Université de Montréal
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La nocturnalité chez les oiseaux côtiers et marins: étude comparative des structures et fonctions rétiniennes

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Thèse présentée à la Faculté des études supérieures en vue de l'obtention du grade de Philosophiae Doctor (Ph.D) en sciences biologiques

Septembre 2006

Identification du jury

Cette thèse intitulée :

La nocturnalité chez les oiseaux côtiers et marins: étude comparative des structures et fonctions rétiniennes

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Résumé

Chez les oiseaux, la grande majorité des espèces sont considérées comme diurnes. Il existe cependant chez les oiseux marins un bon nombre d'espèces qui sont régulièrement ou occasionnellement actives de nuit. L'occupation de niches écologiques nocturnes demande aux espèces qui les colonisent une spécialisation de certains systèmes sensoriels et plus spécifiquement du système visuel. Les conditions lumineuses qui prédominent la nuit imposent en effet d'importantes pressions de sélection sur le système visuel et plus particulièrement sur le système rétinien. Chez les oiseaux, ces pressions sont d'autant plus importantes que la vision guide la plupart de leurs comportements. L'importance que revêt le système visuel pour les oiseaux nous laisse donc supposer de l'existence, chez les espèces marines qui sont actives de nuit, d'adaptations visuelles particulières qui leur confèrent une capacité de vision nocturne. Dans le cadre de la présente thèse nous avons vérifié cette hypothèse en caractérisant et comparant à l'aide de techniques électrophysiologiques (électrorétinographie cornéenne, (ERG)) et histologiques, les structures et fonctions rétiniennes de deux espèces aviaires marines partiellement nocturnes, soit le goéland à bec cerclé (*Larus delawarensis*) et le goéland gris (*Larus modestus*), d'une espèce principalement nocturne, l'océanite cul-blanc (*Oceanodroma leucorhoa*) et d'une espèce diurne, le macareux moine (*Fractercula arctica*). Cette étude comparative nous a fourni des éléments d'appréciation des adaptations rétiniennes chez les oiseaux marins à un mode de vie nocturne et nous a permis de dégager plusieurs conclusions relatives à l'évolution du système rétinien chez ces oiseaux. L'analyse histologique des rétines des espèces étudiées a mis en évidence l'existence d'une variation dans l'organisation structurelle de celles-ci en fonction des niches écologiques nocturnes ou diurnes occupées. Au niveau fonctionnel nous avons également pu observer une variation entre les différentes espèces étudiées, cependant les résultats que nous avons obtenus ne permettent pas d'établir de corrélation nette entre cette variation, les variations structurelles observées et l'occupation de niches écologiques nocturnes ou diurnes. Cette disparité peut s'expliquer par le fait que les différentes ondes de

l'ERG ainsi que leurs caractéristiques varient en fonction de la proportion et la distribution topographique des différents photorécepteurs (cônes et bâtonnets) contenus dans la rétine mais aussi en fonction de l'organisation du réseau nerveux rétinien, cette organisation variant d'une espèce à l'autre. En conclusion, les résultats, que nous avons présentés dans le cadre de cette thèse ont démontré que l'occupation de niches écologiques nocturnes s'accompagne, chez certaines espèces aviaires marines, d'une spécialisation du système visuel et plus particulièrement du système rétinien.

Mots clefs: adaptation à l'obscurité, bâtonnets, comportements nocturnes, cônes, électrorétinographie cornéenne (ERG), goéland à bec cerclé, goéland gris, macareux moine, océanite cul-blanc, rétine, rythmes circadiens, sensibilité rétinienne, sensibilité spectral.

Abstract

Although most bird species are diurnal, several studies have shown that some seabirds are active at night in different aspects of their life cycle. Nocturnal lifestyle requires some specialisation of the different sensory systems and more specifically of the visual system. In fact, light levels occurring at night impose important selective pressures on the visual system and more particularly on the retina. Since birds rely mainly on vision to function in their environment we hypothesised that seabirds which are active at night present some visual adaptations that enable them to function within the luminance range occurring at night. In the present thesis we tested this hypothesis using electrophysiological (corneal electroretinography, (ERG)) and histological techniques. More specifically, we characterised and compared the retinal structures and functions of two seabird species partially active at night, the ring-billed gulls (*Larus delawarensis*) and the gray gulls (*Larus modestus*), one strictly nocturnal species, the Leach's storm-petrels (*Oceanodroma leucorhoa*) and one diurnal species, the Atlantic puffins (*Fractercula arctica*). Overall, this comparative study provided information about retinal adaptations in different seabird species and allowed us to draw several conclusions relating to the evolution of their retinal system. The histological analysis highlighted the existence of a variation in the structural organisation of the retinas of the species studied according to their life-style. At the functional level we also observed some variations between species, however we could not establish a clear correlation between these variations, the structural variations observed and the lifestyle of these species. This disparity can be explained by the fact that ERG responses vary according to the proportions and topographic distribution of the photoreceptors (rods and cones) contain within the retina, but also to the organisation of the retinal nervous network, which may vary from one species to another. In conclusion, the results presented in this thesis showed that nocturnal life-style is accompanied in some seabird species by some specialisation of the visual system and more particularly of the retinal system.

Keywords: Atlantic puffins, circadian rhythms, cones, dark adaptation, electroretinogram (ERG), gray gulls, Leach's storm-petrels, nocturnal behaviours, retinal sensitivity, ring-billed gulls, rods, spectral sensitivity

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Contribution de la doctorante aux articles scientifiques

L'élaboration et la réalisation du projet ont été faites par la doctorante sous la direction des Drs. R. McNeil, T. Cabana et P. Lachapelle. La doctorante a procédé à la collecte de toutes les données brutes, au traitement histologique des rétines et à l'analyse de toutes les données histologiques et physiologiques. Elle a rédigé seule la totalité des textes qui forment les quatre articles présentés dans cette thèse. Des corrections faites par les Drs. R. McNeil, T.Cabana et P. Lachapelle ont été apportées aux différents textes.

Remerciements

Je tiens à remercier mes trois directeurs de recherche, Dr. Raymond McNeil, Dre. Thérèse Cabana et Dr. Pierre Lachapelle pour avoir dirigé cette thèse ainsi que pour leur support financier. Je tiens également à remercier Madame Louise Pelletier pour ses précieux conseils en histologie, Monsieur Jean-Luc Verville pour le montage des photos d'histologie et Dr. Georg Baron qui m'a souvent épaulé lors de moments difficiles. Je veux aussi témoigner de ma gratitude envers mon ami Dr. Vincent Ferretti qui a crée pour moi les programmes informatiques qui m'ont permis de faire l'analyse de mes données. La création de ces programmes a nécessité de longues heures de travail et m'a permis de sauver beaucoup de temps. Merci Vincent. Mon dernier remerciement va à mon conjoint Bruno à qui je dédis cette thèse pour son immense patience.

À Bruno

CHAPITRE 1

Introduction

Tous les animaux, qu'il s'agisse d'invertébrés ou de vertébrés, sont soumis au cours de leur existence aux fluctuations cycliques de l'environnement. L'alternance du jour et de la nuit est l'une des périodicités qui marque le plus la vie des organismes. En fait, de par son influence sur de nombreux éléments abiotiques (comme l'intensité lumineuse, la température et la pression atmosphérique) et biotiques (comme la disponibilité des ressources alimentaires et la présence de prédateurs), cette alternance façonne et forge la structure écologique des communautés animales. Ainsi, les différentes espèces organisent leur temps d'activité et de repos en fonction de cette alternance et en fonction de l'organisation temporelle des autres espèces qui forment une même communauté. Certaines espèces sont diurnes, d'autres nocturnes et d'autres encore ne manifestent que certains comportements spécifiques de jour ou de nuit ou sont arythmiques.

Chez les oiseaux, la grande majorité des espèces sont considérées comme diurnes. Jusqu'à tout récemment, seules quelques espèces appartenant aux ordres des Apterygiformes, Strigiformes, Caprimulgiformes et Apodiformes étaient reconnues comme strictement ou partiellement nocturnes (Martin, 1990). Cependant, depuis une quinzaine d'années environ, plusieurs études ont pu montrer que chez les oiseaux aquatiques (limicoles, de marais, côtiers et marins) un bon nombre d'espèces étaient régulièrement ou occasionnellement actives de nuit (Martin, 1990; Brooke et Prince, 1991; McNeil, 1991; Owen, 1991; McNeil et al., 1992, 1993, 1996; Fasola et Canova, 1993). L'utilisation de nouvelles techniques de télémétrie et de système vidéo à éclairage infrarouge a facilité l'observation des activités nocturnes chez plusieurs de ces espèces et a permis d'établir de façon précise leur cycle d'activité (McNeil et Robert, 1988, 1992; Robert et McNeil, 1989, 1992; Robert et al., 1989; Rompré et McNeil, 1994; Thibault et McNeil, 1994, 1995a,b; McNeil et Rompré, 1995). Les oiseaux aquatiques actifs de nuit se retrouvent au sein d'au moins huit ordres et 27 familles différentes (voir McNeil et al., 1993).

D'une façon générale, chez les oiseaux la vision joue un rôle primordial et guide la plupart de leurs comportements (Hodos, 1993). Ainsi, le vol demande une très bonne perception spatiale et du mouvement, de même qu'une grande acuité visuelle (Meyer, 1986). De plus, une grande majorité d'espèces utilisent des signaux visuels pour la quête alimentaire, la défense du territoire et du nid de même pour le choix du partenaire sexuel (Hodos, 1993). Dans une métaphore, Rochon-Duvigneaud (1943) résume cette importance en définissant l'oiseau comme «...une aile guidée par un œil». En fait, le large espace qu'occupent les globes oculaires dans la boîte crânienne des oiseaux ainsi que les grandes dimensions de leurs lobes optiques par rapport aux autres structures cérébrales témoignent de l'importance de la vision pour cette classe de vertébrés (Jerison, 1977; Boire, 1989). Chez certaines espèces, les yeux possèdent même une masse plus importante que celle du cerveau (Meyer, 1977). Selon Martin (1990, 1994) l'environnement lumineux dans lequel vivent les oiseaux est l'un des facteurs qui impose le plus de demandes sur le système visuel et plus particulièrement sur le système rétinien. L'importance que revêt la vision pour les oiseaux en général nous laisse donc supposer que les espèces aquatiques qui sont actives de nuit, ont développé au cours de leur évolution diverses adaptations visuelles leur permettant de guider leurs comportements nocturnes. Dans le cadre de la présente thèse nous avons voulu vérifier cette hypothèse.

Quelques études ont déjà pu mettre en évidence chez certaines espèces aviaires strictement nocturnes que la taille des globes oculaires, de la cornée, du cristallin et de la pupille est considérablement plus large que chez les espèces diurnes. Cet élargissement des différentes structures de l'œil permettrait de capter une plus grande quantité de lumière et favoriserait la vision dans des conditions de faibles intensités lumineuses (Walls, 1967; Tansley, 1965; Lythgoe, 1979; Meyer, 1977; Martin et al., 1978; Dugan 1981; Pienkowski, 1983a,b; Martin, 1990; Rojas et al. 1997). D'autres études ont pu montrer aussi que la rétine d'espèces nocturnes comme la chouette hulotte (*Strix aluco*), le fulmar boréal (*Fulmarus glacialis*), le bec-en-ciseau (*Rynchops niger*) ou le guacharo des cavernes (*Steatornis caripensis*) contient une

plus grande proportion de photorécepteurs sensibles aux faibles intensités lumineuses (bâtonnets) que celle des espèces diurnes (Lockie, 1952; Martin, 1990; Rojas et al. 1997; 2004). Malheureusement, très peu d'études ont été faites sur le sujet et à ce jour, seul un petit nombre d'espèces ont été étudiées. En fait, hormis les études de Rojas et al. (1997, 1998, 1999a,b), très peu se sont intéressées aux espèces aquatiques. De plus, la grande majorité de ces études se sont limités à des descriptions morphologiques générales et aucune ne s'est intéressée à caractériser et comparer les adaptations développées au niveau des fonctions visuelles et à les corréler avec les différences structurelles observées.

Cette thèse s'insère dans un programme qui vise à étudier les bases visuelles des comportements nocturnes chez les oiseaux aquatiques. Dans le cadre de ce programme d'étude deux projets de doctorat ont été définis, dont un premier qui s'est intéressé aux groupes des oiseaux limicoles et de marais (Rojas, 1998) et le présent projet qui porte sur les oiseaux côtiers et marins.

Le groupe des oiseaux côtiers et marins s'est avéré être un modèle particulièrement intéressant pour notre étude. En effet, d'une part on retrouve dans ce groupe des espèces qui présentent une grande diversité de cycles d'activité, plusieurs espèces étant strictement diurnes, d'autres essentiellement nocturnes et d'autres étant actives de jour comme de nuit ou arythmiques. D'autre part, ces espèces occupent des milieux où les variations lumineuses liées à l'alternance jour/nuit diffèrent considérablement, ce qui nous a permis d'étudier de façon comparative le rôle adaptatif de certaines particularités fonctionnelles et structurelles de leur système visuel. De plus, selon Martin (1990), dans les milieux ouverts, comme les milieux côtiers et marins, l'intensité lumineuse ambiante mesurée la nuit semble être suffisante pour induire des réponses visuelles chez toutes espèces qui possèdent des adaptations visuelles qui confèrent une capacité de vision nocturne.

