (see POLLAK, 1993 and SIMMONS, 1993), for it is very difficult to imagine how a bat brain could achieve such remarkable temporal sensitivity.

In the 1790s the conclusion that bats use their ears to detect obstacles seemed just as incredible as detection of 10 nanosecond time differences seems to neurophysiologists of the 1990s. If further experiments and replications confirm Simmons' conclusions, his critics will turn out to have played a role comparable to that of Georges Cuvier whose ridicule of Jurine and Spallanzani was so effective that they were vindicated only after a century and a half, and the development of wholly new techniques of acoustical analysis. Let us hope that we will not have to wait so long for a resolution of this question.

In short, the echolocation of bats continues to provide surprise after surprise, as investigators apply increasingly penetrating methods of data gathering and analysis. I doubt whether this magic well has yet run dry, and who knows what will be discovered next ?

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The 1939-40 bat experiments that validated Jurine's claim

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Abstract. In 1939 D. R. Griffin and the author conducted a series of experiments on flying bats like those Jurine performed a century and a half earlier, and confirmed his finding that bats deprived of hearing cannot avoid obstacles. Using modern physiological procedures and a collection of physical instruments not available to Jurine we then established, in addition, that bat cochleas generate electrical responses to sounds we cannot hear. This paper describes in detail, using as illustrations some of the original protocols, the experiments that provided the first direct proof that Jurine's explanation was correct.

THE CLAIM : «From these experiments the author concludes : First, that the eyes of the bat are not indispensably necessary to it for finding its way; secondly, that the organ of hearing appears to supply that of sight in the discovery of bodies, and to furnish these animals with different sensations to direct their flight, and enable them to avoid those obstacles that may present themselves» (from "Experiments on Bats deprived of Sight by M. de Jurine" Phil. Mag., 1: 136-30, 1798).

INTRODUCTION

This paper is an account of the scientific enterprise that began a half century ago when Don Griffin asked me whether bat ears respond to sounds above the upper limit of our hearing and ended 18 months later after several experiments had given us clear and consistent answers. These answers were first aired publicly in 1941 at a scientific meeting in Philadelphia (GALAMBOS & GRIFFIN, 1940a, b; GRIFFIN & GALAMBOS, 1940) and then published (GALAMBOS, 1941b, 1942, 1943a, b; GRIFFIN & GALAMBOS, 1941; GALAMBOS & GRIFFIN, 1942). Some years later Griffin summarized the material in a book (GRIFFIN, 1958) and published a brief historical account of our joint efforts (GRIFFIN, 1980). What has not appeared so far, however, are details of the order in which the experimental facts emerged – the dynamics of the discovery process, so to speak. Which experiment came first ? Where was it done, and under what circumstances ? And so on. At the suggestion of the editor of *Le Rhinolophe* I answer questions of this kind in this contribution to the issue of his journal honoring Jurine's discovery 200 years ago.

THE HARD DATA

Two documents supply the main facts in this report : a 300-page laboratory notebook, and the 15-minutes of moving pictures Griffin and I made in 1940 showing flying bats. My notebook, partly summarized in Figure 1, describes, among other things, the bat cochlear potential experiments performed between April 1939 and May 1940. Its entries also make possible a few inferences about the behavioral experiments under way elsewhere at the same time. The contemporary movie showing flying bats, which was thought to be lost until 1991, is a similarly useful record; it succinctly illustrates the many details of the behavioral experiments –the reversible blinding, deafening and silencing of the animals; the altered behavior following these deprivations; and the actual sounds bats produce during successful obstacle avoidance (a videotape copy of these movies was donated to the Jurine archives in Geneva at the time of the Symposium). Unfortunately no notebook describing and dating the behavioral experiments seems to have survived. Other available material includes copies of letters exchanged between us; letters to and from editors and others; reprint requests and/or written comments about the experiments; and clippings of newspaper and magazine reports.

We also retain vivid personal memories-soft data, which we retrieve and compare from time to time, and are amused at how differently two people retell an adventure they shared a half century earlier. But neither of us recalls the circumstances under which our collaboration began. We were graduate students in 1939, two of perhaps 20 in the Harvard University Biology Department in Cambridge, and busily learning our trade. Griffin and G.W. Pierce, a physics professor, had just discovered that bats emit ultrasonic ("supersonic" in those days) cries, but they had not been successful in showing that the flying animals «detect high frequency sounds reflected from objects in their path» (PIERCE & GRIFFIN, 1938). I was then working at the Harvard Medical School in Boston with Professor Hallowell Davis on a new electrophysiological test of hearing that used anesthetized guinea pigs. Presumably it was in early April, 1939, that we decided to find out whether bat ears detect the high frequency cries they emit.

THE COCHLEAR MICROPHONIC EXPERIMENTS

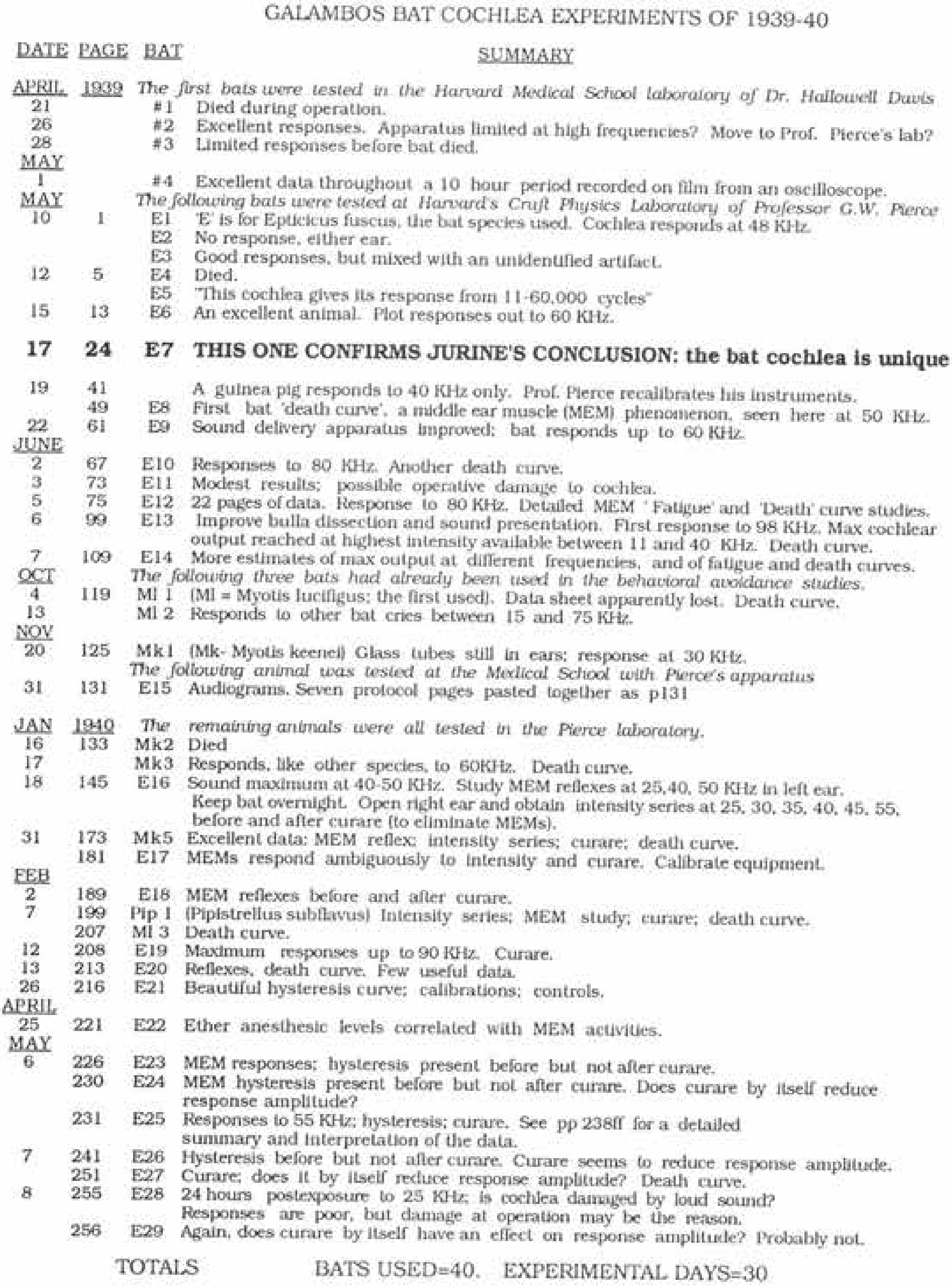
The first experiments tested the proposition that bat cochleas respond to high-frequency sounds inaudible to the human ear. The methods used were minor adaptations of the then-standard guinea pig routines : the cochlea is visualized in the anesthetized animal; active and indifferent electrodes are fixed in place; auditory stimuli are delivered to the ear; and observations are made on the amplified electrical activity cochleas emit when stimulated by sounds.

In Figure 1 each entry summarizes the outcome of one such experiment on a given animal: altogether, 40 bats (4 species) and one guinea pig were studied on 30 experimental days spread through 13 months. The very first bat to survive long enough to be tested responded readily to the highest sound frequencies the available apparatus could generate. The enterprise was then moved across the Charles River to Harvard's Cruft Physics laboratory, where Professor Pierce's specialized high-frequency instruments quickly established the unique high frequency sensitivity of bat cochleas. After January, 1940, emphasis shifted away from frequency responsivity to the activity of the middle ear muscles – bats have unusually large ones – and to the possible damaging effects on the cochlea of loud sounds and the drug curare. Two publications (GALAMBOS, 1941b; 1943a) deal with these experiments.

The experiment of May 17, 1939, the eleventh in the series, is highlighted in Figure 1 because it is the first to provide unequivocal experimental support for Jurine's claim that the ear is essential for bat obstacle avoidance. Let me describe the experiment here. The bat, an adult *Eptesicus fuscus*, had been awakened from hibernation in a laboratory cold room and anesthetized by an intraperitoneal injection of Nembutal (0.04 ml of the then-available commercial solution). The ventral surface of the left bulla was exposed and a silver wire electrode was pushed through a small hole drilled on its surface until it reached the cochlea; this goal was reached when vigorous electrical activity was aroused by jingled keys and hissing sounds (noises whose ultrasonic frequency components provoke impressive startle responses from normal bats resting on a wall). The electrode remained fixed in this position from 11:45 A.M. to 6:45 P.M., when the animal was dead 25 minutes after an intraperitoneal injection of Bouin's solution, a histological fixative. Of the many measurements made during that afternoon three are shown in Figure 2, which is a copy of two graphs pasted into the protocol book. In both plots the ordinate is the meter-reading of Professor Pierce's ultrasonic voltmeter, which measured the cochlear electrical output (NOYES & PIERCE, 1938), and the abscissa is the sound frequency emitted by the magnetostriction bars of his ultrasonic sound generator, which provided the stimuli delivered into the bat's ear (PIERCE & NOYES, 1938).

The upper graph in Figure 2 describes the decline of the cochlear response to a 28,000 Hz tone presented continuously for 25 minutes following injection of the histological fixative; this is a control measurement that shows the meter readings come from normal living tissue, and not after death. The bottom graph plots the cochlear outputs measured at noon and at 5:45 P.M.; different symbols are used, and they overlap, which demonstrates the long-time stability of both preparation and apparatus, and the fact that the upper limit of hearing had not yet been reached at 60,000 Hz, the highest frequency that particular model of the Pierce device could generate (at 2:30 P.M. that day the cochlea had responded at 80,000 Hz to the noise made by compressed air escaping through a small jet).

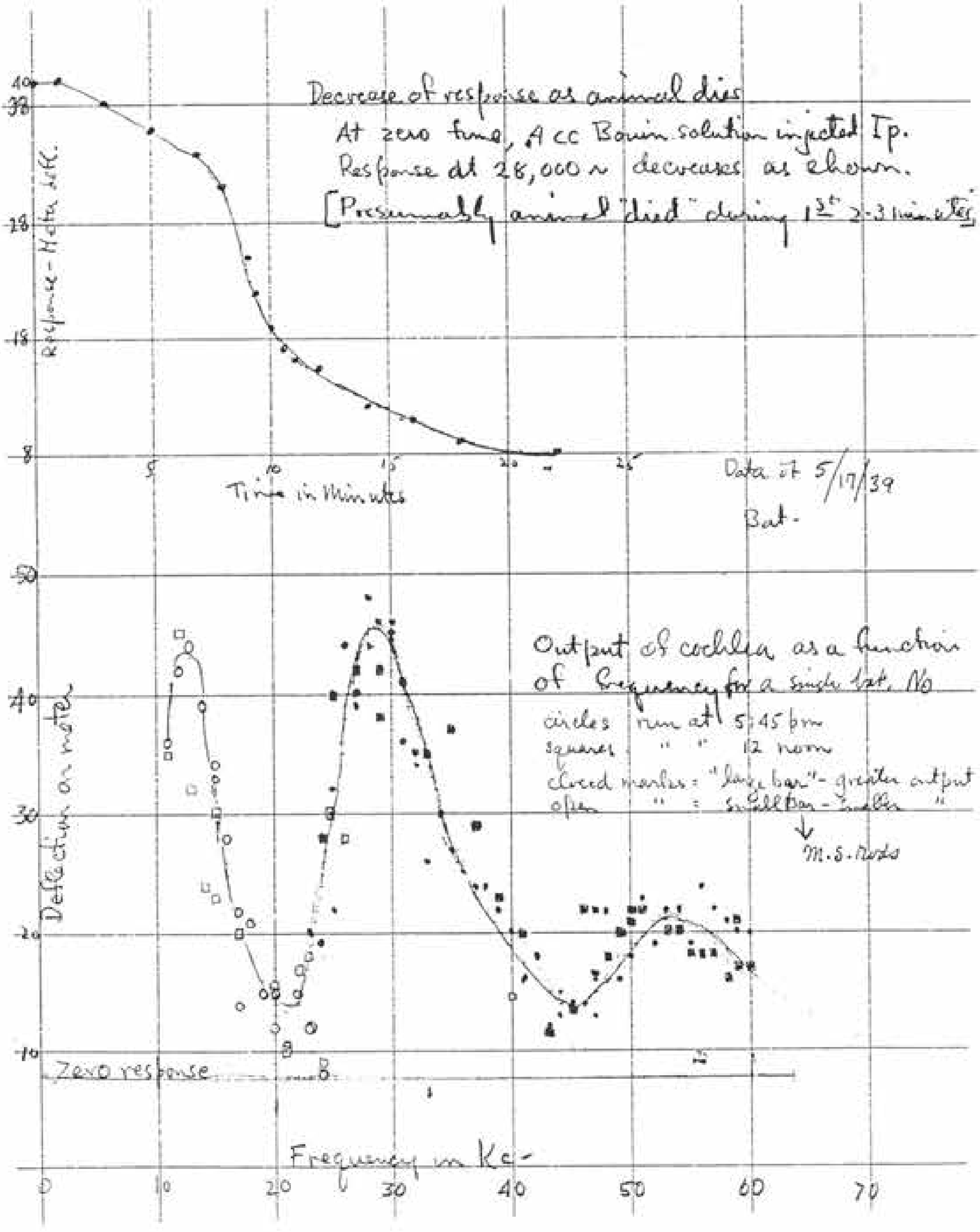
Fig. 1 : Chronological list of the 1939-1940 bat cochlear microphonic experiments. See text for details.



GALAMBOS BAT COCHLEA EXPERIMENTS OF 1939-40

DATE	PAGE	BAT	SUMMARY
APRIL	1939		*The first bats were tested in the Harvard Medical School laboratory of Dr. Hallowell Davis*
21		#1	Died during operation.
26		#2	Excellent responses. Apparatus limited at high frequencies? Move to Prof. Pierce's lab?
28		#3	Limited responses before bat died.
MAY			
1		#4	Excellent data throughout a 10 hour period recorded on film from an oscilloscope.
MAY			*The following bats were tested at Harvard's Cruft Physics Laboratory of Professor G.W. Pierce*
10	1	E1	'E' is for Epticicus fuscus, the bat species used. Cochlea responds at 48 KHz.
		E2	No response, either ear.
		E3	Good responses, but mixed with an unidentified artifact.
12	5	E4	Died.
		E5	"This cochlea gives its response from 11-60,000 cycles"
15	13	E6	An excellent animal. Plot responses out to 60 KHz.
17	**24**	**E7**	**THIS ONE CONFIRMS JURINE'S CONCLUSION: the bat cochlea is unique**
19	41		A guinea pig responds to 40 KHz only. Prof. Pierce recalibrates his instruments.
	49	E8	First bat 'death curve', a middle ear muscle (MEM) phenomenon, seen here at 50 KHz.
22	61	E9	Sound delivery apparatus improved: bat responds up to 60 KHz.
JUNE			
2	67	E10	Responses to 80 KHz. Another death curve.
3	73	E11	Modest results; possible operative damage to cochlea.
5	75	E12	22 pages of data. Response to 80 KHz. Detailed MEM 'Fatigue' and 'Death' curve studies.
6	99	E13	Improve bulla dissection and sound presentation. First response to 98 KHz. Max cochlear output reached at highest intensity available between 11 and 40 KHz. Death curve.
7	109	E14	More estimates of max output at different frequencies, and of fatigue and death curves.
OCT			*The following three bats had already been used in the behavioral avoidance studies.*
4	119	Ml 1	(Ml = Myotis lucifigus; the first used). Data sheet apparently lost. Death curve.
13		Ml 2	Responds to other bat cries between 15 and 75 KHz.
NOV			
20	125	Mk1	(Mk- Myotis keenei) Glass tubes still in ears; response at 30 KHz.
			The following animal was tested at the Medical School with Pierce's apparatus
31	131	E15	Audiograms. Seven protocol pages pasted together as p131
JAN	1940	*The*	*remaining animals were all tested in the Pierce laboratory.*
16	133	Mk2	Died
17		Mk3	Responds, like other species, to 60KHz. Death curve.
18	145	E16	Sound maximum at 40-50 KHz. Study MEM reflexes at 25,40, 50 KHz in left ear. Keep bat overnight. Open right ear and obtain intensity series at 25, 30, 35, 40, 45, 55, before and after curare (to eliminate MEMs).
31	173	Mk5	Excellent data: MEM reflex; intensity series; curare; death curve.
	181	E17	MEMs respond ambiguously to intensity and curare. Calibrate equipment.
FEB			
2	189	E18	MEM reflexes before and after curare.
7	199	Pip 1	(Pipistrellus subflavus) Intensity series; MEM study; curare; death curve.
	207	Ml 3	Death curve.
12	208	E19	Maximum responses up to 90 KHz. Curare.
13	213	E20	Reflexes, death curve. Few useful data.
26	216	E21	Beautiful hysteresis curve; calibrations; controls.
APRIL			
25	221	E22	Ether anesthesic levels correlated with MEM activities.
MAY			
6	226	E23	MEM responses; hysteresis present before but not after curare.
	230	E24	MEM hysteresis present before but not after curare. Does curare by itself reduce response amplitude?
	231	E25	Responses to 55 KHz; hysteresis; curare. See pp 238ff for a detailed summary and interpretation of the data.
7	241	E26	Hysteresis before but not after curare. Curare seems to reduce response amplitude.
	251	E27	Curare; does it by itself reduce response amplitude? Death curve.
8	255	E28	24 hours postexposure to 25 KHz; is cochlea damaged by loud sound? Responses are poor, but damage at operation may be the reason.
	256	E29	Again, does curare by itself have an effect on response amplitude? Probably not.
	TOTALS		BATS USED=40. EXPERIMENTAL DAYS=30

Fig. 2 : Results of the May 17, 1939 bat cochlea experiment. See text for details.



Decrease of response as animal dies
At zero time, A cc Bouin solution injected Ip.
Response at 28,000 ~ decreases as shown.
[Presumably animal "died" during 1st 2-3 minutes]

Data of 5/17/39
Bat.

Output of cochlea as a function of frequency for a single bat. No
circles run at 5:45 pm
squares " " 12 noon
closed marks = "large bar" - greater output
open " = small bar - smaller "
M.S. Notes

Figure 3 assembles the many control measurements performed on that and earlier days (I called them "checks", a term used by my Oberlin college mentor, the psychology professor R.H. Stetson); in the notebook it is a separate sheet pasted near the graphs. The controls, in summary, are these: sounds produced by galton whistles and air-jet noise (and jingling keys, tearing pieces of paper, and the cries of another bat) were as effective as Pierce's magnetostriction rods in generating cochlear electric responses; simply blocking the sound path between Pierce's generator and the bat's ear with a sheet of paper reduced or abolished the response; there was no response if the active electrode was not in contact with a living cochlea; and the response systematically declined to zero as the animal died. Obviously I was convinced by May 17 that bats perceive their high frequency cries. An entry on page 22 of my notebook quotes me as asserting, on the previous day, May 16, «... insectivorous [bats] have cochlea developed for perceiving high frequencies» in a conversation with Professor Glover M. Allen, then the curator of mammals at the Museum of Comparative Zoology. There is no record of when Griffin, who was always the more conservative interpreter of our data, similarly concluded that bats hear the sounds he had discovered.

THE BEHAVIORAL EXPERIMENTS AND THE RECORDING OF BAT CRIES

The summer of 1939 found us separated, with Griffin working on bat obstacle avoidance at the E. N. Huyck Preserve in Rensslerville, N. Y., and I studying invertebrate smooth muscle mechanics at the Bermuda Biological Station (GALAMBOS, 1941a). We came back together in September, a month of important distractions – Hitler had just invaded Poland – but by early October the bat behavioral studies must have been in full swing because the animals that yielded cochlear potentials during October and November had also served as subjects in the behavioral studies (see Figure 1). Griffin describes these behavioral experiments in his book (GRIFFIN, 1958 : 66-74), and I have only one anecdote to add to his account. We regularly sewed glass tubes into the ear canals so that the bat could be reversibly deafened by plugging the tube with a piece of thread. In one bat he inserted tubes that delivered sounds from the right side of the head into the left ear, and from the left side into the right ear; amazingly the animal still avoided obstacles remarkably well.

THREE ABSTRACTS

In the fall of 1940 we decided to present our findings at the annual meeting of the American Society of Zoologists scheduled for January, 1941 in Philadelphia, and on October 29 we submitted the following three abstracts to its Secretary, L.V. Domm. Evidently we had decided by that time – 18 months after the project started – that the obstacle avoidance, sensory deprivation, and ultrasonic cry experiments had all yielded firm and satisfactory conclusions.

The supersonic cries of bats. Robert Galambos
and Donald Griffin, Harvard University
(Introduced by A.C. Redfield).
(Lantern; 15 min.)

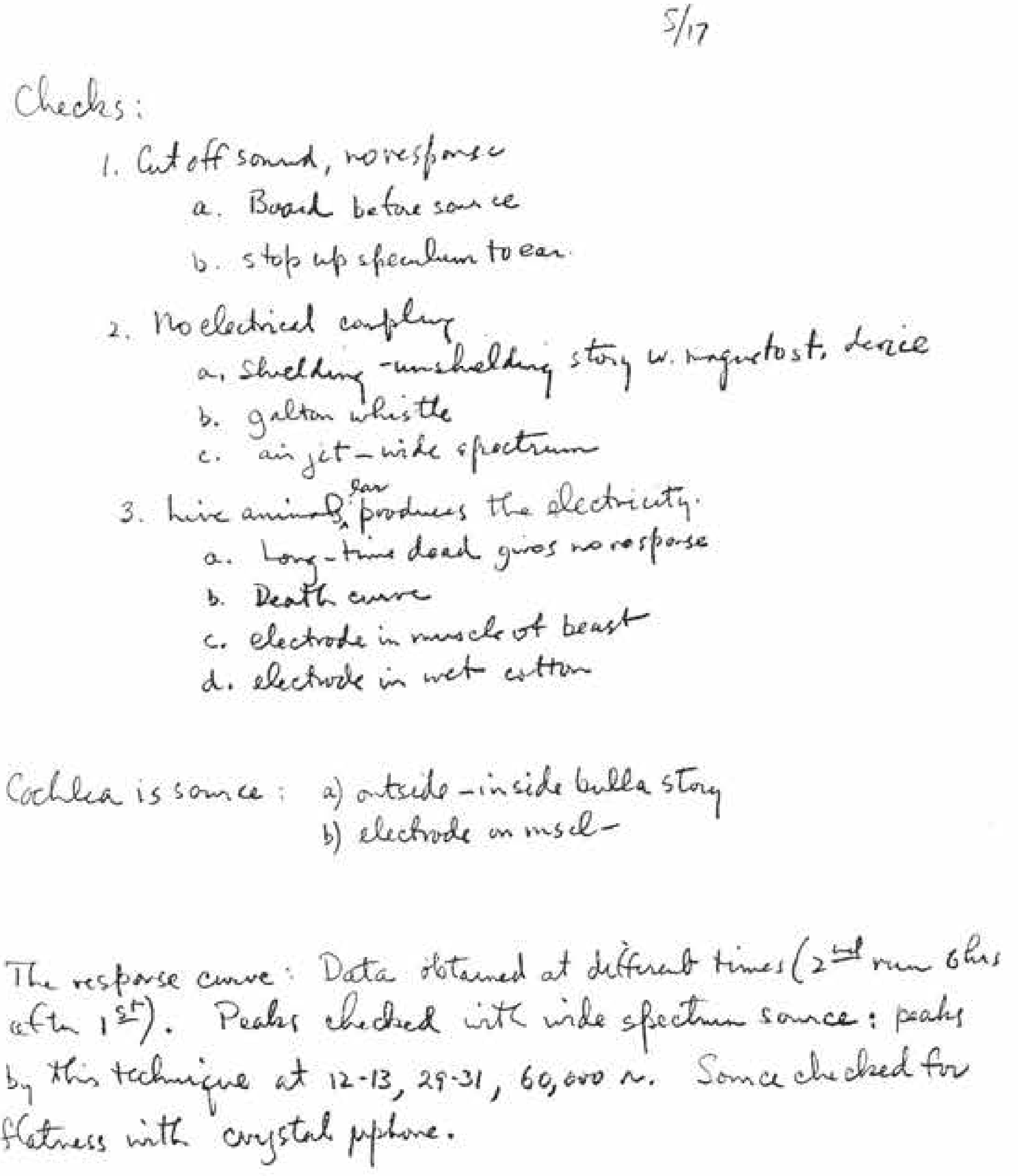
The supersonic cries of bats have been studied with a thermionic device which both converts supersonics into audible sound and makes possible its recording on paper tape. An active bat emits sound frequencies throughout the region 30-70 kc. Of all these, the frequencies near 50 kc. are most intense. Emission is in the form of discrete bursts, each lasting about one-fiftieth of a second. The rate at which these bursts appear varies with the location of the animal in space. Resting bats emit about 5 bursts per second; bats flying in unobstructed space, 25-35; bats approaching obstacles, 50-60. A marked drop in rate of emission of supersonic bursts occurs just before bats dodge obstacles in 90% of the cases; a similar change in rate occurs in only 20% of the cases where bats strike obstacles. Audible sounds practically never were emitted during flight.

This evidence supports the theory that flying bats detect obstacles in their path by (1) emitting supersonic cries, (2) hearing these sound waves reflected back to them by the obstacles, and (3) localizing the source of reflected sound by an auditory mechanism presumably similar to that used by other mammals for sounds audible to them.

Obstacle avoidance by flying bats. Donald R.
Griffin and Robert Galambos, Harvard
University (Introduced by G.H. Parker).
(Lantern; 15 min.).

The ability of bats (mostly *Myotis l. lucifugus*) to avoid obstacles was tested by making them fly through a barrier of vertical wires while a

Fig. 3 : List of control experiments performed during bat cochlear microphonic measurements. See text for details.



5/17

Checks:

1. Cut off sound, no response
   a. Board before source
   b. stop up speculum to ear.
2. No electrical coupling
   a. Shielding-unshielding story w. magnetost. device
   b. galton whistle
   c. air jet–wide spectrum
3. Live animal ear produces the electricity.
   a. Long-time dead gives no response
   b. Death curve
   c. electrode in muscle of beast
   d. electrode in wet cotton

Cochlea is source: a) outside–inside bulla story
b) electrode in mscl–

The response curve: Data obtained at different times (2nd run 6 hrs after 1st). Peaks checked with wide spectrum source: peaks by this technique at 12-13, 29-31, 60,000 ~. Source checked for flatness with crystal μphone.

suitable amplifier recorded their supersonic cries. Average percentage of hits was 36.5%. Bats with eyes covered showed no increase in percentage of hits and no difference in flight. Covering the ears resulted in slower flight and frequent collisions with the walls; the percentage of hits rose to 65 or 70% which is approximately chance average. Controls showed that this effect was not due to injury or irritation. Equally serious impairment of flight and obstacle avoidance resulted when the bat's mouth was covered so that no supersonic sounds could escape.

Bats with one ear free turned away from walls and landed normally, but they struck the wires almost as often as completely deaf bats. One ear was able to locate large obstacles but could not make fine discriminations.

This evidence supports the theory that flying bats detect obstacles in their path by (1) emitting supersonic cries, (2) hearing those sound waves when reflected back to them by the obstacles, and (3) localizing the source of this reflected sound by some auditory mechanism, presumably similar to that used by other mammals for sounds audible to them.

Motion pictures of bats avoiding obstacles.
(Demonstration). Robert Galambos and Donald
R. Griffin, Harvard University
(Introduced by H.W. Rand).

Silent and sound moving pictures of flying bats will be presented to demonstrate and to illustrate the data summarized in the above abstracts. The silent pictures show the normal flight of unimpaired and blindfolded bats as well as the hesitant, erratic flight of bats with ears covered or mouth tied shut. The sound moving pictures demonstrate simultaneously the flight of a normal bat and the supersonic notes it emits.

AN OBSERVATION

It is interesting that our first abstracts do not mention the cochlear microphonic experiments completed 6-7 months earlier. Perhaps we thought it inappropriate to describe and discuss the results of a complicated physiological procedure before the members of a Zoological Society. It is also interesting that in the 50 years since then the chronologically earliest cochlear studies are rarely even referenced in discussions of our bat experiments. I have often wondered why this has been so. Those ear experiments actually represent the final step in a 150-year-long effort to find a plausible, data-based explanation for the behaviors Jurine, Spallanzani, and many others had found so puzzling (GALAMBOS, 1942). The echolocation idea was not new at the time, but there was no credible evidence for it until May, 1939. Professional and popular reports of our experiments do not point this out; instead, they feature our simple replications of the Jurine-Spallanzani sensory deprivation experiments, along with the extensions of them made possible by Pierce's ultrasonic machines. But *only after one has evidence that bats perceive as well as produce ultrasonic cries does the outcome of behavioral experiments such as Jurine's become obvious – predictable before they are performed.* In May, 1939, concrete evidence about what bats hear became available for the first time, and this information finally validated Jurine's claim. What would history say about our contribution if we had decided bat and guinea pig cochleas respond similarly to high frequency sounds ?

THE MOVING PICTURES

The third of the abstracts we submitted promised both silent and sound moving pictures of flying bats, and so we must have considered these to be in near-final form in October, 1940. However, the sound movies certainly were not. The existing version is the second of two. In the first version the sound (on a disc) and the action (on film) were recorded separately and later synchronized, a method apparently widely used commercially at the time. For some reason our technicians could never synchronize the parts. At the very last moment – perhaps as late as the Christmas holidays a week or two before the meetings began – they found the way to record sound and action together and quickly produced the existing version.

The sound movie was made in the Harvard Biology Laboratories. It shows bats flying through the doorway of a small storage room across which black rubber tubing had been stretched after the door had been lifted off its hinges. The silent pictures were made in the sound-deadened room in the basement of Cruft Physics Laboratory where all the sensory deprivation and sound-emission studies had been performed.

THE ISIS PAPER

At the time our collaboration began Griffin had already assembled a bibliography on the Spallanzani bat experiment, including Hahn's important 1908 publication, which confirms the Jurine and Spallanzani behavioral experiments in all important details (HAHN, 1908). Starting from this solid base, I undertook, with occasional help from Griffin and others, a search through the Harvard Widener and Museum of Comparative Zoology libraries for documents related to the bat obstacle avoidance problem. The first chapter of my thesis (now on file at the Widener library) is a 32-page summary of this library research which was subsequently printed with few changes in Isis (GALAMBOS, 1942).

Appendix A in my thesis is a 48-page translation Dale McAdoo and I made of Spallanzani's own account of his bat experiments. The original is found in volume 5 of the 6-volume collection of his works (SPALLANZANI, 1826) and in volume 3 of the 5-volume 1932 edition (SPALLANZANI, 1932). This translation, which was never published, provided much of the information in the Isis paper, and was also used by Griffin in his book. The notebook that supplied Figure 1 also contains a 42-page section in which 89 references related to this historical research are listed and annotated. The first of these is dated May 9, 1940, which suggests that the major part of my library research began long after the experiments had revealed the unique role ultrasonic sounds play in the bat's way of life. It was during this period that I first discovered Jurine –in a letter from Senebier included by Spallanzani in his Opere (SPALLANZANI, 1826, vol. 6 : 253-4) and later in the anonymous 1798 account cited at the beginning of this paper.

THE SCIENTIFIC MONTHLY PAPER

Venerable institutions like Harvard University regularly award prizes to selected students at the time of graduation. In 1941 its Bowdoin Prize – $300 and a medal – was to be awarded to a graduate with a doctoral dissertation in the biological sciences, and my thesis advisor, A.C. Redfield, suggested that I enter my thesis in the competition. The rules specified a document in the form of a short, informative essay submitted under an assumed name. When I proposed to my newly-wed wife – who had already typed numerous thesis drafts, including six copies of the 219-page final version – that she type still another, she struck this bargain : she would do the typing provided I promise that we would begin our family if the essay won the prize. Our first child, a daughter whose middle name is Bowdoin, was born a year or so later.

The Bowdoin Prize essay of 1941, after a few changes – and one more retyping – was accepted by the editor of The Scientific Monthly (GALAMBOS, 1943b).

PRIORITIES AND CREDITS

In 1944 Thomas A. Garnecky of Hillside, New Jersey sent us identical letters asking «who initiated the experiments, and when». Without consulting each other, we both answered his question, then exchanged copies of our letters, and found that we agreed (neither of us recalls ever disagreeing on anything related to the experiments). Griffin responded to my version, on September 22, 1944, as follows :

> «I agree with you 100 per cent in your statement of joint responsibility; not only that, but I admire the masterly way in which you expressed the matter, particularly the final sentence. As far as I am concerned Mr. Garnecky, whatever his motives, has done a great service by eliciting this statement for all time on the matter of the "jointness" of the bat work.»

Griffin liked this paragraph of mine :

> «Your letter gives no hint as to why you request the information I have given you. I wish to stress that Dr. Griffin and I have decided that it is impossible to state which one of us initiated or has prior claim to an experiment or idea. Without his stimulation I should never have undertaken the work on the ear, and without the ear experiments it is unlikely that Dr. Griffin would have pursued the problem much further at that time. We have always made it a point to share any blame or credit equally, and it is our conviction that since we are unable to assess with any precision our individual contributions to the solution of the problem, neither can anyone else.»

Garnecky later wrote Griffin another letter, this time from a New Jersey mental hospital; evidently he wrote the first ones because he believed he, not we, had discovered bat echolocation.

A SUMMARY

The two of us were simply in the right place at the right time. We were lucky, first of all, to have found each other, for it is not likely that either of us would or could have made the measurements alone. Then there are the facts that the laboratories of Professors Pierce and Davis were separated by a few miles, and that their doors opened wide to us the moment we knocked. And finally, every one of our experiments worked out exactly as planned, and they all pointed directly at the ear hypothesis Jurine, and then Spallanzani, knew to be correct. At the moment we were united with our Professors there was only one place in the world where two graduate students could demonstrate that flying bats emit sounds we cannot hear, and that the animals hear and act upon the echoes –and we happened to be there.

ACKNOWLEDGEMENTS

I thank D.R. Griffin and Colán MacArthur for helpful comments.

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Echolocation and body size in insectivorous bats : the case of the giant naked bat *Cheiromeles torquatus* (Molossidae)

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Abstract. Recent hypotheses propose that the maximum size of aerial insectivorous bats is limited by properties of their echolocation system. According to these hypotheses large bats would (A) have to use low call frequencies which may only allow the detection of large prey. However, large prey may be too scarce to meet a large bat's energy requirements. Large bats would (B) have low wing beat frequencies and due to energetic reasons also low call repetition rates. These low call repetition rates, however, may not be sufficient for prey detection. Both hypotheses were tested by analysing the echolocation behaviour of *Cheiromeles torquatus* (150-200 g), the largest aerial insectivorous bat.

Cheiromeles searches for prey by alternating calls with the lowest frequencies at 20 and 28 kHz (call duration 30 and 24 ms respectively) at a repetition rate of 6.3 Hz, and a duty cycle of 18%. The data are discussed in relation to the foraging behaviour of *Cheiromeles*.