Le but de la présente thèse est de caractériser et comparer, à l'aide de techniques électrophysiologiques (électrorétinographie cornéenne (ERG)) et histologiques, les fonctions et structures rétiniennes de deux espèces aviaires côtières partiellement nocturnes dans leurs activités de quête alimentaire et de reproduction, soit le goéland à bec cerclé (*Larus delawarensis*) et le goéland gris (*Larus modestus*), d'une espèce principalement nocturne dans ses activités de reproduction et partiellement nocturne dans ses activités de quête alimentaire, l'océanite cul-blanc (*Oceanodroma leucorhoa*) et d'une espèce diurne, le macareux moine (*Fractercula arctica*). Le choix de ces espèces se justifie, d'une part, par leur accessibilité pour notre étude, et d'autre part, parce qu'elles sont représentatives de la diversité des cycles d'activité observée chez les oiseaux côtiers et marins.

Cette étude nous permettra d'une part de vérifier si les deux goélands et l'océanite cul-blanc possèdent une capacité de vision nocturne pour guider leurs comportements la nuit, et d'autre part d'évaluer si le fait d'être partiellement actif de nuit est suffisant pour induire des adaptations visuelles particulières. À la lumière des résultats obtenus, nous espérons apporter des éléments de plus, à la compréhension des mécanismes visuels impliqués dans la manifestation des comportements nocturnes chez les oiseaux côtiers et marins.

Avant de présenter les hypothèses et objectifs spécifiques de notre étude ainsi que les quatre articles scientifiques qui en résultent, nous ferons état des connaissances sur les comportements nocturnes des oiseaux côtiers et marins et plus spécifiquement des espèces que nous avons choisi d'étudier. Nous présenterons par la suite une description des structures et fonctions du système visuel des oiseaux. Enfin, nous exposerons les fondements théoriques de la méthode d'ERG que nous avons utilisée pour évaluer les différentes fonctions rétiniennes des espèces étudiées.

1.1. Comportements nocturnes chez les oiseaux côtiers et marins

Les connaissances que nous avons sur les comportements nocturnes des oiseaux côtiers et marins sont encore très fragmentaires. Les observations faites de nuit chez les oiseaux marins sont peu nombreuses car, en dehors de la période de reproduction, la très grande majorité de ces oiseaux vivent en mer, souvent loin des côtes. D'une façon générale, les espèces les plus étudiées et sur lesquelles nous possédons le plus de données, quant à leurs comportements nocturnes, appartiennent aux familles des Laridés, Alcidés, Procellariidés et Hydrobatidés.

1.1.1. Les Laridés

Chez les Laridés, les comportements nocturnes les plus observés sont surtout reliés à la quête alimentaire et à la reproduction. Bien que la majorité des goélands, mouettes et sternes s'alimentent principalement de jour, plusieurs études ont montré que certaines espèces s'alimentent aussi régulièrement ou occasionnellement de nuit (Ashmole et Ashmole, 1967; Harris, 1970; Pierotti et Annett, 1987; Neilson, 1989; Garthe et Hüppop, 1996). Ainsi, des études faites sur les contenus stomacaux de la sterne blanche (*Gygis alba*) et du goéland à queue fourchue (*Larus furcatus*) ont montré que ces espèces semblent tirer avantage des migrations verticales nocturnes du micronecton pour s'alimenter (Ashmole et Ashmole, 1967; Harris, 1970). En fait, selon Ashmole (1971), cette migration favoriserait la quête alimentaire nocturne chez plusieurs espèces de Laridés qui s'alimentent à la surface de l'eau. D'autres espèces que l'on retrouve en mer du Nord, comme le goéland à manteau noir (*Larus marinus*), le goéland argenté (*Larus argentatus*), le goéland brun (*Larus fuscus*), la mouette tridactyle (*Rissa tridactyla*) et le goéland cendré (*Larus canus*), s'alimentent également régulièrement de nuit des déchets déversés par les chalutiers commerciaux (Garthe et Hüppop, 1996). Plusieurs autres espèces, comme le goéland argenté, le goéland de l'ouest (*Larus occidentalis*) et le goéland à manteau ardoisé (*Larus schistisahura craveri*), patrouillent régulièrement la nuit les colonies de petits oiseaux

marins comme certains alques et pétrels qui sont actifs de nuit et dont elles sont prédatrices (Pierotti et Annett, 1986; Neilson, 1989). Chez le goéland à queue fourchue et le goéland gris, de nombreux comportements reliés à la reproduction ont pu être observés la nuit (Snow et Snow, 1968).

1.1.1.1. Le goéland à bec cerclé

Le goéland à bec cerclé (Fig.1), bien que principalement diurne, semble être aussi actif la nuit à diverses occasions. Au Canada, il existe deux populations de goélands à bec cerclé. Une première qui niche principalement dans les Prairies (entre 96° et 110° de latitude) et une seconde l'on retrouve le long du corridor des Grands Lacs/Fleuve St-Laurent (entre 54° et 94° de latitude). Les études portant sur les activités nocturnes de cette espèce sont cependant peu nombreuses et ne présentent que peu de données quantitatives. Néanmoins, les études de Fetterolf (1979) ont montré que dans les sites de nidification, les comportements de copulation se font plus nombreux la nuit que le jour, et que d'une façon générale les adultes sont actifs la nuit pendant la période de reproduction. De plus, Hébert et McNeil (1999) ont observé, à l'Île de la Couvée, au sud de Montréal, que chez cette espèce les comportements nocturnes de quête alimentaire et de copulation sont fréquents. Burger et Staine (1993) ont également pu observer dans plusieurs sites du New Jersey qu'en dehors de la période de reproduction le goéland à bec-cerclé s'alimente et vole fréquemment de nuit.

1.1.1.2. Le goéland gris

Chez le goéland gris (Fig. 2) les comportements nocturnes les plus observés sont reliés à la reproduction. Ce goéland que l'on trouve sur la côte pacifique de l'Amérique du Sud (entre 0^0 et 40^0 de latitude) a la particularité de nicher dans l'un des déserts les plus arides du monde, le désert chilien d'Atacama (Howell et al.,1974 ; Meyer 1986 ; Harrison et al., 1983). Les sites de nidification établis dans ce désert

Figure 1: Goéland à bec cerclé (*Larus delawarensis*)

(Photo: Martine Emond, Popam Beach, États-Unis, 1995)

se situent à plus de 30-100 km de la côte (Howell et al., 1974, Howell, 1982). Pendant toute la période de reproduction ces oiseaux couvrent quotidiennement cette distance aller-retour pour pouvoir s'alimenter. Guerra (1987) a estimé que ces trajets se font à des heures régulières, et a établi la durée de ceux-ci à près de deux heures. Ainsi, peu après la tombée de la nuit, soit approximativement vers 20: 00, les oiseaux qui ont passé la journée à s'alimenter ou à se reposer sur les côtes, se rassemblent en volée et quittent pour le désert. Aux environs de 04: 00, les oiseaux se rassemblent de nouveau dans le désert et volent vers la côte pour s'alimenter (Guerra, 1987). Dans les sites de nidification, les adultes semblent être actifs une bonne partie de la nuit. Ainsi, Howell et al. (1974) ont pu constater que les parents changent leur tour de garde au nid et alimentent leurs poussins essentiellement la nuit. De plus, Howell (1974) et Howel et al. (1982) ont pu observer au tout début de la période de reproduction, soit avant la ponte des œufs, que des comportements de cour et de copulation se font essentiellement la nuit. Selon Guerra (1987), deux facteurs écologiques conditionnent les comportements nocturnes de reproduction du goéland gris: la température qui joue un rôle de tout premier ordre et la prédation. Dans le désert d'Atacama, le mercure peut atteindre facilement 60^0C durant le jour. Les adultes, en restant inactifs près de leurs petits pendant le jour, protègent ceux-ci de la chaleur intense en leur faisant de l'ombre et évitent par la même occasion une trop grande dépense énergétique. Les vols de nuit permettraient également aux adultes d'éviter les prédateurs diurnes, comme les faucons.

En dehors de la période de reproduction, Blokpoel et al. (1992) ont pu observer, à quelques reprises, sur les plages de Mollendo, au Pérou, une volée de goélands gris s'alimenter entre 22: 00 et 23: 00.

Figure 2 : Goéland gris (*Larus modestus*)

(Photo : Martine Emond, Antofagasta, Chili, 1996)

1.1.2. Les Alcidés

Chez les Alcidés les activités nocturnes qui ont été les plus observées sont reliées principalement à la reproduction. Ainsi, chez certaines espèces comme l'alque marbrée (*Brachyramphus marmoratus*), l'alque pâle (*Brachyramphus brevirostris*), l'alque à aisselles grises (*Endomychura craveri*), l'alque à cou blanc (*Synthliboramphus antiquus*), l'alque de Cassin (*Ptychoramphus aleutica*) et l'alque à dos noir (*Endomychura hypoleuca*), la garde du nid semble être une activité principalement nocturne (Murray et al., 1983; Vermeer et al., 1987; Eisenhawer et Reimchen, 1990). Chez les alcidés on suppose que les espèces qui se nourrissent principalement de zooplancton, comme l'alque de Cassin, l'alque minuscule (*Aethia pusilla*), l'alque cornue (*Aethia cristatella*) et le mergule nain (*Plautus alle*), sont nocturnes lors de leur quête alimentaire. Bien que la plupart des alcidés soient de très bons plongeurs, ces espèces profiteraient des migrations verticales nocturnes du zooplancton pour s'alimenter (Vermeer et al., 1987). Enfin, plusieurs auteurs ont pu observer chez un bon nombre d'espèces que le départ des jeunes des colonies se fait principalement de nuit. Ainsi, chez le gode (*Alca torda*), la marmette de Brünnich (*Uria lomvia*), la marmette commune (*Uria aalge*), le macareux moine, le guillemot noir (*Cepphus grylle*) et la plupart des alques, les jeunes synchronisent leur départ avec la fin du crépuscule ou aux heures où l'intensité lumineuse est la plus faible pendant les longues journées de l'été arctique (Williams, 1975; Gaston et Nettleship, 1982; Harris et Birkhead, 1985).

1.1.2.1. Le macareux moine

Des quatre espèces étudiées ici, le macareux moine (Fig.3) est celui qui est le plus diurne puisque tous ses comportements reliés à la reproduction et à la quête alimentaire se font essentiellement de jour (Bradstreet et Brown, 1985). En fait le seul comportement nocturne observé chez cette espèce concerne le départ des jeunes des colonies à la fin de la période de reproduction (Bradstreet et Brown, 1985).

Figure 3 : Macareux moine (*Fratercula arctica*)

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1.1.3. Les Procellariidés et Hydrobatidés

Chez les Procellariidés et les Hydrobatidés, un très grand nombre d'espèces sont nocturnes dans leurs comportements de reproduction. Ainsi, chez presque tous les diablotins (*Pterodroma*), un grand nombre de puffins (*Puffinus*) et plusieurs pétrels, les activités d'excavation des terriers, de garde du nid et d'alimentation des poussins se font essentiellement la nuit dans les colonies (revue dans McNeil et al., 1993). De plus, les études de Beck et Brown (1972) et Harper (1983) ont montré que chez le puffin d'Océanie (*Puffinus bulleri*), l'océanite cul-blanc et l'océanite océanique (*Oceanodroma oceaniscus*) les activités de cour et de copulation se produisent dans les terriers en pleine nuit, spécialement lors des nuits sans lune. Les seules espèces dont les activités de reproduction se font essentiellement de jour sont le pétrel de Darwin (*Oceanodroma tethys*) et le puffin d'Audubon (*Puffinus iherminieri*) que l'on retrouve aux îles Galápagos, où aucun prédateur ne leur est connu (revue dans McNeil et al., 1993). En ce qui concerne les activités alimentaires nocturnes de ce groupe, très peu de données sont disponibles. Certaines espèces semblent se nourrir de jour et de nuit, comme le pétrel géant (*Macronectes halli*) (revue dans McNeil et al., 1993), d'autres s'alimentent uniquement de nuit, comme le pétrel de Bulwer (*Bulweria bulwerii*) (Prince et Morgan, 1987).

1.1.3.1. L'océanite cul-blanc

Chez l'océanite cul-blanc (Fig.4), les activités de cour et de copulation se produisent à l'intérieur de terriers en pleine nuit et spécialement lors des nuits sans lune, et la garde du nid et l'alimentation des poussins se font également essentiellement la nuit (Beck et Brown, 1972; Harper, 1983). De plus, tout comme l'alque à cou blanc, l'océanite cul-blanc semble éviter les prédateurs en fréquentant moins souvent les sites de nidification les nuits de pleine lune. Watanaki (1986) a pu en effet observer dans des sites japonais que le goéland à manteau ardoisé, qui est le principal prédateur de l'océanite, survole régulièrement les colonies lorsque les nuits

Figure 4: Océanite cul-blanc (*Oceanodroma leucorhoa*)

(Reproduit avec la permission du ministère des Travaux publics et des Services gouvernementaux du Canada, 2002).

sont claires. En dehors de la période de reproduction, Grubb (1972, 1974) a pu observer que l'océanite cul-blanc s'alimente fréquemment la nuit.

1.2. Origine et rôle de la nocturnalité chez les oiseaux côtiers et marins

La nocturnalité chez les oiseaux côtiers et marins suscite de nombreuses interrogations quant à son origine et à son rôle, notamment au niveau adaptatif. En effet, si elle s'observe chez un bon nombre d'espèces, elle demeure néanmoins occasionnelle. En cherchant les causes de son apparition, McNeil et al. (1993) ont pu mettre en évidence que chez ce groupe d'oiseaux, la nocturnalité résulte plus de facteurs adaptatifs que de facteurs phylogénétiques. En effet, en superposant les comportements nocturnes de plusieurs espèces à l'arbre phylogénétique aviaire établi par Sibley et Ahlquist (1990), ces auteurs ont pu montrer qu'aucune tendance phylogénétique ne se dégageait. De cette analyse ils ont conclu que chez les oiseaux côtiers et marins le caractère de la nocturnalité a émergé, non pas à partir d'une lignée évolutive uniforme et commune, mais plutôt d'un processus de radiation adaptative. Ainsi, la nocturnalité est apparue chez ces différentes espèces de façon indépendante et sous différentes contraintes écologiques.