The call parameters of *Cheiromeles* are far removed from predictions made in both models. When the data of *Cheiromeles* and some other large bats are included in an allometric version of model (A) the prediction of the model changes distinctly indicating that call frequency might only be a weak constraint on body size, if at all. Call repetition rate seems to be correlated to call frequency and not directly to body size as is assumed in model (B). In any case, large bats have lower call repetition rates than wing beat rates and the difference increases with body size. Therefore other factors have to be sought to explain the size distribution of aerial insectivorous bats.

INTRODUCTION

The structure of bat echolocation calls is closely correlated with ecology and the foraging style of the respective species (NEUWEILER, 1983). Rhinolophid bats, for example, which hunt close to vegetation use clutter-resistant, constant-frequency calls, suitable for the detection of moving prey. Not only the general structure of the call, however, seems to be related to foraging behaviour, but special parameters of the echolocation system such as the frequency content of the call (and especially the frequency of maximum energy) and the duration of the call intervals.

Large aerial insectivorous bats use low-frequency calls suitable for the detection of large prey over long distances, whereas small aerial insectivorous bats use high-frequency calls with a short detection range (HELLER & HELVERSEN, 1989; BARCLAY & BRIGHAM, 1991). It has recently been suggested (BARCLAY & BRIGHAM, 1991) that because of this correlation, the body size of aerial insectivorous bats could be restricted : large and fast-flying bats would have to use very low frequencies thereby only detecting large insects due to the physics of sound reflection (PYE, 1993). These insects might be too rarely encountered to provide a sufficient prey for large bats.

Another recent hypothesis (JONES, 1994) suggests that the size of aerial insectivorous bats might be restricted by the physiological costs of echolocation. Call emission is assumed to be cheap only if it is synchronized with the respiratory cycle which is itself synchronized with the wingbeat (SPEAKMAN & RACEY, 1991). The call repetition rate should therefore be the same as or lower than the wingbeat frequency. Wingbeat frequency is negatively correlated to body size so that very large bats are assumed to have call repetition rates too low for effective echolocation and prey detection.

In both of the hypotheses presented above data were limited to bat masses of up to only 60 g or 40 g respectively because no data for larger aerial insectivorous bats seemed to be available (JONES, 1994) or were included (BARCLAY & BRIGHAM, 1991).

In the following, data on the echolocation behaviour of the naked bat *Cheiromeles torquatus* Horsfield, 1824) (Molossidae) are presented. *C. torquatus* is obviously the heaviest of all aerial hawking insectivorous bats (body mass 150-196 g; MEDWAY, 1978; PAYNE *et al.*, 1985) and has the highest aspect ratio and wing tip index (FREEMAN, 1981; this includes the subspecies *C. t. parvidens*; KOOPMAN, 1994). It also has the highest wing loading of all bats (NORBERG & RAYNER, 1987). All these factors indicate a very high flight speed (NORBERG & RAYNER, 1987). The echolocation data are discussed and compared with the predictions made in both of the above mentioned hypotheses.

MATERIALS AND METHODS

The echolocation calls were recorded just outside the Krau Game Reserve at Kuala Lompat (102°15'E, 3°42'N), Pahang, Malaysia on 20.3.1992. At early dusk, between 1945 and 2000 hours, two *Cheiromeles torquatus* were flying above fields with low vegetation at a height of roughly 10-15 m. They were easily recognizable by their huge size. Two days earlier a specimen of this species had been captured in a mistnet placed above a river, less than 50 m from the study location.

Sound recordings were made with a Brüel & Kjaer 6.35 mm microphone (type 4135, with the protecting grid removed), a B & K amplifier 2231 and a videorecorder modified to register sound. The frequency response of the system was flat (± 3 dB) from 3 kHz up to at least 80 kHz. In the laboratory, the registrations were recorded on a RACAL store 4DS recorder operating at 76 cm/s. Sound sequences were analyzed at 1/16 speed with a digital frequency analyser, MOSIP (program SPEKTRO 6.0; Fa Medav, Germany), using a fast fourier transformation. Signal parameters were measured with cursors on the screen, call durations mostly in the amplitude display, and frequency related parameters in the sonagrams (frequency range 80 kHz, frequency resolution 400 Hz, Hanning Window 524 points). The sweep rate was measured during the terminal part of the call, e.g. mostly the last third of the call, where the sweep rate was roughly constant. In the sonagrams of Fig. 1, signals were copied by hand to eliminate echoes reflected from the ground to the microphone.

RESULTS

During the search phase (i.e. prior to detecting a prey), the animals regularly alternated between two types of frequency modulated calls, one ending at about 20 kHz, the other ending at about 28 kHz (Fig. 1, 2). The lowest frequencies typically had also most energy (Fig. 3). According to the bimodal distribution of the lowest frequencies (Fig. 4), calls with lowest frequencies above 25 kHz were classified as high-frequency calls (HFC) and those below 25 kHz as low-frequency calls (LFC). As far as the spectral composition is concerned, LFCs seemed to start suddenly at a defined frequency (Fig. 1, 4) with only very short, steep, downward-modulated sweeps at the beginning, whereas the HFCs started with long, steep sweeps. The highest frequencies (of the first harmonic) in these sweeps differed, probably mainly due to the varying distances from the calling bat to the microphone and to the frequency-dependent atmospheric attenuation. Upper harmonics (2nd and 3rd) could be recognized in many calls (Fig. 1). There was little overlap when the frequency content of both call types was compared, even when the second harmonics were included. The bats, using a combination of both call types, covered a very broad uninterrupted frequency-band (Fig. 3). Call duration varied significantly between the two call types, but call periods (call + following interval) did not (Table 1). Duty cycle, i.e. the proportion of time spent calling (calculated from the call duration divided by the call period), was again significantly different between types due to the differing duration of calls (Table 1).

Eight approaches to prey culminating in final buzzes were recorded. As has been observed in many other bat species, call duration decreased and repetition rate increased during approach. The approach phase is characterized by the continuous reduction of call duration, the terminal phase by the high sweep rate (Fig. 1, 2, 5). The approach calls were typically

Fig. 1 : Sequence of echolocation signals in *Cheiromeles torquatus* showing search, approach, terminal phase (buzz) and search phase again. Upper part : relative sound pressure level; lower part : sonagram. Arrows indicate the beginning of the approach and terminal phase.

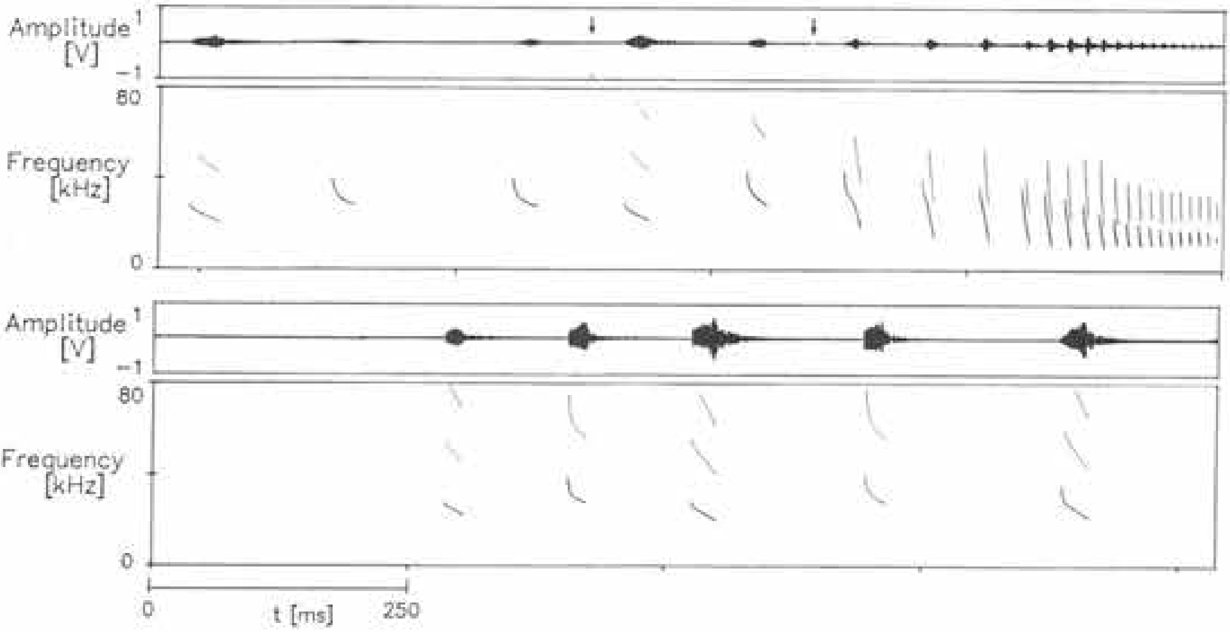


Fig. 2 : The signal parameters of a call sequence including search, approach, terminal and again search phase (a approach phase, t terminal phase; dotted line : call repetition rate)

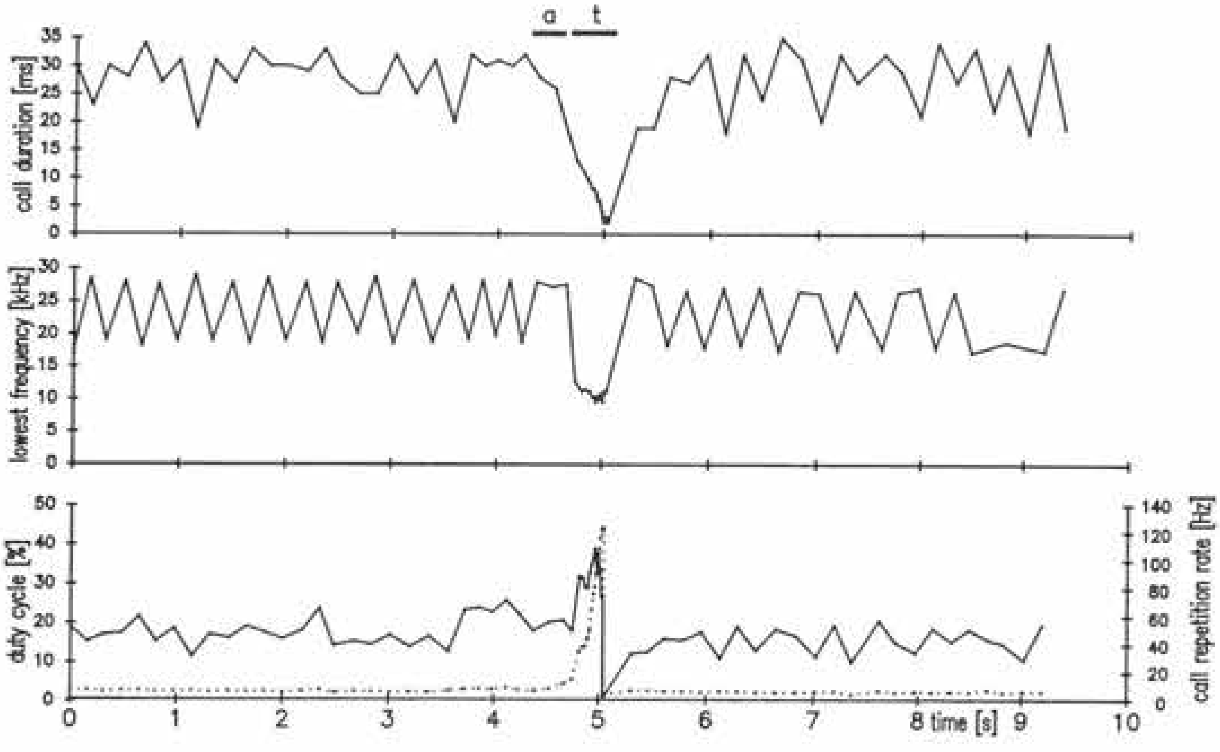


Fig. 3 : Power spectra of a high-frequency call and the following low-frequency call in *Cheiromeles torquatus*.

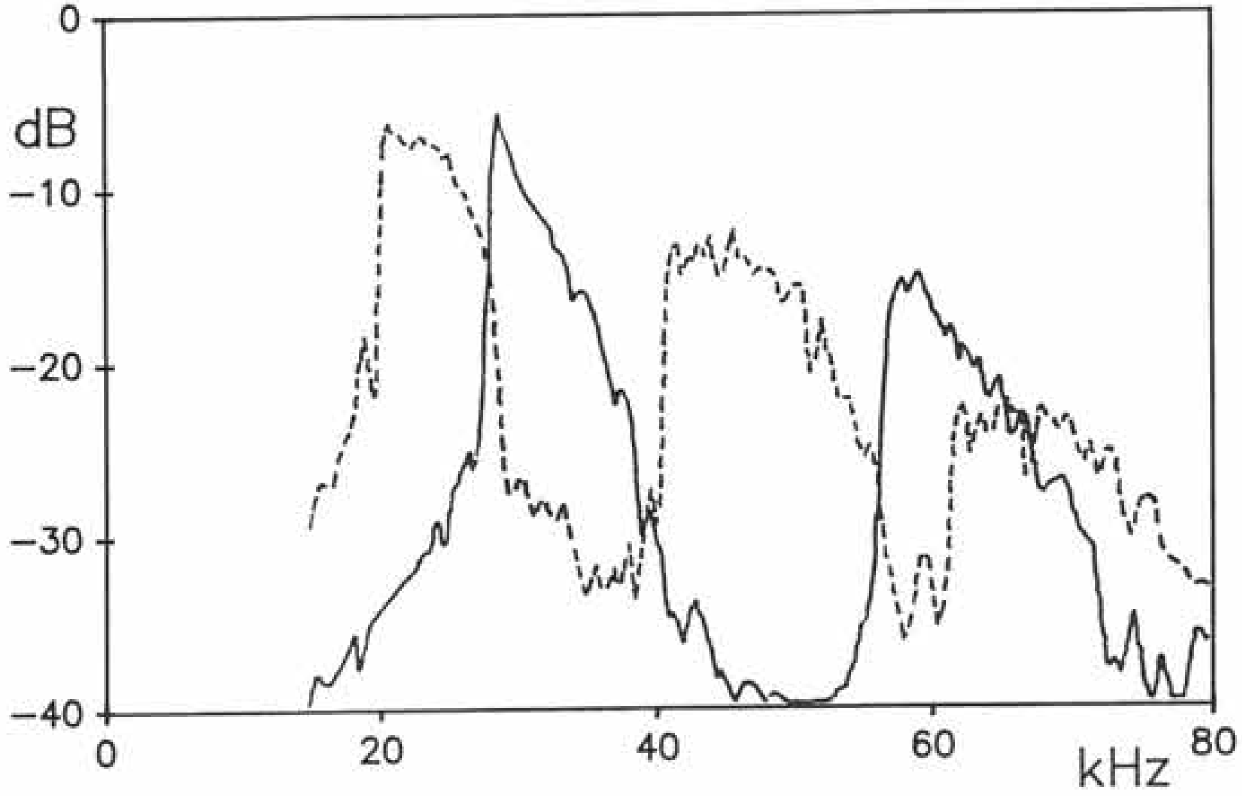
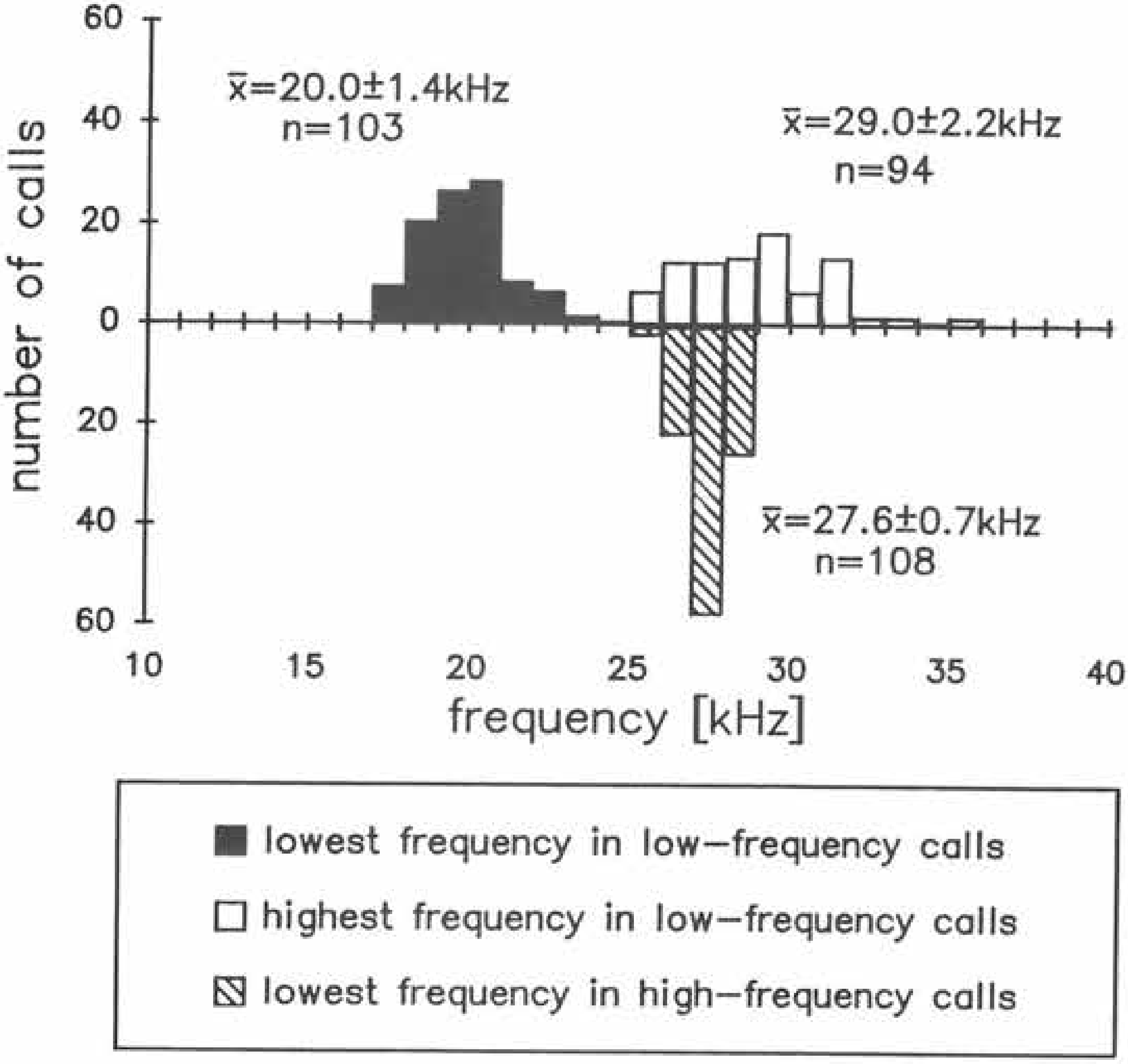


Table 1 : Call parameters (mean ± S.D.) during search phase (data from six call sequences, number of measured calls in brackets, p-values for differences from U-tests).

	Low-frequency calls (LFC)	High-frequency calls (HFC)	
Call duration (ms)	29.0±4.5 (105)	24.9±5.2 (118)	p<0.001
Call period (ms)	164±43 (99)	160±39 (116)	n.s.
Call repetition rate (Hz)	6.1	6.3	
Duty cycle (%)	18.8±4.8 (99)	16.5±4.8 (116)	p<0.001

Fig. 4 : Distribution of call frequencies (mean ± S.D.) during the search sequences in *Cheiromeles torquatus*.



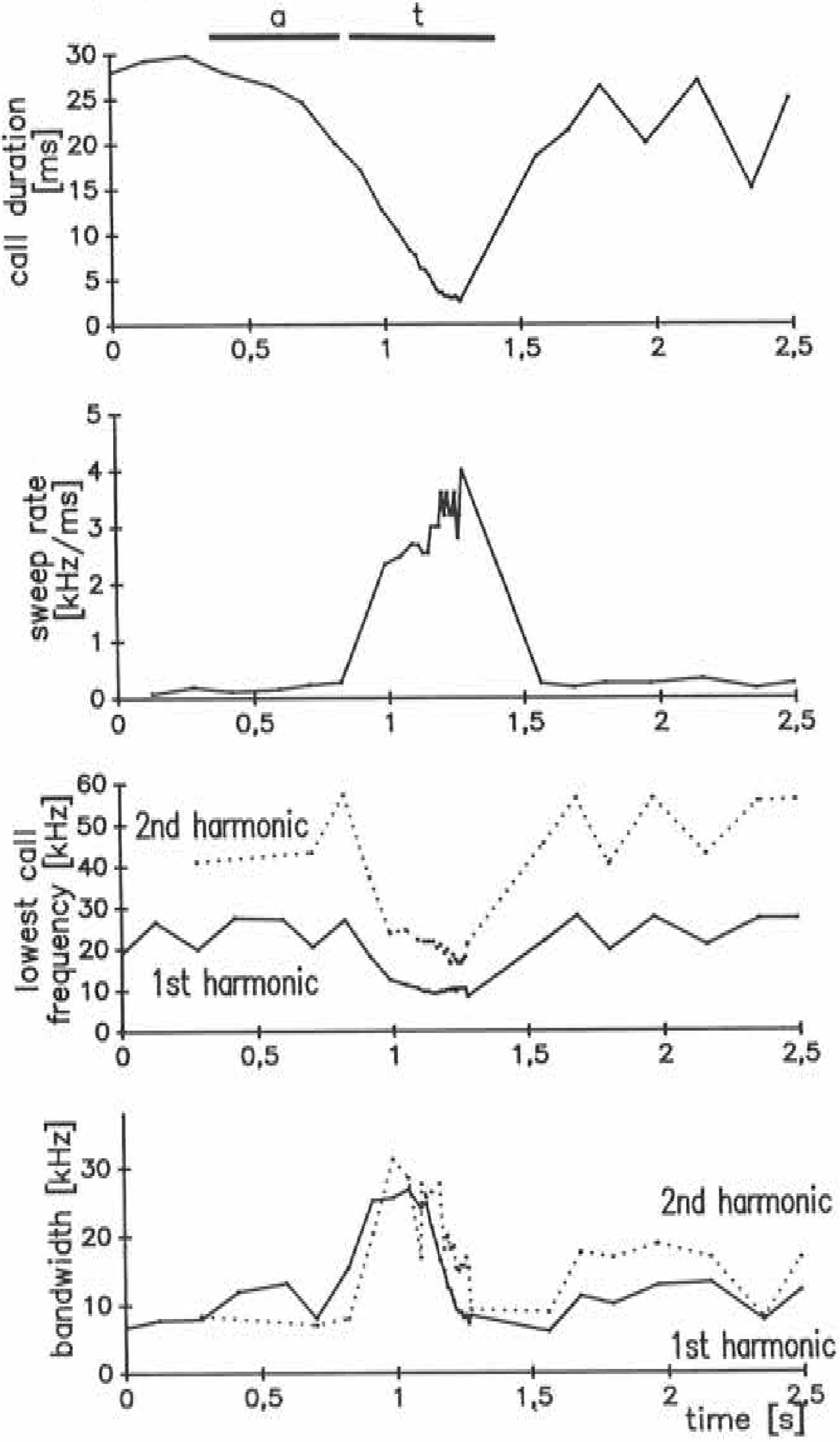
high-frequency calls, but shorter than those emitted during search flight. In two sequences one call was observed at the transition between approach and final buzz, indicating initially the typical frequency modulation of an HFC, but then the high sweep rate of a buzz call (Fig. 1). At the beginning of the buzz, the sweep rate became much higher (up to 4 kHz/ms), the lowest frequency suddenly dropped to about 9 kHz and the calls became much shorter (for the changes in call parameters during the final buzz see Fig. 5). The variability observed in the duration of approach phase and the final buzz was large, as is also found in other bats (e.g. *Myotis daubentonii*; KALKO & SCHNITZLER, 1989). As far as *Cheiromeles* is concerned, the number of buzz calls varied between 10 and 50 (mean : 24) and buzz duration between 250 and 950 ms (mean 460 ms). The final buzzes could be heard by the unaided ear and were very loud.

DISCUSSION

Echolocation behaviour of *Cheiromeles*

The most unusual feature of the echolocation behaviour of *Cheiromeles torquatus* is the regular alternation of two different call types with varying lowest frequencies. An alternation of calls with

Fig. 5 : Change of signal parameters during a terminal phase (buzz) in *Cheiromeles torquatus* (a approach phase, t terminal phase).



different frequencies has been observed only in a few other vespertilionid bats [*Barbastella barbastellus* (AHLEN, 1981); *Nyctalus noctula* (MILLER & DEGN, 1981); *Hesperoptenus blanfordi* (HELLER, 1989); *Chalinolobus gouldi* (JONES & CORBEN, 1993)] and some neotropical emballonurid bats (PYE, 1973; BARCLAY, 1983). In the latter the observed frequency differences between the calls were relatively small (mostly between 2 and 4 kHz), while in some vespertilionids (e.g. *Hesperoptenus blanfordi*) they were in a similar range as that of *Cheiromeles*.

No detailed studies have been performed concerning the function of call alternation. HELLER (1989) proposed two possible advantages for this characteristic : firstly, the bat may enlarge its maximum detection distance which is often considered to be limited by the duration of the call period (FENTON, 1990). A bat should hear the echo from an object before its next call is produced to avoid problems with call-echo-arrangement. By using two alternating call types, a bat could theoretically discriminate between the echoes of the last two calls (WEID & HELVERSEN, 1987) thus doubling its maximum detection range. This may be particularly important for fast flying species such as *Cheiromeles* which hunts above the rain-forest canopy, where the greatly varying height of trees relatively far away might be of interest for the bat. Secondly, the two call types may be used to scan different ranges and prey sizes, HFC for a shorter range and smaller prey size than LFC, an effect of frequency dependent atmospheric attenuation and of echo reflection which is dependent on wave-length. In addition, a related argument has to be considered in *Cheiromeles*. By using the two call types, the bat increases its band-width, covering a broad uninterrupted frequency band from 20 kHz upwards to at least 80 kHz (Fig. 3). A large band-width in echolocation seems to be useful for object identification, because the probability of "coloured echos" is increased (NEUWEILER, 1990). The colours result from the interference of wave-fronts from various parts of an object which differ slightly with their distance from the bat. The hypothesis originally applies to a large bandwidth within one call, but bats may well combine informations from several echoes.

Another unusual feature of *Cheiromeles* is the high duty cycle during echolocation. At 18% it is nearly twice the percentage observed in other aerial insectivorous bats. Duty cycles vary between 2% (*Euderma maculatum*; LEONARD & FENTON, 1984) and 10% (some emballonurid bats; BARCLAY, 1983), with most vespertilionids situated between these extremes. The high duty cycle is probably advantageous for glint detection. A glint, a sudden and short increase in echo amplitude, is produced when an insect's wings are perpendicular to the sound path of the echolocation call (SCHNITZLER *et al.*, 1983). The probability of glint detection increases with increased duty cycle, and *Cheiromeles* may detect glints from large insects with low wingbeat rates.

The high duty cycle is based on a combination of two differing characteristics of echolocation behaviour, calls of long duration and a high call repetition rate. Call durations of up to 40 ms (mean 27 ms; Table 1) in *Cheiromeles* are unusually large, even for aerial hawking insectivorous bats. Except for one observation (50 ms for *N. noctula*; VOGLER & NEUWEILER, 1983) call durations were larger than those observed in any other study of aerial hunting bats (references in BARCLAY & BRIGHAM, 1991 and JONES, 1994). Maximum call duration in large aerial hawking bats (members of the families Molossidae, Emballonuridae, Vespertilionidae) rarely exceed 20 ms (FENTON & BELL, 1981; ALDRIDGE & RAUTENBACH, 1987).

Increasing call duration would enlarge the duty cycle even more. However, due to the call-echo overlap it is unlikely that the bat can detect objects whose echoes arrive before the end of the call (signal overlap zone; KALKO & SCHNITZLER, 1993). In search flight, *Cheiromeles* may be "blind" to objects in the range of 4-5 m in front of it. The clutter overlap zone (KALKO & SCHNITZLER, 1993) is of the same distance, i.e. *Cheiromeles* is probably unable to detect insects which are closer than 4-5 m from obstacles.

Since *Cheiromeles* is a very large and fast flying bat, it can be expected to hunt not only at heights of 10 to 15 m above ground as observed here, but often also much higher. Comparing the flexibility of the echolocation signals of other bat species (KALKO & SCHNITZLER, 1993), *Cheiromeles* also may alter its echolocation behaviour in such situations. For most call parameters, however, detailed predictions will be difficult.

Call frequency and body size

The call frequencies used by *Cheiromeles* seem to be extraordinarily high for a bat of its body mass, at least when compared to the prediction made in the model of BARCLAY & BRIGHAM (1991). According to their calculations, the echolocation calls of *Cheiromeles torquatus* should have most energy at "minus 12.3 kHz". Using this model, BARCLAY & BRIGHAM (1991) argue that aerial insectivorous bats must be small because large bats would have to use low frequencies with long wavelengths, making detection of small prey impossible. On the other hand, the bats might encounter large prey too rarely to survive. This semilogarithmic model, however, may be not appropriate for the situation because it predicts negative frequencies for bats with a body mass above 85 g. A model, based on an allometric relationship between call frequency (f; kHz) and body mass (M; kg) ($f = aM^b$), has the same correlation coefficient as BARCLAY & BRIGHAM's (1991) model for the same data :

$$f = 2.85 * M^{-0.550};\ r^2 = 0.59;\ p < 0.001 \quad (I)$$

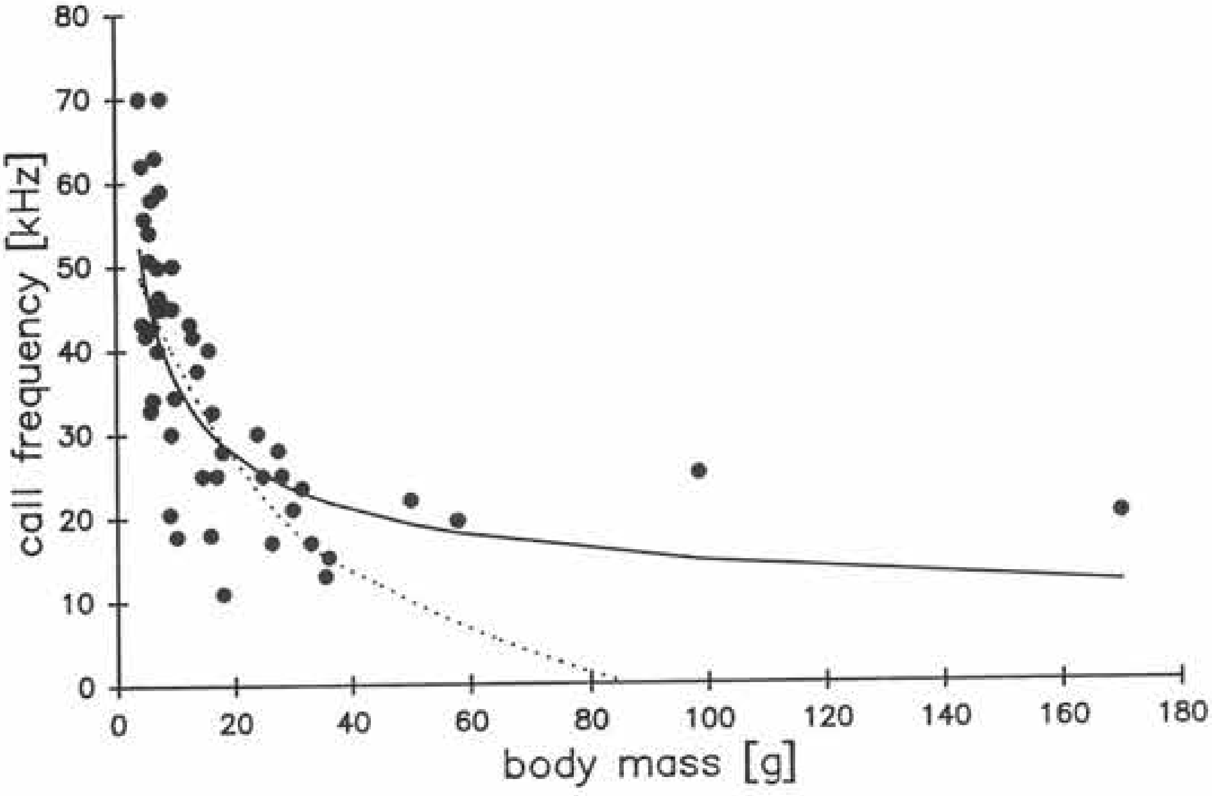
Its predictions for call frequencies in large bats, however, are much closer to the observed values (e.g. 7.3 Hz for *Cheiromeles*). Including the data from *Cheiromeles* (LFC) and three other large bats (*Taphozous peli*; call frequency 25 kHz (PYE, 1980), body mass 98.5 g (KINGDON, 1974); *Saccolaimus saccolaimus* 22 kHz (HELLER, 1989), 50 g (MEDWAY, 1978; PAYNE *et al.*, 1985); *Nyctalus lasiopterus* 19.5 kHz (WEID & HELVERSEN, 1987), 58 g (SCHOBER & GRIMMBERGER, 1987) in this model results in a distinctly lower slope than before, but also a weaker correlation (Fig. 6 : solid line) :

$$f = 5.85 * M^{-0.396};\ r^2 = 0.52;\ p < 0.001 \quad (II)$$

The observed exponent of 0.40 for the regression equation is not far removed from 0.33, the value expected from the very simple model that call frequency is determined by the length of the vocal cord, a linear dimension of body size. Besides body size, however, other factors may also be important in determining call frequency. For example, moth-feeding bats may use very low echolocation frequencies outside their preys' hearing range (RYDELL & ARLETTAZ, 1994).

When the argument that call frequency might limit prey detection is considered, it is important to remember (JONES, 1994) that the calls of many bat species contain higher frequencies than the

Fig. 6 : Relationship between the frequency of maximum intensity of echolocation calls and body mass in aerial insectivorous bats. Dotted line : regression line according to BARCLAY & BRIGHAM, 1991, solid line : regression line based on an allometric model (see text, equation II).



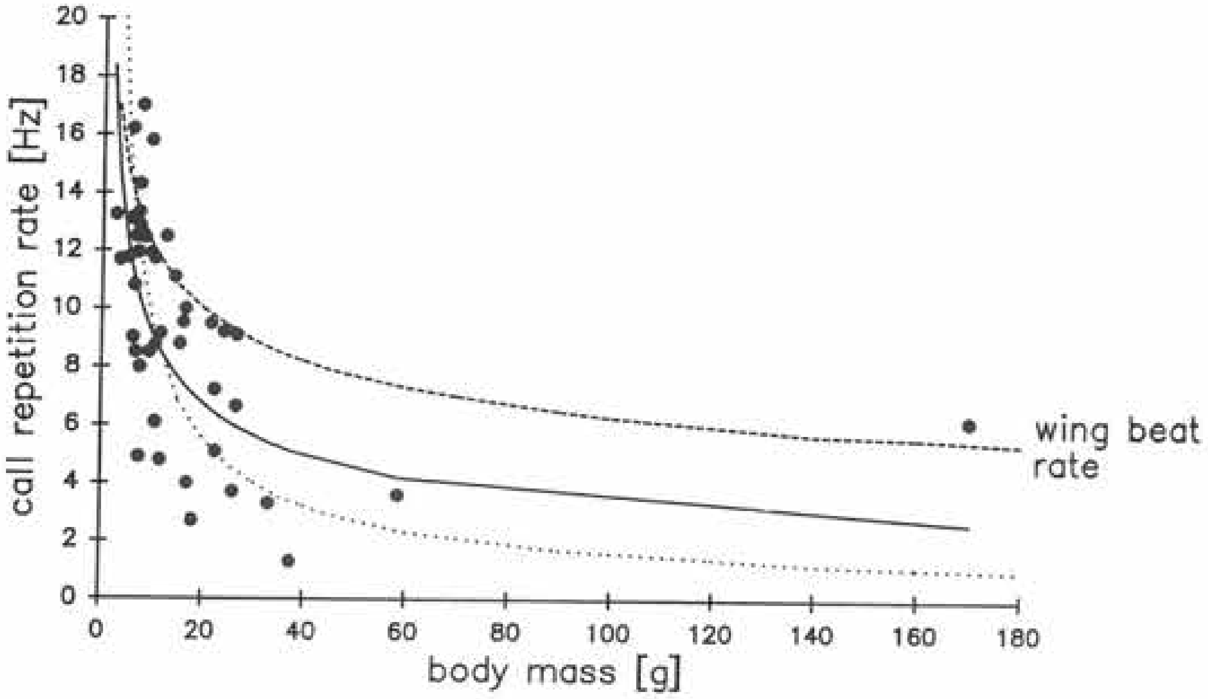
frequency of maximum energy. When considering the large frequency span of the calls of *Cheiromeles* (Fig. 3), it can easily be understood that these animals are able to detect small insects, although the range of the high frequency components may be distinctly smaller than that of the lowest components. While the unusual thickness of its jaws and the large sagittal crest (FREEMAN, 1981) suggest that *Cheiromeles* may feed mainly on large and heavily sclerotized insects such as beetles, it is known to feed at least sometimes on termites (MEDWAY, 1978) and flying ants (FREEMAN, 1981). Thus it would appear agile enough to catch such small prey detected at a relatively short distance. Another large bat, *Noctilio leporinus* (50-90 g), was also observed feeding predominantly on small insects during the wet season (BROOKE, 1994). *Noctilio*, however, has a most prominent echolocation frequency of 60 kHz (SCHNITZLER *et al.*, 1994) and probably a lower flight speed than *Cheiromeles* (NORBERG & RAYNER, 1987). Estimating a flight speed of 13 m/s (using data from NORBERG & RAYNER, 1987 and their equations on page 380), *Cheiromeles* may travel distances of 3 to 12 m (mean 6 m) during the final buzz alone.