McNeil et al. (1993) retiennent trois principales hypothèses écologiques pour expliquer l'apparition des comportements nocturnes chez les espèces aviaires côtières et marines. Selon une première hypothèse (*supplementary hypothesis*), certaines espèces s'alimenteraient de nuit lorsque leurs besoins nutritifs et énergétiques ne peuvent être comblés par les aliments qu'elles se procurent le jour. Cette hypothèse s'appliquerait à plusieurs espèces marines des pays de climat tempéré qui ne migrent pas l'hiver. Les demandes énergétiques étant beaucoup plus importantes l'hiver, ces oiseaux s'alimenteraient fréquemment la nuit pendant la saison hivernale pour combler des carences énergétiques (Brooke et Prince, 1991).

Selon la deuxième hypothèse (*preference hypothesis*), la quête alimentaire nocturne permettrait à certaines espèces de profiter d'une plus grande disponibilité de proies la nuit, comparativement au jour. Dans les milieux côtiers et marins, la disponibilité des aliments est en effet fortement influencée par les cycles de marée. Ainsi, de nombreux invertébrés et poissons migrent à la surface de l'eau pendant la nuit, fournissant ainsi une plus grande abondance de nourriture (Ashmole et Ashmole, 1967). Cette deuxième hypothèse expliquerait les comportements de quête alimentaire nocturne d'un bon nombre d'espèces côtières et marines qui ne sont pas plongeuses, comme les sternes, plusieurs goélands, de nombreux pétrels, albatros, diablotins et puffins qui profitent des migrations nocturnes du zooplacton et des autres organismes marins pour s'alimenter (Ashmole et Ashmole, 1967; Harris, 1970; Imber, 1973, 1975, 1976; Hasegawa et DeGange, 1982; Thomas, 1982; Harper, 1983; Prince et Morgan, 1987).

Selon la troisième hypothèse (*predation avoidance hypothesis*), certains comportements nocturnes seraient liés à un besoin d'éviter les prédateurs diurnes et de contrer le kleptoparasitisme de nombreux chapardeurs qui sont actifs de jour. Cette dernière hypothèse s'appliquerait particulièrement aux espèces marines de petite taille, comme les pétrels et les alques, qui sont les proies de nombreux goélands dans leur aire de nidification (Vermeer et al., 1987; Jones et al., 1990).

Les facteurs écologiques les plus déterminants dans la manifestation des comportements nocturnes chez les oiseaux côtiers et marins semblent donc être liés à la disponibilité des ressources alimentaires, aux stratégies qu'utilisent les différentes espèces pour acquérir ces ressources, et à la présence de prédateurs.

1.3. Le système visuel des oiseaux : structures et fonctions

Le système visuel des oiseaux est à toute fin pratique semblable à celui des autres vertébrés. Les structures et les rôles fonctionnels des éléments qui le

composent se comparent en effet à ceux des poissons, reptiles et mammifères (Butler et Hodos, 1996). Au-delà de ces ressemblances générales le système visuel des oiseaux possède cependant ses propres particularités et présente toute une variété d'adaptations structurelles et fonctionnelles qui reflètent leurs différents modes de vie (Tansley, 1965; Martin, 1990, 1994).

1.3.1. Structures de l'œil

Tout comme chez les autres vertébrés, l'œil des oiseaux se compose de trois tuniques: une première constituée de tissu conjonctif et qui est dite fibreuse (la plus externe), une deuxième vasculaire appelée uvée et une troisième sensitive (la plus interne) la rétine. La tunique fibreuse se divise en deux parties: une partie antérieure qui fait saillie et forme la cornée, et une partie postérieure qui forme la sclérotique. La tunique vasculaire se compose quant à elle de trois éléments: la choroïde, le corps ciliaire et l'iris. La choroïde est une membrane très vascularisée qui forme la partie postérieure de la tunique vasculaire. Elle s'unit dans la partie antérieure de celle-ci au corps ciliaire par une jonction appelée l'*ora serrata*. Le corps ciliaire est formé principalement de faisceaux musculaires lisses qui régissent la forme du cristallin. L'iris, la partie antérieure de la tunique vasculaire, est aussi constitué de muscles lisses et, à la manière d'un diaphragme, contrôle l'ouverture et la fermeture de la pupille et par le fait même l'entrée de la lumière dans l'œil (Figure 5) (Meyer, 1986). Ainsi, lorsque l'intensité lumineuse est élevée, les muscles lisses de l'iris se contractent et diminuent le diamètre de la pupille pour éviter l'éblouissement. De même, lorsque la lumière ambiante diminue, la pupille s'élargit afin de faire entrer plus de lumière dans l'œil. Chez presque toutes les espèces aviaires, la pupille est de forme ronde ; seul le bec-en-ciseaux noir (*Rynchops niger*), qui est une espèce nocturne, possède une pupille en fente verticale qui permet une obturation complète de celle-ci lorsque l'oiseau est actif de jour (Zusi et Bridge, 1981; Rojas et al, 1997).

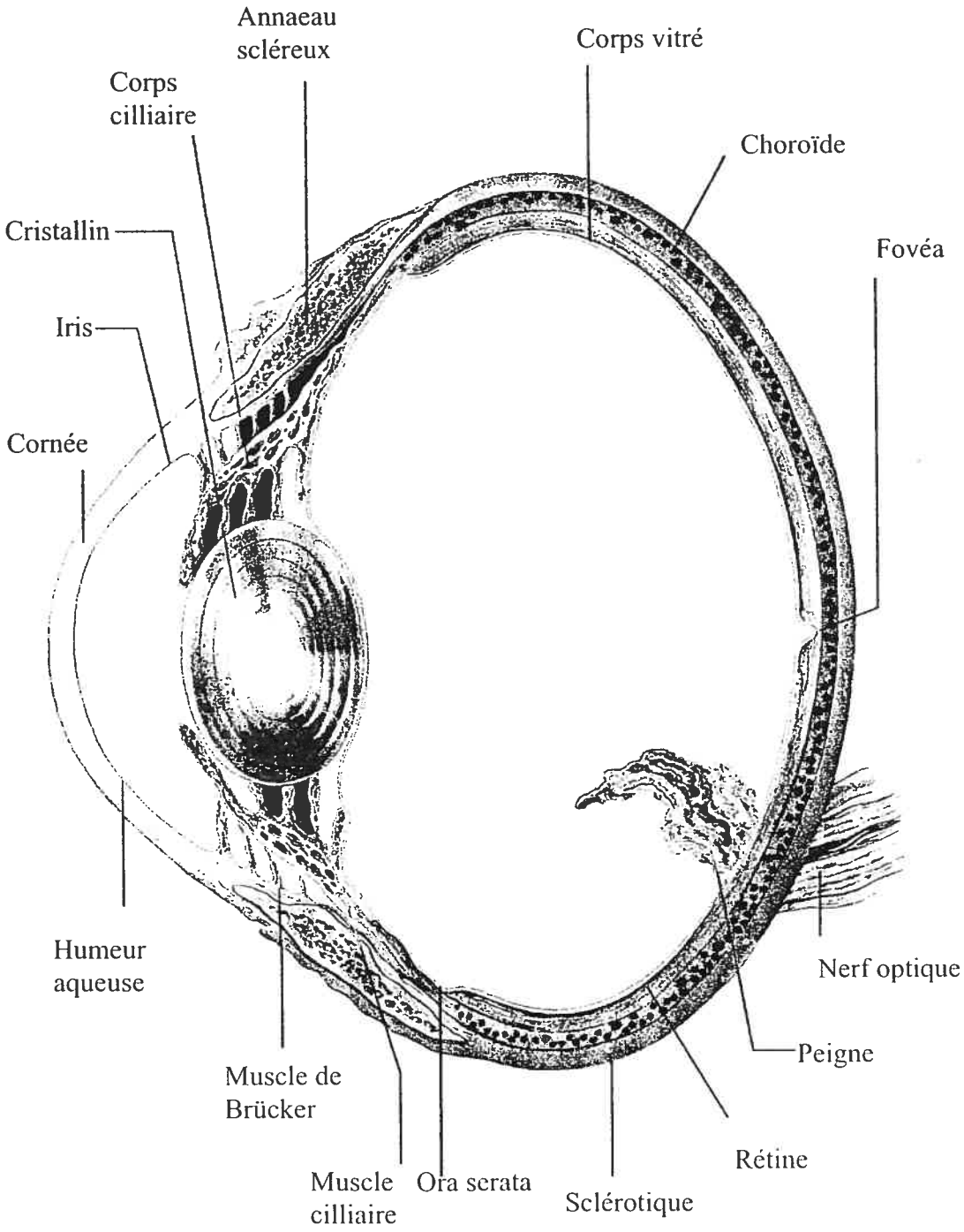

Figure 5: L'oeil de l'oiseau

(Tirée et modifiée de del Hoyo J, Elliott A et Christie DA (Eds). Handbook of the Birds of the World, 1999)

À l'intérieur de l'œil, on distingue deux chambres : une antérieure qui contient un liquide transparent, l'humeur aqueuse, et une postérieure qui est remplie d'une substance gélatineuse et transparente, le corps vitré. La frontière entre ces deux chambres est délimitée par le cristallin. Cette structure, qui agit comme une lentille dans le processus de vision, est soutenue verticalement à l'intérieur de l'œil grâce à des ligaments suspenseurs. Lorsque la lumière ambiante atteint l'œil, elle traverse successivement la cornée, l'humeur aqueuse, le cristallin et le corps vitré avant de stimuler la rétine.

Chez les oiseaux, contrairement aux mammifères, la sclérotique est cartilagineuse et se prolonge à l'avant par un anneau scléreux ossifié qui entoure la région ciliaire. C'est cet anneau qui confère à l'œil sa forme. D'une façon générale, l'œil des oiseaux est très volumineux par rapport à la taille de la tête. Chez les espèces nocturnes, l'œil est généralement très grand par rapport aux dimensions de la tête, comparativement à ce qui est observé chez les espèces diurnes (Meyer, 1977, 1986). Ainsi, on retrouve chez les espèces nocturnes une cornée élargie, un très gros cristallin, une large pupille et une grande chambre antérieure (Meyer, 1977). De fait, l'élargissement de toutes ces structures permet à l'œil de capter une plus grande quantité de lumière, ce qui favorise la vision dans des conditions de faible luminosité. La forme de l'œil varie également en fonction des espèces et de leur mode de vie. En fait, on distingue trois grandes catégories de forme: l'œil plat que possèdent la plupart des espèces, l'œil globuleux des rapaces diurnes et l'œil tubulaire que l'on retrouve chez les espèces strictement nocturnes. Bien qu'aucune corrélation n'ait été encore établie de façon satisfaisante, la forme tubulaire favoriserait la vision nocturne. En fait, cette forme permettrait d'avoir un œil relativement gros dans une boîte crânienne relativement petite et favoriserait l'entrée d'une plus grande quantité de lumière (Martin, 1985; 1990; 1994).

Une autre particularité de l'œil de l'oiseau est le peigne. Cette structure est une membrane richement vascularisée qui s'étend dans la chambre postérieure, à partir du

point où le nerf optique émerge de la rétine et qui se projette dans l'humeur vitrée. Le rôle de cette structure est encore mal connu. Le peigne semble avoir une fonction nutritionnelle et/ou jouer un rôle dans la sensibilité au mouvement ou dans l'orientation dans l'espace (Meyer, 1986).

1.3.2. Structure de la rétine

La rétine des oiseaux, comme celle des autres vertébrés, se compose de deux couches: une couche pigmentaire externe et une couche nerveuse interne (Figure 6). La couche nerveuse se divise en trois couches cellulaires: la couche nucléaire externe qui est constituée des photorécepteurs (les cônes et les bâtonnets), la couche nucléaire interne qui comprend les cellules bipolaires, horizontales, amacrines et interplexiformes, et la couche ganglionnaire qui est composée principalement de cellules ganglionnaires et de cellules amacrines dites déplacées. Entre la couche nucléaire externe et la couche nucléaire interne se trouve une zone de connexions synaptiques appelée couche plexiforme externe. Entre la couche nucléaire externe et la couche ganglionnaire se trouve une autre zone de connexions synaptiques, la couche plexiforme interne. Les cellules horizontales, grâce à des connexions latérales, permettent le transfert de l'information entre les récepteurs et les cellules bipolaires. De même, les cellules amacrines permettent un transfert latéral entre les cellules bipolaires et les cellules ganglionnaires. Les cellules interplexiformes, quant à elles, forment des contacts postsynaptiques avec les cellules amacrines et présynaptiques avec les cellules bipolaires. La rétine contient aussi un autre type de cellules, les cellules gliales de Müller qui traversent radialement les trois couches cellulaires ; elles forment la membrane limitante interne (Hayes, 1982).