Call repetition rate and body size

The call repetition rate (CRR) of *Cheiromeles* seems to be unusually high for a bat of this size. JONES (1994) found a significant correlation between call repetition rate and body mass in aerial insectivorous bats. According to this relationship (CRR = $0.264^{*} M^{-0.775}$; F = 35.0; M bodymass in kg; regression with reduced major axis; Fig. 7 : dotted line. CRR = $0.71^{*} M^{0.547}$; $r^2 = 0.49$; F = 39.6; own calculation; normal linear regression on log-transformed data) a rate of 1.1 Hz could be expected for *Cheiromeles*, while in actual fact 6.2 Hz was observed. Including *Cheiromeles* in the data set used for calculation improves the prediction (2.6 Hz; Fig. 7 : solid line: CRR = $1.196^{*}M^{-0.437}$; $r^2 = 0.42$; $p < 0.001$; normal linear regression on log-transformed data), but the correlation becomes weaker.

However, an analysis of the data (data set combined from data of BARCLAY & BRIGHAM, 1991 and of JONES, 1994, supplemented with frequency data for *Saccopteryx bilineata* (BARCLAY, 1983) and *Lasionycteris noctivagans* (BARCLAY, 1986), which were not used by BARCLAY & BRIGHAM, 1991) with a stepwise multiple regression showed

Fig. 7 : Relationship between call repetition rate, wing beat rate and body mass in aerial insectivorous bats. Dotted line : regression line for call repetition rate according to JONES, 1994, solid line : regression line using data from JONES and including *Cheiromeles torquatus* (regression equation see text), broken line : regression line for wingbeat rate according to JONES, 1994 (all bats).



that CRR can be predicted more accurately when using call frequency than by means of body mass. In fact, after including call frequency, CRR is not significantly correlated to body mass at all (Table 2). Inclusion of *Cheiromeles* does not alter matters. The correlation between CRR and call frequency is easily understandable, because call frequency has a very strong effect on the range of the echolocation signal and therefore the time interval during which echoes are to be expected. Thus bats with low frequency calls receive echoes a longer time after the call (and from greater distances) than bats with high frequency calls, and should therefore apply larger call intervals. Using this correlation (calculation does not include body mass)

$$CRR = 0.195 * f^{1.071};\ r^2 = 0.71;\ p < 0.001 \quad (III)$$

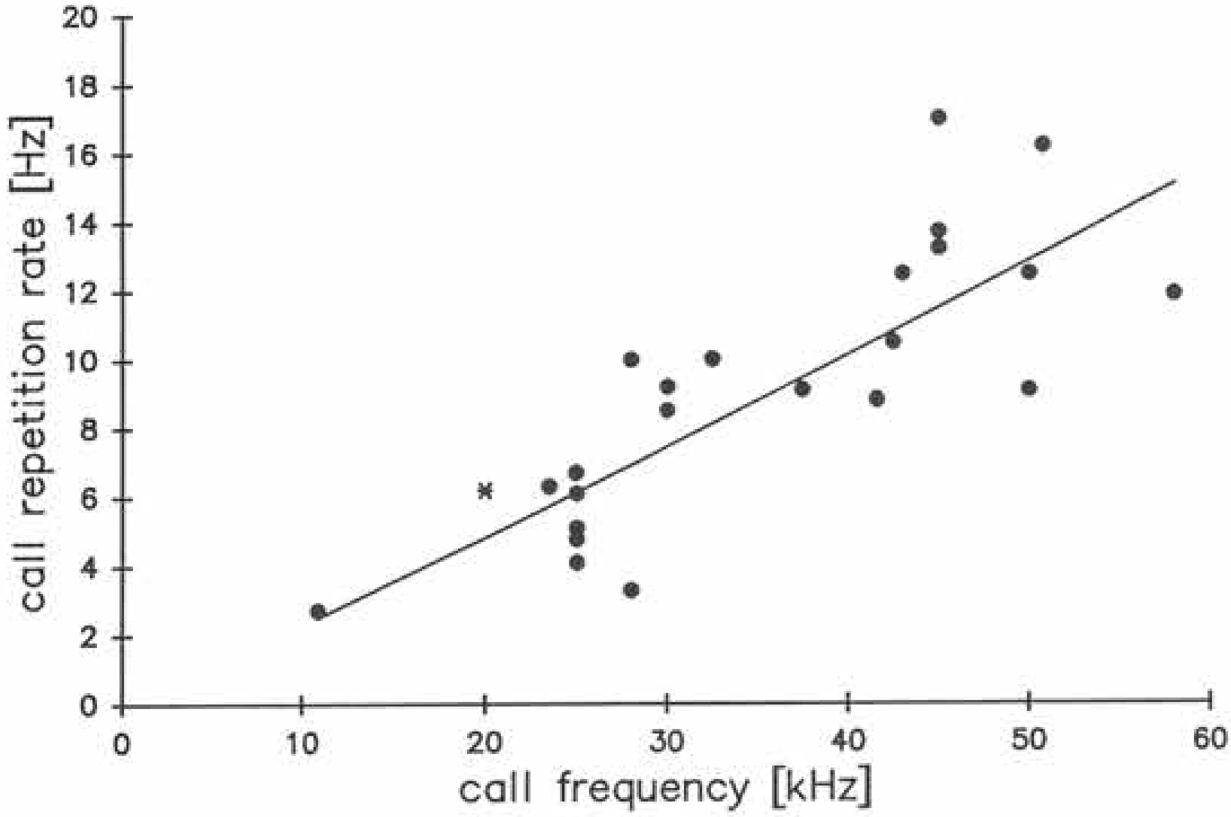
a call repetition rate of 4.8 Hz (for LFC) or 6.8 Hz (for HFC) is predicted for *Cheiromeles* (Fig. 8). The observed mean rate of 6.2 Hz lies between these two values. A CRR of 6.2 Hz is also close to the predicted wing beat frequency of 5.5 Hz (JONES, 1994) (Fig. 7), and *Cheiromeles* probably emits one call per wing beat. Many other bats with low CRR and low call frequencies, however, often emit only one call per two or three wingbeats, as can be seen in the multimodal distributions of call periods (AHLEN, 1981; HELLER, 1989). The interval between the modes often comes close to the wingbeat period which can be predicted from the body mass (JONES, 1994). These findings are contradictory to the hypothesis that body size in aerial insectivorous bats is limited by the CRR

Table 2 : The relationship between CRR (call repetition rate), call frequency and body mass as indicated by a multiple regression on CRR (log CRR)

Variable	coeff	SE	t	P
constant	0.72	0.22	-3.20	0.004
log call frequency	0.97	0.22	4.46	<0.001
log body mass	-0.08	0.14	-0.59	0.56

(n = 24 species) $r^2 = 0.69$

Fig. 8 : Relationship between call repetition rate and call frequency (* *Cheiromeles torquatus*; regression equation : see text).



(JONES, 1994) : large bats with low call frequencies typically emit less than one call per wingbeat (see regression lines for the wingbeat rate and CRR when compared with body mass in Fig. 1 in JONES, 1994).

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Le Rhinolophe (1995) **11** : 39-40

The influence of landscape elements on the echolocation of the pond bat *Myotis dasycneme*

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Abstract. Instead of crossing open areas many bat species seem to prefer flying close to the vegetation of landscape elements like hedgerows and tree lanes. Apart from being relatively rich in insects and providing shelter to bats, (linear) landscape features may be used as sonar guidelines for orientation. Pond bats (*Myotis dasycneme*) were studied when commuting over canals of different width. In order to find out whether bats keep "in touch" with elements in their environment, inter-pulse intervals and pulse lengths were related to the distance from bat to canal bank. For instance, if a pond bat adjusts its "sonar time window" to the canal bank, a correlation between the interpulse intervals and the distance to the bank can be expected. Pulse lengths and canal width were correlated as well. Some preliminary results are presented.

Some bat species like Daubenton's bat, *Myotis daubentoni*, and the common pipistrelle, *Pipistrellus pipistrellus*, are claimed to prefer flying close to linear landscape elements when commuting between roost and foraging areas. We hypothesize that this behaviour can be explained in three ways : landscape elements (i) provide relatively high insect densities, (ii) provide shelter from wind/predators, and/or (iii) facilitate the echo-orientation of bats. The last hypothesis was tested on the pond bat, *Myotis dasycneme*. In the Netherlands, pond bats usually commute over canals in relatively open polder landscapes. This enabled us to study the relation between the pond bat's echolocation and the distance between bat and canal bank. Thus, canal width (13, 19, 25 and 30 m) was related to pulse lengths and inter-pulse time intervals. Figure 1 shows that mean pulse lengths increase from the 13 m to the 25 m wide canal, resp. from 8.02 to 10.33 ms (T-test : all mutually significant, $P < 0.05$).

Figure 2 shows the mean pulse interval lengths at different canal widths. Only at the 30 m wide canal pulse intervals were longer than at the other canals (T-test : $P<0.05$).

For all (including the longest) pulses emitted, bat-to-bank distances were too large to cause pulse-echo overlap. More likely, the bats increase their pulse lengths at wider canals to improve long distance perception. The long pulse intervals observed at the 30 m wide canal enable the bats to avoid interference of returning echo's with new outgoing pulses, which would often occur in the case of 90 ms intervals. Our preliminary results thus indicate a relationship between echolocation and the surrounding landscape, suggesting that bats with a restricted range of echolocation signals prefer to follow landscape elements instead of crossing open areas.

Fig. 1 : Mean pulse lengths at different canal widths based on time expanded recordings

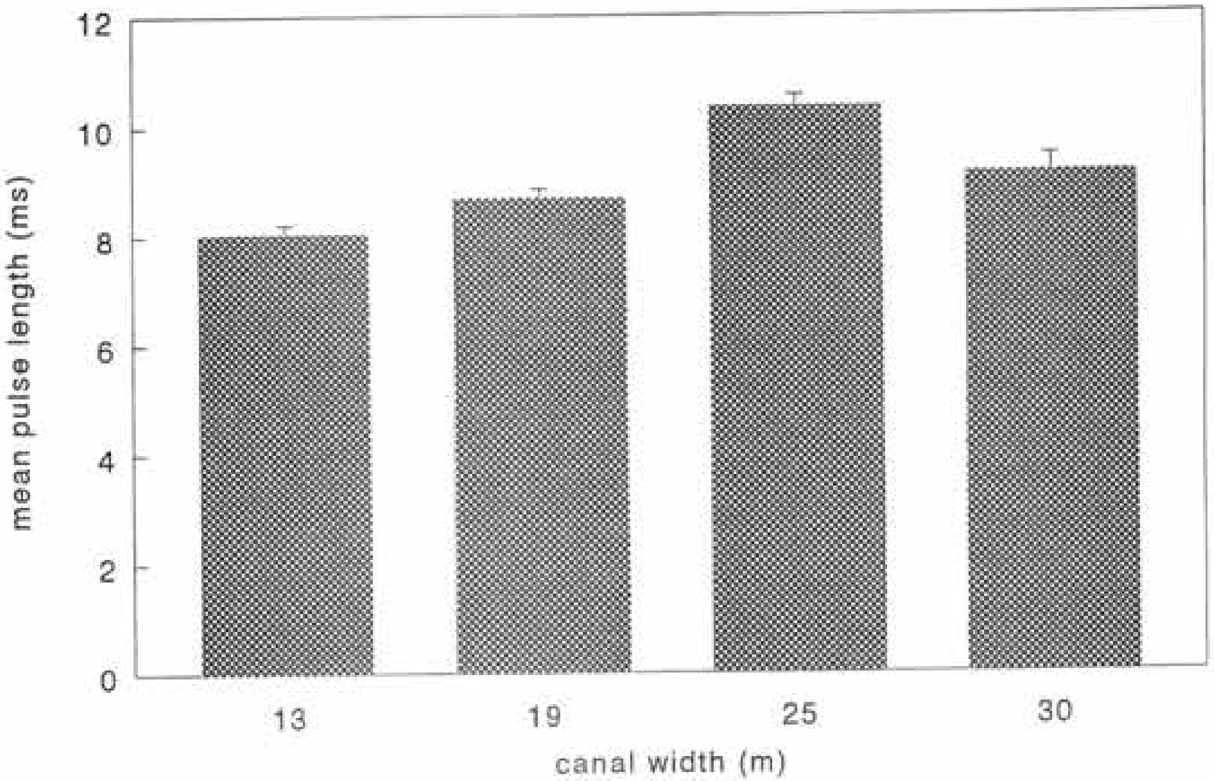
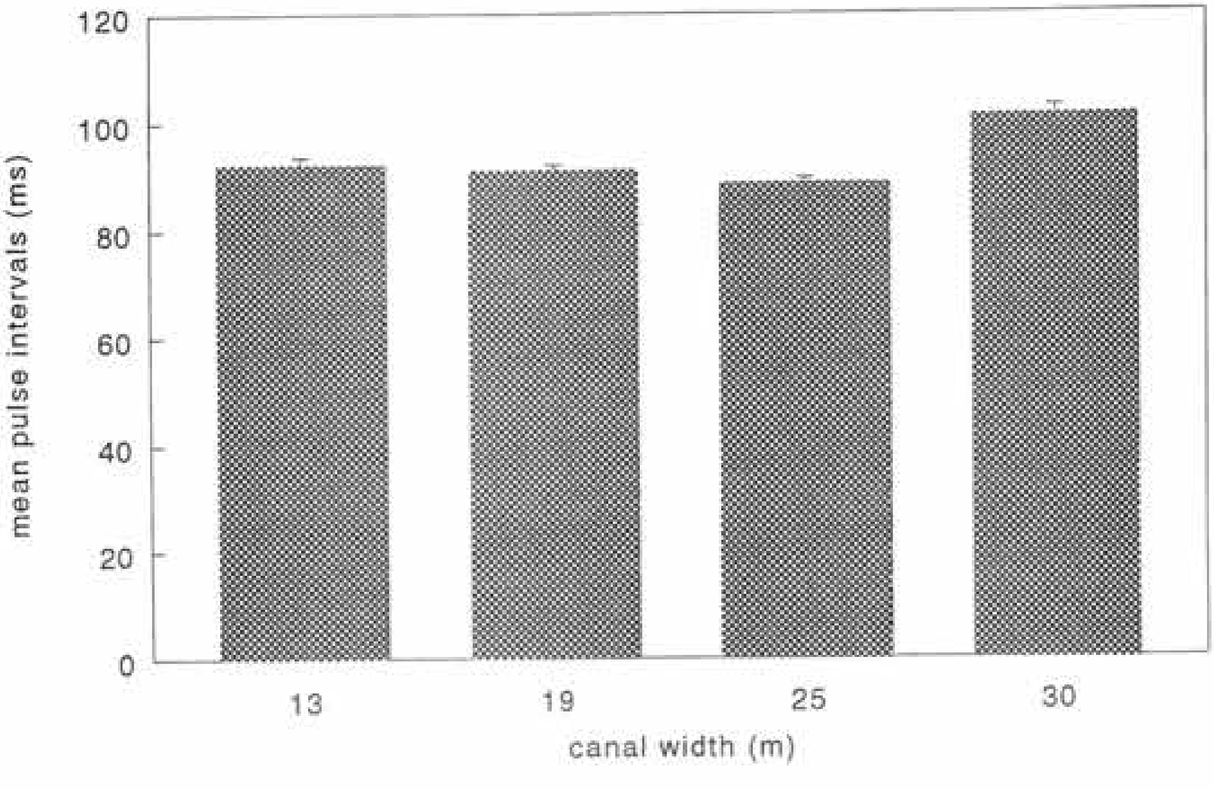


Fig. 2 : Mean pulse intervals at different canal widths based on heterodyned recordings



Le Rhinolophe (1995) **11** : 41-52

Bat echolocation, electronics and field research : a fruitful symbiosis ?

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Abstract. In recent years the use of microtechnology in field research has become more and more widespread and modern field instrumentation for bat reseach is currently being developed towards all-in-one solutions with sophisticated realtime analysis capabilities. Will this lead into the legendary "black-box bat recorder" which promises to record and analyse bat sounds, determine the species on the fly and correlate the results with the flight behaviour, the flight path and the ecological context ? Is this a desirable evolution ? Who can take profit from such technology and where in the dark do the dangers lurk ? Who does really need sophisticated equipment and whom may it deter from searching for more innovative approaches in bat research ?

The article points at these and similar questions and moves along to critically review the benefits and dangers of the application of modern bioacoustic methods in field research on bats.

Now may be the right time to stop for a short while and discuss the implications which all the new technologies and methods may have. How will they influence the way we pose our biological questions and which will be their effect on the long term goals of bat research ?

INTRODUCTION

The aim of this paper is to encourage the discussion about the future ways to go in bat echolocation research and about the role microtechnology could or should play in the game. Most of its content is not new research data but reflects opinions based on my experience in research on dolphin and bat echolocation behaviour over the past 20 years.

Modern research on echolocation is based on sophisticated instrumentation and it is difficult to imagine how it could evolve without a simultaneous development in electronics. History shows that whenever new equipment was made available, the recording techniques and techniques of signal analysis have also evolved considerably.

The modern trend goes towards the application of digital or hybrid black boxes to record, analyse and maybe re-transmit bat signals. It is obvious that the use of black box instruments in scientific research could be disastrous in the hands of the unwary. Thus two questions arise :

1. Is the black box approach unavoidable ?
2. Who would possibly profit from a black box bat recorder ?

These two questions will now be discussed in more detail.

IS THE BLACK BOX APPROACH UNAVOIDABLE ?

Serious bioacoustic research calls for a careful control of all important parameters, e.g.

- the goals of the research project and any boundary conditions have to be well known and controlled;
- recording and analysing techniques have to be carefully set up and standardised and should be transparent to the user.

The first statement leads to a focus on experimental research in the laboratory, where it is easier to meet these requirements. In other words it leads generally away from descriptive field research. This trend is enforced by todays career mechanisms in the scientific community where field studies in general do not yield results fast enough and useful results are less guaranteed within a limited time period, thus leading to a disadvantage of field researchers in a competitive system.

The second part of the second statement is difficult to fulfil with modern computerised instrumentation. Digital instruments may indeed make the unexperienced believe that everything he or she is measuring is done at a very high accuracy and is not prone to significant measuring errors since the results are already expressed in numbers and computers are known to make no mistakes when doing calculations. When working in the field with these instruments there is even less control of possible pitfalls. On the other hand the miniaturization of recording and measuring electronics opens exciting new possibilities even for realtime data evaluation in the field.

How can this controversial situation be resolved ? Which way should we go ?

In order to answer this we should go back to the second question : Who could profit from a black box bat recorder ?

This may depend on whether one is interested to investigate the bat sonar system in its own right or whether one wants to use bat echolocation sounds as a resource to gain access to related information : detecting hunting bats, measuring their flight activity or determining bat species by means of their sounds are methods which are commonly used by a growing number of people nowadays.

- For bioacoustic research black boxes are definitely not desirable. When recording and analysing bat signals it is essential to dispose of a very good knowledge in physics and data acquisition techniques but also of the behaviour of the animals under investigation. Furthermore the equipment which is used should be well known and its response to known signals tested beforehand.
- If echolocation sounds are used as a means to detect, count or determine bats within the frame of ecological studies or in order to assess bat populations in an area, the black box approach may be perfectly tolerable or even desirable, provided the researchers working with the equipment are carefully trained.

Three examples illustrate these statements :

Example A : Signal structure in the time and frequency domain

Let us take the example of a dolphin echolocation signal in order to illustrate the first statement. It consists of a series of almost identical, very short echolocation clicks (Fig. 1), which form a so called "click train" with varying repetition rate. The oscillogram of the signal describes all its properties adequately. If, however, the signal is analysed by means of a sonagraph, a complex pattern of harmonic frequency bands may emerge (Fig. 2). The sonagram pattern will depend on the click repetition rate at any one moment and on the filter bandwidth used for the analysis. If we analyse a variety of click trains of a moving dolphin, we will inevitably end up with a huge variety of sonagram patterns, differing in the amplitude distribution in the frequency domain and differing in the spacing between harmonic bands. Without ever looking at an oscillographic representation of the signals, the next step will then be to classify the signals, put them into categories and so on. Examples of research work following this pattern are numerous in older cetological literature. In some cases kilometres of tapes have been analysed and categorised in this way.

If, however we know about some basic physical relationships between time and frequency representations of a signal and have a look at the oscillogram of the signal, we can easily realise that the harmonic frequency pattern represents the repetition rate of structurally identical clicks and that the harmonic interval changes according to the changes in repetition rate.

If we know about the directive properties of high frequency, broadband signals, then it becomes clear that shifts in the spectral maximum may simply be due to the directivity pattern of the sound field when a dolphin is moving. In short words : All those numerous categories do not have any biological significance and the signal variability is much overestimated.

In order to analyse very short signals the sonagraph is not the ideal instrument. We should not forget that the sonagram always represents a compromise between the resolutions in the frequency and in the time domain. If we increase the analysing filter bandwidth, this will lower the frequency resolution but increase the time resolution. Decreased filter

Fig. 1 : Echolocation click of a river dolphin (*Platanista indi*) : oscillogram and frequency spectrum. The spectrum was obtained through a 1/3 octave filter bank. Adapted from PILLERI *et al.*, 1976 and ZBINDEN, 1982.

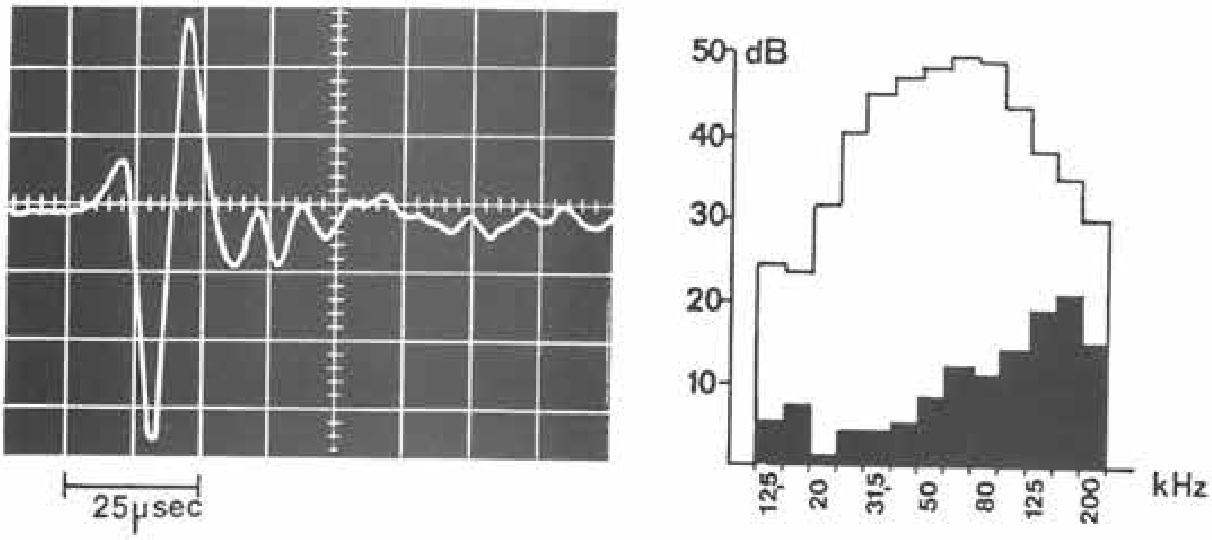
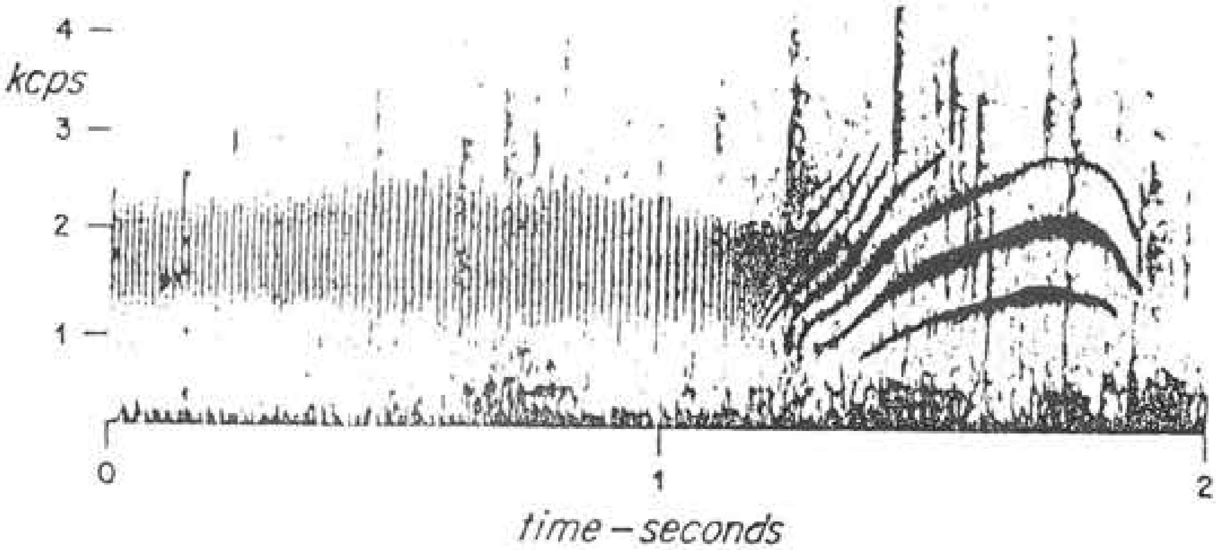


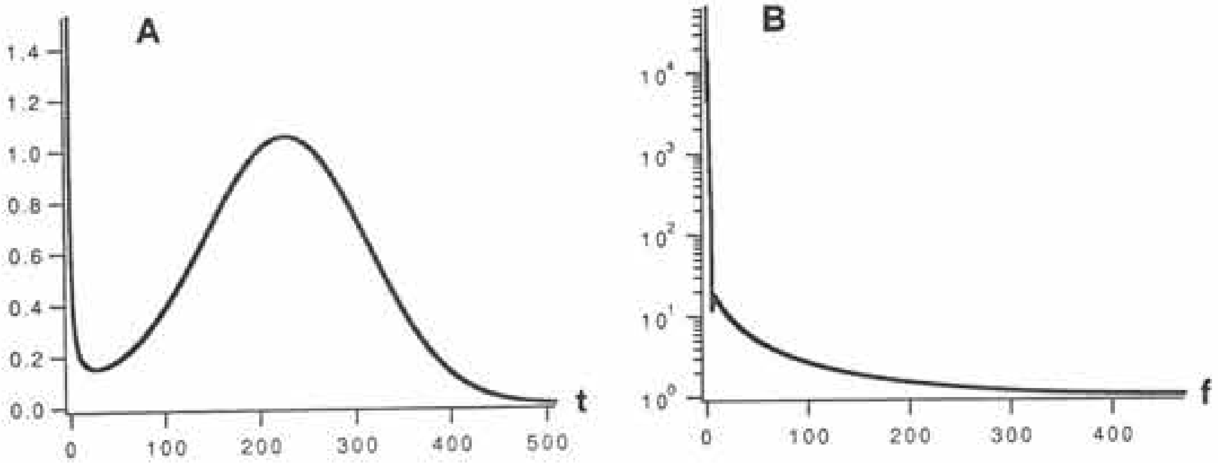
Fig. 2 : Sonagram representation of a click series of a porpoise (*Phocoena phocoena*) with increasing repetition rate over a time interval of 2 s (low frequency component shown only). Modified after WATKINS (1966).



bandwidth on the other hand provides a better frequency resolution but the sonagram will be smeared along the time scale.

The same principle applies in fact to the signals themselves : the frequency of a very short signal is not well determined as the example of a dolphin echolocation click demonstrates. The frequency of a long, constant frequency signal by contrast is defined much more accurately, but the longer the signal, the less precise are any estimates of the time of its occurrence. This principle resembles very much Heisenberg's uncertainty relationship in physics. To illustrate this, imagine an artificial signal which contains two very different signal components (Fig. 3). The temporal representation of the signal starts with a very short spike of high amplitude and

Fig. 3 : Model signal to demonstrate the uncertainty relationship. A : oscillogram, B : frequency spectrum obtained by an FFT-Transformation. See text for further explanations.



ends with a long, gaussian shaped curve of low amplitude. The representation of this signal in the frequency domain again shows two distinct components : The sharp peak at the low frequency end represents the frequency contents of the gaussian shaped curve whose time of occurrence is not very accurately defined. The second component which extends over almost every frequency shown in the diagram represents the frequency contents of the sharp spike in the oscillogram. If the spike had been of zero width (e.g. as represented by a step function), its frequency spectrum would in fact have become constant over all frequencies.

Example B : Digital signal analysis

When analysing bat signals by means of digital equipment, gliding time windows are often used, in order to represent the variation of the signal frequency over time. When deciding about the type and the duration of the time window, it is important to know about the side effects of this procedure. The application of a time window is a multiplication process between the signal and the window function. In the process the spectra of the two signals are folded and the resulting combined spectrum has a peculiar form which depends on the type of the window used. If a rectangular window is chosen, each signal frequency component will not be represented smoothly but artificial sidelobes will be introduced (Fig. 4). It is therefore essential to chose a time window which keeps the deformation of the resulting spectrum to a minimum. This is achieved by using gaussian, hanning or hamming window functions. The drawback of their use is that the resulting filter bandwidth still depends on the duration of the window function. The practical implications of this become evident, if say a long, narrowband bat echolocation signal is analysed by means of a very short, gliding time window : the resulting signal bandwidth may appear much too large.

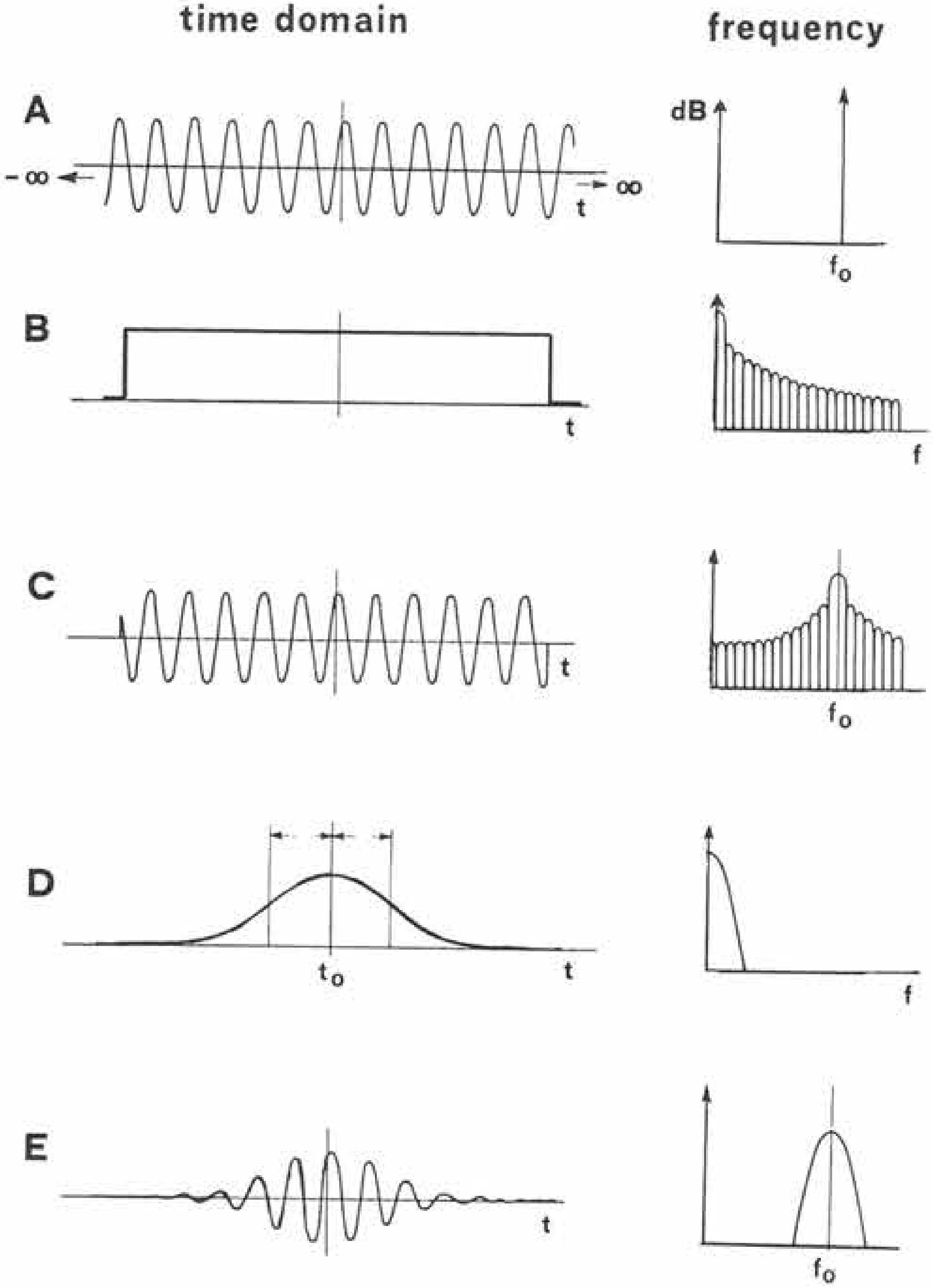
- As a conclusion it can be stated that for bioacoustic research the physics behind a measuring setup and the measuring procedure must be very well understood and if black boxes are unavoidable, their transfer characteristics must have been thoroughly tested using artificial signals with known properties.

Example C : Determination of bat species by analysing their echolocation sounds

I have stated that the use of black boxes may be useful to gain information on related questions of general biological relevance. It may in fact not be very important to the average user of a bat detector to know the exact signal transfer characteristics of the instrument, as long as he follows certain standardised measuring procedures and working rules.

An example : when an unexperienced observer tries to determine bat species by means of a detector it is important for him or her to know which signal parameters to consider and which part of the bat's behaviour is suitable to the task. This background and appropriate restrictions must have been laid

Fig. 4 : Schematic representation of the effects of a rectangular and a Gauss-shaped windowing function applied to a sinusoidal waveform. Left columns and right columns : time domain and frequency domain representations of the signal and window functions. A : long duration sinewave. Its spectrum consists of a single line at f_0. B : Rectangular window function. Its spectrum has a complex structure with multiple side lobes. C : Waveform and spectrum resulting from the application of the rectangular window to the sine wave. The side lobes introduced by the window function are clearly visible in the spectrum and the signal bandwidth is now spreaded over a much larger area of the spectrum. D : Gaussian shaped window function. Its spectrum has a Gaussian shape as well. E : signal shape and spectrum resulting from the application of the Gaussian window to the sine wave. The resulting signal bandwidth appears larger than that of the long duration sine wave but the spectrum contains no side lobes. The shorter the window function, the larger will be the resulting frequency span of the signal in the frequency representation. Modified after RANDALL (1973).



down beforehand by bioacoustics specialists.

One important restriction will be that a suitable detector has to provide broadband output and the signal has to be recorded and checked in the laboratory by an experienced person. Another restriction concerns the conditions during sound registration : Only echolocation signals of a bat which was in search flight during the recorded phase should be evaluated and the approximate distance of the hunting bat to nearby objects and to the ground should be known (ZBINDEN, 1989; RYDELL, 1990, 1993). ZINGG (1990) has developed a quantitative approach to species determination by ultrasound in European bats. A useful, short discussion of the relative value of different bat detector types to perform this task is given in ZINGG, 1994.

WHICH IS THE CURRENT STATE OF KNOWLEDGE ON BAT ECHOLOCATION ?

Since Griffins' and Galambos' discovery of echolocation in bats (see GRIFFIN & GALAMBOS, 1941 and GALAMBOS & GRIFFIN, 1942), phenological descriptions of the echolocation signals of numerous species have been elaborated. Most of the signals were recorded from bats kept in captivity or recorded in the field without knowing much about the behavioural context.