1.3.2.1. Les photorécepteurs: structures et fonctions

La rétine des oiseaux contient trois différents types morphologiques de photorécepteurs, soit les cônes simples, les cônes doubles, qui sont des cônes simples

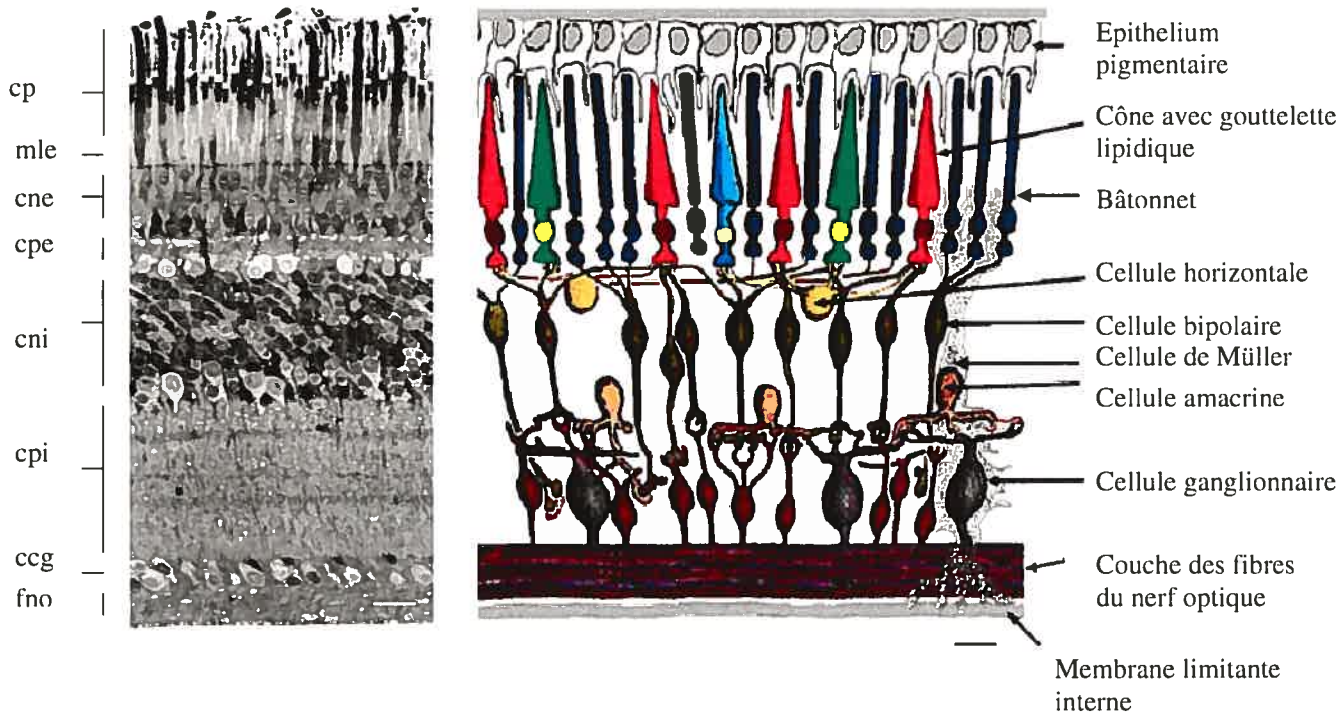

Figure 6: Photomicrographie de la rétine du goéland à bec cerclé (*Larus delawarensis*) (gauche) et schéma de son organisation structurelle (droite) (Tiré et modifié de Kolb et al., 2005). Abréviations : cp = couche des photorécepteurs ; mle = membrane limitante externe ; cne = couche nucléaire externe ; cpe = couche plexiforme externe ; cni = couche nucléaire interne ; cpi = couche plexiforme interne ; ccg = couche des cellules gaglionnaires ; fno = fibres du nerf optique. Echelle = 20 µm (gauche) et 50 µm (droite).

associés au niveau de leur membrane par des jonctions de type électrique («gap junctions») et les bâtonnets (Hart, 2001). Les cônes (simples et doubles) et les bâtonnets sont constitués des mêmes éléments structuraux. Ainsi, ils possèdent un segment interne contenant un noyau et une terminaison synaptique, un segment intermédiaire contenant un cil connecteur, constitué de neuf paires de microtubules, et un segment externe contenant le pigment photosensible. Ils se distinguent cependant par la forme et la taille de leur segment externe. Ainsi, le segment externe des bâtonnets a une forme allongée et est constitué de disques libres empilés, alors que celui des cônes est conique et constitué d'une membrane basale repliée sur elle-même qui forme des invaginations horizontales sans disques libres. De plus, les cônes des oiseaux possèdent des gouttelettes lipidiques situées à la jonction de leurs segments interne et externe. Ces gouttelettes contiennent différents pigments caroténoïdes (principalement l'astaxanthine, le zeaxanthine et le galloxanthine) et, selon le type et la quantité de caroténoïde, elles sont soit transparentes, soit de couleur jaune-pâle, jaune, orange, rouge ou verte (Goldsmith et al., 1984; Varela et al., 1993).

Le nombre, la densité, de même que la distribution topographique des différents photorécepteurs varient selon les espèces et leur mode de vie, résultant en d'importantes différences régionales ayant des conséquences fonctionnelles. Ainsi, chez les espèces strictement diurnes, il est possible d'identifier une ou plusieurs régions où la densité des cônes est très élevée. Ces régions peuvent prendre différentes formes. Chez le pigeon, par exemple, elle est de forme ovale tandis que chez plusieurs espèces de procellariiformes elle s'étend dans l'axe temporo-nasal en une sorte de ruban (Hayes, 1982). Au centre des régions de haute densité de cônes on retrouve une dépression, la fovéa, où les structures rétiniennes contiguës sont déplacées vers le côté, permettant ainsi à la lumière d'atteindre directement les photorécepteurs sans traverser les autres couches de la rétine, ce qui permet une meilleure acuité visuelle. En fait, l'acuité visuelle est optimale lorsque l'éclairement est élevé. Au niveau de la fovéa les rayons lumineux arrivent directement aux photorécepteurs sans interférence puisque dans cette région les structures rétiniennes

contiguës sont déplacées vers le côté. Certaines espèces prédatrices diurnes possèdent deux fovéas, une centrale et une autre dans la portion dorso-temporale de la rétine (Pearson, 1982).

Les bâtonnets contiennent de la rhodopsine, un photopigment composé d'une protéine de type opsine, et d'un aldéhyde dérivé de la vitamine A_1, le rétinène. Lors de la stimulation lumineuse, le rétinène change de conformation spatiale et passe de la forme 11-*cis* à la forme *trans*. Cette isomérisation provoque plusieurs transformations structurelles de la protéine, et lorsque celle-ci est sous la forme de métarhodopsine II, elle se dissocie complètement de la molécule de rétinène. C'est au cours de cette dissociation que les bâtonnets émettent des signaux électriques (Fain et al., 1996). Bien que l'on connaisse encore mal le processus de transduction qui survient dans les cônes, le mécanisme biochimique dont il découle semble être le même que celui des bâtonnets (Dowling, 1987). Le photopigment contenu dans les cônes, l'iodopsine, est composé cependant d'une opsine différente de celle qui constitue la rhodopsine des bâtonnets (Dowling, 1987).

Cette différence confère aux cônes et aux bâtonnets des fonctions propres. Ainsi, ils présentent des seuils d'excitation distincts. D'une façon générale, les bâtonnets sont plus sensibles que les cônes, c'est-à-dire qu'ils répondent à des intensités lumineuses beaucoup plus faibles que ces derniers et servent donc à la vision nocturne. Les cônes, quant à eux, demandent des intensités lumineuses beaucoup plus fortes pour être fonctionnels et servent à la vision diurne (Dowling, 1987). En fait, un seul photon est capable de provoquer une réponse dans un bâtonnet alors qu'il en faut une centaine pour provoquer la même réponse dans un cône. Par conséquent, une moins grande quantité de photons est nécessaire pour évoquer une réponse maximale des bâtonnets comparativement aux cônes (Baylor et al., 1979). De plus, l'organisation synaptique convergente des bâtonnets avec les cellules bipolaires accroît leur sensibilité car elle permet d'amplifier les réponses

évoquées par de faibles intensités lumineuses en «additionnant » les signaux des bâtonnets (Cohen, 1992).

En plus de présenter différents seuils d'excitabilité, les photopigments des bâtonnets et des cônes n'absorbent pas les mêmes longueurs d'onde de lumière. Le pic d'absorption maximale de la rhodopsine se situe aux environs de 500 nm (Dowling, 1987). Chez les oiseaux, on reconnaît généralement quatre types fonctionnels de cônes qui se distinguent par le spectre d'absorption des différents photopigments qu'ils contiennent. Ainsi, ils possèdent des pics d'absorption maximale (λ_{max}) variant entre 541-571 nm (rouge), 497-510 nm (vert) et 430-463 nm (bleu) selon les espèces et certaines espèces possèdent également un λ_{max} au environ de 362-426 nm ce qui leur confère une vision dans le spectre du violet et de l'ultraviolet (Hart, 2001). En fait, la sensibilité spectrale des oiseaux se définit par le spectre d'absorption des photopigments contenus dans leurs cônes et par celui des gouttelettes lipidiques (Varela et al., 1993). En agissant comme des filtres qui absorbent les longueurs d'onde les plus courtes, les gouttelettes lipidiques permettent une discrimination plus fine des différentes longueurs d'onde (Bowmaker, 1977).

1.3.2.2. Les cellules horizontales

Les cellules horizontales se situent dans la partie externe de la couche nucléaire externe et leurs terminaisons horizontales font synapse avec les photorécepteurs et les cellules bipolaires et assurent la transmission latérale de l'information dans la rétine des oiseaux (Husband et Shimizu, 2001). Chez les téléostéens, urodèles, reptiles et oiseaux, on distingue principalement deux types morphologiques de cellules horizontales, soit les étoilées et les en brosse (Rodieck, 1973). On distingue également deux types physiologiques de cellules horizontales, soit les cellules horizontales qui hyperpolarisent ou dépolarisent en fonction de la longueur d'onde de la stimulation lumineuse (chromaticité ou type C), et celles qui hyperpolarisent en fonction de l'intensité de la luminosité, indépendamment de la longueur d'onde de la

stimulation (luminosité ou type L) (Rodieck, 1973). A ce jour, chez les oiseaux, seules les cellules horizontales de type L ont été identifiées (Husband et Shimizu, 2001).

1.3.2.3. Les cellules bipolaires

Chez les oiseaux tout comme chez les autres vertébrés, les cellules bipolaires assurent la jonction entre les photorécepteurs et les cellules ganglionnaires. Elles peuvent être soit de type ON (se dépolarisant à la stimulation lumineuse), soit de type OFF (s'hyperpolarisant à la cessation de la stimulation lumineuse). Chez les oiseaux, on distingue principalement deux types de cellules bipolaires, les cellules bipolaires à large champ dendritique et celles à petit champ dendritique (Rodieck, 1973). Le degré d'arborisation dans la couche plexiforme interne des différents types de cellules bipolaires semblent varier selon les espèces et permettrait à certaines de traiter plus efficacement les signaux lumineux à faible contraste et par le fait même d'augmenter la sensibilité de la rétine (Husband et Shimizu, 2001).

1.3.2.4. Les cellules amacrines

Les cellules amacrines, tout comme les cellules horizontales, assurent la transmission latérale de l'information dans la rétine. En fait, elles modulent l'information provenant des cellules bipolaires vers des cellules ganglionnaires (Dowling, 1990). Chez différentes espèces de vertébrés, on a pu identifier à ce jour plus de 20 types morphologiques de cellules amacrines qui utilisent au moins huit neurotransmetteurs différents (Kandel et al., 1993). Leur implication dans le fonctionnement de la rétine est donc fort complexe. Très peu d'études cependant ont été faites chez les oiseaux et on ignore le nombre exact des différents sous-types de cellules amacrines que l'on peut rencontrer chez les différentes espèces. Chez le pigeon, il semble exister des variations régionales dans la densité des cellules amacrines ; on observe en effet chez cette espèce un nombre élevé de cellules

amacrines dans le champ rouge (axe dorso-temporal) de la rétine (Nalbach et al., 1993).

1.3.2.5. Les cellules ganglionnaires

La rétine des oiseaux se distingue de celle des autres vertébrés par le nombre élevé de cellules ganglionnaires qu'elle contient. En effet, la rétine du pigeon contient un peu plus de deux millions de cellules ganglionnaires, tandis que celle du singe rhésus, par exemple n'en contient qu'un million (Thompson, 1991). Ces cellules se distinguent des autres cellules rétiniennes par le fait qu'elles sont les seules à produire des potentiels d'action (Kandel et al., 1993). Chez les oiseaux tout comme chez les autres vertébrés, on distingue trois sous-types de cellules ganglionnaires : les cellules W qui sont de petite taille et qui se caractérisent fonctionnellement par une vitesse de conduction lente ainsi que par leur rôle dans les réponses d'orientation des yeux et de la tête vers un objet en mouvement, les cellules X qui sont de taille moyenne et qui ont une vitesse de conduction rapide (en fait ces cellules ont la capacité de moduler leur propre rythme de décharge et d'intégrer l'information spatiale des réponses qu'elles émettent, elles ont donc un pouvoir de résolution très élevé par rapport à leur pouvoir de résolution temporelle, faisant d'elles des analyseurs de contrastes spatiaux) et les cellules Y qui sont de grande taille et qui ont une très grande vitesse de conduction. Physiologiquement les cellules Y possèdent des propriétés inverses de celles des cellules X. Ainsi, on leur reconnaît une incapacité de moduler leur rythme de décharge et de faire de la sommation spatiale linéaire. Elles ont par contre un très bon pouvoir de résolution temporelle, ce qui fait d'elles des détecteurs de mouvements (Buser et Imbert, 1987). De façon générale, le nombre et la distribution des cellules ganglionnaires que l'on retrouve dans la rétine tendent à varier en fonction des comportements et de l'habitat plus que de la phylogénie des espèces (Thompson, 1991). Ainsi, la rétine des animaux nocturnes contient moins de cellules ganglionnaires que celle des espèces diurnes (Husband et Shimizu, 2001). Par contre, chez les espèces diurnes, la densité de cellules

ganglionnaires est très élevée et est associée avec une densité élevée de cônes, ce qui résulte en une aire de grande acuité visuelle (Husband et Shimizu, 2001).