In a few species we now have a detailed knowledge of signal structure, variability and the accuracy of echolocation under laboratory conditions. In very few species only, some of the mechanisms of echo elaboration in the ear and of processing by the central nervous system are known. Although brilliant research work has been done by a number or research groups such as those of J.D. Pye, J. Simmons, H.U. Schnitzler, G. Neuweiler, N. Suga and many others, we still do not even know the whole acoustic repertoire of a single bat species under natural conditions, nor do we know the exact mechanism of echo analysis in the bat brain. Thus a lot remains to be investigated.

In 1987 at the Helsingør conference on Animal Sonar Systems I had proposed to intensify the research on the signal variability of echolocating bats under natural conditions. In the mean time many field projects have successfully been undertaken and valuable new data have been collected.

But unfortunately the scientific trends have changed again and many research groups have returned to the laboratory.

WHAT TYPE OF RESEARCH DO WE NEED ?

By obvious reasons we need both, laboratory and field investigations.

- Laboratory research allows an accurate, experimental assessment of echolocation mechanisms. The danger of research under restricted, experimental conditions however is, that the behavioural context is lost and the observer remains ignorant about the biological relevance of a behaviour or mechanism.
- In field research the observed behaviour is by definition of a certain biological relevance and it is often possible to judge the relative importance of a certain item of the acoustical behaviour. Very often however, it is difficult if not impossible to keep and overview on all the important parameters and it is very rare that the behaviour can be tracked down to the level of the underlying mechanisms.

Nevertheless I think that the emphasis of future bioacoustic research on bats ought to be laid on field research :

- Why emphasize field research ?
- What could we investigate ?
- How can we do it ?

WHY COULD IT BE REWARDING TO PUT THE EMPHASIS ON FIELD RESEARCH ?

An example : At the Frascati conference in 1966 Cahlander was the first to present ambiguity diagrams in order to describe the accuracy by which bats might measure distance and velocity of a located object using an optimal receiver model (CAHLANDER, 1966). Since then passionate discussions have been hold about whether bats do use optimal receivers or not. After Cahlander, others such as BEUTER (1976), PYE (1980), HARTLEY (1985) and myself (ZBINDEN, 1988a) have described the characteristics of bat echolocation signals by means of similar concepts. SIMMONS & GRINNELL (1988), Schnitzler and Menne (MENNE, 1988) and MØHL (1988) have conducted sophisticated experiments in the laboratory in order to prove or disprove the concept.

Which was the result ? In some laboratory experiments the bats seemed to behave as if they had optimal receivers in other experiments they showed a much poorer performance. Thus from laboratory experiments alone we can not give a definitive answer. If we can't find optimal receiver behaviour in bats in the laboratory this does not preclude that the bats may be able to reach such an accuracy under natural conditions - if the situation calls for it.

We must assume that a bat is able to focus its attention on a certain task depending on the amount of its complexity. Thus although the bat might be able to perform as an ideal receiver it may not always be necessary to exploit that full potential, or in other words : The bat may pay more or less attention to an echolocation problem, depending on the difficulty of the task and its performance may vary accordingly.

After years of research done by a large number of scientists it has become clear that the sonar system of bats has a very high plasticity, both with respect to its history and degree of evolution and with respect to the range of acoustic behaviours of bat species.

Whenever the physical constraints were prominent, the echolocation signals of different bat species may have evolved in a convergent manner. An example for this is the signal sequence prior to prey capture which is very similar in almost all of the aerial hunting bats.

On the other hand signal types may have evolved in a divergent manner between bat species whenever this helped to exploit certain ecological niches which in turn imposed different physical constraints. Typical for this are search flight calls where we find the most prominent differences among species.

If our aim is to study the evolution of echolocation or the capabilities of bats to adapt their signals to changing requirements, it is evident that this is best done in field studies. Only the natural surroundings can challenge the adaptive capabilities of a bat to the full and only there we will find the whole palette of individual and interspecific variability.

This gives us the answer to our second question : What should we investigate ?

A few proposals are given in the following paragraphs.

INTRASPECIFIC AND INTERSPECIFIC VARIABILITY

Intraspecific variability can give us an estimate of the adaptive capabilities of a bat species, e.g. of its behavioural and ecological flexibility.

Interspecific variability gives us clues about different ecological niches covered by different bat species.

In order to investigate both types of variability it is necessary to have knowledge about the following parameters :

- the flight behaviour / flight tracks
- spatial parameters of the surroundings
- elements of general behaviour

All these parameters have to be assessed synchronously, so that correlations with the acoustic behaviour become possible.

When comparing different signal types in this context, ambiguity diagrams may give us interesting hints about possible adaptations to solve certain tasks.

FOCUS ON THE ECHO

Whenever an animal emits echolocation signals it is not the transmitted signal which is of primary interest but its **echo**. The echo carries all the important information for the echolocating animal. In some cases the fine structure of a transmitted signal in the frequency domain may be almost irrelevant as long as its bandwidth is large enough. Let us consider the extreme example of a dolphin echolocation signal. The click of a bottle-nosed dolphin is extremely short, less than 100 µsec long (Fig. 5). Such an echolocation signal has a rather broad bandwidth and it is difficult to indicate its exact frequency (ref. uncertainty relationship). The echo of the signal after reflection from a complex target however, has become much longer and has a rather complex structure both in the time and frequency domains. The peaks and valleys in the frequency spectrum of the echo contain useful information about the target size, shape and surface structure (Fig. 6).

Thus a structurally very simple signal of large bandwidth whose exact frequency structure is uncritical may yield a wealth of different echos from different targets. It is these echos which carry the relevant information for the animal. As one can imagine, it is difficult to get accurate echo data in a field study. This leads us back to the third question : How can we do it ?

Again I shall make a few proposals : we could

- intensify directed observation,
- intensify experimental field work,
- utilise optical equipment (night vision cameras) in synchronization with bioacoustic equipment,
- undertake field studies over a long time span.

In order to obtain good results from field experiments it is necessary to express innovative and may be sometimes unconventional ideas. How could the spatial characteristics of a natural hunting habitat be utilised to study the adaptation of signals against internal and external requirements ? Is it feasible to make use of the curiosity of bats or of their stereotype flight paths to conduct a field

Fig. 5 : Typical waveform and frequency spectrum of a click of a bottle-nosed dolphin (*Tursiops truncatus*). Modified after AU (1993).

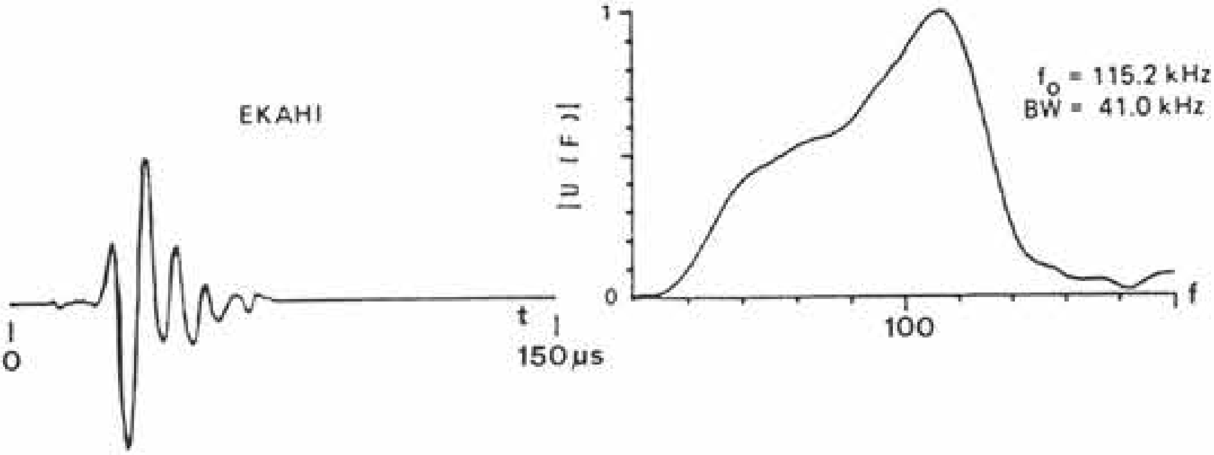
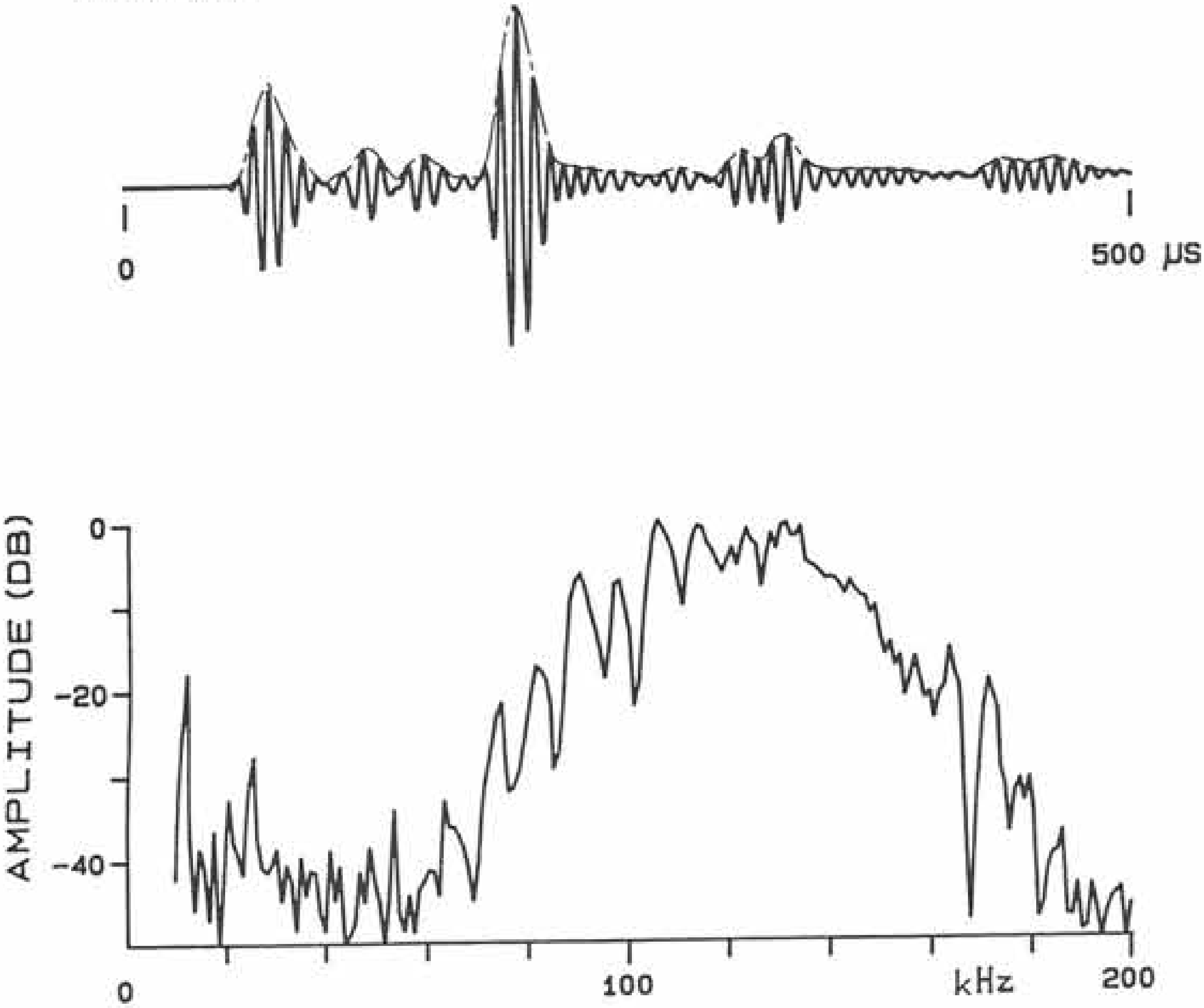


Fig. 6 : Echo of a single, simulated dolphin echolocation click after its reflection from a water filled steel sphere. After AU (1993).



experiment ? Which possibilities exist to get close to the bat in order to achieve decent recordings ? How can we do this without distracting the bat and without disturbing its natural echolocation behaviour ?

A good example of how this can be done was presented by D. Hartley and J.D. Pye (HARTLEY, 1985) who disguised their recording microphone in the form of an artificial lure which used to be mistaken by the bats for prey. With their field experiment they were able to get an exact correlate of the bat's flight speed (measured by means of a doppler microwave radar), its distance from the target and the characteristics of the emitted echolocation signals.

Miniaturised, portable equipment is essential for this type of field study. Every effort should be made to elaborate a careful and detailed documentation about the bat's behaviour in its natural milieu. It is very dangerous to already elaborate the data in the field (modern equipment may now allow data compression in realtime) because valuable details are lost which could make up links to other aspects of a bat's behaviour. If data compression is used extensively in the field, errors can often not be traced down because the raw data are lost.

When working experimentally it is essential that the sounds and the behaviour of the bat are recorded simultaneously. A good example of such a procedure has been put forward by E. Kalko in Schnitzler's group in Germany, where multiflash protography was combined with acoustical recordings in order to investigate echolocation signals emitted during prey capture (KALKO & SCHNITZLER, 1989). Night vision video is now used by our group in conjunction with broadband detectors in the form of a highly mobile unit which allows us to track down the bat's acoustic behaviour under difficult field conditions and gives us a powerful tool to assess the adaptive capabilities of the acoustic system of a bat species under various circumstances.

When tracking the behaviour of bats in the field it has been an important requirement for a long time to measure the exact flight path of a bat. In 1982, J.D. Pye and K. Zbinden (unpublished results) tried to triangulate flight paths of bats by means of recording their echolocation sounds by a spatial arrangement of microphones and then enhancing the spatial resolution by correlation processing. By various reasons the project was not followed on at that time but the problem has been taken up independently by AUBAUER (1994) who has developed a computerised system which allows the tracking of bats almost in real time.

My last proposal was to promote long term field studies. Two approaches are possible :

- investigate the whole or a major part of the bat population in a certain area and set up a web of correlations between selected ecological parameters and the flight behaviour and the acoustic behaviour of different bat species,
- follow the acoustic behaviour of one species under different circumstances which impose different constraints on echolocation.

Both of these approaches will profit from a follow up over several years by the same person or research group and might provide access to novel concepts in bat behaviour.

In order to get interesting acoustic data in the field it is not always necessary to work with expensive equipment, however. On the contrary : a lab full of equipment needs maintenance and presents a massive technical overhead which has to be mastered before any efficient work in the field can be done. As a minimum configuration for bioacoustic field work I propose the following :

- Ultrasound detector with broadband output (divider)
- High quality cassette tape recorder (such as a Sony TC-D5 or a DAT recorder)
- Testsignal generator (pulse burst generator with piezo transducer)
- Computer program for data acquisition and analysis or digital oscilloscope.

A test signal generator is important because it allows regular checks of the recording and analysing equipment.

WHAT ARE THE REQUIREMENTS OF A BAT WORKER WHO WANTS TO USE BIOACOUSTIC TECHNIQUES AS A RESOURCE TO STUDY OTHER TOPICS ?

In order to facilitate the use of bioacoustic techniques by non-specialists we must find out about the appropriate equipment and about the rules of its application in the field.

As I have pointed out earlier, the black box approach may be feasible for this type of application, provided its users have received a decent training beforehand. Bat detector workshops are useful for this and it would be desirable to elaborate generally accepted conceptions about the signal parameters to consider when echolocation sounds are used for species determination.

What are the minimum requirements for a suitable equipment ?

If only bat activity in general is to be assessed, a simple heterodyning or broadband divider detector is perfectly adequate. Moeschler and Blant were among the first to use such a system to sample the abundance of bats in a certain area and correlate it with landscape elements (MOESCHLER & BLANT, 1990).

If the goal is to accurately determine species, however, all the presently known detector systems are complementary and it is advantageous to combine them.

The following list shows what a system should ideally provide to be up to this task :

- Heterodyne mode for maximum sensitivity and rough on site measurements of frequency parameters,
- Broadband divider mode operating in realtime,
- Digital memory to store short signal sequences (>= 1 Mbyte memory),
- Period plot calculation,
- Screen to plot waveform and period,
- Parallel outputs of divider and memory to facilitate simultaneous recording on tape.

The "PUSP" (Portable ultrasound processor, see also S350, reviewed by ZBINDEN, 1988b) recently developed by Ultrasound Advice in Britain goes along these lines. Unfortunately the instrument is still quite expensive. Advances in signal processor design will hopefully change this situation very soon.

Checklist of knowledge which is needed by the user of such a device :

He or she should

- be familiar with important signal parameters (duration, frequency measures, modulation, harmonics, etc.),
- know the traps inherent to digital signal acquisition,
- know about the variability of bat echolocation signals due to adaptive behaviour.

Except for assessing the distribution of bat activity and for determining bat species in the field, echolocation signals can also be used to count bats emerging from multiple roost entrances, in caves or even in the hunting habitat. "Batmeteo" (ZBINDEN, 1994) is an example for the use of a bat detector to monitor the effect of changes that have been made to a bat hunting site. The system consists of an automatic logging station which measures a range of meteo parameters and counts ultrasonic activity picked up by a Mini-2 detector.

When we take a look back at the last decade of bat research it becomes clear that a lot of effort has gone into the development of new methods and technology of which Jurine at his time could not even have dreamed of.

I firmly hope that much of this scientific power will go into future field research. After all it is only the field results which do finally allow us to test our hypothesis and models of bat behaviour for its biological relevance.

For our experimental field work I wish us all more inspiration, more phantasy and a lot of luck with a lovely picture (Fig. 7) reproduced from the interesting book and in memoriam of Denise Tupinier.

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Fig. 7 : Disguised bat, XIX century. Adapted from TUPINIER (1989).

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Variation in bat echolocation : implications for resource partitioning and communication

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Abstract. I review factors affecting call frequency in echolocating bats. In five families, frequency scales with body mass with exponents between -0.36 and -0.48. Exponents are similar in all families, though for their body mass rhinolophids and hipposiderids emit higher frequency calls than do bats in other families. This is related to the use of second harmonics by most rhinolophoid bats. Most echolocating bats are small, and probably need to be small to produce ultrasonic frequencies used in the echolocation of small targets. Within species, call frequency decreases with body size in certain age and sex classes of two species of FM bats, and is highest in intermediate-sized bats in one hipposiderid. Females emit higher frequencies than males in 3 species of rhinolophoid bats, males call at higher frequency in one species, and there are no differences in call frequency between sexes in two species. In 5 species, first-year bats emit lower frequencies than do older individuals, and age related changes in the echolocation of greater horseshoe bats provide evidence that the fine-tuning of call frequency may have a learnt component. Body temperature and condition may affect frequency. Variation in call frequency may have implications for jamming avoidance, signalling, and resource partitioning. Cryptic species of bats are found where morphological similarity masks large differences in echolocation call frequency. I suspect that more cryptic species of bats may be described fom their echolocation calls, and suggest some ways in which potential links between call frequency, body size, mating calls and resource partitioning may influence speciation in bats.

INTRODUCTION

All bats in the Order Microchiroptera studied to date are able to produce calls for use in echolocation. Although echolocation is not always used in prey detection, it remains an important sensory method for orientation. Passive listening for prey generated noises is used for the location of prey in by some species (FIEDLER, 1979), but many insectivorous bats use echolocation to detect and track prey. This paper will mainly be concerned with the echolocation calls of insectivorous bats. The aims of the paper are as follows :

1) to review inter- and intra-specific variation in the frequency of echolocation calls, and to determine whether any general principles can be applied which help explain the causes of this variation.
2) to ask whether any intra-specific variation has implications for resource partitioning, communication and speciation. For example, if call frequency determines echo strength in relation to the size of insect prey, bats that use different frequencies in echolocation calls may be able to specialise in eating different sized insects. Moreover, if frequency is correlated with body size, selection for changes in body size may result in changes in call frequency of bats, and this could have implications for the evolution of new dietary niches. In terms of communication, if features of call frequency can reveal aspects of, for example, the sex, or age of an animal, conspecifics may obtain information about the status of the signaller. Such communicative aspects of echolocation may be important because we expect echolocation calls to be honest signals (FENTON, 1994).

I will consider in detail echolocation calls and species diversity in pipistrelle bats. My work on the calls of European pipistrelles *P. pipistrellus* (JONES & PARIJS, 1993) suggests that one of Britain's commonest mammals is in fact two species. Bats show large numbers of cryptic species, and it could be that selection on features of their echolocation calls has implications for speciation in bats.

INTERSPECIFIC SCALING OF CALL FREQUENCY

Larger bat species tend to emit lower frequency echolocation calls (HELLER & HELVERSEN, 1989; BARCLAY & BRIGHAM, 1991). The scaling between dominant call frequency and body mass holds in at least 5 families, with exponents of the relation varying between -0.36 and -0.48 (JONES, 1996 –using standard linear regression, not reduced major axis). A negative relation between size and frequency is expected, because drum membranes and strings produce lower frequency as size increases, and the frequencies of many air-filled pipes and diaphragms also show similar relations (PYE, 1979). The differences in exponents between families is not significant, but the Hipposideridae and Rhinolophidae tend to emit higher frequencies for their body mass than do bats in other families. These bats channel most energy into their second harmonics, and this may allow them to specialise in eating tympanate moths, whose frequencies of best hearing are usually 20-50 kHz (FULLARD, 1987). Among the rhinolophids and hipposiderids, species that emit higher frequency calls eat more moths (JONES, 1992). Although selection for predation on tympanate moths may not have been the primary selective force responsible for the evolution of harmonic shifting, it is clear that rhinolophoid bats that emit long duration calls gain considerable benefits from shifting most energy into the second harmonic in reducing their apparency to moths, since long duration calls are initially apparant to moth ears.

It is important to realise that although the use of high frequencies brings certain benefits, it may also involve a number of costs. High frequencies suffer more from atmospheric attenuation and are more directional than low frequencies (PYE, 1993). Bats are small mammals, with 70% of microchiropterans for which data are available weighing under 20 g (JONES, 1996). It could be that many bats need to be small in order to produce the high frequency sounds used in the echolocation of small insects, since high frequencies at least in theory give stronger echoes from smaller targets (PYE, 1979; 1993; see below).

HOW FIXED IS CALL FREQUENCY ?

Bats can change features of their echolocation calls according to the situations in which they fly. Calls tend to shorten in duration, and become more frequency-modulated (FM) when bats fly in cluttered habitats, for example (PYE, 1980; KAPTEYN, 1993; KALKO & SCHNITZLER, 1993). The relative importance of behavioural variation and inbuilt constraints in limiting the range of call plasticity may depend on echolocation call design. RYDELL (1993), for example, argued that behavioural factors were more important that inbuilt constraints associated with sex and age in *Eptesicus nilssonii*. Despite this behavioural plasticity, features such as dominant call frequency in bats that use constant frequency (CF) components in their search phase calls may be fairly constrained within individuals because of the specialised hearing mechanisms of these bats. Some authors have argued that bats shift call frequency when flying in groups of conspecifics, so that by calling at a different frequency from surrounding bats, jamming can be avoided (HABERSETZER, 1981; MILLER & DEGN, 1981). Such observational data have not been supported by experimental studies, however, where bats have been flown first alone and then in groups. Jamming avoidance predicts that a wider range of frequencies should be produced by the bats during group flight, and this was not seen to any great extent in any of three experimental studies (SCHMIDT & JOERMANN, 1986; JONES *et al.*, 1993, 1994). Any small changes in call frequency noted in the group flights of hipposiderid bats were probably attributable to slower flight speeds then, with an associated reduction in the need to Doppler-shift compensate. I would therefore argue that call frequency may be constrained within certain limits in at least some bat species. The greatest constraints may be in CF bats with acoustic foveae (SCHULLER & POLLAK, 1979), such as rhinolophids and hipposiderids, since a bat's cochlear and neural tuning may be extremely inflexible, at least in the short term. It is now opportune to show how call frequency may vary at the intraspecific level to determine whether frequency can be predicted from certain characteristics of a bat such as its size or sex.

INTRASPECIFIC RELATIONS BETWEEN BODY SIZE AND CALL FREQUENCY

Given that frequency scales negatively with body size across species, does a similar scaling relation hold within species ? The evidence to date suggests that it does in some species, not in others.

The dominant frequency of the main harmonic decreases with body size in some trawling insectivorous bats that emit FM calls. In *Myotis adversus* of Australia, males with longer forearms emit lower frequency calls as determined from peaks of power spectra (JONES & RAYNER, 1991). In *Myotis daubentonii* studied in Poland, lowest frequency of calls decreased with increasing body size in first-year males only (JONES & KOKUREWICZ, 1994). Thus in some FM bats, there is evidence that frequency may decrease as body size increases. Measurements of upper frequencies are subject to extreme atmospheric attenuation, and they are therefore dependent on distance to the microphone and direction, however. Lowest frequencies, or frequencies containing most energy are more accurate measures of call frequency in bats, but the power spectra of FM calls often fail to show peaks which are easy to measure. The frequency containing most energy is easier to measure in CF calls, where most of the energy is channelled into a very narrow bandwidth. Frequency peaks (where the call contains most energy) are also relatively easy to measure in bats that mix FM and CF components in calls. There is no correlation between call frequency and forearm length in either phonic type of the FM/CF bat *Pipistrellus pipistrellus* (JONES & PARIJS, 1993). Are there any relations between frequency and body size in CF bats ?

In the hipposiderid *Asellia tridens*, the relation between call frequency and body mass is best described by a polynomial relation, with frequency initially increasing and then decreasing as forearm length increases (JONES *et al.*, 1993). Frequency is therefore highest in bats of intermediate size. Frequency is not related to body size in *Rhinolophus rouxi* of Sri Lanka (NEUWEILER *et al.*, 1987), or in *R. ferrumequinum* or *R. hipposideros* (JONES *et al.*, 1992; JONES & RANSOME, 1993). Thus overall, there is evidence for a relation between body size and call frequency for at least three species. In two species frequency decreases as body size increases, in one other it follows a more complex relationship.

OTHER FACTORS AFFECTING CALL FREQUENCY

I will now consider how two other factors, sex and age, affect call frequency in bats. I will then discuss how the evidence for age-related effects in *Rhinolophus ferrumequinum* implies that aspects of the fine-tuning of call frequency involve learning from mothers by offspring in this species.

The effects of sex on call frequency

Females emit calls of higher frequencies than males in the following species : *Rhinolophus rouxi* (NEUWEILER *et al.*, 1987), *R. hipposideros* (JONES *et al.*, 1992), and *Asellia tridens* (JONES *et al.*, 1993). There is no evidence for sexual size dimorphism in *R. rouxi*, while females tend to be the larger sex in *R. hipposideros*. Males are the larger sex in *A. tridens*. Sex does not influence frequency in *R. ferrumequinum* (JONES & RANSOME, 1993) or *Hipposideros fulvus* (JONES *et al.*, 1994), where females are the larger sex.

Males emit calls of higher frequency in *Hipposideros speoris*, where no sexual size dimorphism is apparent (JONES *et al.*, 1994). Thus, in conclusion, of 6 CF bat species studied to date, females emit higher frequency calls than males in 3 species, males emit higher frequencies in one species, and call frequency does not differ between the sexes in 2 species. There is no general rule to relate sexual differences in call frequency to sexual size dimorphism.

The effects of age on call frequency

In all species studied to date, first-year bats consistently emit calls of lower frequency than older bats. This effect has been noted in the FM bats *M. daubentonii* (JONES & KOKUREWICZ, 1994) and *M. lucifugus* (D.L. PEARL, unpublished), and in the CF bats *Asellia tridens* (JONES *et al.*, 1993), *Rhinolophus hipposideros* (JONES *et al.*, 1992), *R. ferrumequinum* (JONES & RANSOME, 1993). The fact that this relation exists in five species of bats, some of which have different ancestry, suggests that a common rule associated with maturation may link age and call frequency in bats.

The situation in *R. ferrumequinum* has been studied in detail, and provides evidence that the fine-tuning of call frequency may have a learning component in this species (JONES & RANSOME, 1993). In *R. ferrumequinum*, frequency increases over the first 2-3 years of life, and then remains fairly stable until the bats reach about 10 years of age. After this age, frequency decreases again. The frequency emitted by any bat therefore changes as it ages, and there are also seasonal changes (see below). The frequencies emitted by mothers and offspring are positively correlated. Differences in the frequencies emitted by offspring born to old and young mothers support the theory that frequency is at least caused partly by learnt effects in this species. Old females (> 5 years) raised infants with lower frequencies than did young females, and this pattern was statistically significant for both male and female offspring. Old females would have emitted higher frequencies as young breeders, and, if frequency were determined in a purely genetic manner, there is no reason to expect a relation between maternal age and offspring frequency. Indeed, if frequency were determined purely genetically, infants born to old females should emit higher frequencies than the ones we recorded, perhaps more similar to those of their mothers during their earlier reproductive life. This argument only applies to the fine tuning of call frequency –presumably the infant has a genetic template for the basic call structure, since deafened young bats can still emit adult-like echolocation calls in *Rhinolophus rouxi* (RÜBSAMEN & SCHÄFER, 1990). Learning of social calls has been demonstrated in *Phyllostomus discolor* by ESSER (1994).

Other factors affecting frequency : temperature and body condition

A positive correlation exists between call frequency and body temperature in the CF bat *Pteronotus parnelli* (HUFFMAN & HENSON, 1993a), and shifts occur in cochlear and neural tuning which are concomitant with changes in frequency (HUFFMAN & HENSON, 1993b). Seasonal changes in the frequencies emitted by *R. ferrumequinum* are in the directions expected from a positive relation between body temperature and call frequency (JONES & RANSOME, 1993).

In the Indian hipposiderid *Hipposideros fulvus*, CF frequency was highest in bats of highest body condition (mass/forearm length; JONES *et al.*, 1994). Body size on its own did not correlate with frequency, and the relation between frequency and condition was apparent for both males and females. Perhaps bats in poorer condition attempt to save energy by reducing body temperature, and this consequently reduces call frequency.

POSSIBLE CONSEQUENCES OF VARIATION IN CALL FREQUENCY

Why might intraspecific variation in call frequency be important for bats ? There are at least three possible reasons for its potential importance.

1. Jamming avoidance

Jamming from the echoes of conspecifics' calls might be reduced if individuals emit different call frequencies. Any advantages associated with jamming avoidance would probably be most important in CF bats that have acoustic foveae close to the call frequency emitted during resting (SCHULLER & POLLAK, 1979). If individuals differ in the frequency of echolocation calls, sorting one's own echoes from those of conspecifics during group flight might be facilitated.

2. Signalling in communication

If frequency is related to body size, sex, or age then conspecifics may be able to gain information about the status of other bats according to call frequency. In *R. rouxi*, for example, all calls emitted above 77 kHz were produced by females (NEUWEILER *et al.*, 1987). If a male was searching for females to mate with, he could ignore bats that emitted frequencies under 77 kHz.

3. Resource partitioning

Arguably the most important consequence of variation in call frequency is related to resource partitioning. This is because call frequency can be thought of as an echolocating bat's equivalent of a bird's bill. In birds, bill size can determine the size of prey handled most effectively (e.g. GRANT, 1986). Prey size may be related to call frequency in ways outlined below.

When the wavelength of sound [= velocity of sound in air (i.e. 340 m/s at 16°C)/ frequency] is longer than the circumference of the target, echo intensity falls off rapidly as wavelength increases, at least for spheres (PYE, 1993). The strength of the backscatter from a sphere reaches a maximum when the wavelength of the sound equals sphere circumference, and then fluctuates somewhat until object circumference reaches about 10 wavelengths, above which echo intensity becomes proportional to the cross-sectional area of the object. This complex relation was derived for simple spheres (PYE, 1993), and the modelling of target strengths from real biological targets may be impossible (MØHL, 1988). Measurements of target strengths from pinned insects show target strength to be seemingly independent of frequency between 20-100 kHz (WATERS *et al.*, in press), so the sphere model may not be applicable to insects. Nonetheless, until more data are available, it seems reasonable to assume that calls whose frequencies have wavelengths longer than target circumference will return much weaker echoes to the bat than will calls whose wavelength equals or is shorter than target circumference. Thus bats that use higher frequencies may be expected to specialise in eating smaller prey, and call frequency may be an effective mechanism for dietary niche partitioning.

HELLER & HELVERSEN (1989) studied 12 sympatric rhinolophoid bats in Malaysia, and found that the distribution of call frequencies used by the bats was more even than that expected by chance. Frequencies lying close together were avoided, supporting the hypothesis that divergence in frequency may be a mechanism by which dietary resource partitioning could be achieved. Three species of sympatric hipposiderid bats in India southern India show little overlap in call frequency, perhaps as a mechanism for avoiding interspecific competition for insect prey (JONES *et al.*, 1994). Studies of call frequency in areas where similar species are absent would be revealing, to see whether ecological release of call frequency occurs. Although resource partitioning might be a realistic expectation for bats species that use different call frequencies, whether it would occur given the limited variation in frequency within species is more contentious.

CALL FREQUENCY AND CRYPTIC SPECIES IN BATS

Pipistrelle (*P. pipistrellus*) bats in Europe were long believed to be of one species. Detailed study of their echolocation calls showed that two phonic types are present, however (JONES & PARIJS, 1993). One phonic type echolocates with a call frequency (frequency containing most energy) averaging about 46 kHz, the other at about 55 kHz. Maternity roosts consist of bats of only one phonic type, and the two types are sympatric over much of their European range (see, for example ZINGG, 1990). Given the large differences in call frequency between the two types, it is surprising that the species are very difficult to distinguish by morphology. Moreover, there is a large genetic divergence between the two types, with a portion of the cytochrome b gene of mtDNA showing about an 11% sequence divergence (BARRATT *et al.*, in prep.). *P. pipistrellus* is clearly two cryptic species, and large differences in echolocation calls and genetics of the two species are masked by similarities in the bats' general appearance.

Cryptic species are commonly found in bat faunas. In Europe, for example the sibling species pairs *Plecotus auritus* and *P. austriacus* and *Myotis mystacinus* and *M. brandti* were only recognised as good biological species within the past 35 years (SCHOBER & GRIMMBERGER, 1989). It is possible that radiations of cryptic species can result as the consequence of echolocation call frequency influencing resource partitioning. It is easy to classify two sibling species of bats as being almost identical on the basis of their appearance, since humans are predominantly visual animals. Morphologically similar bat species may in fact use different call frequencies, and major differences may lie in the acoustic domain. Selection pressure for divergence in call frequency may be much greater than that for divergence in external morphology, so bats which look similar to our eyes may be radically different in their acoustics. The sibling species *Hipposideros caffer* and *H. ruber* of Africa, for example, have puzzled taxonomists for some time because of their similar external appearances. In the Gambia, however, bats keyed as *H. caffer* echolocate with CFs between 128-153 kHz, while *H. ruber* used 121-136 kHz. There was very little overlap in the frequencies used by the two sibling species (JONES *et al.*, 1993). Bimodal echolocation is seen in other African hipposiderid bats (PYE, 1972), and there may be analogous situations here to that described for pipistrelles above, with many cryptic species yet to be described.

It is interesting to contrast the echolocation calls of bats with vocalisations produced by birds and orthopterans. In the latter, the elaborate song structures may be driven by sexual selection, while the echolocation calls of bats are shaped primarily by natural selection. Bats presumably have optimal call designs for performing tasks associated with the acoustic recognition of targets, while bird and orthopteran songs may be acoustic equivalents of the peacock's tail, shaped largely by female choice. Might there be speciation mechanisms unique to echolocating bats because of the possible links between call frequency and resource partitioning ? I believe that there may indeed be, and two potential mechanisms are explored below.

1. Selection on body size might cause call frequency to diverge in species

In those species where body size and call frequency are correlated, selection acting on body size could drive divergence in echolocation call structure. There may be energetic reasons for animals of a particular size to be favoured by selection, and differences in body size would translate into differences in call frequency, and ultimately to differences in prey size.

2. Song flights, social calls and echolocation call divergence

Pipistrelle bats emit "social calls" when foraging. Such calls are complex in structure, consisting of a number of "V" shaped components between 18-35 kHz (AHLÉN, 1981). The two phonic types of pipistrelles emit statistically distinguishable social calls, with the 46 kHz type emitting calls lower in frequency than those of the 55 kHz type (K.E. BARLOW & G. JONES, unpubl.). Males repeat the social calls during song flights in the autumn in order to attract mates (LUNDBERG & GERELL, 1986). Female choice for, say, low frequency songflight calls could drive echolocation frequency to lower frequencies if echolocation call frequency was correlated with songflight call frequency. Speciation could in theory be achieved sympatrically by this mate choice model, with bats that use higher frequency calls specialising on smaller prey, and hence moving into a new ecological niche. This speciation mechanism could be unique to bats, though at this stage is proposed only as a possibility.