1.4. Électrorétinographie cornéenne

L'électrorétinographie (ERG) cornéenne, comme son nom l'indique, est une technique électrophysiologique qui permet d'enregistrer l'activité rétinienne à partir d'une électrode active placée au niveau de la cornée. En fait, elle permet l'enregistrement graphique des potentiels qui surviennent au niveau de la rétine lorsque celle-ci est stimulée par de brefs éclairs de lumière, on parle ainsi de potentiels évoqués. Même si cette mesure représente la somme de plusieurs réponses cellulaires, il est possible en faisant varier les paramètres de stimulation (intensité, durée, fréquence, longueur d'onde de l'éclair lumineux) et en analysant les caractéristiques des ondes qui résultent de cette variation, d'évaluer différentes fonctions rétiniennes. Ainsi, l'ERG cornéenne peut être utilisée pour déterminer l'activité des bâtonnets et/ou des cônes, de même que leurs fonctions d'adaptation à la lumière et à l'obscurité et leur sensibilité spectrale (Jayle et al., 1965, Brown, 1968; Armington, 1974; Dowling, 1987; Marmor, 1989; Berson, 1992; Bayer et al., 2001).

Chez les vertébrés, il est possible d'identifier quatre ondes principales. Une première onde *a* négative, une onde *b* positive, une autre onde positive mais celle-ci plus lente, l'onde *c,* et enfin une onde *d* qui correspond à la fin de la stimulation lumineuse (Jayle et al. 1965; Armington, 1974). Ces différentes ondes se caractérisent par leur morphologie, leur temps de latence, leur amplitude, leur durée et leur temps de culmination. La présence de ces différentes ondes ainsi que leurs caractéristiques varient en fonction des espèces étudiées et plus particulièrement en fonction de la proportion de bâtonnets et de cônes contenus dans leur rétine et de son organisation structurelle, mais aussi en fonction des paramètres de stimulation et des conditions d'adaptation de la rétine (Jayle et al. 1965; Armington, 1974). La figure 7 montre des exemples d'ERG obtenus chez différentes espèces de vertébrés. Nous

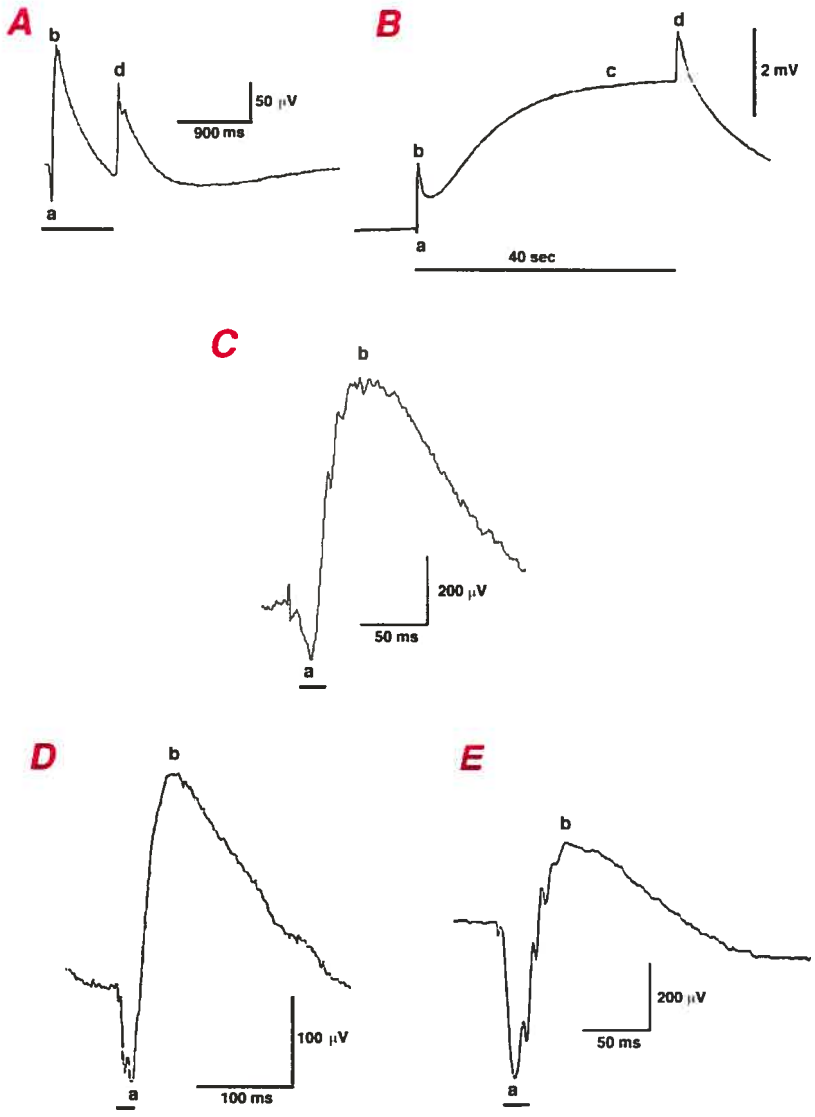

Figure 7 : Exemples d'ERG obtenus chez différentes espèces de vertébrés. En condition photopique (adaptation à la lumière), A) l'ERG de la tortue se caractérise par la présence des ondes *a* et *b* suivie d'une onde *d* (Linn et al, 1998), B) chez la grenouille, l'ERG se caractérise par une onde *c* très lente qui apparaît entre l'onde *b* et *d* (Oakley, 1977). En condition scotopique (adaptation à l'obscurité) C) chez l'oiseau, D) le lapin (Dong and Hare, 2000) et E) l'humain (Asi and Perlman, 1992) seules les ondes *a* et *b* sont apparentes.

pouvons constater qu'en condition photopique (adaptation à la lumière), l'ERG de la tortue se caractérise par la présence des ondes *a* et *b* suivies d'une onde *d* (Figure. 7A; Linn et al, 1998), tandis que chez la grenouille, une onde *c* très lente apparaît entre l'onde *b* et *d* (Figure. 7B; Oakley, 1977). En condition scotopique (adaptation à l'obscurité), chez l'oiseau (Figure. 7C), le lapin (Figure. 7D; Dong et Hare, 2000) et l'humain (Figure. 7E; Asi et Perlman, 1992), seules les ondes *a* et *b* sont apparentes.

1.4.1. Origines des principales ondes de l'ERG

1.4.1.1. L'onde a

L'onde *a* est un potentiel négatif qui résulte principalement de trois événements, dont deux proviennent de l'activité des photorécepteurs et l'autre des cellules gliales de Müller. Lorsque les photorécepteurs s'hyperpolarisent en réponse à la lumière, deux potentiels se créent, un premier dit «précoce» qui résulte du changement de configuration des molécules de photopigment lors de la stimulation, et un deuxième, le potentiel récepteur tardif, qui provient de la réponse des photorécepteurs (Dowling, 1987 ; Breton et al., 1994 ; KangDrewent et Lisenmeier, 2001). Le courant extracellulaire qui se crée le long des cellules de Müller en réponse à la baisse de concentration de potassium produite par l'hyperpolarisation des récepteurs représente le troisième élément qui participe à la genèse de l'onde *a* (Breton et al., 1994).

1.4.1.2. L'onde b

On a longtemps cru que l'onde *b* était générée principalement par les cellules de la couche nucléaire interne, et plus particulièrement par les cellules bipolaires. Cependant plusieurs études ont montré que les cellules de Müller jouent aussi un rôle important dans la formation de cette onde (Miller et Dowling, 1970; Dick et Miller, 1978; Kline et al., 1985). Selon une hypothèse généralement acceptée, l'onde *b* tire son origine des courants extracellulaires qui font suite à la dépolarisation des cellules

bipolaires. En fait, cette dépolarisation provoque une augmentation de la concentration de potassium dans les couches plexiformes interne et externe, créant ainsi trois courants : deux entrant dans les cellules de Müller et un autre sortant. L'onde *b,* qui est un potentiel positif, proviendrait de ce courant (Neuman et Frishman, 1991 ; Xu et Karwoski, 1994).

1.4.1.3. L'onde c

L'onde *c* est un potentiel positif qui suit l'onde *b* et représente la somme de deux principaux événements. Le premier tire son origine d'une baisse de concentration extracellulaire du potassium qui survient dans l'espace entourant les segments externes des photorécepteurs lorsque ceux-ci sont stimulés par la lumière, créant ainsi un potentiel négatif. Le second, provient de l'hyperpolarisation des cellules épithéliales qui est provoquée par cette même baisse de potassium. A la suite de cette hyperpolarisation, un autre potentiel se crée, mais cette fois positif. Ces deux potentiels s'additionnent pour former l'onde *c* (Steinberg, 1985 ; Zeumen et al., 1994).

1.4.1.4. L'onde d

L'onde *d* de l'ERG est une onde positive qui marque la fin de la stimulation lumineuse lors des enregistrements photopiques. En condition scotopique la cessation de la stimulation ne présente qu'une très légère dépression négative. Des études faites chez la grenouille et le necturus ont montré que ce potentiel résulte en partie de l'arrêt de l'activité des photorécepteurs et en partie des courants potassiques extracellulaires qui proviennent de l'activité des cellules horizontales et/ou de l'hyperpolarisation des cellules bipolaires (Frishman et Karwoski, 1991). Des enregistrements intrarétiniens faits chez le singe ont en effet montré que cette onde représente la fin du potentiel récepteur tardif (Brown, 1968). De façon générale, chez

les mammifères, l'onde *d* semble prendre son origine uniquement des cônes (Naarendorp et Williams, 1999).

1.5. Exposé du projet de recherche

Comme nous avons pu le voir précédemment, la nocturnalité semble avoir émergé chez les oiseaux côtiers et marins à partir d'un processus de radiation adaptative (voir McNeil et al., 1993). Sous l'effet de différentes pressions de sélection, plusieurs espèces ont adopté ce mode de vie afin de maximiser leur chance de survie et leur succès de reproduction (voir McNeil et al., 1993). Les conditions lumineuses qui prédominent la nuit imposent cependant d'importantes pressions de sélection sur le système visuel (Tansley, 1965; Lythgoe, 1979; Martin, 1990, 1994). Chez les oiseaux, ces pressions sont d'autant plus importantes que la vision guide la plupart de leurs comportements, tel que le vol, la quête alimentaire, le choix du partenaire sexuel et la défense du territoire (Hodos, 1993 ; Hart, 2001). L'importance que revêt le système visuel pour les oiseaux nous laisse donc supposer de l'existence chez les espèces qui sont actives de nuit d'adaptations visuelles particulières qui leur confèrent une capacité de vision nocturne.

D'une façon générale, la capacité de vision nocturne se définie principalement par le seuil de sensibilité de la rétine (Dowling, 1987). Plus ce seuil est bas et plus la rétine est sensible. Plusieurs facteurs peuvent influencer le seuil de sensibilité de la rétine. Le nombre de bâtonnets contenu dans la rétine est l'un des facteurs les plus déterminants. Ainsi, plus la rétine d'un animal contient de bâtonnets, plus celle-ci est sensible à la lumière. Il existe aussi des mécanismes physiologiques et biochimiques qui peuvent augmenter la sensibilité rétinienne de façon plus ponctuelle. Certains de ces mécanismes répondent instantanément aux faibles intensités lumineuses et permettent à l'œil de s'adapter rapidement à ces conditions. Ainsi, à l'obscurité la pupille se dilate et atteint une ouverture maximale afin de faire entrer une plus grande

quantité de lumière dans l'œil. Chez certaines espèces aviaires nocturnes, comme la chouette hulotte (*Strix aluco*) la pupille est particulièrement large (Martin, 1990).

D'autres mécanismes, plus lents et de nature chimique, permettent aussi d'augmenter la sensibilité rétinienne en augmentant la capacité d'absorption des photons par le pigment visuel. Ces mécanismes induisent la transformation du rétinène contenu dans les bâtonnets en rhodopsine lorsque ceux-ci sont placés à l'obscurité, ce qui a pour effet d'accroître la concentration de rhodopsine et par le fait même la sensibilité rétinienne (Dowling, 1987; Hart, 1992; Lamb et Pugh, 2004). Ce phénomène constitue l'adaptation à l'obscurité. Cette adaptation se fait très lentement pendant les premières minutes passées dans l'obscurité et devient de plus en plus rapide par la suite (Dowling, 1987; Fain, 2001).

D'autres mécanismes permettent également d'augmenter la sensibilité rétinienne en prévision des fluctuations de l'alternance jour/nuit. Ces mécanismes, communément appelés oscillateurs endogènes fonctionnent selon un rythme approximatif de 24 heures (rythmes circadiens). En absence de toute stimulation externe cependant, ce rythme peut varier entre 22 et 25 heures. Pour assurer une parfaite synchronisation entre les rythmes rétiniens endogènes et le cycle solaire de 24 heures, ces oscillateurs sont 'remis à l'heure' par certains indices temporels externes ("zeitgeber"), comme par exemple l'intensité lumineuse ambiante (Turek, 1994; Green et Beshares, 2004). Ainsi, chez plusieurs espèces, la rétine devient plus sensible la nuit comparativement au jour, et ce peu importe les conditions d'adaptation dans laquelle elle se trouve (conditions d'adaptation à l'obscurité ou à la lumière) (Cahill et Beshares, 1995; Green et Beshares, 2004).

Chez les espèces aviaires actives de nuit nous nous attendons donc à ce que ces mécanismes soient optimisés pour favoriser une capacité de vision nocturne. C'est ce que nous avons voulu vérifier dans la présente thèse. Pour ce faire, nous avons poursuivi quatre objectifs qui correspondent aux quatre articles présentés ici. Dans

ces articles, nous avons étudié certaines particularités fonctionnelles et structurelles du système rétinien du goéland à bec cerclé, du goéland gris, du macareux moine et de l'océanite cul-blanc et évalué leurs caractères adaptatifs à un mode de vie nocturne.

Le goéland à bec cerclé et le goéland gris étant deux espèces côtières partiellement actives de nuit, nous avons émis l'hypothèse qu'il existe au niveau de la structure et des fonctions de leurs rétines des adaptations qui leur donnent une certaine capacité de vision nocturne. Pour vérifier cette hypothèse nous avons, dans le premier article, caractérisé et comparé la sensibilité rétinienne de ces deux espèces en établissant des courbes d'intensité-réponse pour les ondes *a* et *b* de l'ERG et en étudiant le décours temporel de la fonction d'adaptation à l'obscurité. En parallèle, nous avons caractérisé et comparé leur structure rétinienne en évaluant la densité relative des bâtonnets et des cônes ainsi que leurs distributions topographiques.

L'optimisation des mécanismes qui favorisent une capacité de vision nocturne se fait généralement au détriment de certaines autres habilités visuelles nécessaire à une bonne vision diurne. Ainsi, l'absence de cônes dans la rétine des espèces strictement nocturnes confère une grande sensibilité à leur rétine mais la rend inapte à percevoir les détails et/ou les couleurs. Le goéland à bec cerclé et le goéland gris étant aussi actif de jour, nous avons voulu vérifier si leurs rétines étaient aussi adaptées pour percevoir les couleurs. Dans le deuxième article, nous avons caractérisé et comparé la sensibilité spectrale du goéland à bec cerclé et du goéland gris. Des courbes de réponse spectrale ont été établies, en conditions scotopique et photopique, pour l'onde b de l'ERG en présentant des flashs lumineux d'une même intensité mais de huit longueurs d'onde différentes couvrant un spectre de 400 nm à 700 nm. Nous avons également identifié les différents types de gouttelettes lipidiques contenues dans les cônes de ces deux espèces et établi leurs distributions topographiques.

Chez les oiseaux, la rétine joue un rôle particulier dans la synchronisation des rythmes biologiques avec l'environnement. En effet, d'une part elle représente la voie par laquelle transite l'information sur l'intensité lumineuse ambiante vers le principal centre circadien (la glande pinéale) et d'autre part elle semble être capable, tout au moins chez certaines espèces, d'engendrer localement des rythmes au niveau de plusieurs fonctions visuelles comme par exemple la sensibilité rétinienne, la sensibilité spectrale ou encore le processus d'adaptation à l'obscurité (Schaeffel et al., 1991; Lu et al., 1995). Cette rythmicité, comme ont pu le montrer les études de Schaeffel et al. (1991) et de Lu et al. (1995), s'exprime très nettement au niveau d'enregistrements électrorétinographiques (ERG). On ignore actuellement s'il existe des différences entre des animaux nocturnes et diurnes dans l'expression de ces mécanismes. Dans le cadre de notre étude nous avons tenté de répondre à cette question en utilisant l'électrorétinographie cornéenne. Ainsi, nous avons utilisé les différentes caractéristiques de l'ERG pour définir différentes fonctions rétiniennes et pour démontrer l'existence d'une rythmicité circadienne au niveau de ces fonctions chez des espèces aviaires diurnes et nocturnes.

L'observation chez le goéland à bec cerclé et le goéland gris d'une augmentation de la sensibilité rétinienne la nuit comparativement au jour en condition d'adaptation à l'obscurité nous a amenée à étudier de façon plus systématique les rythmes circadiens des différentes fonctions rétiniennes chez ces deux espèces. La photopériode étant l'un des principaux synchroniseurs des rythmes circadiens, nous avons émis l'hypothèse qu'il existait une différence dans l'organisation fonctionnelle de ces rythmes chez les deux espèces étudiées puisque qu'elles occupent des environnements où la photopériode varie considérablement. Dans le troisième article, nous avons établi des courbes d'intensité-réponse à partir des ondes *a* et *b* de l'ERG ainsi que des courbes de sensibilité spectrale à différentes heures de la journée, tout en respectant les conditions d'alternance jour/nuit auxquelles sont soumises les deux espèces étudiées dans leur milieu naturel.

Finalement, dans le quatrième article (en préparation), nous avons caractérisé et comparé la sensibilité rétinienne d'une espèce marine strictement diurne, le macareux moine, et d'une espèce presque essentiellement nocturne, l'océanite cul-blanc, en établissant des courbes d'intensité-réponse pour les ondes a et b de l'ERG. En parallèle, nous avons caractérisé et comparé la structure rétinienne des deux espèces en évaluant la densité relative des photorécepteurs en fonction de différentes régions de la rétine, de même qu'en établissant le rapport cônes/bâtonnets.

CHAPITRE 2

Comparing the retinal structures and functions in two species of gulls (*Larus delawarensis* and *Larus modestus*) with significant nocturnal behaviours

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Article paru en ligne dans la revue

Vision Research
(2 mai 2006)

2.1. Abstract

Ring-billed gulls (*Larus delawarensis*) and gray gulls (*Larus modestus*) are two species active both by day and night. We have investigated the retinal adaptations that allow the diurnal and nocturnal behaviours of these two species. Electroretinograms (ERG) and histological analyses show that both species have a duplex retina in which cones outnumber rods, but the number of rods appears sufficient to provide vision at night. Their retinas respond over the same scotopic dynamic range of 3.4 log cd.m^{-2}, which encompasses most of the light levels occurring at night in their photic environment. The amplitudes of the scotopic saturated a- and b-wave responses, the photopic saturated b-wave response and the photopic sensitivity parameter S are however higher in ring-billed gulls than in gray gulls. Moreover, in ring-billed gulls it took 71.60 min to the b-wave to saturate, while in gray gulls it took 41.59 min. In both species, these values appear much slower than what is observed in other bird species. Our results suggest that both species have acquired in the course of their evolution functional adaptations that can be related to their specific photic environment.

Keywords: birds, cones, dark adaptation, electroretinogram (ERG), nocturnal behaviour, retina, rods.

2.2. Introduction

Animals active both by day and by night face complex visual problems. Unlike strictly diurnal or nocturnal species, which are exposed to a restricted range of light intensities during their daily activities, they may cope with great variations of light levels, from the full intensity of the zenith sun to the darkness of night. Thus, in open environment, the ambient light intensity may vary over a range of nearly 9.5 log units during a 24-hour cycle (Martin, 1990). Moreover, in some latitudes, light level can change by as much as one log unit every 10 minutes at dawn and dusk (Lythgoe, 1979).

Most bird species are diurnal, however some gulls Laridae are in different aspects of their life cycle partly active at night (McNeil et al., 1993). For instance, ring-billed gulls (*Larus delawarensis)* have been reported to forage and fly frequently at night (Burger and Staine, 1993; Hébert and McNeil, 1999), chick feeding and aggressive interactions have sometimes been observed during nighttime in this species (Fetterolf, 1979). Gray gulls (*Larus modestus*) also have nocturnal activities. These birds breed in the desert of Atacama about 30–100 km from the coast of northern Chile and most of their reproductive behaviours take place at night. Thus, beginning in July, adults congregate every day at dusk in large flocks along the coast and initiate spiralling flights until complete darkness, after which they leave to their nesting territories in the desert where nest building begins (Guerra, 1987). A few weeks later, courtship and copulation take place exclusively at night. During incubation and brooding, the parents alternate in foraging flights, departing from the coast to the desert at around 21:30 h, they feed their chicks during darkness, and leave the nesting sites before sunrise at around 04:00 h to return back to the coast (Howell et al., 1974; Guerra, 1987). Outside the breeding season, foraging occasionally takes place at night (Blokpoel et al., 1992).

Since light intensity is considered to be the most important selective pressure

responsible for specialised adaptations in the eye (Lythgoe, 1979), we hypothesised that ring-billed gulls and gray gulls present visual adaptations that enable them to function in the nocturnal as well as in the diurnal luminance range. Our results support our claim that the retina of each species has acquired in the course of their evolution specific structural and functional adaptations, which can be related to their photic environment.

2.3. Methods

2.3.1. Animals

Experiments were performed on 29 adult ring-billed gulls (350-475 g) and 25 adult gray gulls (325-400 g) following the guidelines of the Canadian Council on Animal Care (1993). Ring-billed gulls were captured near Montréal (45°50'N, 73°58'W), Canada, between June and September, and gray gulls in Antofagasta (23°65'S, 70°40'W), Chile, during the austral fall (April). All the experiments were done during the day between 0800 h and 1600 h in Montreal and Antofagasta. Since the electroretinographic procedure used in this study was not invasive, the birds not kept for histology were allowed to recover from anaesthesia and returned to their natural habitat.

2.3.2. ERG procedures

Birds were anaesthetised with a solution of ketamine hydrochloride (50 mg/kg, i.m.; Ketaset, Ayerst) and xylazine hydrochloride (5 mg/kg, i.m.; Rompun, Bayer), and placed on a custom-made recording holder inside a Ganzfeld dome of 41 cm in diameter (LKC Ganzfeld-2503B) so that only the left eye was stimulated. Eyelids and nictitating membrane were retracted with a speculum, the cornea was anaesthetised with 0.5% proparacaine hydrochloride and the pupil fully dilated with

1% Tropicamide. A DTL electrode (X-static silver coated conductive nylon yarn, Sauquoit Industries, Scranton, PA, USA) was placed on the cornea to act as the active electrode. Reference and ground electrodes (Grass subdermal electrodes, Astro-med Inc., Warwick, RI, USA) were inserted into the scalp and under the skin of the chest, respectively. Responses were evoked to flashes of white light of 0.52 log cd.sec.m^{-2} and 20 μs duration delivered with a photostimulator (Grass PS-22) through the Ganzfeld and the stimulus luminance was attenuated with Kodak Wratten neutral density (ND) filters (Kodak Ltd, Rochester, NY, USA). Responses were recorded within a bandwidth of 0.3 to 500 Hz, amplified 10,000 X, averaged and stored on hard disc using an EPIC2000 computer-controlled electrodiagnostic system (LKC Technologies, Inc., Gaithersburg, MD).

Birds were dark adapted for 4 h after which they were prepared as described above under dim red light illumination. Scotopic responses were first obtained using increasing flash luminances from -4.68 to 0.52 log cd.sec.m^{-2} in steps of 0.4 log unit. For each luminance, the responses to 6 successive flashes presented at an inter-stimulus interval of 10.1 sec were averaged. Birds were then light adapted to a white light background of 1.55 log cd.m^{-2} for 15 min and photopic responses were obtained using increasing flash luminances of -1.48 to 0.52 log cd.sec.m^{-2} in steps of 0.4 log unit. For each luminance, the responses to 10 successive flashes presented at an inter-stimulus interval of 4.2 sec were averaged. Fewer stimuli were used in scotopic (6) than in photopic (10) condition and they were separated by longer intervals to ensure that the retina retained its dark-adapted state.

The kinetic aspect of dark adaptation was studied in an additional group of 14 ring-billed gulls and 10 gray gulls. Birds were light adapted to the above background light for 15 min, the light was then turned off and the ERGs, evoked to a single flash of white light of –1.48 log cd.sec.m^{-2} presented at 10 min intervals, were recorded over a period of 120 min.

The percentage of visual pigment bleached by the background light was evaluated according to Breton et al. (1994). For a rod outer segment of 32.08 to 33.24 μm in length and 4.79 μm in diameter, the total pigment content was estimated to be 1.05 x 10^{9} molecules and the effective collecting area 11.92 μm^{2}. The retinal irradiance was established to be 2.37 x 10^{7} photons μm^{-1} per troland in ring-billed gulls and 3.28 x 10^{7} in gray gulls. Hence, the background light delivered 2.83 x 10^{7} and 3.93 x 10^{7} units of photoisomerisation per rod in ring-billed gulls and gray gulls, respectively, and therefore bleached about 3–4% of the rhodopsin in both species. For this calculation, the pre-retinal media transmissivity and the rod outer segment optical density of rock doves (*Columba livia*; Bowmaker, 1977) were used since these parameters are not available for ring-billed gulls and gray gulls or any other species of wild birds.

2.3.3. Histology

Following the photopic ERG recordings (light adaptation), 5 individuals of each species were given a lethal dose of sodium pentobarbital. Their eyes were removed under this photopic illumination and the axial length (AL), equatorial diameter (ED) and maximal entrance pupil were measured (Martin, 1986). The left eye was injected with 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH = 7.2) and bathed 30 min in this fixative. The anterior part of the eye was removed at the equator and the retina, still attached to the choroid, was cut into nine sectors using the pecten as a landmark (Fig.1), according to the procedure of Rojas de Azuaje et al. (1993). Each sector was further subdivided into smaller portions of approximately 2 mm^{2} and kept in the fixative for 3 h. Tissues were then prepared as previously described (Rojas et al., 2004).