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Sound stimulation activates Fos-like immunoreactivity in the auditory neurons of echolocating bats

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Abstract. Using c-fos immunocytochemistry as a rapid and sensitive technique, we examined sound activated Fos-like immunoreactive neurons in the cerebral cortex, the cerebellum and subcortical nuclei of the big brown bat, *Eptesicus fuscus*. When both-ears were opened for sound stimulation, 19-43% of neurons in all subcortical auditory nuclei, the auditory cortex, the superior colliculus, the pontine nuclei and the cerebellar deep nuclei were found to be Fos-like immunoreactive. These Fos-like immunoreactive neurons were bilaterally and symmetrically distributed in all brain centers examined. When one ear was plugged, sound stimulation activated a larger (28-74%) number of Fos-like immunoreactive neurons in all contralateral auditory nuclei from the level of the nucleus of the lateral lemniscus down and in all ipsilateral auditory nuclei from the level of the inferior colliculus up. In addition, a larger number of Fos-like immunoreactive neurons were distributed in all ipsilateral superior colliculus, pontine nuclei and cerebellar deep nuclei. Implications of these observations in relation to known mammalian auditory pathways and electrophysiological studies are discussed.

INTRODUCTION

In mammalian cells, many extracellular stimuli induce rapid but transient induction of nuclear proto-oncogenes. This signal transduction is likely to be of direct relevance to the nervous system (HALL, 1992; SHENG & GREENBERG, 1990). Because of this, stimulus induced proto-oncogene expression can be used to study the stimulus activated nervous activity. For example, by utilizing the fact that the proto-oncogene c-fos is expressed in many neurons following pharmacological, electrical and physiological stimulation, c-fos immunocytochemistry has been used as a rapid and sensitive marking technique for identification of stimulus activated neurons in the nervous system (BULLITT, 1990; DRAGUNOW & ROBERTSON, 1987; DRAGUNOW & FAULL, 1989; HUNT *et al.*, 1987; LE GAL LA SALLE & NAQUET, 1990; MENETREY *et al.*, 1989; MORGAN & CURRAN, 1989; MORGAN *et al.*, 1987; SAGAR *et al.*, 1988; SATO *et al.*, 1992; SHENG & GREENGBERG, 1990). In contrast to the electrophysiological recording method, this immunocytochemical technique has the advantage of providing an overall profile of the stimulus activated activity within a specific sensory system of a single animal. Recently, this c-fos immunocytochemistry has been successfully used to examine the activated neurons caused by sound stimulation in mice and Sprague-Dawley rats (EHRET & FISCHER, 1991; FRIAUF, 1992; REIMER, 1993; SATO *et al.*, 1992). Under free-field stimulation conditions, we have extended these studies to examine the sound activated Fos-like immunoreactive neurons in the subcortical nuclei, the auditory cortex and the cerebellum of the big brown bats, *Eptesicus fuscus*, which heavily rely upon sound processing for survival (GRIFFIN, 1958).

The present study shows that when both ears were opened, sound activated Fos-like immunoreactive neurons were bilaterally and symmetrically distributed in all auditory nuclei, the superior colliculus, the pontine nuclei and the cerebellar deep nuclei. In contrast, when one ear was plugged, sound activated Fos-like immunoreactive neurons were bilaterally but asymmetrically distributed in all brain centers examined. There were 31-70% more Fos-like immunoreactive neurons in all contralateral auditory nuclei from the level of the nucleus of the lateral lemniscus down and in all ipsilateral auditory nuclei from the level of the inferior colliculus up. In addition, predominant distribution was observed in all ipsilateral superior colliculus, pontine nuclei and cerebellar deep nuclei.

MATERIALS AND METHODS

Six *Eptesicus fuscus* were used for this study. Each bat, either with both-ears opened or one-ear plugged (with dental cement), was placed inside a 10 x 10 x 10 cm^3 cage made of aluminum mesh and was transferred into a sound proof room in total darkness for 2 hours to adapt to the new environment. The bat was then stimulated with either 30 kHz, 79 dB SPL or 50 kHz 79 dB SPL sounds (4 ms, 0.5 ms rise-decay times delivered at 2 pulses/sec) for 45 minutes. That is, the bat was stimulated with the 4 ms pulse for a total of 21.6 sec over the 45-minute period. At the end of sound stimulation, the bat was deeply anaesthetized with Nembutal and perfused transcardially with phosphate buffered saline (PBS) (0.1 M PBS, pH 7.4) followed by 2% paraformaldehyde in 0.1 M phosphate buffer (pH 7.4). After removing the skull, the brain was fixed in 2% paraformaldehyde for 4 hours before being placed in 30% sucrose/PBS solution overnight at 4°C. Coronal sections were cut at 20µm on a freezing microtome (Leitz 1208). Adjacent consecutive sections were divided into three series and were thoroughly washed in PBS before being mounted on microscope slides (Fisher) and air-dried overnight. One series of sections were stained with Nissl stain in order to count the total number of neurons in each section. The other two series were used for c-fos immunocytochemistry processing. These two series were dipped in acetone three times (3 minutes each time) and rewashed in PBS three times for incubation in 1.5% normal goat serum in PBS for 1 hour. All sections were rewashed in PBS between successive steps of protocol.

At room temperature, one series were reacted with the primary antibody, a polyclonal rabbit IgG to the Fos protein (c-fos 4; Cat # SC-52, Santa Cruz Biotechnology, Inc) at a dilution of 1: 100 in PBS overnight before being processed immunocytochemically with the avidin-biotin-peroxidase method (VECTOR ABC kit). Peroxide reaction was carried out with DAB (0.04%), NiCl (0.04%) and H_2O_2 (0.01 %) in phosphate buffer before being rinsed, dehydrated and embedded in Permount. The other series (control) were processed in the same way but with goat serum rather than the primary antibody for Fos. An additional control experiment was also performed by testing the Fos immunoreactivity of brain sections of one bat which received no sound stimulation.

To determine the effect of sound activation under different stimulation conditions, the total number of Fos-like immunoreactive neurons and the Nissl stained neurons in five consecutive coronal sections of each series were respectively counted for each brain center under the light microscope with the aid of a reticule. The percentage of Fos-like immunoreactive neurons relative to Nissl stained neurons at each brain center was then calculated.

RESULTS

Stimulation under both ears opened conditions

Fos-like immunoreactive neurons were rarely found in the auditory cortex, the cerebellum and the subcortical nuclei of the control bats. When the bat was stimulated with sound under both-ears opened conditions (referred to as symmetrical sound stimulation), 19-43% (Tables 1, 2, left two columns vs middle two columns) of neurons in dorsal and ventral cochlear nuclei (DCN, VCN) (Fig 1A$_l$,B$_r$), the nucleus of the trapezoidal body (NTB), both lateral and medial superior olivary nuclei of the superior olivary complex (SOC) (Fig 1 E$_l$,F$_r$), the nucleus of the lateral lemniscus (NLL) (Fig 1 C$_l$,D$_r$), the inferior colliculus (IC) (Fig 1 G$_l$,H$_r$), the dorsal and ventral divisions of the medial geniculate body (MGB) (Fig 1 I$_l$,J$_r$) and the auditory cortex (AC) (Fig 2 A$_l$,B$_r$), the superior colliculus (SC) (Fig 2 C$_l$,D$_r$), the pontine nuclei (PN) (Fig 2 E$_l$,F$_r$), the cerebellar fastigial (NFC) (Fig 2 G$_l$, Hr), interpositus (NIC) and (NDC) dentate nuclei (Fig 2 I$_l$,J$_r$) were found to be Fos-like immunoreactive. These Fos-like immunoreactive neurons were bilaterally and symmetrically distributed in all these brain centers (Figs 1-3). Thus at each brain level, the number of Fos-like immunoreactive neurons observed in the right and left brain centers are almost the same. In addition, both 30 kHz, 79 dB SPL and 50 kHz, 79 dB SPL sounds appeared to activate about the same number and percent of Fos-like immunoreactive neurons in each brain center (Tables 1, 2, middle two columns).

Although two different sound frequencies were used for stimulation, differential distribution of the Fos-like immunoreactive neurons according to sound

Table 1 : Number and percent Fos-like immunoreactive and Nissl stained neurons in five coronal sections of each brain center when stimulated with 30 kHz, 79 dB SPL sound under two different ear conditions. AC : auditory cortex; DCN : dorsal cochlear nucleus; IC : inferior colliculus; MGB : medical geniculate body; N : number of neurons; NDC : cerebellar dentate nucleus; NFC : cerebellar fastigial nucleus; NLL : nucleus of lateral lemniscus; NIC : cerebellar interpositus nucleus; NTB : nucleus of trapezoidal body; PN : pontine nuclei; SC : superior colliculus; SOC : superior olivary complex; VNC : ventral cochlear nucles. Note : percent Fos-like immunoreactive neurons in each brain center was obtained by dividing the number of immunoreactive neurons by the number of Nissl stained neurons in the same brain center relative to the same ear. In the two far right columns, the side of each brain center which contains a higher percentage of Fos-like immunoreactive neurons is marked with an asterisk.

Brain centers	Nissl stained neurons				Fos-like immunoreactive neurons							
	both-ears opened				both-ears opened				left-ear plugged			
	left		right		left		right		left		right	
	N	%	N	%	N	%	N	%	N	%	N	%
DCN	455	(100),	445	(100),	168	(37),	167	(37),	180	(40),	252	(57)*,
VCN	443	(100),	436	(100),	107	(24),	105	(24),	98	(22),	147	(33)*,
NTB	376	(100),	386	(100),	129	(34),	125	(32),	125	(33),	174	(45)*,
SOC	276	(100),	277	(100),	104	(38),	101	(37),	95	(34),	146	(53)*,
NLL	920	(100),	925	(100),	184	(20),	193	(21),	189	(20),	282	(31)*,
IC	1262	(100),	1250	(100),	336	(27),	356	(28),	537	(43)*,	342	(27),
SC	1257	(100),	1238	(100),	365	(29),	383	(31),	501	(40)*,	359	(29),
PN	381	(100),	384	(100),	161	(42),	164	(43),	282	(74)*,	177	(46),
MGB	584	(100),	572	(100),	212	(36),	212	(37),	332	(57)*,	215	(38),
AC	1670	(100),	1657	(100),	319	(19),	330	(20),	463	(28)*,	333	(20),
NFC	240	(100),	241	(100),	93	(39),	89	(37),	129	(54)*,	89	(37),
NDC	278	(100),	278	(100),	87	(31),	88	(32),	115	(41)*,	85	(31),
NIC	290	(100),	293	(100),	73	(25),	70	(24),	114	(39)*,	74	(25),

frequency was only observed in the NLL and the MGB. Whereas 30 kHz sounds activated Fos-like immunoreactive neurons in both the dorsal and ventral NLL, the dorsal and intermediate divisions of the MGB, 50 kHz sounds activated Fos-like immunoreactive neurons in the ventral NLL,ventral and intermediate divisions of the MGB (Fig 3 A vs B).

Stimulation under monaurally plugged conditions

When the bat was stimulated under the monaurally plugged conditions (referred to as asymmetrical sound stimulation), observed Fos-like immunoreactive neurons were bilaterally but asymmetrically distributed in all brain centers examined (Fig 4). Fos-like immunoreactive neurons were observed in 19-47% (Tables 1, 2, far right two columns) of neurons in all ipsilateral DCN and VCN (Fig 5 A_l), NTB, SOC (Fig 5 E_l), NLL (Fig 5 C_l), and all contralateral IC (Fig 5 H_r), MGB (Fig 5 J_r), AC (Fig 6 B_r), SC (Fig 6 D_r), PN (Fig 6 F_r), NFC (Fig 6 H_r) and NDC (Fig 6 J_r). This range of percentage of Fos-like immunoreactive neurons is comparable that observed in the corresponding brain center of the bat which received symmetrical sound stimulation (Tables 1, 2, two middle columns). In contrast, Foslike immunoreactive neurons were observed in 28-74% of neurons in all contralateral DCN and VCN (Fig 5 B_r), NTB, SOC (Fig 5 F_r), NLL (Fig 5 D_r), and all ipsilateral IC (Fig 5 G_l), MGB (Fig 5 I_l).SC (Fig 6 C_l), AC (Fig 6 A_l), PN (Fig 6 E_l), NFC (Fig 6 G_l) and NDC (Fig 6 I_l). A comparison of the number of Fos-like immunoreactive neurons between two corresponding nuclei at each brain center shows a difference of 31-70 %.

Similar to the symmetrical sound stimulation condition (Fig 3), asymmetrical stimulation with 30

Table 2 : Number and percent Fos-like immunoreactive and Nissl stained neurons in five coronal sections of each brain center when stimulated with 50 kHz, 79 dB SPL sound under two different ear conditions. AC : auditory cortex; DCN : dorsal cochlear nucleus; IC : inferior colliculus; MGB : medical geniculate body; N : number of neurons; NDC : cerebellar dentate nucleus; NFC : cerebellar fastigial nucleus; NLL : nucleus of lateral lemniscus; NIC : cerebellar interpositus nucleus; NTB : nucleus of trapezoidal body; PN : pontine nuclei; SC : superior colliculus; SOC : superior olivary complex; VNC : ventral cochlear nucles. Note : percent Fos-like immunoreactive neurons in each brain center was obtained by dividing the number of immunoreactive neurons by the number of Nissl stained neurons in the same brain center relative to the same ear. In the two far right columns, the side of each brain center which contains a higher percentage of Fos-like immunoreactive neurons is marked with an asterisk.

Brain centers	Nissl stained neurons		Fos-like immunoreactive neurons			
	both-ears opened		both-ears opened		right-ear plugged	
	left N %	right N %	left N %	right N %	left N %	right N %
DCN	439 (100),	444 (100),	170 (39),	177 (40),	248 (56)*,	171 (39),
VCN	433 (100),	424 (100),	101 (23),	100 (24),	148 (34)*,	100 (24),
NTB	376 (100),	387 (100),	121 (32),	116 (30),	214 (57)*,	126 (33),
SOC	275 (100),	278 (100),	103 (38),	100 (36),	145 (53)*,	98 (35),
NLL	932 (100),	939 (100),	191 (21),	182 (19),	285 (31)*,	183 (20),
IC	1264 (100),	1250 (100),	337 (27),	356 (28),	355 (28),	549 (44)*,
SC	1260 (100),	1240 (100),	367 (29),	383 (31),	361 (29),	513 (41)*,
PN	380 (100),	396 (100),	158 (42),	173 (43),	177 (47),	268 (68)*,
MGB	601 (100),	589 (100),	213 (35),	221 (37),	229 (38),	331 (56)*,
AC	1668 (100),	1649 (100),	332 (20),	326 (19),	315 (19),	468 (28)*,
NFC	245 (100),	236 (100),	91 (37),	96 (41),	94 (38),	134 (57)*,
NDC	275 (100),	282 (100),	86 (31),	82 (29),	87 (32),	112 (40)*,
NIC	288 (100),	282 (100),	82 (28),	68 (24),	75 (26),	110 (39)*,

and 50 kHz sounds only generated differential distribution of the Fos-like immunoreactive neurons in the NLL and MGB (Fig 4 A vs B). When stimulated with 30 kHz sounds, Fos-like immunoreactive neurons were observed in both the dorsal and ventral NLL as well as the dorsal and intermediate divisions of the MGB of the bat. In contrast, when stimulated with 50 kHz sounds, Fos-like immunoreactive neurons were observed in the ventral NLL, ventral and intermediate divisions of the MGB.

DISCUSSION

Fos-like immunoreactive neurons in auditory system

C-fos expression elicited by sound stimulation has been successfully demonstrated in mice (EHRET & FISCHER, 1991; REIMER, 1993) and rats (FRIAUF, 1992; ROUILLER *et al.*, 1992; SATO *et al.*, 1992). These studies showed that c-fos immunocytochemistry is a reliable method for identification of neuronal activity and tonotopic organization in the auditory system. Whereas the studies on mice (EHRET & FISCHER, 1991; REIMER, 1993) and rats (SATO *et al.*, 1992) primarily examined c-fos positive neurons and tonotopy in the CN and/or IC, two studies on rats (FRIAUF, 1992; ROUILLER *et al.*, 1992) examined sound elicited c-fos positive neurons throughout the entire auditory system. These two studies reported that neurons expressing c-fos were either not observed in the SOC and the ventral division of the MGB (ROUILLER *et al.*, 1992) or were infrequently observed in the MGB and the AC but

Fig 1 : Photomicrographs showing Fos-like immunoreactive neurons in representative sections of the left and right CN (DCN, VCN)(A_l, B_r), NLL (C_l, D_r), SOC (E_l, F_r), IC (G_l, H_r), MGB (I_l, J_r) of a bat when symmetrically stimulated with 50 kHz and 79 dB SPL sounds. Note there are about a same number of Fos-like immunoreactive neurons observed in both sections of each nucleus. A representative Fos-like immunoreactive neuron in each section is indicated by an arrow head. Two enlarged Fos-like immunoreactive neurons in VCN (Br) and SOC (F_r) are shown in K and L. l : left; r: right.

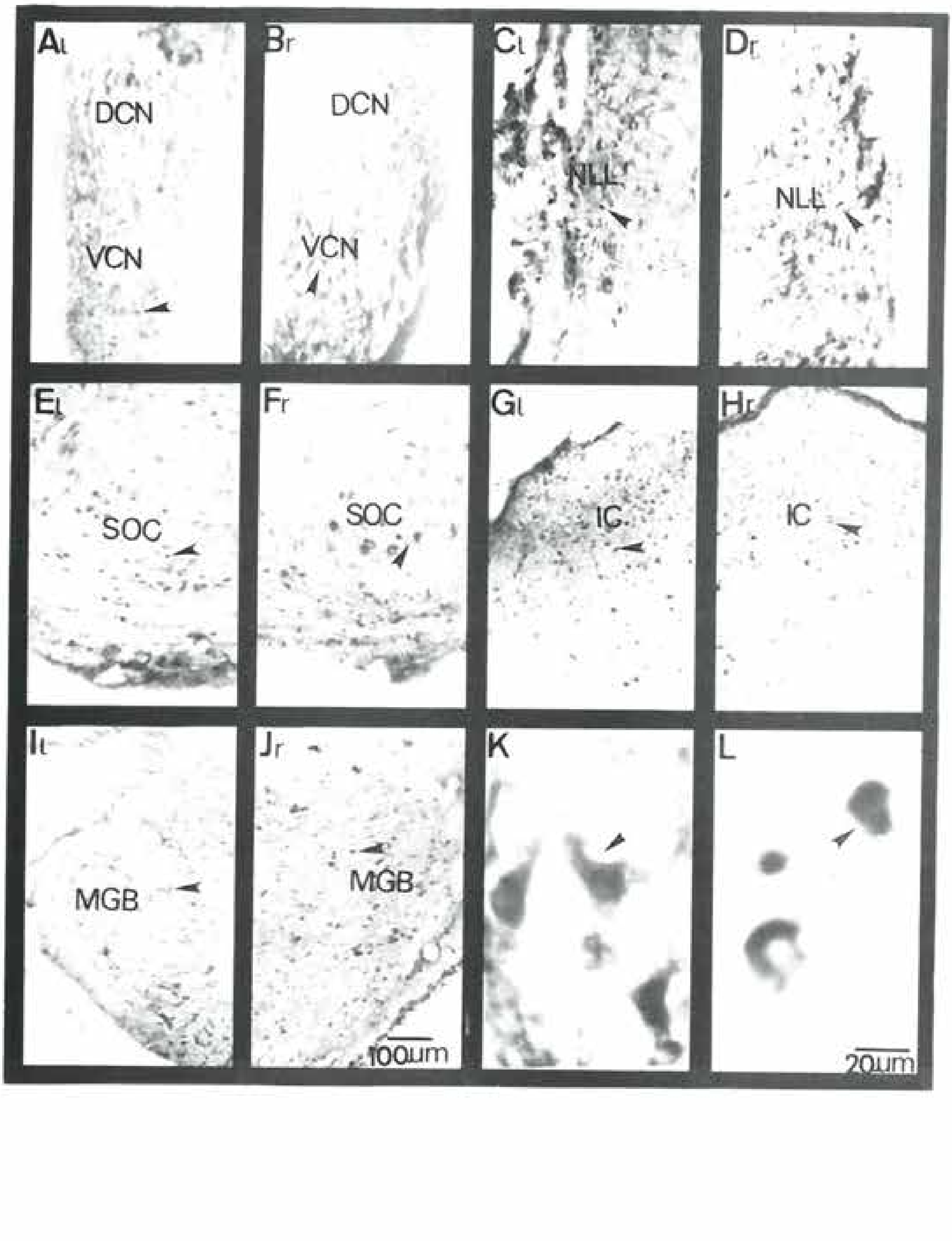


Fig 2 : Photomicrographs showing Fos-like immunoreactive neurons in representative sections of the left and right AC (A_l, B_r), SC (C_l, D_r), PN (E_l, F_r), NFC (G_l, H_r) and NDC (I_l, J_r) of a bat when symmetrically stimulated with 50 kHz and 79 dB SPL sounds. Note there are about a same number of Fos-like immunoreactive neurons observed in both sections of each brain center. A representative Fos-like immunoreactive neuron in each section is indicated by an arrow head. Two enlarged Fos-like immunoreactive neurons in NFC (G_l) and NDC (I_l) are shown in K and L. l : left; r: right.

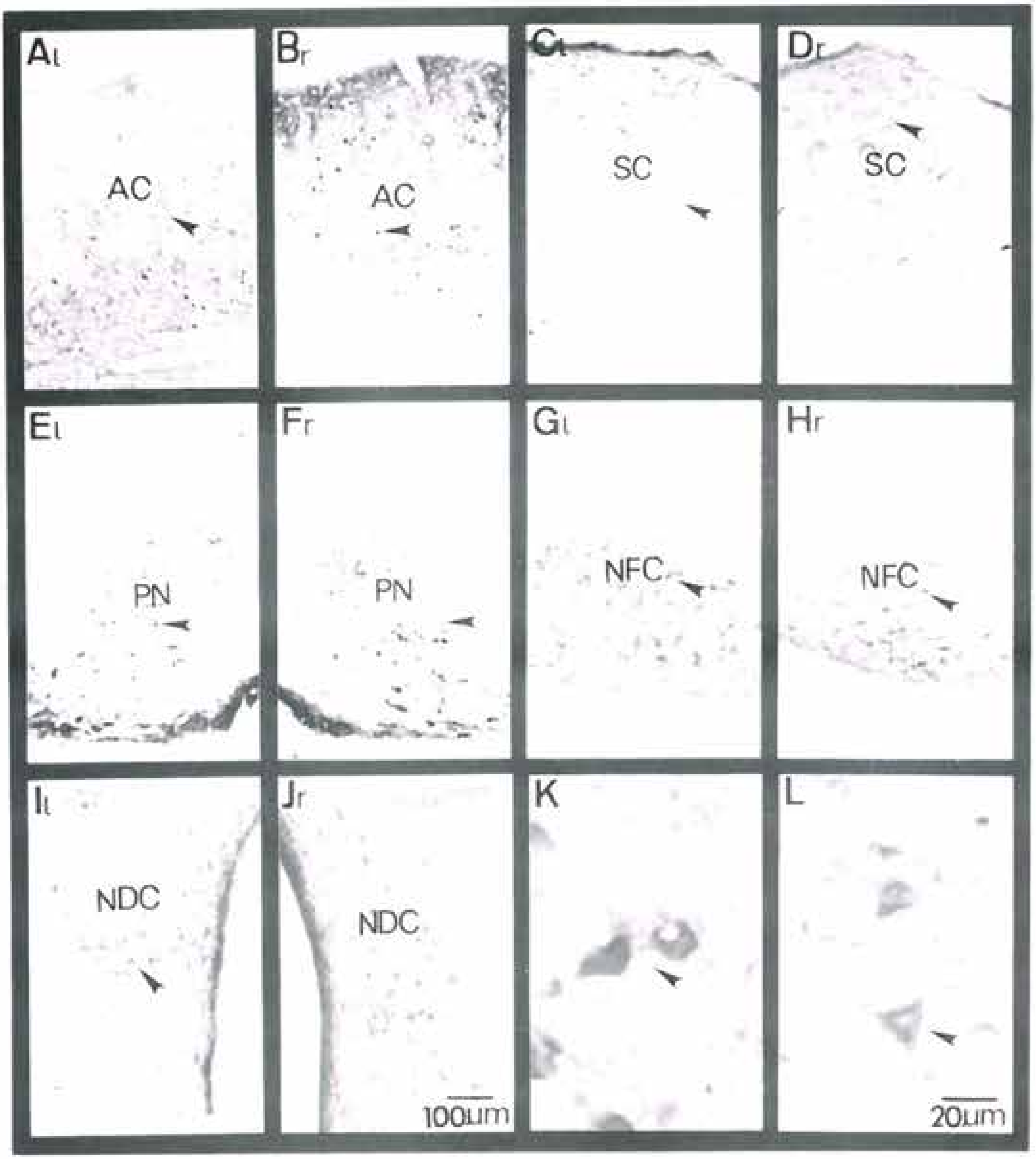


Fig 3 : Drawings of brain sections showing bilateral and symmetrical distribution of Fos-like immunoreactive neurons (black dots) elicited by symmetrical sound stimulation (A: 30 kHz, 79 dB SPL; B: 50 kHz, 79 dB SPL) in the cortex and subcortical nuclei of two big brown bats, *Eptesicus fuscus*. These Fos-like immunoreactive neurons were found in the dorsal and ventral cochlear nucleus (DCN and VCN), the superior olivary complex (SOC), the nucleus of lateral lemniscus (NLL), the nucleus of trapezoidal body (NTB), the inferior colliculus (IC), the superior colliculus (SC), the medial geniculate body (MGB), the auditory cortex (AC), the pontine nuclei (PN), the cerebellar fastigial and dentate nuclei (NDC and NFC).

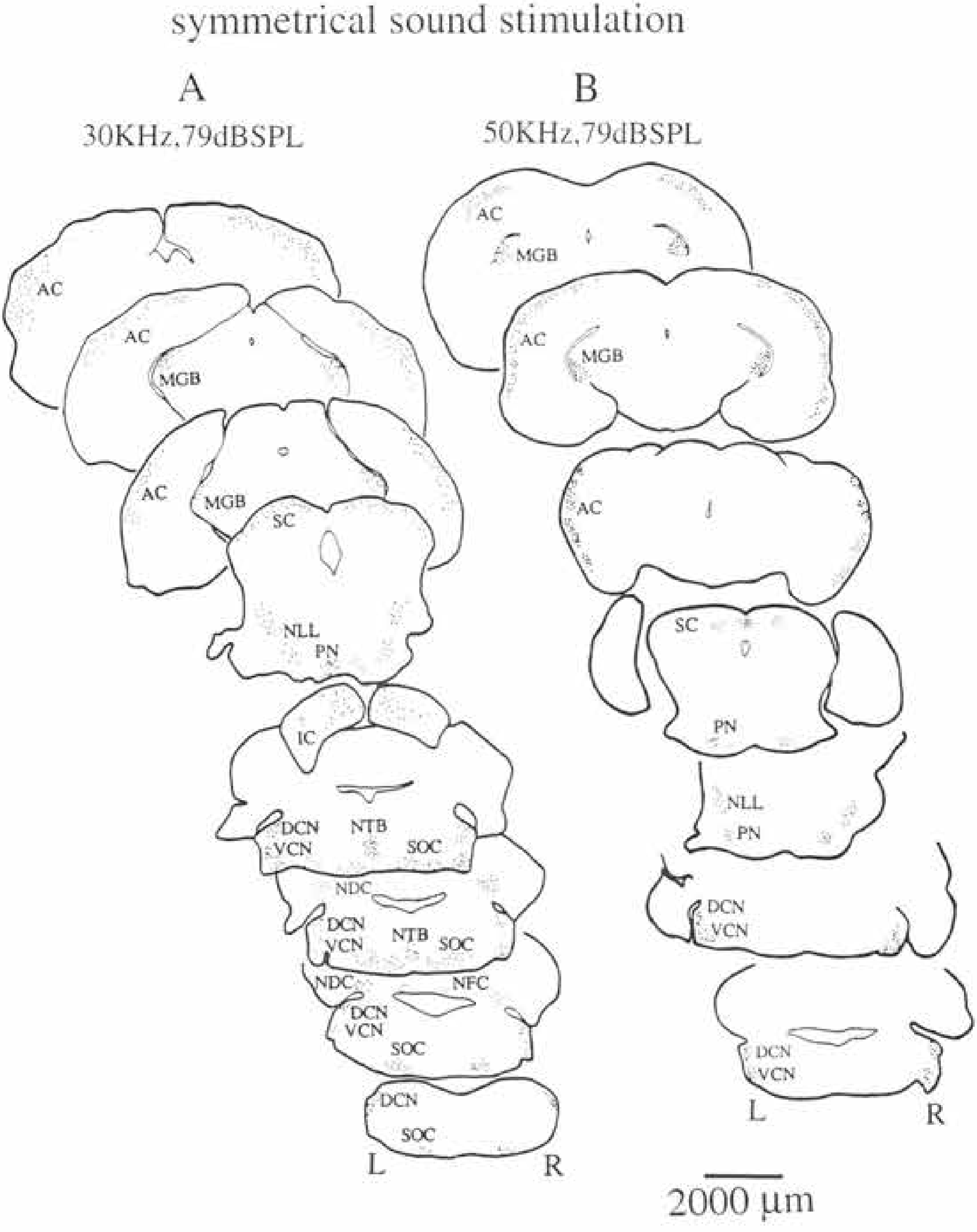


Fig 4 : Drawings of brain sections showing bilateral but asymmetrical distribution of Fos-like immunoreactive neurons (black dots) elicited by asymmetrical sound stimulation (A: 30 kHz, 79 dB SPL; B: 50 kHz, 79 dB SPL) in the cortex and subcortical nuclei of two monaurally plugged big brown bats, *Eptesicus fuscus.* Note Fos-like immunoreactive neurons were predominantly found in contralateral CN, SOC, NTB, NLL and ipsilateral IC, SC, MGB, AC, PN, NFC and NDC. Drawings in A were based upon the results obtained from a left-ear plugged (Lp) bat which was stimulated with 30 kHz, 79 dB SPL sounds. Drawings in B were based upon the results obtained from a right-ear plugged (Rp) bat which was stimulated with 50 kHz and 79 dB SPL sounds.

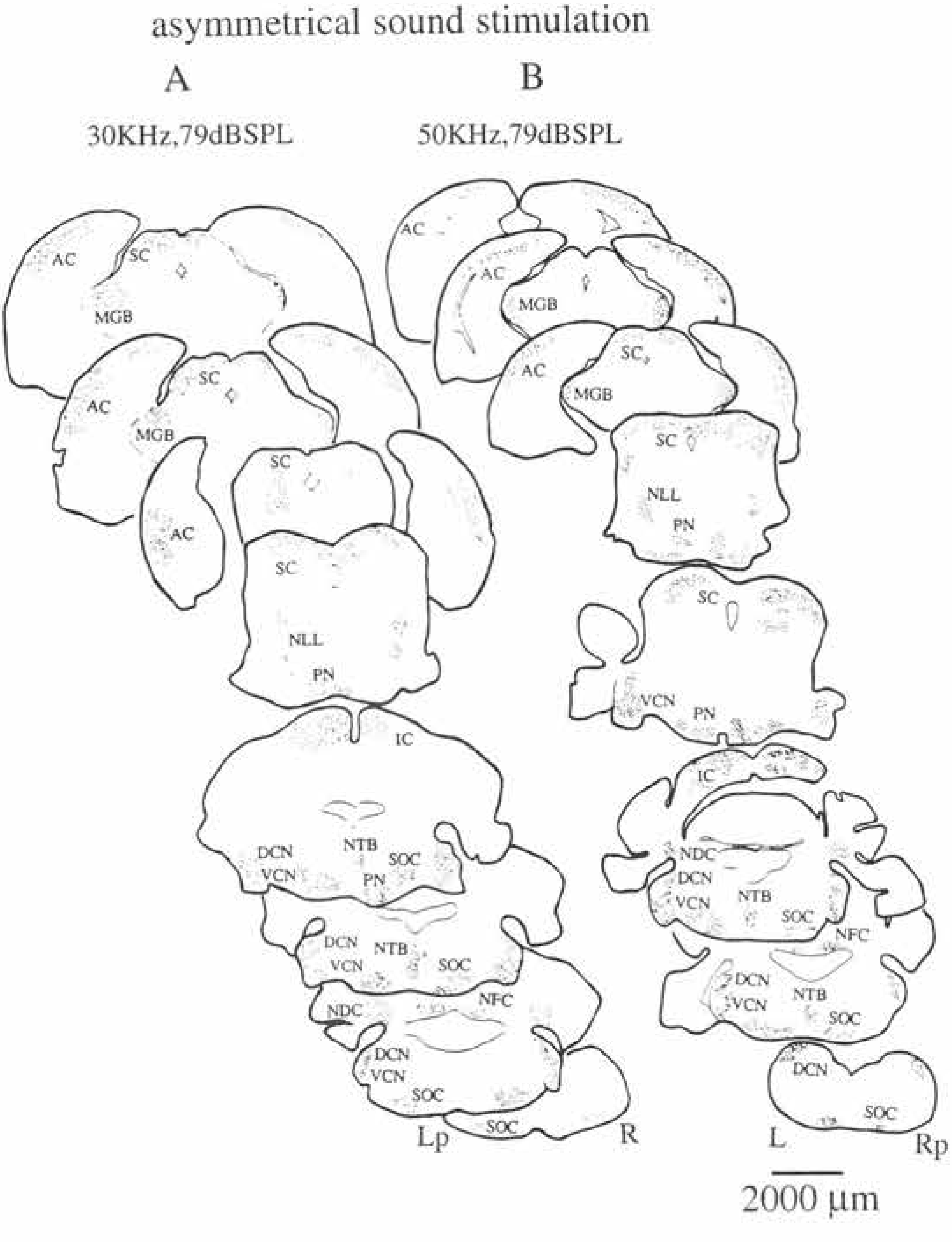


Fig 5 : Photomicrographs showing Fos-like immunoreactive neurons in representative sections of left and right CN (DCN,VCN) (A_l, B_r), NLL(C_l, D_r), SOC (E_l, F_r), IC (G_l, Hr), MGB (I_l, J_r) of a left-ear plugged bat which was stimulated with 30 kHz and 79 dB SPL sounds. A representative Fos-like immunoreactive neuron in each section is indicated by an arrow head. Note more number of Fos-like immunoreactive neurons are observed in the contralateral DCN and VCN (B_r), SOC (F_r), NLL (D_r), and ipsilateral IC (G_l), MGB (I_l) than in corresponding counterpart sections (A_l; C_l; E_l; H_r; J_r). Two enlarged Fos-like immunoreactive neurons in VCN (B_r) and SOC (F_r) are shown in K and L. l : left; r: right.