Transverse semithin (0.7 μm) sections were cut with an ultramicrotome, mounted onto glass slides, stained with toluidin blue and examined with the light

microscope. Rods and cones were counted in a field of 310 µm from 15 sections randomly selected for each sector to calculate their average densities. The length and diameter of the outer and inner segments of 5 rods and 5 cones randomly selected for each of the 15 sections, as well as the thickness of each retinal layer were measured using a calibrated grating.

To check the presence of a tapetum in the eye of gray gulls, the choroids, as well as the retinal epithelial cells were examined since it has been reported that the tapetum lies in either structure (Arnott et al., 1970; Nicol and Arnott, 1974; Braekevelt, 1981, 1982, 1983, 1984, 1986). The choroid was observed on fresh preparations. The right eye was hemisected along the equator; the vitreous and the retina were removed, thus exhibiting the inner surface of the choroid. The retinal epithelium cells were observed from the pieces of epon-embedded tissues, which were cut into thin (50–70 nm) sections, collected on copper grids coated with formvar, stained with uranyl acetate and lead citrate, and examined with a Jeol JEM-100 transmission electron microscope.

2.3.4. Data analysis

Luminance-response curves were constructed for the scotopic and photopic a- and b-waves of the ERG by plotting the amplitude of these waves as a function of the stimulus luminance. The amplitude of the a-wave was measured from baseline to trough, that of the b-wave from the trough of the a-wave to the peak of the b-wave or, when no a-wave was present, from baseline to peak.

The thresholds of the scotopic and photopic a- and b-waves were obtained by extrapolating from the luminance-response curves the luminance that produced a criterion response of 10 µV, which was the response amplitude just above the average value of the baseline amplitude in all animals tested.

The scotopic and photopic a-wave luminance-response curves were fitted by a least-squares algorithm (Matlab, MathWorks, Natick, MA) to the equation:

$$P_3(I,t) \cong \{1 - \exp[-I \cdot S \cdot (t - t_d)^2]\} \cdot R_{max\,(P3)} \text{ for } t > t_d \qquad (1)$$

which describes the transduction mechanisms of photoreceptors in vertebrates according to the Lamb and Pugh (1992) model, and where P_3 represents the sum of the individual photoreceptor responses as a function of flash energy I and time t after the occurrence of a short flash, S is a sensitivity parameter that scales the intensity of the flash required to generate a response equal to ½ R_{max} (semisaturation constant), R_{max} the maximum response amplitude, and t_d a brief delay (Hood and Birch, 1990, 1993, 1997). Similarly, the scotopic and photopic b-wave luminance-response curves were fitted by a least-squares algorithm to the equation (SAS Information Delivery System for UNIX, Version 6.07.02; SAS Institutes Inc., Cary, NC):

$$V/V_{max} = I^n / (I^n + \sigma^n) \qquad (2)$$

which models the activity of the inner retina in vertebrates (Naka and Rushton, 1966, 1967) and where V represents the response to stimulus luminance I, V_{max} the maximum response, σ a parameter of sensitivity which scales the luminance required to generate a response equal to ½ V_{max} (semisaturation constant), and n the slope of the function.

Dark adaptation curves were obtained by plotting the amplitudes of the a- and b-waves as a function of time during recovery from the bleach. Using a least-squares algorithm, the dark adaptation curves were then fitted by a general logistic growth equation estimated to produce the best fit to the a- and b-wave responses in both species (SAS Information Delivery System for UNIX, Version 6.07.02; SAS Institutes Inc., Cary, NC):

$$V = V_{max} / \{1 + T [\exp (-n \cdot t)]\} \quad (3)$$

where V represents the response to time t, V_{max} the maximum response, T the time at which a response is equal to ½ V_{max}, and n the slope of the function.

Statistical analyses were performed using analysis of variance (ANOVA) to evaluate differences between species in their ERG responses and in their retinal cytoarchitecture parameters. Post hoc Holm-Sidak tests were applied for evaluation of significant differences between the groups. Data fitting a non-parametric distribution were tested for significance using the Kuskal-Wallis ANOVA by ranks test with Dunn's post hoc comparison when comparing groups (Statistica for Windows version 5.0; StatSoft Inc., Tulsa, Oklahoma). Data are presented as means ± SD and in all cases the $p < 0.05$ level was used to determine statistical significance.

2.4. Results

2.4.1. Eye and pupil measurements

The eyes of ring-billed gulls and gray gulls have approximately the same size and present a typical flat shape. The colour of their iris however differs remarkably, the iris of ring-billed gulls being yellow and that of gray gulls dark brown. In ring-billed gulls, the average equatorial diameter (ED) and axial length (AL) measure 17.8 ± 0.9 mm and 16.7 ± 1.7 mm, respectively, compared to 17.0 ± 0.8 mm and 16.0 ± 1.1 mm in gray gulls, which gives a AL: ED ratio of 0.94 for both species. The pupil of ring-billed gulls reaches a maximum diameter of 5.9 ± 0.4 mm, and that of gray gulls 5.3 ± 0.36 mm.

2.4.2. Retinal function

Fig. 2 shows representative ERG responses obtained in a ring-billed gull and a

gray gull to a range of flash stimuli under scotopic (A) and photopic (B) conditions. It shows that under scotopic condition the general form of the ERGs is very similar in both species. At low stimulus luminances, a positive potential (b-wave) predominates the waveforms and as luminance increases a negative potential (a-wave) with a shorter latency begins to dip below the baseline. The amplitude of both waves also increases as a function of the stimulus luminance. Under photopic condition, the morphology of the ERGs of both species appears quite different. Thus, in ring-billed gulls, at the highest luminance (0.52 log cd.sec.m^{-2}), both the a- and b-waves are well defined, whereas in gray gulls the a-wave presents a round shape and the b-wave is barely profiled. In photopic condition, as under scotopic condition, the amplitudes of both waves increase as a function of the stimulus luminance in both species.

Fig. 3 provides the mean luminance-response curves derived from the ERGs. The lines represent the least-squares fit of equations 1 and 2 to the amplitude of the a- and b-waves, respectively. The mean values of the parameters of the luminance-response function are given in Table 1. The 10 μV criterion thresholds, for the scotopic a- and b-waves as well as the luminances at which these waves saturate, are almost identical in both species. Therefore, the retina of both species functions over the same scotopic dynamic range of luminance, i.e. between -4.21/-4.25 and -0.8 log.cd.sec.m^{-2}, which gives an overall scotopic dynamic range of 3.4 log cd.sec.m^{-2}. Within this range, however, the retina of both species behaves quite differently. ANOVA tests reveal that under scotopic condition, the amplitudes of saturated responses of the scotopic a-wave (R_{max}) (Holm-Sidak method, $t = 4.04$; $p < 0.05$) and b-wave (V_{max}) (Dunn's method, $Q = 3.91$; $p < 0.05$) are significantly higher in ring-billed gulls than in gray gulls. Under photopic condition, the parameters S (Holm-Sidak method, $t = 2.48$; $p < 0.05$) and V_{max} (Dunn's method, $Q = 3.80$; $p < 0.05$) are also higher in ring-billed gulls than in gray gulls.

2.4.3. Kinetic of dark adaptation

The dark adaptation curves obtained from ring-billed gulls and gray gulls after a 15-min period of light adaptation, which bleached about 3-4% of their visual pigment, are shown in Fig. 4. The dots represent the mean amplitude of the a-and b-waves, and the solid lines the least-squares fit of equation 3 to the amplitude of both waves. It can be seen that in ring-billed gulls the a-wave reaches saturation more rapidly than the b-wave (Holm-Sidak method, $t = 3.16$; $p < 0.05$). Thus, the amplitude of the a-wave increases slightly for the first 40 min and saturates approximately after 50 min, whereas the b-wave increases more markedly in a nearly linear fashion for the first 40 min, then continues to increase slightly between 40-70 min to finally reach saturation after more than 70-80 min. In gray gulls both the a- and b-waves reach saturation at approximately the same time, the amplitude of both waves increases linearly for approximately the first 40 min and attains saturation after about 50 min. The mean values of the parameters of the dark adaptation function obtained from both species are given in Table 2. It can be seen that in ring-billed gulls, the b-wave reaches saturation about 19.36 min after the a-wave. Furthermore, the time at which the b-wave reaches saturation (T_{vmax}) and half-saturation (T) is approximately twice longer in ring-billed gulls than in gray gulls (Holm-Sidak method, T_{vmax}: $t = 4.81$; $p < 0.05$; T: $t = 3.26$; $p < 0.05$). No difference was observed between species for the a-wave parameters.

2.4.4. Retinal structures

Light photomicrographs from the central retina (sector 5) of ring-billed gulls and gray gulls are presented in Fig. 5. In both species, three morphologically distinct photoreceptors were found: single cones, double cones (comprising a principal element closely linked to an accessory one) and rods. Cones and rods were easily differentiated by the length and diameter of their outer segments, which are smaller in the cones, and by the presence of an oil droplet at the apical portion of the cone inner

segment. In the single cones as well as in the principal element of the double cones, the oil droplet is large and coloured, whereas in the accessory element of the latter it is smaller and colourless. Table 3 presents the rod and cone morphometric measurements obtained in both species. Since, for both species, no clear difference was observed between retinal sectors, only the overall measurements are given in Table 3. Except for the rod inner segment, which is significantly longer (Holm-Sidak method, $t = 2.87$; $p < 0.05$) in gray gulls than in ring-billed gulls, the other photoreceptor measurements are not significantly different between species.

Because the difference between single cone and principal element of double cones was difficult to assess with certainty at the light microscope, each double cone was counted as two cones for the calculation of photoreceptor density. In both species, cones outnumber rods and comprise about 70% of the total photoreceptors (Fig. 6). The overall relative cone density tends to be slightly higher in gray gulls (55.7/310 µm field ± 7.7) than in ring-billed gulls (52.4/310 µm field ± 10.5), while the overall relative rod density is not significantly different between species (23.2/310 µm field ± 1.0 vs. 23.4/310 µm field ± 3.87). The topographical distribution of cones varies across the retina in approximately the same pattern in both species. Thus, the relative density of cones reaches a peak in the central retina (sector 5) and declines towards the ventral retina where the lowest density is attained in sector 9 (Fig.6). In contrast, rods are evenly distributed across the entire retina. The rods and cones are therefore not complementary in their distribution, i.e. the increase in cones in the central retina is not compensated by a decrease in rod number. In both species the cone: rod ratio is approximately 3:1 in the central retina while it is 2:1 in all other sectors.

The thickness of the retinal layers was identical in both species and the same sectorial trends were observed (Fig. 7). Thus, the outer and inner nuclear layers, the inner plexiform layer and the ganglion cell layer tend to be thicker in central sector 5,

while the optic nerve fiber layer tends to be thicker in ventral sector 9.

With regard to the presence of a tapetum in the eyes of gray gulls, when the retina was removed, the outer surface of the attached pigment epithelium as well as of the choroid appeared dark brown and no reflexive layer was seen. The pigment epithelial cells observed under transmission electron microscope (Fig. 8) presented numerous inclusions such as melanosomes, but no inclusion suggestive of a tapetum.

2.5. Discussion

Our electrophysiological and histological data show that ring-billed gulls and gray gulls have a duplex retina which is sensitive to the nocturnal as well as in the diurnal luminance range. Both species possess a retina clearly dominated by cones, but the number of rods appears to be sufficient to provide vision at night in their natural environment.

Fig. 9 presents the range of luminances that may occur in open habitat during a 24-h cycle. A comparison of Fig. 9 and Table 1 reveals that most of the luminances occurring at night are above the scotopic b-wave thresholds of both species (-4.21 and –4.25 log cd.sec.m^{-2}, respectively), and that the luminance at which their scotopic b-wave saturates (V_{max}) corresponds approximately to the light level occurring just before the end of the civil twilight period under clear sky. Therefore, the retina of both species responds over a scotopic dynamic range of about 3.4 log cd.m^{-2}, which encompasses most of the light levels that may occur during the night in their natural photic environment. Whether these levels of luminance are sufficient to allow adequate visual acuity and depth perception for nocturnal flight and/or foraging is difficult to assess. However, our results give information about limits at which these nocturnal behaviours can be guided by vision, and make clear that both species possess a retina which can detect luminances in the nocturnal range.

Although both species have the same scotopic and photopic dynamic ranges, the analysis of the luminance-response reveals that within these ranges their retinas respond differently to light, such that the amplitudes of the scotopic and photopic saturated a- and b-waves (R_{max} and V_{max}) are significantly higher in ring-billed gulls than in gray gulls. R_{max} can be related to the number of photoreceptors, and V_{max} to the number of cells within the inner nuclear layer (INL; bipolar and amacrine cells) (Hood and Birch, 1993). This would suggest that the retina of ring-billed gulls contains a greater absolute number of photoreceptors and cells in the INL than gray gulls, however our histological data do not support this interpretation. Indeed no difference was found between species in the relative rod density or INL thickness, and both species have approximately the same eye size. Therefore, other factors may explain the above physiological difference between species. The ocular pigmentation of ring-billed gulls and gray gulls differs remarkably, the iris of ring-billed gulls being yellow and that of gray gulls dark brown. Some studies have shown that the amplitude of the ERG decreases with a decrease in the transparency and the light-scattering characteristics of the eye through accumulation of eye pigment (Aufdembrinke, 1982; Lachenmayr et al., 1994; Johansson and Sandström, 2003).