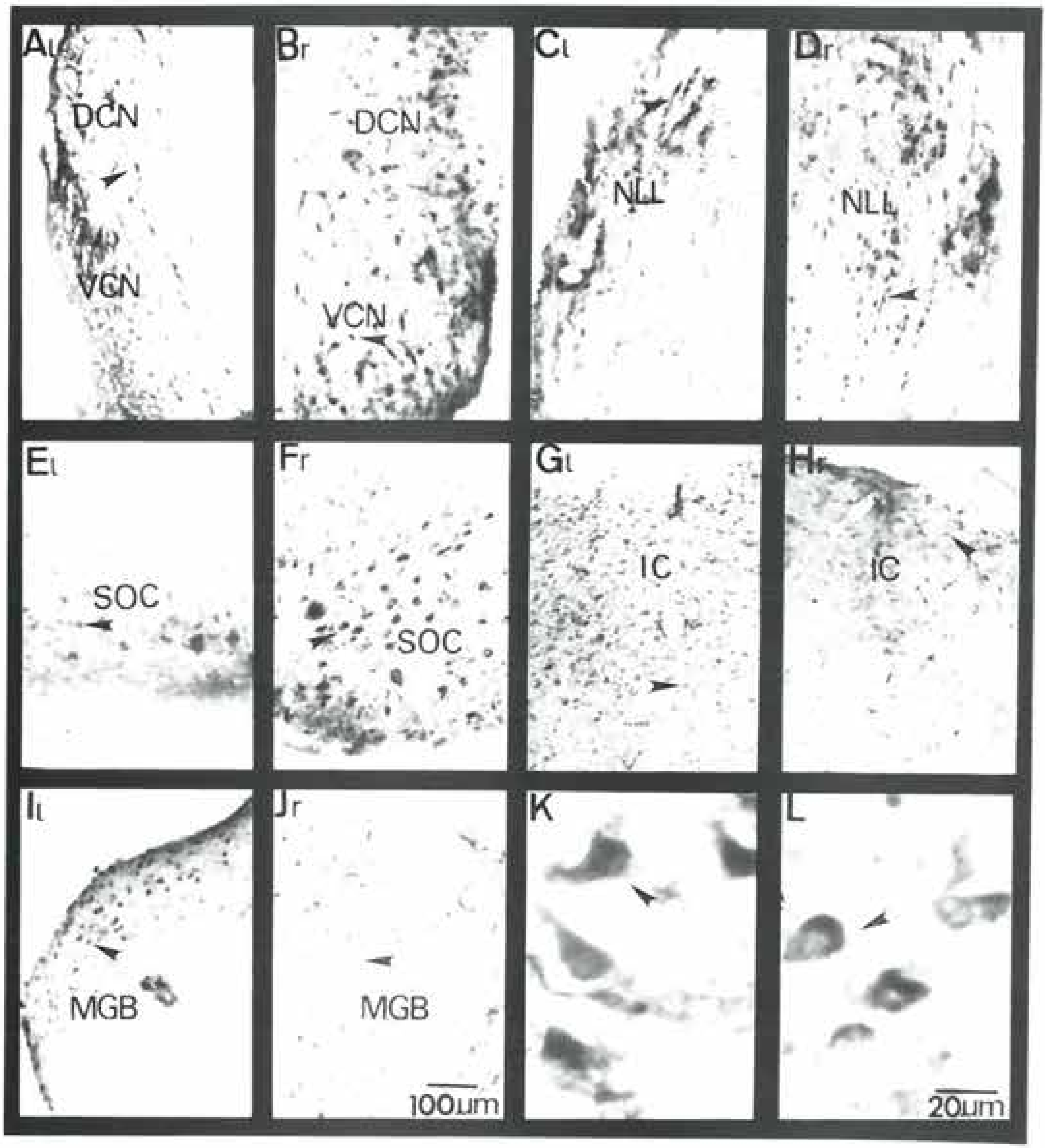
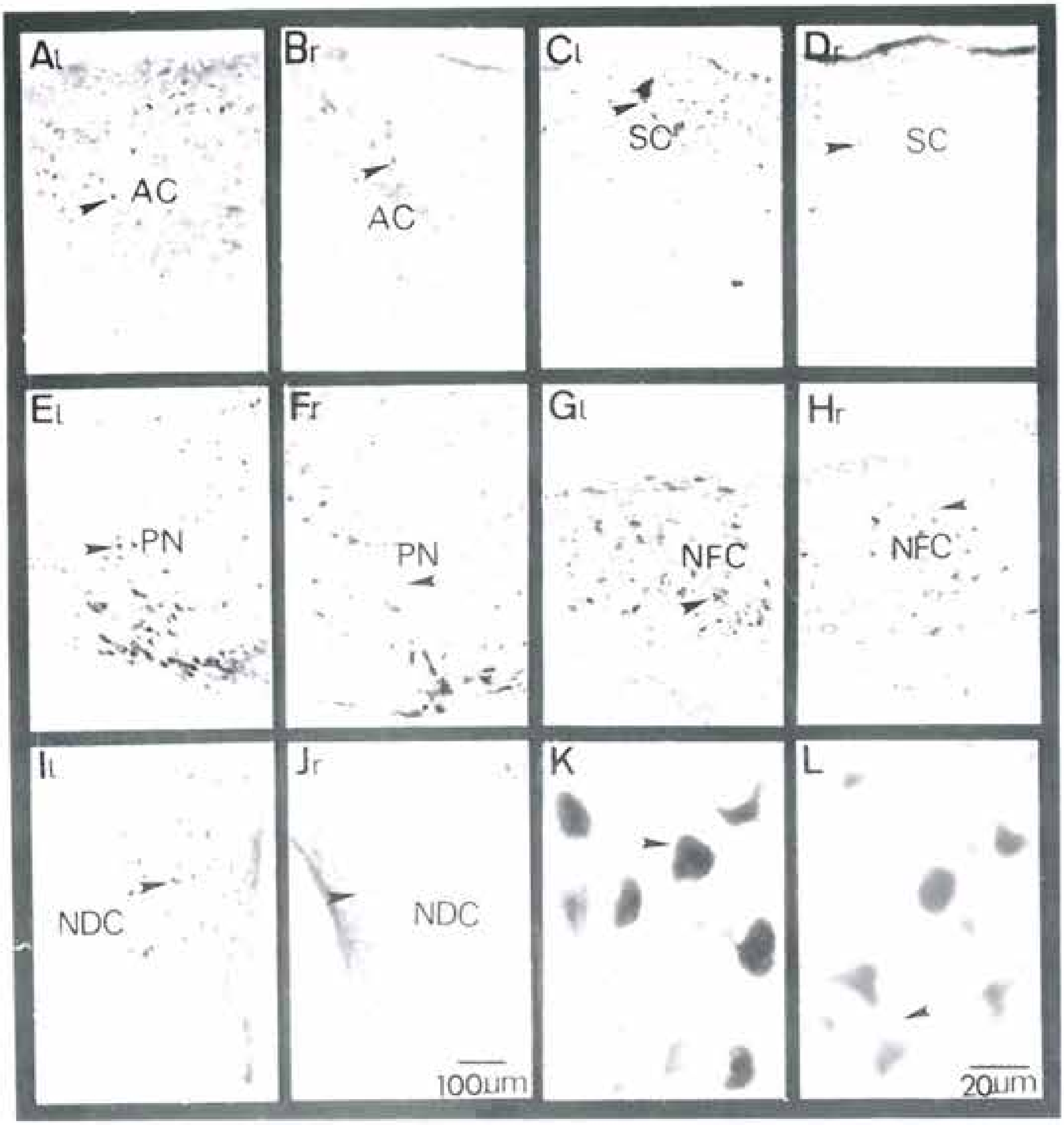


Fig 6 : Photomicrographs showing Fos-like immunoreactive neurons in representative sections of left and right AC (A_l, B_r), SC (C_l, D_r), PN (E_l, F_r), NFC (G_l, H_r) and NDC (I_l, J_r) of a left-ear plugged bat which was stimulated with 30 kHz and 79 dB SPL sounds. A representative Fos-like immunoreactive neuron in each section is indicated by an arrow head. Note more number of Fos-like immunoreactive neurons are observed in the ipsilateral AC (A_l), SC (C_l), PN (E_l), NFC (G_l) and NDC (I_l) than in corresponding counterpart sections (B_r; D_r; F_r; H_r; J_r). Two enlarged Fos-like immunoreactive neurons in PN (F_l) and NFC (Hr) are shown in K and L. l : left; r : right.



not at all in the medial superior olivary nucleus (FRIAUF, 1992).

In the present study, neurons expressing Fos-like immunoreactivity were observed in both lateral and medial superior olivary nuclei, the ventral division of the MGB and the AC. Because sound intensity used in these two studies and ours were all comparable (80-90, 80, and 79 dB SPL respectively), these different observations are more likely due to species-specific difference rather than different stimulus conditions. Perhaps the much more extensive sound activated Fos-like immunoreactivity in the auditory system of bats is related to the fact that the bats, which heavily rely upon acoustic signal processing for survival (GRIFFIN, 1958), have a highly developed auditory system (NEUWEILER, 1980; POLJAK, 1926; ZVORYKIN, 1959). In addition, their auditory neurons are extremely sensitive to sound stimulation (BUSNEL & FISH, 1980; NACHTIGALL & MOORE, 1988).

In this study, tonotopical distribution of Fos-like immunoreactive neurons due to different sound frequencies was only observed in the NLL and the MGB. However, previous studies have demonstrated tonotopical distribution of Fos immunoreactive neurons in the CN and the IC (EHRET AND FISCHER, 1991; ROUILLER *et al.*, 1992, SATO *et al.*, 1992, REIMER, 1993). The lack of tonotopical distribution of Fos-like immunoreactive neurons in most auditory centers of the bat is likely due to the strong sound intensity used for stimulation. Both 30 kHz, 79 dB SPL and 50 kHz, 79 dB SPL sounds used in this study likely activated most auditory neurons in each brain center which made tonotopical study impossible.

Stimulation duration required for Fos immunoreactivity expression

In activating Fos immunoreactive neurons, four previous studies used either sound pulses ranging from 50 to 200 ms (EHRET & FISCHER, 1991; FRIAUF, 1992; ROUILLER *et al.*, 1992; REIMER, 1993) or continuous pure tones (SATO *et al.*, 1992) for stimulation. Although differed in stimulus parameters (i.e. pulse duration, repetition rate), the total amount of time used for sound stimulation in these studies ranged from 6 to 36 minutes over a period of 10 to 80 minutes. In contrast, 4 ms pulses were delivered in only 21.6 sec over a period of 45 minutes in this study. This effective method of auditory stimulation in activating fos immunoreactivity in auditory neurons was first discovered by SCHEICH and his coworkers (Federal Instituts for Neurobiology, Magdeburg, Germany).

Fos-like immunoreactive neurons in non-auditory brain centers

In this study, Fos-like immunoreactive neurons were also observed in the superior colliculus, the pontine nuclei and the cerebellar deep nuclei (Tables 1, 2, Figs 2 C-J, 3, 4, 6 C-J). These observations are consistent with the electrophysiological findings that neurons in the superior colliculus (JEN *et al.*, 1984b, 1993b; POUSSIN & SCHLEGEL, 1984; SHIMOZAWA *et al.*, 1984; SUN *et al.*, 1983), the cerebellum (JEN & SCHLEGEL, 1980; JEN *et al.*, 1984a; KAMADA & JEN, 1990; SUN *et al.*, 1987) and the pontine nuclei (JEN *et al.*, 1993a; KAMADA *et al.*, 1992; TENG, 1991; TENG & JEN, 1990; WU, 1993; WU & JEN, 1993) of this bat species respond to sound stimulation.

Fos-like immunoreactive cerebellar granule cells were not observed in the present study although they presumably respond to sound stimulation (JEN & SCHLEGEL, 1980). Because the 79 dB SPL sound used in this study should theoretically activate cerebellar granular cells according to previous electrophysiological studies (JEN & SCHLEGEL, 1980; JEN *et al.*, 1984a; KAMADA & JEN, 1990), we can only speculate that the cerebellar granule cells apparently did not initiate a cellular immediate early response at this level of sound activation. A previous study has reported that a transcriptional response in cerebellar granule cells was not induced even with seizures (LE GAL LA SALLE & NAQUET, 1990).

Fos immunoreactivity under symmetrical vs asymmetrical sound stimulations

In the auditory pathway of the bat, neurons in the IC, the MGB and the AC mainly receive their auditory inputs from the contralateral cochlea while neurons in all auditory nuclei below the IC receive theirs from the ipsilateral cochlea (NEUWEILER, 1980). Because the left and right auditory pathways are symmetrical, one can predict that when a bat is symmetrically stimulated, all brain centers at both sides of the auditory system are equally stimulated. Such sound stimulation will generate a same number of Fos-like immunoreactive neurons in all brain centers examined (Figs 1-3, Tables 1, 2, middle two columns). In contrast, when monaurally plugged bats were stimulated, ear plugging reduces the stimulus intensity to neurons in all ipsilateral auditory nuclei from the level of the NLL down and in contralateral auditory nuclei from the level of the IC up. This unequal sound stimulation will result in bilateral but asymmetrical distribution of the Fos-like immunoreactive neurons in all brain centers examined (Figs 4-6, Tables 1, 2, right two columns). The present study also observed asymmetrical and predominant distribution of Fos-like immunoreactive neurons in the ipsilateral SC, PN and cerebellar deep nuclei (Figs 4, 6, Tables 1, 2, right two columns) under asymmetrical sound stimulation. This finding is consistent with previous studies that these nuclei receive predominant auditory inputs indirectly from the contralateral cochlea (SCHULLER *et al.*, 1991; TENG, 1991; TENG & JEN 1990; 1991, ZHANG *et al.*, 1987).

In all brain centers examined, we found that asymmetrical sound stimulation produced a larger number of Fos-like immunoreactive neurons than symmetrical sound stimulation did in some ipsilateral or contralateral auditory nuclei (Figs 4, 6, Tables 1, 2, middle two columns vs right two columns). This is likely due to the fact that most binaural EI neurons, which receive excitation from one ear and inhibition from the other, were not activated when both ears were stimulated. However, they were likely activated by sound stimulation when the inhibitory input from the plugged ear was greatly attenuated. In addition, an earlier study has demonstrated that some neurons in the cochlear nucleus could be inhibited by contralateral sound stimulation (MAST, 1970) which perhaps was mediated via the centrifugal pathways (DESMEDT, 1975; PICKLES, 1982). This study may explain the fact that attenuation of the inhibitory effect from the plugged ear during sound stimulation activated more Fos-like immunoreactive neurons in the contralateral CN.

Advantage of Fos immunocytochemistry

Similar to other studies on mice (EHRET & FISCHER, 1991; REIMER, 1993) and rats (FRIAUF, 1992; ROUILLER *et al.*, 1992; SATO *et al.*, 1992), our present study has demonstrated that c-fos immunocytochemistry can be a very useful method to map the sound activated neurons in the auditory system of bats. Although 2-deoxyglucose autoradiography has been used to map the auditory responses in bats (MELZER, 1985; QIAN, 1988), c-fos immunochemistry method appears to have finer resolution at the single cell level in addition to lower cost and greater safety. This method may prove to be a useful complement to electrophysiological studies of the responses of auditory neurons to specific signal features.

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Directional sensitivity of inferior collicular neurons of the big brown bat *Eptesicus fuscus*, determined with temporally varied sound pulses

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Abstract. Under free field stimulation conditions, directional sensitivity of 72 inferior collicular neurons of the big brown bat *Eptesicus fuscus*, was studied by using three pulse trains with varied pulse durations and repetition rates. The directional sensitivity of a neuron was studied by recording its number of impulses discharged to each pulse train delivered from 9 selected azimuthal angles. The sharpness of directional sensitivity of a neuron was determined in terms of the angular range of its directional sensitivity curve at 10% below the maximal response. All 72 collicular neurons recorded in this study discharged less than 5 impulses to each presented pulse. Excluding one neuron which did not show any obvious sensitivity to sound direction, all remaining 71 neurons discharged maximally to all three pulse trains delivered either from a specific azimuthal angle or from contralateral hemi-field. Whereas all three pulse trains did not affect the overall shape of directional sensitivity curves or the angular range of maximal directional sensitivity of most neurons (73.5%), they affected the sharpness of directional sensitivity curves of all 71 neurons. In general, pulse trains with contained pulses delivered at higher repetition rates and shorter durations generated sharper directional sensitivity curves. In addition, the number of impulses discharged to sequentially presented pulse within the 35.7 and 91 pps pulse trains decreased logarithmically with pulse number.

INTRODUCTION

Insectivorous bats such as *Eptesicus fuscus* emit ultrasonic signals and listen to the returning echoes to extract information about the size, direction, relative velocity of the target (GRIFFIN, 1958). They systematically increase the pulse repetition rate, shorten the pulse duration and decrease the pulse intensity as they search, approach and finally zero in on a localized target (OBRIST, 1989; SIMMONS *et al.*, 1979) or negotiate obstacles (GRIFFIN, 1958; JEN & KAMADA, 1982). Presumably, these changes in pulse parameters avoid pulse-echo overlap, ensure optimal echo intensity and increase target information for better target detection and localization. Previous studies on bats have shown that the number of impulses and the response latency of auditory neurons vary with pulse intensity, duration and repetition rate (BUSNEL, 1967; BUSNEL & FISH, 1980; CASSEDAY *et al.*, 1994; CHEN & JEN 1994; NACHTIGALL & MOORE, 1988; POLLAK & CASSEDAY, 1989; WU *et al.*, 1992). In addition, the number of impulses of inferior collicular neurons varied with temporally patterned sound pulses which varied in intensity (MORIYAMA *et al.*, 1994). These studies suggest that the bats can potentially extract information about the localized target from the response properties of their auditory neurons to variation in echo parameters during different phases of hunting. As an extension of these studies, we examine how temporally varied sound pulses may affect the directional sensitivity of the auditory neurons.

MATERIALS AND METHODS

Under Nembutal anesthesia (45-50 mg/kg b.w.), the flat head of a 1.8 cm nail was glued onto the anterior dorsal part of the skull of each of three big brown bats, *Eptesicus fuscus* (18-23 g body weight, b.w.) with acrylic glue and dental cement. During recording, each bat was tranquilized with neuroleptanalgesic Innovar-vet (0.08 mg/kg b. w. of fentanyl, 4 mg/kg b.w. of droperidol). The bat was tied ventrally onto an aluminum plate and its head immobilized by fixing the shank of the nail into a metal rod with a set screw (SUGA & SCHLEGEL, 1972). The cut skin was sutured back to restore the drooped pinnae to the natural position. Its head was oriented such that the eye-snout line pointed toward 0° in azimuth and 5° down in elevation of its frontal auditory space.

A loudspeaker (AKG model CK 50, 1.5 cm diameter, 1.3 g) was attached to an aluminum arm creating a distance of 23 cm from the bats head. By means of two small electric motors, the loudspeaker could be placed under remote control at any specific angle within ± 90° in azimuth and ± 55° in elevation of the bats frontal auditory space. Its position was monitored on a calibrated screen of an oscilloscope placed outside the sound proof room (Industrial Acoustics Company, temperature 28-30°C). The loudspeaker was calibrated with a B and K 1/4 inch microphone (4135) placed at the bat's head and its output was expressed in dB SPL referred to 0.0002 dyne/cm^2 root mean square.

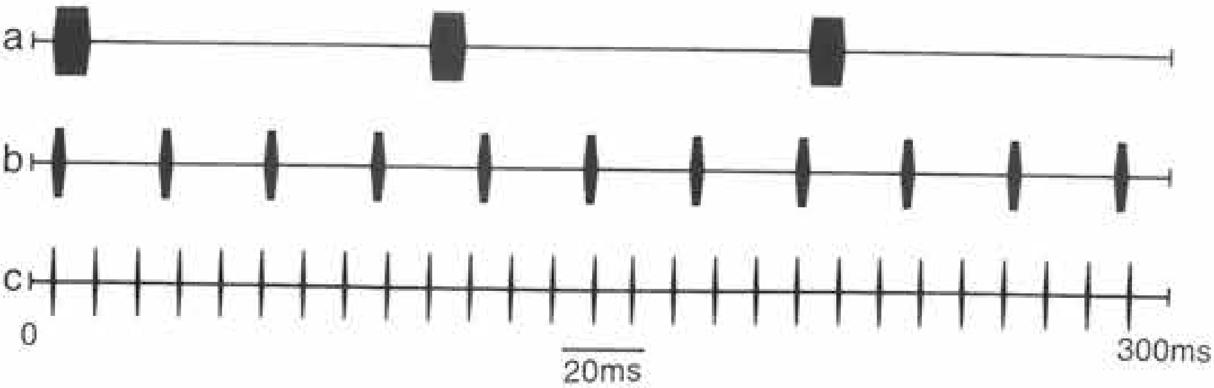
A small hole was made on the skull overlying the inferior colliculus for insertion of 3M KCl glass microelectrodes dorsoventrally to record acoustic evoked neural activities extracellularly. Recording depths were read in µm from the display of a microdrive (David-Kopf). Each inferior collicular neuron was first isolated with 3 ms tone pulses (0.25 ms rise-decay times) delivered at 2 pulses per second (pps) from the loudspeaker which was placed at 30° contralateral to the recording site. The stimulus intensity and frequency were then systematically adjusted in order to determine the neuron's best frequency (BF) and minimum threshold (MT). At the MT, the neuron had 50% response probability. The neuron's MT to one of three frequency-modulated (FM) pulses (90 to 45 kHz, 70 to 35 kHz and 45 to 20 kHz) sweeping downward across its BF was redetermined. The specific sound pulse (i.e., BF or FM pulses) that generated the lowest MT was then used to study the directional sensitivity of each recorded neuron.

To study how temporally varied sound pulses may affect the directional sensitivity of collicular neurons, three pulse trains consisted of chosen BF or FM pulses were used for stimulation. The temporal characteristics of these pulse trains are typical of echoes occurring during three different phases of hunting. Respectively, they consist of 3 pulses of 11 ms (100 ms interpulse interval = 10 pps) (Fig 1 a), 11 pulses of 3 ms (28 ms interpulse interval = 35.7 pps) (Fig 1 b) and 27 pulses of 1.2 ms (11 ms interpulse interval = 91 pps) (Fig 1 c). Regardless of variation in repetition rate and duration, the total sound stimulation in terms of the sum of all pulse durations in each pulse train was about 33 ms.

During study, each pulse train with the contained BF or FM pulses set at 20 dB above a neurons MT was delivered at 1 train/s from nine selected azimuthal angles (i.e. contralateral and ipsilateral 20°, 40°, 60°, 80° and 0°). Recorded action potentials were amplified with conventional techniques and monitored audiovisually by means of an oscilloscope and audiomonitor. They were also sent to an IBM AT (286) computer for acquisition of post-stimulus-time (PST) histograms (300 ms sampling period) and dot-raster patterns of the neuron's responses over 20 trials of each pulse train. The PST histogram, the dot-raster pattern and the total number of impulses collected at each azimuthal angle provide the temporal discharge pattern and the quantified response of each neuron in response to each presented pulse train. The number of impulses discharged to each sequentially presented pulse within a pulse train was also calculated.

The directional sensitivity of a collicular neuron was studied by measuring its number of impulses to each pulse train delivered from all nine selected azimuthal angles. A directional sensitivity curve was drawn for each neuron to study the relationship between the number of impulses and sound direction. Because all three pulse trains used in this study contained different numbers of pulses, a given neuron discharged different numbers of impulses to these three pulse trains even when they were delivered from the same angle. In order to determine the effect of these three pulse trains on the overall shape of directional sensitivity curve and the angle of maximal sensitivity of a neuron, all directional sensitivity curves obtained with these three pulse trains were normalized. Normalization of each curve was performed by converting a neuron's response obtained at each azimuthal angle into percent response relative to the maximal response. A neuron was considered to be sensitive to a particular angle only when its responses obtained from the most and least preferred angles differed by at least 50%. In addition, the sharpness of a neurons directional

Fig 1: Sketches of three pulse trains used to study the directional sensitivity of inferior collicular neurons of the big brown bat, *Eptesicus fuscus.* The pulse repetition rate and duration of these pulse trains are varied in a way typical of echo trains occurring during three different phases of hunting. Respectively, these pulse trains consist of 3 pulses of 11 ms (100 ms interpulse interval = 10 pps)(a), 11 pulses of 3 ms (28 ms interpulse interval = 35.7 pps)(b) and 27 pulses of 1.2 ms (11 ms interpulse interval 91 pps)(c). IPI: interpulse interval, PD: pulse duration, PRR(pps): pulse repetition rate in pulses per second.



	PD (ms)	IPI(ms)	PRR(pps)
a	11	100	10
b	3	28	35.7
c	1.2	11	91

Train rate: 1 train/s
Pulse rise-decay times: 0.25 ms

sensitivity was determined in terms of the angular range of its directional sensitivity curve at 10% below the maximal response.

RESULTS

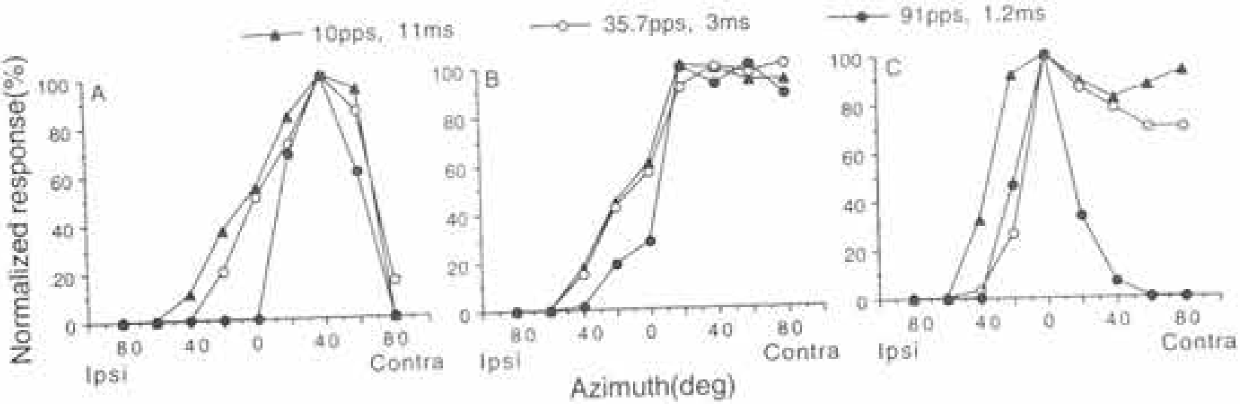
All 72 collicular neurons isolated in this study discharged less than 5 impulses to each presented sound pulse. According to the lowest MT obtained for these neurons, BF pulses were used to study the directional sensitivity of 58 neurons and FM pulses were used to study the remaining 14 neurons.

The directional sensitivity curves

According to the shape of the directional sensitivity curves obtained with all three pulse trains used in this study (Fig 1), directional sensitivity of 67 neurons can be mainly described into following three groups. The first group of neurons (N=26, 36%) always have inverted V-shape directional sensitivity curves when stimulated with all three pulse trains (Fig 2A). They discharged maximally to all three pulse trains delivered from a specific azimuthal angle (the angle of maximal sensitivity) between 0° and 40° contralateral. The angles of maximal sensitivity determined with these three pulse trains are either the same (N=13) or differ by less than 20° (N=13). In addition, the maximal discharge of these neurons is always at least 50% larger than the two minimal responses determined at two other azimuthal angles. Directional sensitivity curves of the second type of neurons (N=27, 37.5%) arise from an ipsilateral angle by more than 50% and reach a plateau level or decline by less than 50% thereafter over a wide range of contralateral angles (Fig 2B). For convenience, these directional sensitivity curves are called contralateral hemi-field sensitive curves. The third type of neurons (N=14, 19.5%) either have two contralateral hemi-field sensitive curves and one inverted V-shaped directional sensitivity curve or vice versa. For example, the neuron of Fig 2C generated an inverted V-shape directional sensitivity curve which peaked at 0° when determined with a 91 pps pulse train. It generated contralateral hemi-field sensitive curves when determined with 10 and 35.7 pps pulse trains because its responses to these two pulse trains delivered from the contralateral hemi-field never differed by more than 50%.

Besides the above three main types of directional sensitivity curves, there were 5 (7%) neurons which

Fig 2: Directional sensitivity curves of 3 representative collicular neurons determined with three pulse trains shown in Fig 1. Directional sensitivity curves determined with different pulse trains are shown in different symbols (shown at the top). Ordinates and abscissae represent the normalized response in percent and azimuthal angle in degrees. Ipsi or contra: azimuthal angles which are located at the ipsilateral or contralateral hemisphere relative to the recorded neuron (see text for details).



either had three different (N=4, 5.5%) directional sensitivity curves or did not show any sensitivity to a particular azimuthal angle (N=1, 1.5%) when determined with all three pulse trains.

The sharpness of directional sensitivity curves

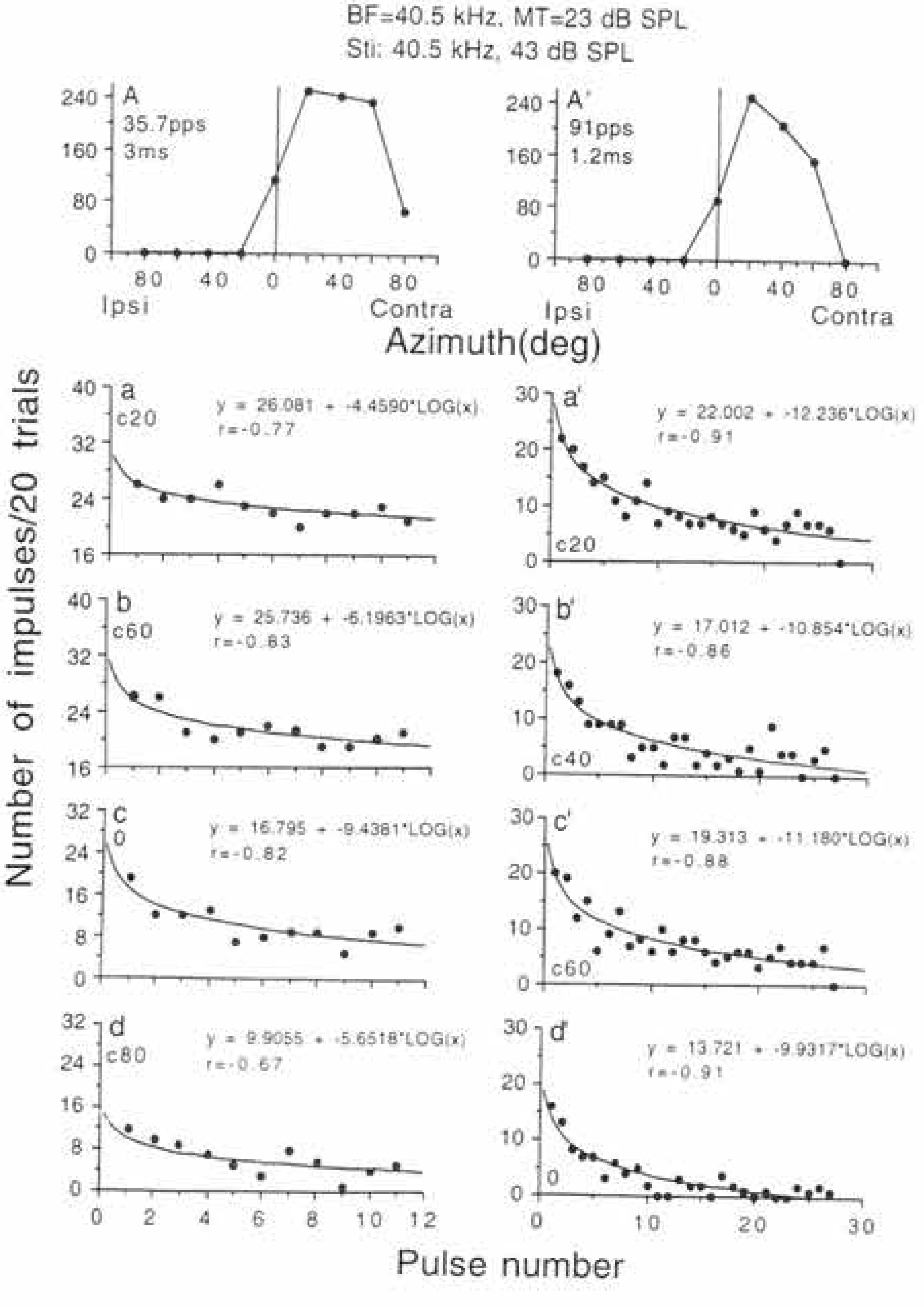
The effect of all three pulse trains on the sharpness of directional sensitivity curves of each neuron was studied by comparing the angular ranges of all three directional sensitivity curves determined at 10% below the maximal response. When a neuron had a hemi-field sensitive curve in which the contralateral limb did not decline by 10% from the maximal response (e.g. Fig 2B, 35.7 pps curve), the angular range was determined between the ipsilateral angle corresponding to 10% below the maximal response and 80° contralateral (i.e. the farthest contralateral angle tested in this study).

Excluding the neuron which did not show any sensitivity to sound direction, 46 (65%) neurons had the smallest angular range when determined with 1.2 ms pulses delivered at 91 pps; 19 (27%) had the smallest angular range when determined with 3 ms pulses delivered at 35.7 pps. Only 6 neurons had the smallest angular range when determined with 11 ms pulses delivered at 10 pps. Thus most collicular neurons had sharper directional sensitivity and smaller angular range to pulse trains which had the contained pulses delivered at higher pulse repetition rates and shorter durations. For example, the neuron of Fig 2C had two contralateral hemi-field sensitive curves when determined with 10 pps and 35.7 pps pulse trains but it generated a smaller angular range at 10 % below the maximal response for the 35.7 pps pulse train. This neuron generated an inverted V-shape directional sensitivity curve and had the smallest angular range at 10% below the maximal response when determined with 91 pps pulse train.

Number of impulses discharged to each pulse

The effect of these three pulse trains on the directional sensitivity of a neuron was also examined by analyzing the neuron's number of impulses discharged to sequentially presented pulses within a pulse train. Whereas the number of impulses discharged to each pulse of the 10 pps pulse train was comparable, it varied in different degrees when stimulated with 35.7 pps and 91 pps pulse trains. For example, Fig 3 (A and A') shows a collicular neuron that only discharged impulses to 35.7 pps and 91 pps pulse trains delivered from certain azimuthal angles. The number of impulses of this neuron discharged to sequentially presented pulses was not only different for a given pulse train delivered from the same and different angles but also different between two different pulses trains delivered from the same angle. In general, the number of impulses started with a high value to the first pulse and declined to a plateau level to the later pulses. The extent of such response adaptation was more drastic for 91 pps pulse train than for 35.7 pps pulse train such that the plateau level was also lower for the former than for the latter pulse train. The plateau level was always the highest when each pulse train was delivered

Fig 3: A and A': directional sensitivity curves of a representative neuron determined with two different pulse trains varied in pulse repetition rate and duration (3 ms pulse at 35.7 pps or 1.2 ms pulse at 91 pps). Ordinates and abscissae represent the number of impulses per 20 trials of a pulse train and the azimuthal angle in degrees. Bottom (a-d, a'-d'): variation of number of impulses of this neuron discharged to sequentially presented pulses within each pulse train delivered from selected azimuthal angles. Ordinates and abscissae represent the number of impulses per 20 trials of each pulse train and pulse number within each pulse train. Note the distribution of the number of impulses discharged to sequentially presented pulses within each pulse train can be best described by a logarithmical equation as shown at the upper portion of each panel. The solid line and r represent the best fitted line and the coefficient of correlation. The azimuthal angle from which each given pulse train was delivered to obtain the response of the neuron was also shown within each panel. (see Figure 2 for legends).



from the angle of maximal sensitivity (e.g. Fig 3 a vs b, c, d and a'vs b',c', d'). In addition, a logarithmic regression analysis of distribution of number of impulses per pulse generated a higher correlation of coefficient (r) than a linear regression analysis did.

DISCUSSION

During hunting, the big brown bats systematically change the parameters of the emitted pulses in order to better extract information about the relative velocity, size, direction and distance of the ever changing target from the returning echoes (OBRIST, 1989; SIMMONS *et al.*, 1979). Previous studies have demonstrated that most collicular neurons of *Eptesicus fuscus* discharged maximally to sound pulses delivered at a specific pulse repetition or duration (CASSEDAY *et al.*, 1994; PINHEIRO *et al.*, 1991; WU *et al.*, 1992). In addition, their responses are highly directional so that they discharged maximally to a sound delivered from a specific azimuthal angle (SCHLEGEL *et al.*, 1988; POON *et al.*, 1990; JEN *et al.*, 1991; JEN & WU, 1993). If these responses properties are utilized by a bat, the bat certainly can extract the information about the repetition rate and duration of the echo trains as well as the directional information of the localized target. However, if variation in pulse repetition rate and duration during different phases of hunting changes the directional sensitivity of a neuron, accurate detection of the target would be greatly impaired.

The present study has demonstrated that the pulse trains with varied pulse repetition rates and durations did not affect either the overall shape of directional sensitivity curves or the angular range of maximal directional sensitivity of most neurons (73.5%). In contrast, pulse trains with higher pulse repetition rates and shorter pulse durations sharpened the directional sensitivity (Fig 2A,B) and reduced the angular range of maximal sensitivity (Fig 2C) of most collicular neurons. These results suggest that a bat not only can reliably utilize the directional sensitivity of collicular neurons to determine the direction of a target but also can improve the localization of the target as it searches, approaches and finally zeroes in on the target.

The effect of temporally patterned sound pulses on the responses of inferior collicular neurons of the same bat species has been examined in a previous study (MORIYAMA *et al.*, 1994). This study demonstrated that the number of impulses of the collicular neurons discharged maximally to a pulse train in which the amplitude of contained pulses of constant duration linearly varied in a specific slope. We have extended this study by examining the responses of collicular neurons to temporally patterned sound pulses varied in repetition rate and duration. Because the repetition rate and duration of pulses in three pulse trains used in this study were varied in a way typical of echoes occurring in three different phases of hunting, directional sensitivity of collicular neurons obtained in this study can be considered as an approximation of their directional sensitivity during different phases of hunting. However, the fact that both pulse duration and repetition rate varied in each pulse train makes it difficult to determine the dominant parameter which affects the sharpness of directional sensitivity of collicular neurons studied. In order to have the answer, experiments are being conducted in our laboratory to study the directional sensitivity of collicular neurons with sound pulses which only varied either in pulse repetition rate or duration.

Whereas response adaptation of a neuron to sequentially presented pulses was small to 10 pps pulse train, it was more obvious when stimulated with 91 pps pulse train than with the 35.7 pps pulse trains (Fig 3 a-d vs a'-d'). This is likely due to the fact that the shorter interpulse interval in the 91 pps pulse train prevents a neuron from fully recovery to its response to the previous pulse. When stimulated with a given pulse train, the degree of response adaptation varied with the azimuthal angle from which the pulse train was delivered. The plateau level was the highest when the pulse train was delivered from the angle of maximal sensitivity (Fig 3). We suggest that different degrees of response adaptation to a given pulse train when delivered from different azimuthal angles are primarily due to variation of the neurons minimum threshold with sound direction which contributes to the neurons directional sensitivity to the pulse train.

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Analyse fine des cris sonar des chauves-souris : évolution et perspectives

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Abstract. During these last thirty years, bat sonar signals sharp analysis has been going through important evolutions. The periodmeter has first highlighted frequency modulations. Afterwards, the sonagraph became of common use. It gave better knowledge of modulations behaviour and brought harmonics which escape the periodmeter. At present, we have simple and fast computer means to obtain graphic representations of spectrogram.

However, these methods have a few limitations and other representations can give more precise signal description. Wigner-Ville distribution and its smoothed versions give a better localisation of signal components in time as well as in frequency. Unlike spectrogram, time and frequency resolutions are not linked. These representations show interferences between own components of the signal. These terms can make the time-frequency image interpretation difficult, but they also can give signs of low energetic components existence, like high order harmonics. Other representations can also be used, but a method suited to all signal structures does not exist. Each of these methods give complementary descriptions.

INTRODUCTION

Cette dernière décennie a vu se développer les détecteurs d'ultrasons. Cela a eu pour effet de favoriser l'observation acoustique des chauves-souris. Comme l'essentiel des émissions sonores de ces animaux est inaccessible à l'oreille humaine, les zoologistes spécialistes des chiroptères se sont très rapidement intéressés aux représentations graphiques des cris sonar. L'amélioration de la qualité et le volume des enregistrements ont favorisé l'application d'analyses de plus en plus fines afin de discerner ce qui revient à l'espèce observée de ce qui est le reflet du comportement. Comme encore actuellement il n'existe pas de méthode d'analyse qui puisse être appliquée avec rigueur à tous les types d'émission, nous avons recherché les méthodes les mieux adaptées aux diverses émissions sonores des chauves-souris.

1. Du période-mètre au sonagraphe

Si parfois l'allure du signal temporel laisse supposer que les fréquences qui le composent ne sont pas stables au cours du temps, le premier outil qui a permis de visualiser ces évolutions fréquentielles est le période-mètre. On a pu en imaginer plusieurs versions, mais on peut retenir celle qui consiste à mesurer la durée de chaque "période" entre deux passages à zéro du signal. Un des premiers exemples d'application aux cris sonar des chauves-souris est fourni dans CAHLANDER *et al.* en 1964.

On peut trouver de nombreuses illustrations dans CAHLANDER (1966) qui montrent que ces dispositifs présentent malgré tout quelques limitations. Si le signal comporte une composante modulée et un de ses harmoniques, le période-mètre ne rend en général pas compte de la présence de cette seconde composante, surtout si son énergie est faible (Fig. 1a). Si cet harmonique est très énergétique, c'est lui qui sera au contraire exhibé au détriment de la composante fondamentale (Fig. 1b). En cas de signal fortement bruité, le résultat est fort bruité lui aussi (Fig. 1c). Enfin, la mesure de la période doit être effectuée avec une finesse suffisante, sinon le résultat est erroné.

L'utilisation du sonagraphe a permis de pallier ces problèmes. Ce dispositif fait son apparition dans le milieu des années 40 pour l'analyse de la parole (KOENIG *et al.*, 1946). On trouve des publications de résultats obtenus à l'aide de ce matériel pour les chauves-souris dans les années 60.

Le sonagraphe opérait en fréquence. Le signal était préalablement enregistré sur un disque magnétique. Pendant une rotation de ce disque, on filtrait le signal par un filtre passe-bande, puis on matérialisait la puissance en sortie du filtre par noircissement d'un papier sensible disposé sur un cylindre solidaire du disque. Au cours des rotations successives, on hétérodynait le signal, ce qui conduisait à explorer fréquence par fréquence la bande utile du signal. Cette opération, équivalente à une analyse par une batterie de filtres en parallèle, peut se modéliser par :

$$S_x(t,\nu) = \left| \int_{-\infty}^{+\infty} X(n)\, H(n-\nu)\, e^{2i\pi nt}\, dn \right|^2$$

où $X(n)$ est la transformée de Fourier du signal $x(t)$ à analyser et $H(n)$ le gain complexe du filtre d'analyse.

On trouve aujourd'hui des versions modernes de ce matériel qui est toujours utilisé. Cependant, l'apparition des algorithmes de transformation de Fourier rapide dans le milieu des années 60 et la progression remarquable des moyens de calculs ont conduit à l'utilisation d'autres procédés.

2. Le spectrogramme

Le sonagramme possède une interprétation duale dans le domaine temporel. Il peut s'exprimer de manière équivalente comme suit :

$$S_x(t,\nu) = \left| \int_{-\infty}^{+\infty} x(s)\, h^*(s-t)\, e^{-2i\pi\nu s}\, ds \right|^2$$

Cette formulation fait intervenir la réponse impulsionnelle h du filtre d'analyse utilisé dans le sonagramme. Elle met en évidence une structure équivalente de calcul du type "observation à court terme du signal à travers une fenêtre suivie d'une analyse spectrale locale". On désigne cette approche sous le nom de spectrogramme.

Le spectrogramme, positif, peut s'interpréter comme une densité d'énergie dans le plan temps-fréquence ce qui est un atout satisfaisant. Mais il présente quelques inconvénients majeurs.

Les supports temporels et fréquentiels de la représentation ne sont pas strictement limités aux domaines d'existence du signal.

Les résolutions temporelles et fréquentielles sont complètement liées, dépendant de la durée et de la nature de la fenêtre d'analyse h. Ainsi, le choix de cette durée se révèle souvent délicat pour des signaux modulés. L'analyse de la parole, par exemple, passe souvent par deux types d'analyses complémentaires dits bande étroite ou bande large utilisés suivant la nature des informations à extraire.

Pour des signaux modulés linéairement en fréquence, il est possible d'établir la durée de fenêtre d'analyse fournissant la résolution optimale en fonction de la durée de la composante modulée et de la bande qu'elle occupe (STOREY, 1953; FLANDRIN, 1993). Mais pour d'autres types de modulation, et en particulier celles d'allure hyperbolique, une fenêtre ne peut être optimale que pour une portion de signal. De plus, ce choix peut être convenable pour une composante, mais ne le sera pas pour son éventuel harmonique.

On peut constater cette difficulté en examinant la figure 2 où une fenêtre de longueur donnée semble convenir pour l'étude de la partie finale de la composante fondamentale et de l'harmonique relativement faiblement modulé, et où le choix d'une autre durée de fenêtre d'analyse convient pour analyser plus finement la première partie du fondamental.

3. Les représentations de la famille Wigner-Ville

Le spectrogramme appartient à l'ensemble des représentations temps-fréquence qui sont des distributions d'énergie. Il fait partie des représentations bilinéaires covariantes par translation dans le plan temps-fréquence regroupées sous le nom de classe de Cohen (FLANDRIN, 1993; COHEN, 1966; HLAWATSCH & BOUDREAUX-BARTELS, 1992).

Dans cette famille, une représentation occupe une place centrale. C'est la représentation de Wigner-Ville

$$W_x(t,\nu) = \int_{-\infty}^{+\infty} x(t+\frac{\tau}{2})\, x^*(t-\frac{\tau}{2})\, e^{-2i\pi\nu\tau}\, d\tau$$

et toutes les distributions de la classe de Cohen peuvent s'en déduire par

Fig. 1 : Evolution des périodes estimées à l'aide d'un période-mètre.
Horloge de mesure des passages à zéro à la cadence 0.5 µs
(a) *Barbastella barbastellus* : le signal a plusieurs harmoniques de faible énergie.
(b) *Plecotus auritus* : le signal présente un harmonique fortement énergétique dans sa seconde partie.
(c) *Pipistrellus pipistrellus* : le signal a une seule composante, mais est fortement bruité.
(d) *Rhinolophus ferrumequinum*: le signal est à fréquence pure.

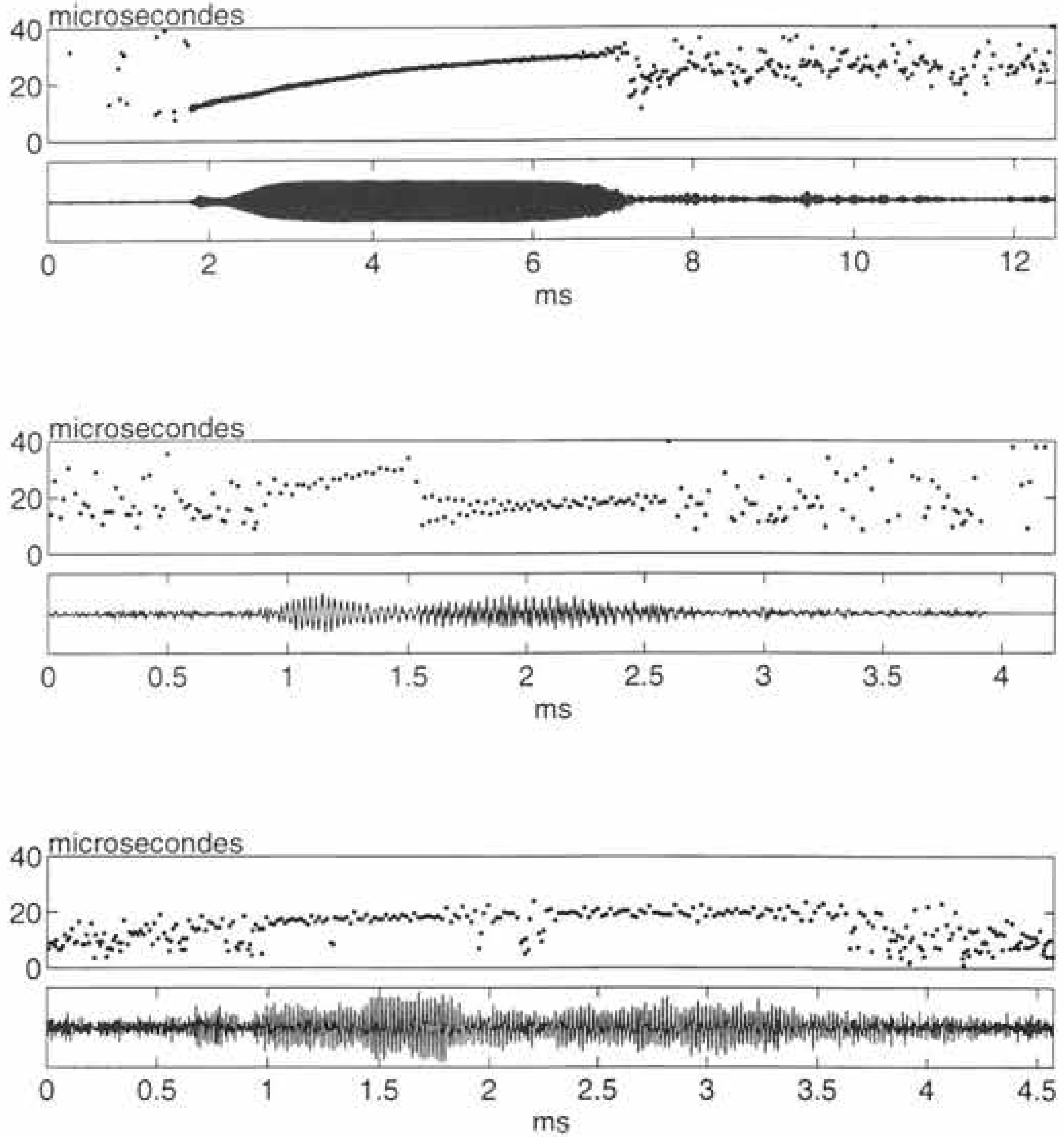
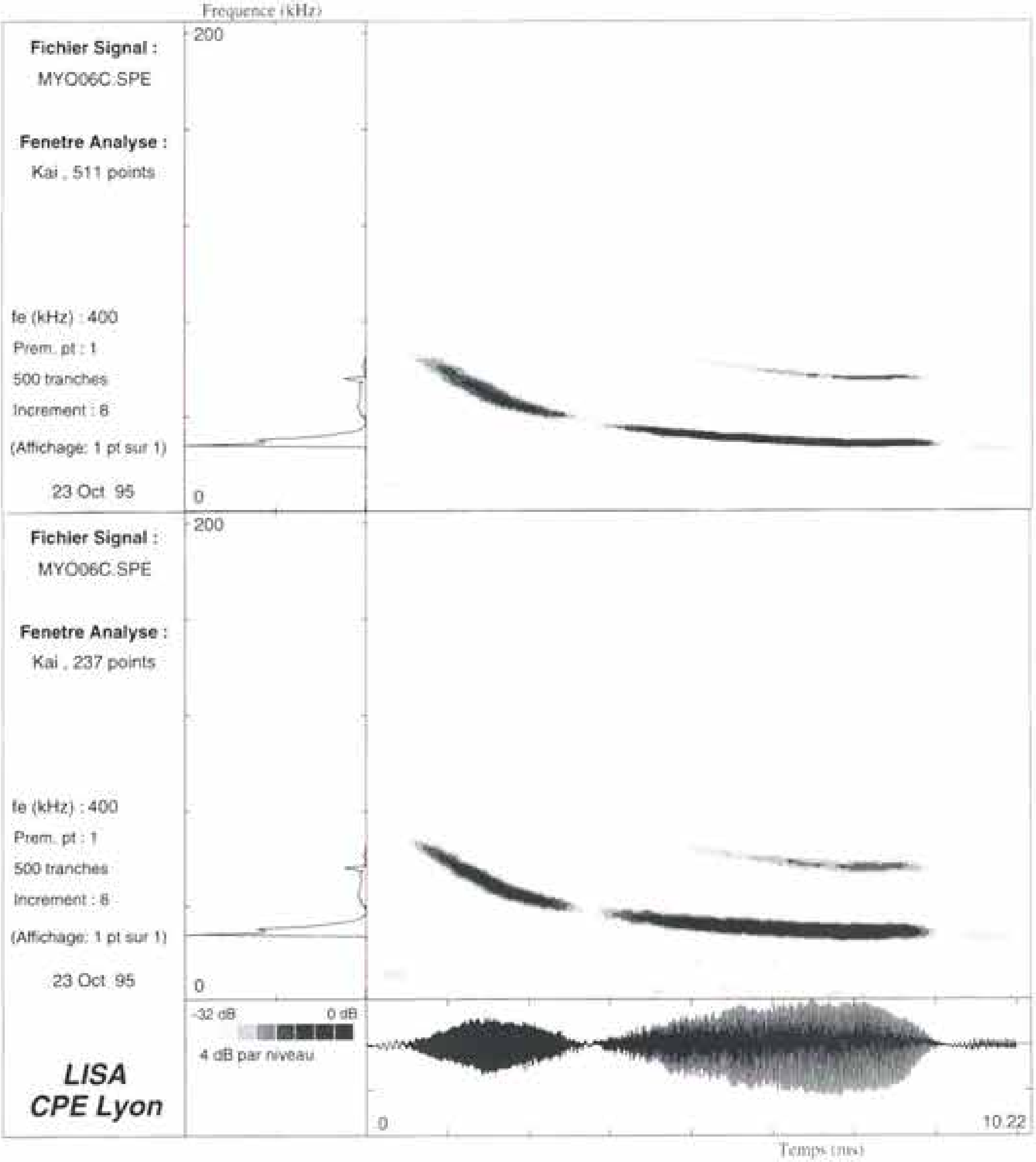


Fig. 2 : *Myotis myotis*. Comparaison de spectrogrammes
(a) Fenêtre d'analyse de type Kaiser-Bessel de 511 points soit environ 1,25 ms
(b) Fenêtre d'analyse de type Kaiser-Bessel de 237 points soit environ 0,6 ms



$$C_x(t,\nu) = \int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty} \Pi(s-t,\xi-\nu)\, W_x(s,\xi)\, \mathrm{d}s\, \mathrm{d}\xi$$

où Π est une fonction de paramétrisation.
Parmi les propriétés souhaitables pour une représentation temps-fréquence, la distribution de Wigner-Ville en possède plusieurs.

Dans le cadre d'une analyse fine de signaux, on peut noter que :

- La distribution de Wigner-Ville n'existe que sur les supports temporels et fréquentiels où existe le signal.
- Intégrée sur chacun des axes temps ou fréquence, elle fournit les distributions marginales, soit respectivement la densité spectrale et la puissance instantanée.
- Elle ne présente pas en tant que telle de limitation en termes de résolution fréquentielle.
- Les moments d'ordre un de la représentation d'une composante coïncident avec la fréquence instantanée et le retard de groupe.

Le spectrogramme, membre de la classe de Cohen, peut s'interpréter comme une version lissée de la représentation de Wigner-Ville

$$S_x(t,\nu) = \int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty} W_x(s,\xi)\, W_h(s-t,\xi-\nu)\, \mathrm{d}s\, \mathrm{d}\xi$$

où W_h est la transformée de Wigner-Ville de la fenêtre d'analyse du spectrogramme. Mais, il ne possède aucune des propriétés inventoriées ci-dessus et est surtout pénalisé par la contrainte de résolution liée en temps et en fréquence.

La distribution de Wigner-Ville ne possède pas que des avantages. Si elle est réelle, elle n'est pas positive, ce qui interdit son interprétation en termes de densité énergétique. De plus, sa lecture est parfois délicate en raison de la présence de termes d'interférences dus à la structure bilinéaire de cette représentation. La structure de ces interférences est bien établie (HLAWATSCH & FLANDRIN, 1993), qu'il s'agisse d'interférences entre composantes d'un signal ou d'interférences dites internes.
On trouve sur la figure 3 illustration de la présence de ces termes. Pour les cris sonar, on les rencontre essentiellement entre les différents harmoniques du signal s'il en existe. Il faut remarquer que ces interférences sont de nature oscillante et peuvent atteindre des amplitudes deux fois supérieures aux composantes propres du signal.

Afin de limiter ces termes, il faut déjà travailler sur le signal analytique associé au signal à étudier. Ceci permet de ne pas avoir d'interférences entre composantes aux fréquences positives et négatives. Compte tenu de la structure oscillante des interférences, on peut lisser la représentation en utilisant d'autres distributions de la classe de Cohen et ceci en jouant sur la fonction de paramétrisation Π. On souhaitera conserver certaines propriétés fondamentales, au prix, bien sûr, de l'abandon d'autres caractéristiques.

Une première modification est souvent nécessaire au vu de la taille des données à analyser (parfois plusieurs milliers de points pour un signal de quelques ms échantillonné à 400 kHz) et compte tenu des capacités de calcul disponibles. On peut alors résoudre ce problème en utilisant une distribution appelée pseudo-Wigner-Ville qui devient une analyse à court terme par l'introduction d'une fenêtre h(τ) telle que

$$PW_x(t,\nu) = \int_{-\infty}^{+\infty} h^*\left(\frac{\tau}{2}\right) h\left(-\frac{\tau}{2}\right) x\left(t+\frac{\tau}{2}\right) x^*\left(t-\frac{\tau}{2}\right) e^{2i\pi\nu\tau}\, \mathrm{d}\tau$$

On peut interpréter l'action de la fenêtre h comme une opération de lissage fréquentiel, ce qui limitera l'importance d'éventuelles interférences entre composantes situées à des dates distinctes.
Cette représentation conserve un certain nombre des propriétés dont dispose la distribution de Wigner-Ville. En particulier, son moment d'ordre un fournit toujours la fréquence instantanée d'une composante.

Si les interférences restent gênantes pour l'interprétation, on peut avoir recours à un lissage complémentaire de la représentation qui sera cette fois de nature temporelle et limitera les interférences entre composantes de fréquences distinctes. C'est la distribution dite pseudo-Wigner-Ville lissée (PWL):

$$PWL_x(t,\nu) =$$

$$\int_{-\infty}^{+\infty} h^*\left(\frac{\tau}{2}\right) h\left(-\frac{\tau}{2}\right) \left[\int_{-\infty}^{+\infty} g(s-t)\, x\left(s+\frac{\tau}{2}\right) x^*\left(s-\frac{\tau}{2}\right) \mathrm{d}s\right] e^{2i\pi\nu\tau}\, \mathrm{d}\tau$$

Cette représentation (Fig. 4) permet d'améliorer la lisibilité des images temps-fréquence. Il est important de remarquer que dans le cas de la représentation *PWL*, la fonction de paramétrisation Π est une fonction séparable en temps et fréquence. Ceci permet de régler indépendamment résolution fréquentielle (fixée par la durée de la fenêtre d'analyse *h*) et résolution temporelle (fixée par la durée de la fenêtre de lissage *g*), ce que l'on ne peut

Fig. 3 : *Pipistrellus pipistrellus*. (a) Spectrogramme. (b) Représentation de Wigner-Ville.

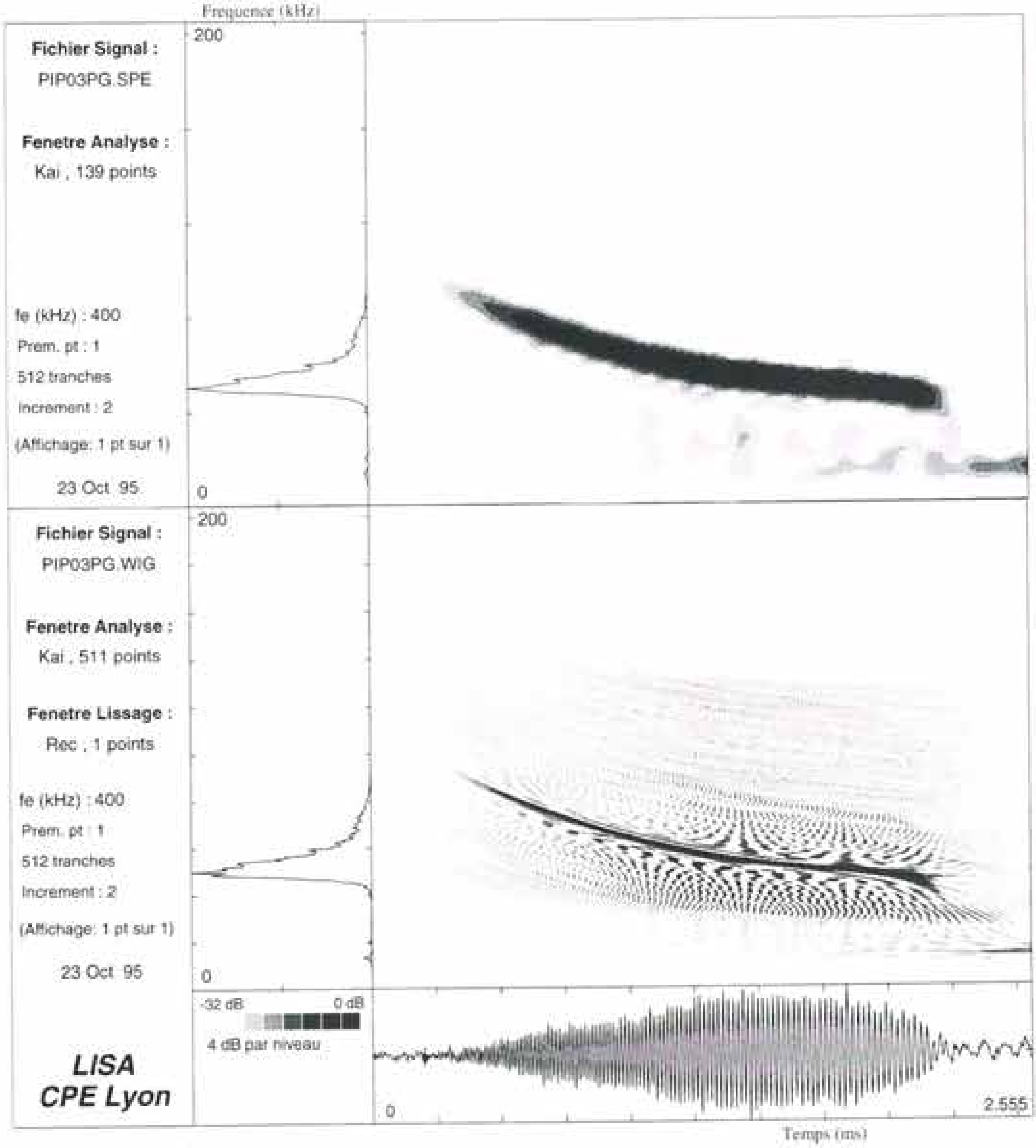
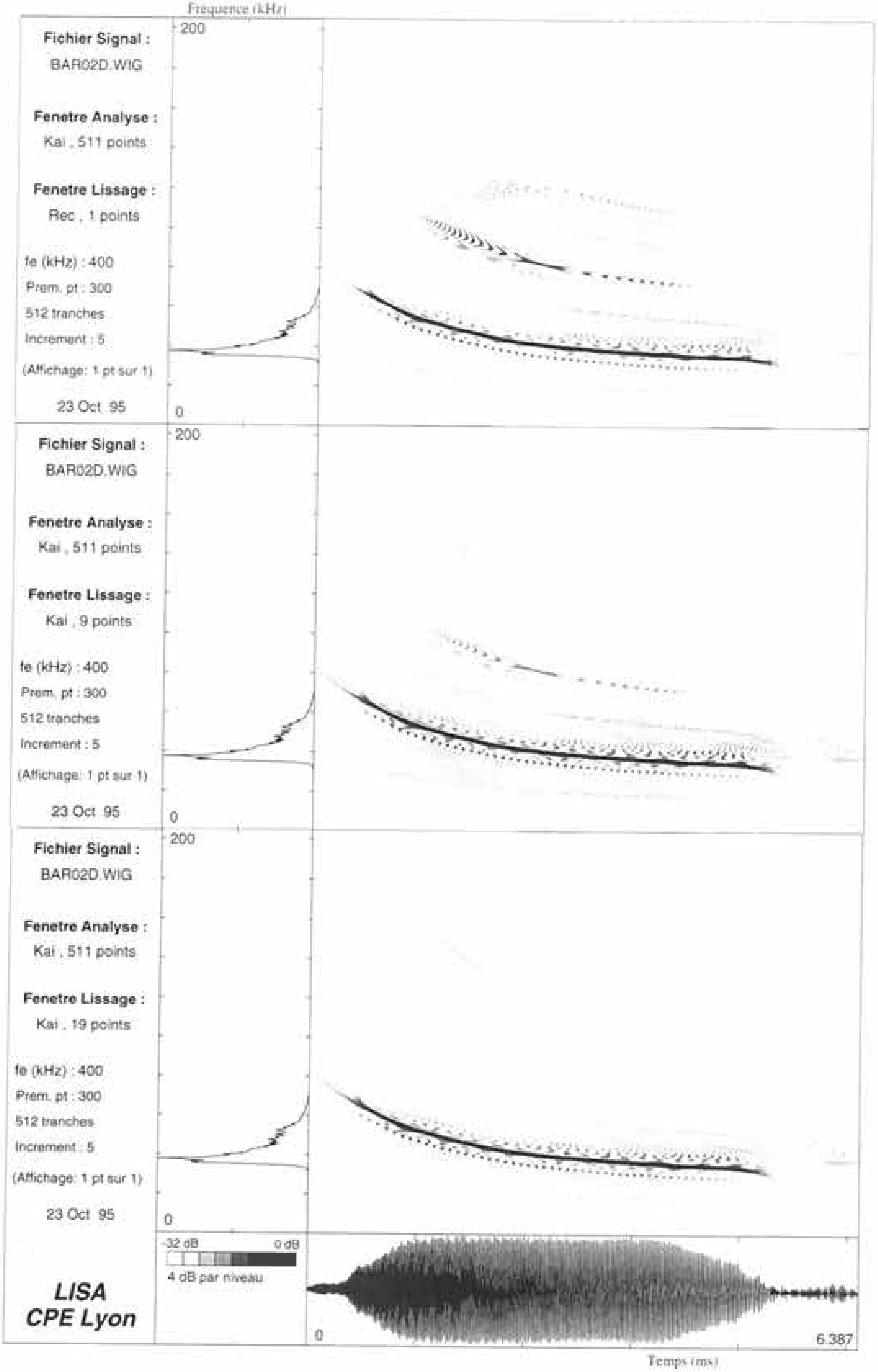


Fig. 4 : *Barbastella barbastellus*, Pseudo Wigner-Ville Lissées. Comparaison de lissages



Fichier Signal : BAR02D.WIG
Fenetre Analyse : Kai , 511 points
Fenetre Lissage : Rec , 1 points
fe (kHz) : 400
Prem. pt : 300
512 tranches
Increment : 5
(Affichage: 1 pt sur 1)
23 Oct 95

Fichier Signal : BAR02D.WIG
Fenetre Analyse : Kai , 511 points
Fenetre Lissage : Kai , 9 points
fe (kHz) : 400
Prem. pt : 300
512 tranches
Increment : 5
(Affichage: 1 pt sur 1)
23 Oct 95

Fichier Signal : BAR02D.WIG
Fenetre Analyse : Kai , 511 points
Fenetre Lissage : Kai , 19 points
fe (kHz) : 400
Prem. pt : 300
512 tranches
Increment : 5
(Affichage: 1 pt sur 1)
23 Oct 95

pas faire pour le spectrogramme. La perte de résolution occasionnée par l'utilisation d'une PWL reste toutefois acceptable, étant toujours supérieure aux résultats du spectrogramme.

On cherche souvent à éliminer les interférences, mais elles peuvent jouer un rôle informatif intéressant. Leur présence au-dessus de composantes bien marquées est un indice de l'existence d'harmoniques de rang supérieur de très faible énergie. Le spectrogramme est en général impuissant à fournir de telles informations.

CONCLUSIONS ET PERSPECTIVES

Les résultats exposés ci-dessus font état de notre expérience, mais il est clair que d'autres représentations peuvent être utilisées avec profit. On trouvera dans HLAWATSCH & BOUDREAUX-BARTELS (1992) des exemples de mises en oeuvre d'autres représentations appliquées à l'analyse de cris sonar de chauves-souris. On peut envisager d'autres approches telles que les analyses paramétriques évolutives où on analyse un modèle du signal (GRENIER, 1986). Une autre direction consisterait à s'intéresser aux distributions temps-échelle issues de la classe affine (FLANDRIN, 1993). Certaines possèdent des propriétés de localisation sur des lois de fréquence instantanée du type $1/v\alpha$, propriétés à explorer dans le cas de signaux sonar à modulation d'allure hyperbolique.

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Récepteur temps-fréquence et paquet d'ondelettes continues : un modèle possible pour le récepteur sonar des chauves-souris

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Abstract. Taking into account results published by J.A. Simmons *et al.* about the sonar behaviour, the sonar receiver may be modelled by a time frequency correlator. The "neurograms" exhibit a processing way able to get estimations of time and intensity, related to the various "glints" due to the target (prey). Time resolution and identification of targets by bats are analysed and modelled by P. Saillant, J.A. Simmons *et al.* as the SCAT receiver built from correlated spectrograms.

Starting with such a result a possible way to model the space time processing by bats (angular estimation) is to get a cross-correlation between the two "received" (or echo) spectrograms. A parallel way is to deal with cross-correlation between echo spectrogram with a copy of the emission spectrogram.

As indicated by J.A. Simmons the cochlear receiver may be described as a bank of filters, similar to a "wavelet" receiver. Such a point implies that an improved model has to take into account these results and present a generalized model. The neural systems may be represented as filters, or wavelets, which may be matched at any time t and frequency ν to the frequency modulation $\nu_i(t)$ of the emitted signal of the echo. This new model, related to the SCAT one, is dealing with a "continuous wavelets packet", deriving time frequency cells (or boxes) centered on the derivative of $\nu_i(t)$. This model is deeply related to "time-relative frequency" (or time-scale) representations, as a generalized and improved receiver using constant relative bandwith wavelets.

INTRODUCTION

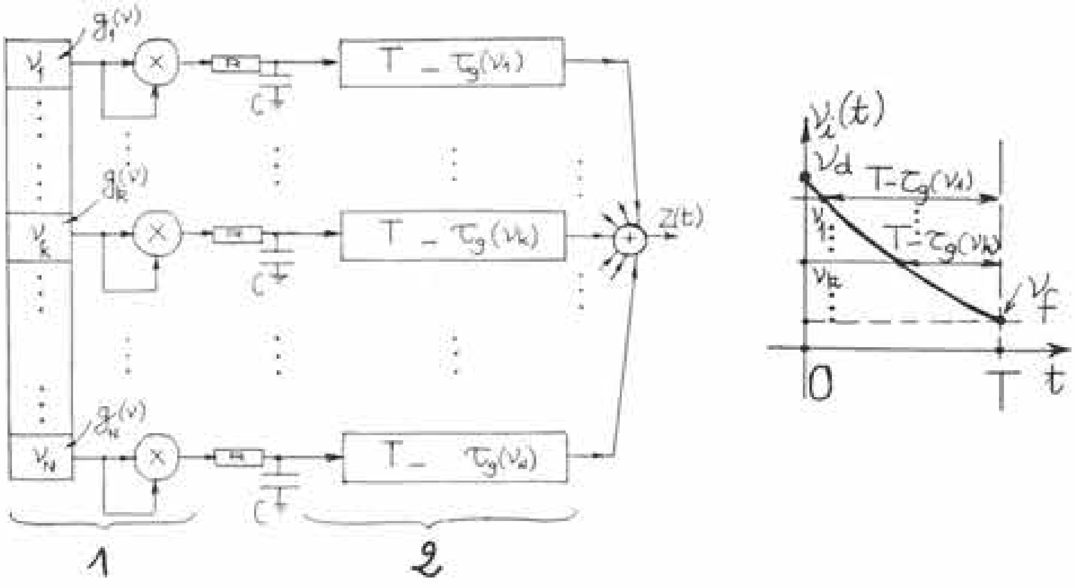
Les travaux réalisés depuis 10 ans, tant dans l'étude des systèmes SONAR des chauves-souris, que dans le traitement par ondelettes, permettent d'envisager actuellement l'étude de modèles possibles. Les résultats obtenus par Simmons *et al.* ont dégagé une structure vraisemblable du récepteur SONAR neuroacoustique (SAILLANT *et al.*, 1993; SIMMONS *et al.*, 1992; SIMMONS *et al.*, 1990a, b). Les études menées par GROSSMANN *et al.* laissent envisager des représentations adaptées aux divers éléments des récepteurs neuroacoustiques (DELPRAT *et al.*, 1992; REYNAUD & TORRESANI, 1991).

1. MODELE DE RÉCEPTEUR SPECTROGRAMME

Le schéma général d'un tel type de récepteur est représenté dans la figure 1.

Le signal SONAR de fréquence instantanée $\nu_i(t)$ permet d'associer à chaque fréquence ν_k, le retard de groupe $\tau_g(\nu_k)$, caractéristique de la date d'apparition de cette fréquence. La partie 1 du récepteur réalise le spectrogramme tel que

Figure 1



$$S_Z(t, \nu) = \left| \int_{IR} h(\nu_k - n) z(n) e^{2i\pi\nu n} dn \right|^2$$

où $z(\nu)$ est la transformée de Fourier du signal $Z(t)$. La partie 2 réalise le regroupement des composantes de fréquence ν_k autour de la date T. C'est l'opération de démodulation, ou compression ("dechirping") décrite par SIMMONS (SAILLANT *et al.*, 1993). La figure 2 en illustre le principe.

La seconde phase du traitement est de type corrélatif selon un procédé décrit par ALTES et discuté dans ses diverses variantes par FLANDRIN (1988; 1993). Il consiste à réaliser dans le plan temps-fréquence (t,ν) la corrélation entre $S_Z(t, \nu)$ dû au signal émis avec celui de l'observation $S_V(t, \nu)$. $V(t)$ est le mélange écho et bruit reçu

$$V(t) = \alpha Z(t-\tau_0)+B(t)$$

où τ_0 est la date d'apparition de l'écho, et B(t) un bruit parasite à large bande.

On calcule alors

$$\int_{(C)} S_Z(t'-t,\nu) S_V(t',\nu) dt'$$

au long de la courbe (C) alignée sur la loi de modulation.
Une variante consiste à réaliser la corrélation sur les composantes regroupées par le procédé décrit auparavant. La figure 3 représente cette opération.

Le caractère optimal, ou sous-optimal, de tels récepteurs fut discuté par FLANDRIN par l'analyse d'un récepteur soit cohérent (filtrage adapté par corrélation de représentation Wigner-Ville), soit partiellement cohérent (FLANDRIN, 1988).

2. LE MODELE SCAT PROPOSÉ PAR SAILLANT, SIMMONS *et al.*

2.a. Le modèle SCAT (SAILLANT *et al.*, 1993)

Les divers résultats obtenus par SIMMONS *et al.* depuis 1990 ont permis d'obtenir des renseignements précis sur la validité d'un tel modèle. Partant des structures du récepteur cochléaire les résultats présentés ont mis en évidence (SAILLANT *et al.*, 1993; SIMMONS *et al.*, 1992) :

- l'obtention d'une image "spectrogramme" de l'émission,
- l'acquisition de "réponses" (neurogrammes) conditionnées par l'émission et approchant ainsi la corrélation entre les deux spectrogrammes,
- l'estimation des retards dans le plan (t,ν).

La possibilité de distinguer des échos à composantes complexes est envisagée par une analyse temps-fréquence permettant (SAILLANT *et al.*, 1993; SIMMONS *et al.*, 1992) :

- l'estimation de la densité spectrale des échos,
- la mise en évidence des zéros de la densité spectrale,
- une lecture temporelle des échos séparés par retour vers la variable temps.

En effet, pour les signaux fortement modulés (grand produit durée x bande) à fréquence instantanée hyperbolique, le caractère asymptotique (déferlement lent de l'enveloppe et de la fréquence avec le temps) est évident, comme l'indique l'exemple

Figure 2 d'après SIMMONS *et al.*, 1989

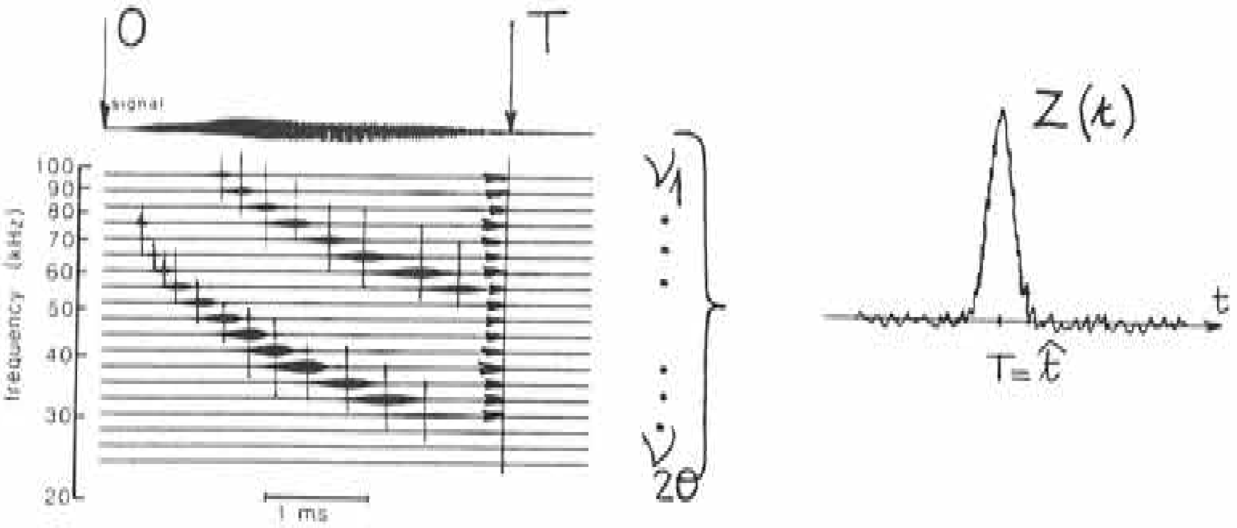


Figure 2 bis

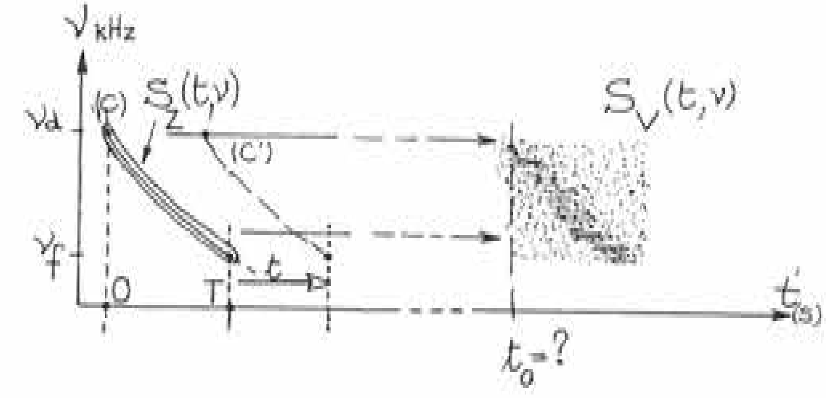
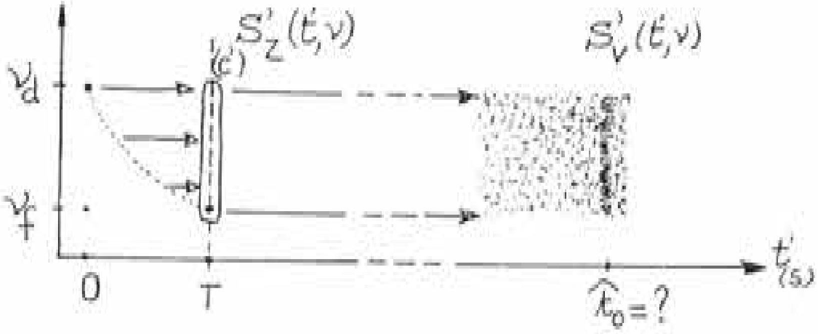


Figure 3



suivant :

$\nu_i(t) = \dfrac{\nu_d}{1+\dfrac{nt}{T}}$ avec $\nu_d = 75$ kHz, $\nu_f = 30$kHz, $T = 2$ ms

$B = \nu_d - \nu_f = 45\ kHz,\ BT = 90,\ \lambda = 2\pi \dfrac{\nu_d T}{n} = 350$

soit λ et $BT >> 1$

Dans un tel cas, le regroupement temps-fréquence par les retards $T\text{-}\tau_g(\nu)$ fournit $\gamma_Z(\nu)\,|H(t\text{-}T)|^2$ où $\gamma_Z(\nu)$ est la densité spectrale du signal émis, comme la figure 4 le montre.

En présence d'échos multiples ("glints" selon J.A. SIMMONS *et al.*), la densité spectrale présente des maxima et des minima significatifs (courbe pointillée) pour la densité spectrale observée $\gamma_V(\nu)$. Par l'emploi d'une analyse par des vecteurs de base adaptés [warped basis (SAILLANT *et al.*, 1993)] la séparation d'échos est possible (SAILLANT *et al.*, 1993).

2.b. Une variante spatio-temporelle

Un tel modèle de récepteur est corrélatif entre émission $Z(t)$ et signal écho observé $V(t) = \alpha Z(t\text{-}\tau_o) + B(t)$. Une variante de ce procédé serait d'utiliser ce modèle pour justifier de la corrélation entre signaux reçus spatialement par les deux récepteurs auditifs de la chauve-souris. En notant que de précédentes expériences de résolution angulaire avaient montré que la réponse obtenue s'identifiait à la fonction de corrélation du signal émis, il est possible d'envisager une structure de récepteur binaural corrélatif illustré par la figure 5 (BARD *et al.*, 1978).

Figure 4

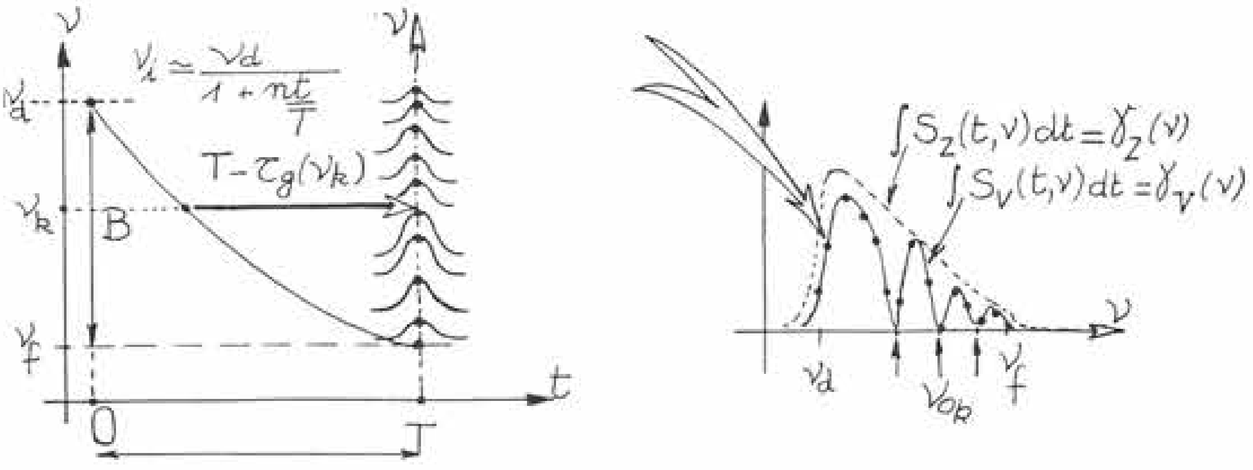
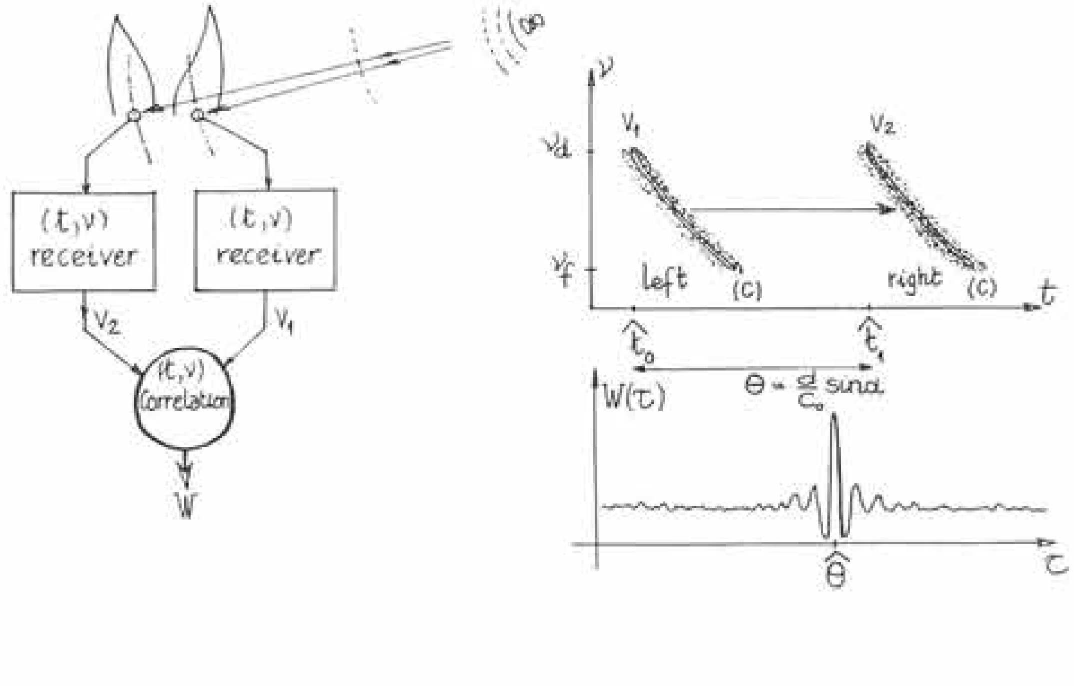


Figure 5



Une telle structure suppose que le récepteur temps-fréquence équivalent puisse fournir par corrélation une réponse liée à l'autocorrélation du signal reçu ou une version pondérée filtrée de celui-ci.

3. LE MODELE D'ANALYSE PAR ONDELETTE (DELPRAT *et al.*, 1992)

Une remarque fondamentale peut être faite au sujet de la modulation hyperbolique en fréquence:

$$\nu_i(t)=\frac{\nu_d}{1+\frac{nt}{T}}$$

En appelant bande dynamique, la grandeur liée à la vitesse de modulation

$$\frac{\partial\nu_i}{\partial t}=\frac{-\nu_d\, n/T}{\left|1+\frac{nt}{T}\right|^2},\quad B_d=\frac{1}{T_r}=\left(\left|\frac{\partial\nu_i}{\partial t}\right|\right)^{1/2}$$

on peut définir la cellule temps-fréquence (B_d, T_r) où se localise l'énergie dans le plan (t,ν) (figure 6). La surtension équivalente

$$Q=\frac{\nu_i(t)}{\left|\frac{\partial\nu_i}{\partial t}\right|^{1/2}}=\sqrt{\frac{\nu_d T}{n}}$$

chiffre la bande fréquentielle relative à une cellule associée à un filtre sélectif de bande passante

$$B_d(t)=\sqrt{\left|\frac{\partial\nu_i}{\partial t}\right|}$$

Cette propriété de localisation énergétique autour de $\nu_i(t)$ à bande fréquentielle relative constante, ou surtension constante, suggère immédiatement l'emploi de la représentation par ondelette, dont c'est la propriété fondamentale (DELPRAT *et al.*, 1992) :

$$T_Z(t,\eta)=\sqrt{\eta}\int_{IR}G^*(\eta(u-t))Z(u)\,du$$

où G est l'ondelette d'analyse et η le facteur d'échelle. Notons que T_Z, représentation en ondelette de Z est l'interambiguïté entre G et Z.
Si on admet que le filtre d'analyse (ondelette) $G(u)$, de gain complexe $g(\nu)$, est un filtre sélectif du type $G(t) = A(t)e2^{i\pi\nu_0 t}$, A amplitude pouvant être une fonction gaussienne (ondelette MORLET-GROSSMANN), un récepteur analogue à celui de la figure 1 est appelé scalogramme (DELPRAT, 1992) :

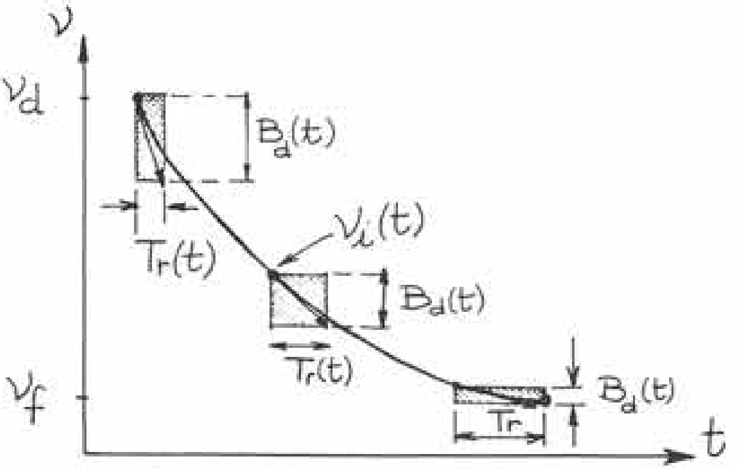
$$|T_Z(t,\eta)|^2=$$

$$\left|T_Z\left(t,\eta=\frac{\nu}{\nu_c}\right)\right|^2=\left|\sqrt{\eta}\int_{IR}G^*(\eta(u-t))Z(u)\,du\right|^2.$$

La figure 7 représente l'effet de changement d'échelle $\eta=\nu/\nu_c$ lié à la fréquence relative rapportée à la fréquence centrale $\nu_c=\nu_0$ de l'ondelette choisie pour l'analyse.

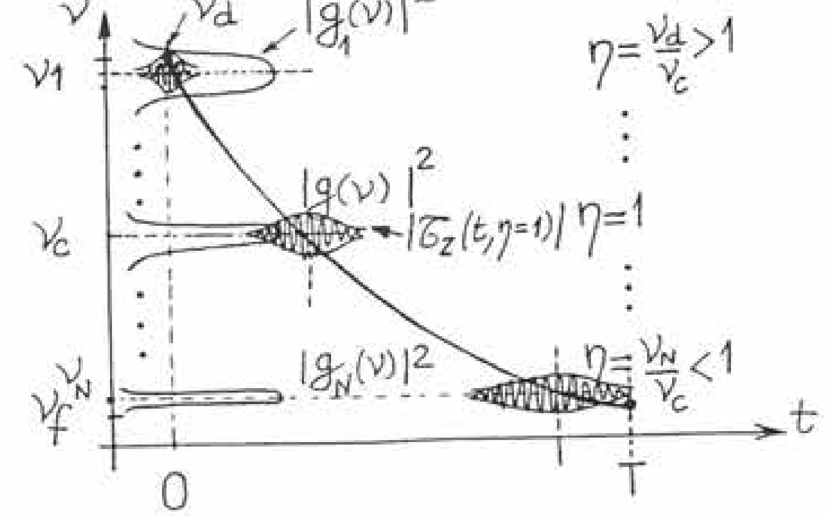
A chaque date $t_k=\tau_g(\nu_k)$, où $\nu_k=\nu_i(t)$, le filtre de fréquence centrale ν_k, telle que $\eta_k=\nu_k/\nu_c$, est traversé par une modulation de fréquence dont la pente est $\left(\frac{\partial\nu i}{\partial t}\right)_{t_k}$
comme représenté ci-dessus. La bande $\Delta\nu_k$ de ce

Figure 6



$$\frac{\nu_i(t)}{B_d(t)}=Q=\sqrt{\frac{\nu_d T}{n}}$$

Figure 7



filtre est adaptée à la rapidité de modulation.

Au lieu d'une représentation de type scalogramme, comme représenté figure 8, on peut imaginer un regroupement temporel des réponses des filtres par un retard adapté $T-\tau_g(\nu_k)=T-\tau_g(\eta_k)$, $\eta_k=\nu/\nu_c$, ce qui conduit à un regroupement autour de la date T avec une pondération temporelle $G(\eta_k t-T)$ liée à l'échelle η_k considérée. Un processus de corrélation entre une observation $T_Y(t,\eta)$ avec une référence $T_Z(t\eta)$ est alors envisageable dans une telle représentation.

4. UNE SYNTHESE DE RÉCEPTEUR COHÉRENT PAR ONDELETTES (ESCUDIE & TORRESANI, 1990)

La représentation par ondelette permet de réaliser une approche de récepteur cohérent, comme la structure de la figure 8 le laisse deviner. Dans un tel cas, chaque paquet d'onde, issu du filtre de rang ν_k de gain complexe

$$g_k(\nu) = g\left(\frac{\nu}{\eta_k}\right),$$

est convenablement regroupé par le retard $T-\tau_g(\nu_k)$ afin d'obtenir la sortie du filtre adapté à $Z(t)$, comme la figure 9 le montre (ESCUDIE & TORRESANI, 1990).

Il est à remarquer qu'en fait le signal de sortie $Z'(t)$ est égal à $\Gamma_Z(t).\Gamma_G(t)$ où $\Gamma_G(t)$ est la fonction d'autocorrélation de l'ondelette G d'analyse. Une autre utilisation de ces informations serait de considérer la représentation en ondelette $T_Z(t,\eta)$ regroupée autour de la date finale T du signal par la transformation $T_Z(t,\eta) \rightarrow T_Z(t'+\tau_g(\eta)-T,\eta)$ avec $\tau_g(\eta)=\tau_g\left(\frac{\nu}{\nu_c}\right)$ retard de groupe caractéristique du paquet d'onde de fréquence centrale $\nu=\eta\nu_c$, comme la figure 8 le suggère pour $|T_Z(t,\eta)|^2$.

5. UN MODELE DE RÉCEPTEUR À PAQUET D'ONDELETTES CONTINUES

5a. Le paquet d'ondelettes continues (REYNAUD & TORRESANI, 1991)

Dans l'analyse par ondelettes continues, on dispose de 2 variables de description :
- la date,
- l'échelle $h= \frac{\nu}{\nu_c}$

La figure 10 présente le mode d'analyse mis en oeuvre pour la représentation d'un signal modulé en fréquence par une ondelette d'enveloppe $A(t)$ et de fréquence centrale ν_c.
A chaque date $t_d+\tau_g(\nu_k)$ correspondant à l'apparition du paquet d'onde de fréquence $\nu_k=\eta_k\nu_c$, on dispose de la variable de décalage $t=t_d+\tau_g(\nu_k)$ et du facteur d'échelle η_k pour faire coïncider la fréquence instantanée $\nu_i(t)$ et la fréquence centrale changée d'échelle $\eta_k\nu_c$:

Figure 8

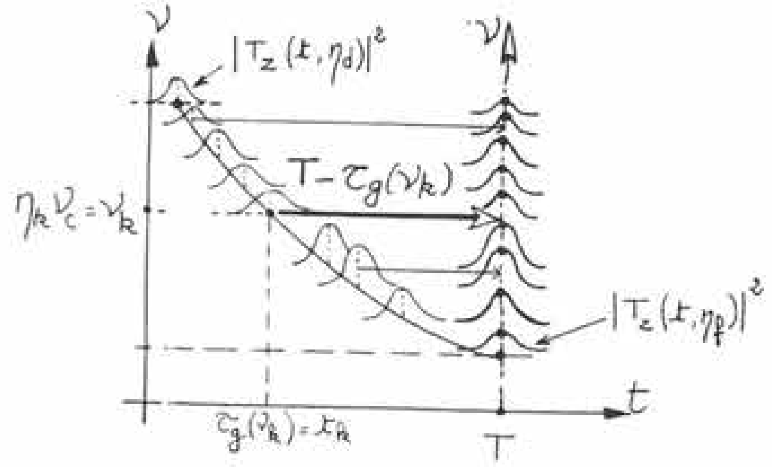


Figure 9

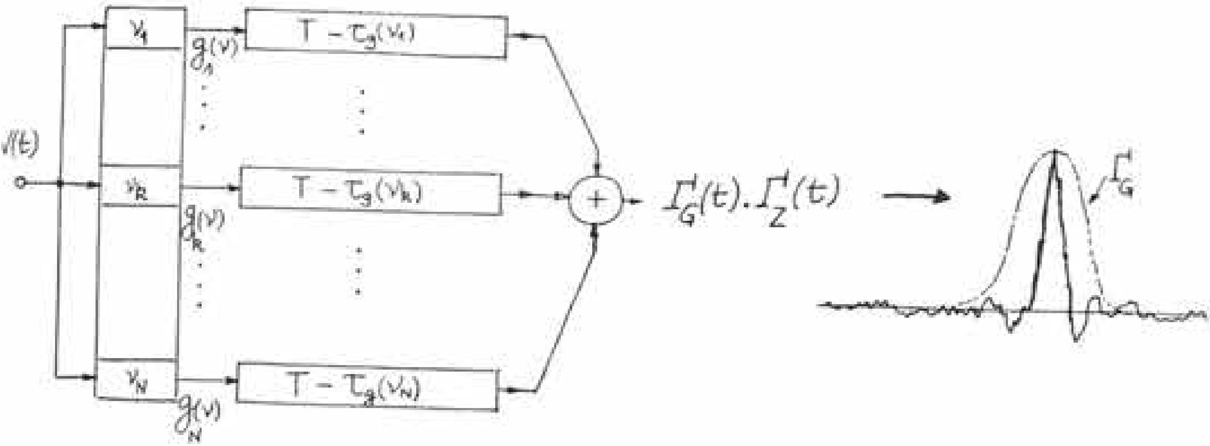
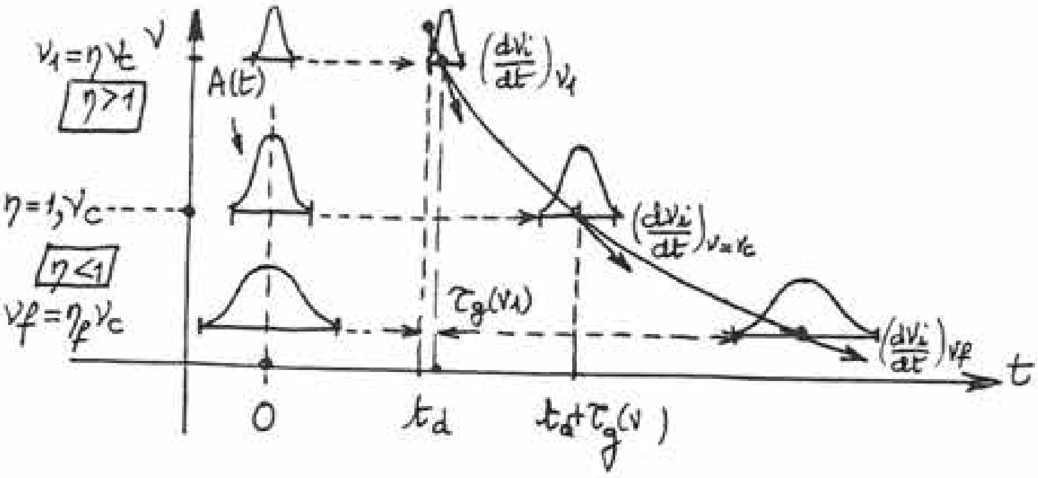


Figure 10



$$T_Z(t,\eta)=\sqrt{\eta}\int_{IR}G^*(\eta(u-t))Z(u)\,du$$

Le module de la représentation est alors exprimé en fonction de la différence de pente entre $\nu_i(t)$ et $\nu_k=\eta_k\nu_c$ qui est une constante.

Le perfectionnement apporté par la notion de paquet d'ondelettes continues est de rendre en tout point la fréquence instantanée de l'ondelette G tangente à $\nu_i(t)$ fréquence instantanée du signal $Z(t)$. Ceci amène à considérer l'ondelette à fréquence modulée suivante :

$$G(t)=A_G(t)e^{2i\pi(\nu_0 t-\frac{B_G}{2T_G}t^2)}=A_G(t)e^{i\Phi_G(t)}$$

de fréquence instantanée

$$\nu_G(t)=\nu_0-\frac{B_G}{T_G}\,t,$$

comme présenté à la figure 11.

Dans une telle représentation, on dispose en fait de trois paramètres : la date t, le facteur d'échelle η, et la pente de modulation

$$\beta B=\frac{\partial\nu_G}{\partial t}=-\frac{B_G}{T_G}.$$

A toute date t, on pourra donc obtenir

$$\nu_i(t)=\frac{\nu_d}{1+\frac{nt}{T}} \qquad \text{d'où}$$

$$\frac{\partial\nu_i}{\partial t}=-\frac{\nu_d n}{T}\;\frac{1}{\left(1+\frac{nt}{T}\right)^2}=-\eta^2\,\frac{B_G}{T_G}$$

car on réalise le changement de variable $t\to\eta t$, ce qui entraîne $\Phi_G(\eta t)=2\pi(\nu_0\eta t+\frac{\beta_G}{2}\eta^2t^2)$.

Le récepteur ainsi constitué localise l'énergie dans une cellule du plan $(t,\eta=\frac{\nu}{n_c})$ (Fig. 12)

dont la diagonale autour du point (t,ν) est alignée sur la pente de modulation du signal $\frac{\partial\nu_i}{\partial t}$.

Ce procédé revient à construire un filtre d'analyse dont la modulation de fréquence est calquée, ou adaptée en chaque point $(t,\eta=\frac{\nu}{n_c})$

à celle du signal analysé. Une expression de la représentation obtenue est alors exprimable dans le cas d'un signal SONAR de chauve-souris moyennant une approche de type phase stationnaire pour signaux asymptotiques (DELPRAT *et al.*, 1992; FLANDRIN, 1993; ESCUDIE & TORRESANI, 1990).

L'approche d'un récepteur scalogramme est alors possible ainsi que celle des procédés à corrélation. Une démarche conduisant à un modèle analogue au modèle SCAT est envisageable afin de détecter la présence de l'écho, d'estimer sa date, et d'extraire divers paramètres.

CONCLUSION

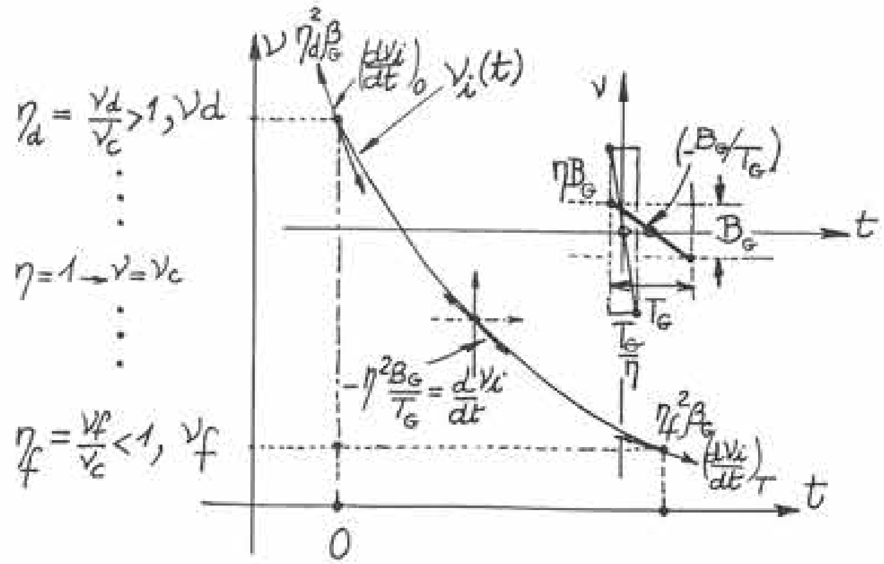
Si on tient compte des résultats acquis depuis quelques années, une modélisation vraisemblable des neurorécepteurs acoustiques des chauves-souris semble possible. La structure corrélative de ces récepteurs conduit à les doter d'une représentation de type spectrogramme, ou mieux "scalogramme"

Figure 11

Ondelette MORLET GROSSMANN

Ondelette MLF,
ou paquet d'ondelettes continues

Figure 12



pour tenir compte des propriétés observées pour les cellules de la cochlée.

La représentation en ondelette fournit alors un moyen d'approche efficace, même en vue de l'approche d'un récepteur cohérent. Un perfectionnement possible est d'envisager un paquet d'ondelettes continues à l'aide d'une ondelette à modulation linéaire de fréquence. Elle permet alors une localisation adaptée des composantes dans le plan temps-fréquence. Des variantes du modèle SCAT, proposé par Simmons *et al.* sont alors envisageables en vue de l'extraction des composantes d'échos SONAR complexes.

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Abstracts of the Symposium papers not appearing in this volume

Louis Jurine (1751-1819), l'observateur et l'expérimentateur

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L'oeuvre scientifique de Louis Jurine est analysée en termes de contenu et de méthode. Si son oeuvre est multiple, disparate même, et souvent confidentielle, on peut cependant essayer d'en déterminer les constantes et de caractériser la méthode de ses investigations. Une méthode qui passe par l'observation, suivie d'interventions expérimentales dans le champ de la physiologie animale, de la médecine et de la chirurgie, une méthode aussi de taxonomie systématique dans ses travaux de naturaliste collectionneur.

La méthode utilisée dans quelques travaux particuliers sera présentée afin de déterminer les caractères constants présents dans des recherches différentes.

Les sources probables qui inspirent Jurine dans ses choix méthodologiques sont à chercher dans la pratique médicale de la fin du XVIII^{e}, mais aussi chez les naturalistes parisiens (Cuvier) et genevois, ainsi que chez Spallanzani. Le rôle d'intermédiaire joué par Jean Senebier est attesté par diverses sources.

La méthode de Jurine sera également considérée dans son contexte et on envisagera son influence sur d'autres naturalistes, ainsi que les raisons qui ont favorisé le relatif oubli dans lequel il est tombé.

Ce travail s'inscrit dans la continuité de ceux que nous avons déjà présentés et qui contribuent à la connaissance de l'évolution des méthodes dans les sciences de la vie comme champ autonome (M. Buscaglia. 1994. Pour une histoire spécifique de la méthode en biologie. *Archs Sci. Genève*. 47 : 137-154).

Conflicts and Compromises in Frequency Modulated Echolocation

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In frequency modulated echolocation, as used by many bats, there is a conflict between obtaining accurate range information and a detailed image of objects ahead. Revolving detail is also incompatible with scanning a large volume. Bats that fly in open conditions have evolved systems that scan large volumes while bats that fly in cluttered conditions are optimised to scan a small area ahead with good discrimination of detail. The way in which the compromises are made will be discussed in terms of computer models and by reference to vespertilionid bats. Consideration of the difficulty of echolocating in cluttered conditions also reveals the advantage of gleaning for bats flying close to foliage.

Der Schalldruckpegel des Echos beeinflusst die Entfernungsmessung bei der Fledermaus *Eptesicus fuscus*

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Neurophysiologische Untersuchungen an cortikalen Neuronen, die auf Laufzeiten abgestimmt sind, lassen vermuten, dass der Schalldruckpegel (SPL) des Echos eine wichtige Grösse für die Entfernungsmessung ist [Berkowitz & Suga (1989) Hearing Res. 41:255-264). Um diese Hypothese im Verhaltensexperiment zu überprüfen, wurden 4

Eptesicus fuscus in einer Zweifach-Wahldressur darauf dressiert, zwei unterschiedlich weit entfernte Phantomziele bei variablem Echo SPL zu unterscheiden. Die Echoortungslaute wurden mit zwei Mikrofonen aufgenommen, elektronisch verzögert und über einen von zwei Lautsprechern zurückgespielt. Der SPL der Echos wurde von Lauf zu Lauf variiert und betrug -10 dB, -20 dB, -30 dB, -40 dB oder -50 dB relativ zum Aussendelaut. Alle Versuche wurden doppelblind durchgeführt.

Die Ergebnisse zeigten, dass die Unterscheidungsleistung vom SPL der Echos abhängt und bei relativen Echo SPLs zwischen -20 dB und -40 dB am besten ist. Lange Trainingsphasen verbesserten die Leistungen bei einem relativen Echo SPL von -50 dB, hatten aber keinen Effekt auf die Leistung bei -10 dB. Dies unterstützt die Hypothese, dass paradoxe Latenzzeitverschiebung ein möglicher Mechanismus für die Entfernungsmessung ist.

A new kind of echolocation signal in the neotropical molossid bat *Molossops temminckii*

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The echolocation signals of *Molossops temminckii* were recorded from hand-held, released free-flying and flying in the wild bats in the "Hato el Frío" country estate (Estado Apure, Venezuela), in the Venezuelan wooded savannah of the Orinoco plains.

The calls *M. temminckii* uses in echolocation during the search phase have surprising characteristics and are radically different from those emitted by other molossids, and also different to the signals described by now in any kind of bat. They consist in an initial upward steep frequency modulated (FM) sweep which gradually shallows coming to an aproximately constant frequency (CF) segment that ends in a short shallow downward FM segment. The signals closely resemble a mirror image of the fish-catching bats (*Noctilio* sp.) echolocation calls. During the approach phase the bat alternates typical molossid downward period linear modulated pulses with the upward FM-quasi CF pulses. The terminal phase is a typical molossid buzz made up of very short and very steep FM pulses in quick sucession.

The information gathered strongly suggests that *M. temminckii* is using a narrow-frequency analysis sonar. The implications of this "evolutive novelty" for understanding the evolution of echolocation in bats and its possible adaptative significance are discussed.

Acoustic Tracking of a Bat's Flight Path : A New Method for Investigating Echolocation and Flight Behaviour of Hunting Bats in the Field

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In a joint project of the U. of Erlangen and TH. Darmstadt, a new technique was developed for tracking flight paths of bats in the field. The technique is based on computing the time delay of echolocation calls between eight different microphones.

Our new method allows to correlate flight and echolocation behaviour with respect to the proximal and more distant environment. Up to now, 75 flightpaths of 5 bat species at 6 different field locations were analyzed. The flight paths of the noctule bat could be reconstructed up to a distance of 50 meters from the recording microphones, those of the pipistrelle and Savi's pipistrelle up to 20 meters, and those of the smaller *Myotis* species up to 15 meters. Preliminary results show that these sympatrically living species are hunting in different parts of the shared habitat.

Die Suchlaute der Fledermäuse und ihre Abhängigkeit von den ökologischen Randbedingungen

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Es wird angenommen, dass bei jeder Fledermausart in der Evolution die Struktur der Echoortunglaute an die Lösung artspezifischer Ortungsaufgaben angepasst wurde. Dies führt zu der Frage, welche Ortungsaufgaben in verschiedenen Habitaten zu lösen sind. Es wird gezeigt, dass Aufgaben wie die

Detektion, die Klassifikation und die Lokalisation von Nutzechos und die Unterdrückung von Störechos von Bedingungen wie Habitat, Jagdstil und Nahrung abhängen. Entsprechend dieser ökologischen Randbedingungen werden die verschiedenen Fledermausarten zu Gilden zusammengefasst. Vergleichende Betrachtungen zeigen, dass die Fledermäuse einer Gilde ähnliche Ortungsaufgaben zu lösen haben und deshalb in der Evolution mit ähnlichen Echoortungssystemen ausgestattet wurden. Dies wird am Beispiel der Suchlaute genauer ausgeführt.

Lazzaro Spallanzani and his "Journal of Bats"

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The recent publication of Lazzaro Spallanzani's manuscript "Journal of Bats" has thrown additional light on the experiences concerning the "new" sense of bats which the famous Italian naturalist conducted in Scandiano and in Pavia at the end of the XVIII Century. His influence on the discoveries of Jurine is also discussed.

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Le Rhinolophe, revue internationale de chiroptérologie, est édité par le Muséum d'histoire naturelle de Genève et le Centre de coordination ouest pour l'étude et la protection des chauves-souris (Suisse).

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