The phenomena of photostasis, which is a structural and functional adaptive process related to daily variations in luminous environment and whose purpose is to regulate the total amount of photons caught per day, could also contribute to the physiological discrepancies observed. It is well known that rhodopsin concentration and length of the rod outer segment change in response to modifications of the luminous environment of animals (Williams et al., 1999; Daly et al., 2004). For instance, previous studies have shown that rods of rats raised in a dim light environment contain more rhodopsin, and therefore are more sensitive to light, than those of rats raised in a bright environment (Penn and Williams, 1986; Williams et al., 1999). Since ring-billed gulls live in a habitat (temperate latitude) where the ambient light is less intense than that of gray gulls (desert at the equator latitude), this

would suggest that the rods of ring-billed gulls contain more rhodopsin and therefore are more sensitive to light than those of gray gulls.

The results obtained for the dark adaptation experiment were unexpected and surprising. First, the process of recovery after the bleach was extremely slow in both species. It took more than 70 min in ring-billed gulls and 40 min in gray gulls to reach the saturation level for a bleach of 4-5%. Second, our results give evidence that the two species exhibit different patterns of dark adaptation. In ring-billed gulls, the data show that the sensitivity of the retina is governed by photoreceptors but also by adaptive mechanisms within the inner retina, which are not linked to the sensitivity changes of the photoreceptors during the process of dark adaptation. The discrepancy observed between the a-wave and b-wave demonstrates that, in this species, a non-receptoral adaptive mechanism exists and governs visual sensitivity after 40 min of dark adaptation. In gray gulls, the kinetic of dark adaptation followed by the b-wave was exactly the same as the a-wave, suggesting that the sensitivity of the retina of this species is governed mainly by photoreceptors.

In mammals, changes in ERG b-wave amplitude during dark adaptation have been related to regeneration of the visual pigment in the dark after exposure to light; in fact, the time course of dark adaptation follows roughly the time course of pigment regeneration (Dowling, 1960). However, some studies have indicated that other factors are involved in this process, such as adjustments within the neural circuitry of the retina (Rushton and Cohen, 1954; Dowling, 1963; Fain et al., 2001). Other factors may also explain the more gradual attainment of maximum sensitivity. Douglas and Wagner (1982) have shown evidence for a direct relationship between the increase in sensitivity during the course of dark adaptation and retinomotor movements in the rainbow trout (*Salmo gairdneri*). Indeed, when the fishes are shifted from light to darkness, their rods shorten in such a way that the outer segments are removed from the shielding effect of the pigment epithelium, a process

that increases the number of rods being exposed to light and, consequently, enhances sensitivity. Such retinomotor movements are also present in birds (Meyer, 1977; Menger et al., 2005). In our study, the effect of regeneration of the visual pigment was probably negligible since less than 5% of the rhodopsin was bleached. Therefore, the increase in the amplitude of the b-wave may be attributed to retinomotor movements and the difference between the two species could be linked to a more rapid retinomotor mechanism in gray gulls than in ring-billed gulls. The difference in ocular pigmentation observed between the two species may also explain the fact that the process of dark adaptation was about 30 min faster in gray gulls than in ring-billed gulls. Previous studies have shown that albino rats have a slower dark-adaptation process than pigmented rats (Behn et al., 2003). This has been related to the fact that calcium, which is involved in the phototransduction cascade, binds strongly to the pigmented tissue due to the presence of melanin (Drager, 1985).

The fact that saturation is attained more rapidly during the process of dark adaptation in gray gulls than in ring-billed gulls may have behavioural and ecological significance. The transition from day to night is more rapid close to the equator than at higher latitudes and days are less bright and nights are less dark at higher latitudes. A more rapid dark adaptation process in condition of rapid transition from day to night could be advantageous to gray gulls which, during the breeding season, fly at sunset from coastal feeding areas to nesting territories in the desert, where they perform most of their activities at night.

Both gull species possess a duplex retina in which 70% of the photoreceptors are cones and 30% are rods, a proportion similar to what was found in cattle egrets (*Bubulcus ibis*), tricolored egrets (*Egretta tricolor*) and American white ibises (*Eudocimus ruber*), three strictly diurnal species (Rojas et al., 1999a). The topographical distribution of the photoreceptors is quite identical in both gull species, with similar higher cone density in central sector 5 resulting in a distinct thickening of this area (Fig. 8). Sectors of higher cone density represent areas of highest visual

acuity (Walls, 1967; Meyer, 1977). Furthermore, in both species the rods are evenly distributed across the retina, which may maximise visual sensitivity in all parts of the visual field. Many gull species locate their preys from the water surface as they fly, which, according to Ashmole (1971), requires good vision in all parts of the visual field. The uniform distribution of their rods would therefore have some behavioural and ecological significance since both gulls forage during the night. In most nocturnal shorebird and wading bird species studied so far and that do not forage while flying, rods tend to be more numerous in sector 5 than in other sectors (Rojas et al., 1999 a,b). The rod distribution of ring-billed gulls and gray gulls differs from what is generally found in strictly diurnal species, such as american robins (*Turdus migratorius*) and mourning doves (*Zenaida macroura*) in which rods tend to be less numerous in the central retina (McNeil et al., 2005). Finally, contrary to what has been suggested by Howell et al. (1974), the eye of gray gulls does not contain a tapetum. Under intense flashes, eye-shine can be detected in eyes without a tapetum, due to a small proportion of the light being reflected at the retinal surface before it reaches the photoreceptors. For instance in ostriches (*Struthio camelus*), the light reflection has been attributed to the *lamina vitrea* between the pigment epithelium and choroid (Walls, 1967).

In conclusion, the present study shows that the dynamic range of the retina of ring-billed gulls and gray gulls encompasses all of the light levels that may occur in their natural photic environment. Both gull species live in open habitats, forage and fly between feeding sites or from roosting sites to feeding grounds under nocturnal light levels (McNeil et al., 1993). However, we do not know if vision is sufficient to account for all the nocturnal behaviours that have been observed in both species, notably nocturnal foraging. Gray gulls have been reported to feed at night like sandpipers (*Emerita analoga*) by probing the wet sand behind the retreating waves for mole crabs (Blokpoel et al., 1992). In ring-billed gulls, there is also indication of tactile nocturnal feeding while standing on water bodies (Hébert and McNeil, 1999). This may suggest that both species, like some shorebird species do, e.g.,

Catoptrophorus and *Tringa* species (McNeil and Rompré, 1995; Rompré and McNeil, 1996), could switch from a visual day-time foraging strategy to a tactile strategy at night. However more behavioural studies are needed in ring-billed gulls and gray gulls to test this hypothesis.

Acknowledgements

This work was realised by M.P.E. as partial requirement for the M.Sc. and Ph.D. degrees at the Université de Montréal and was supported by the Natural Sciences and Engineering Research Council of Canada and the Université de Montréal (R.M. and T.C.) and by the CIHR (P.L.). We thank Dr Luz-Marina Rojas for the teaching of the ERG and histology techniques, Dr. Vincent Ferretti for the mathematical advice for the analysis of the data and the programming of the models, Alejandra Malinarich and Consuelo Pastey for their invaluable assistance during the ERG recording in Antofagasta (Chile).

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Fig. 1. Schematic representation of the retina showing the nine sectors. D, N, T, and V correspond to dorsal, nasal, temporal and ventral sectors, respectively. The thick line between sectors 8 and 9 represents the pecten.

Fig. 2. Representative ERG waveforms obtained for a ring-billed gull and a gray gull to a range of flash stimuli presented under scotopic (A) and photopic (B) conditions. Abbreviations: a = peak of the a-wave; b = peak of the b-wave.

Fig. 3. Luminance-response curves of the a- and b-waves derived from the ERGs. The lines represent the least-squares fit of Eqs. (1) and (2) to the mean amplitudes of the a- and b-waves, respectively.

Fig. 4. Dark adaptation curves derived from the ERGs of ring-billed gulls and gray gulls. The lines represent the least-squares fit of Eq. (3) to the amplitude of the a- and b-waves.

Fig. 5. Light photomicrographs of the central retina (sector 5) of a ring-billed gull and a gray gull. A) Toluidine bleu-stained transverse sections showing the organisation of the retinal layers. Abbreviations: p.l. = photoreceptor layer; o.l.m. = outer limiting membrane; o.n.l. = outer nuclear layer; o.p.l. = outer plexiform layer; i.n.l. = inner nuclear layer; i.p.l. = inner plexiform layer; g.c.l. = ganglion cell layer; o.f.l. = optic fiber layer; i.l.m. = inner limiting membrane. B) Magnified view of the photoreceptor layer.

Fig. 6. Mean cone and rod densities (± SD) calculated in 5 ring-billed gulls and 5 gray gulls in each of the nine retinal sectors.

Fig. 7. Mean thickness (μm) of retinal layers (± SD) measured in 5 ring-billed gulls and 5 gray gulls in each of the nine retinal sectors.

Fig. 8. Electron micrographs through the retina (A), the pigmented retinal epithelium (B), and the choroid (C) of a gray gull. Abbreviations: C = cone; OD = oil droplet; M = melanosome, included within melanocytes.

Fig. 9. The range of natural luminance (log $cd.m^{-2}$) of natural surface in open habitats under clear and cloudy skies. Adapted from Fig. 2.5 of Martin (1990).

Figure 1

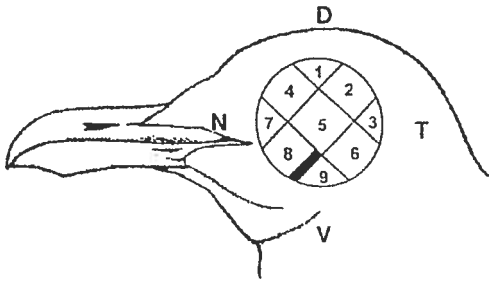

Figure 2

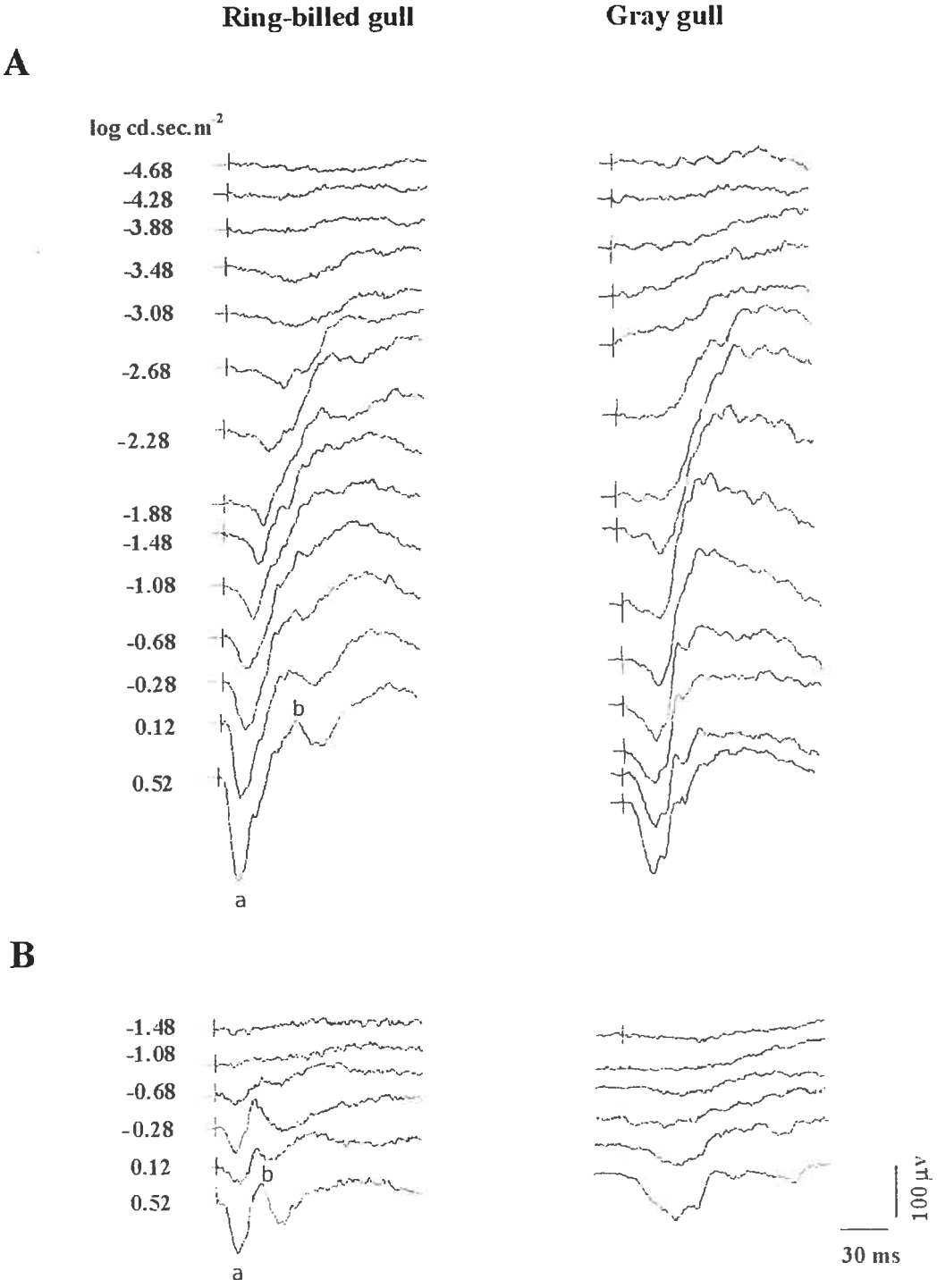
Ring-billed gull
Gray gull
A
log cd.sec.m-2
-4.68
-4.28
-3.88
-3.48
-3.08
-2.68
-2.28
-1.88
-1.48
-1.08
-0.68
-0.28
0.12
0.52
a
b
B
-1.48
-1.08
-0.68
-0.28
0.12
0.52
a
b
100 µv
30 ms

Figure 3

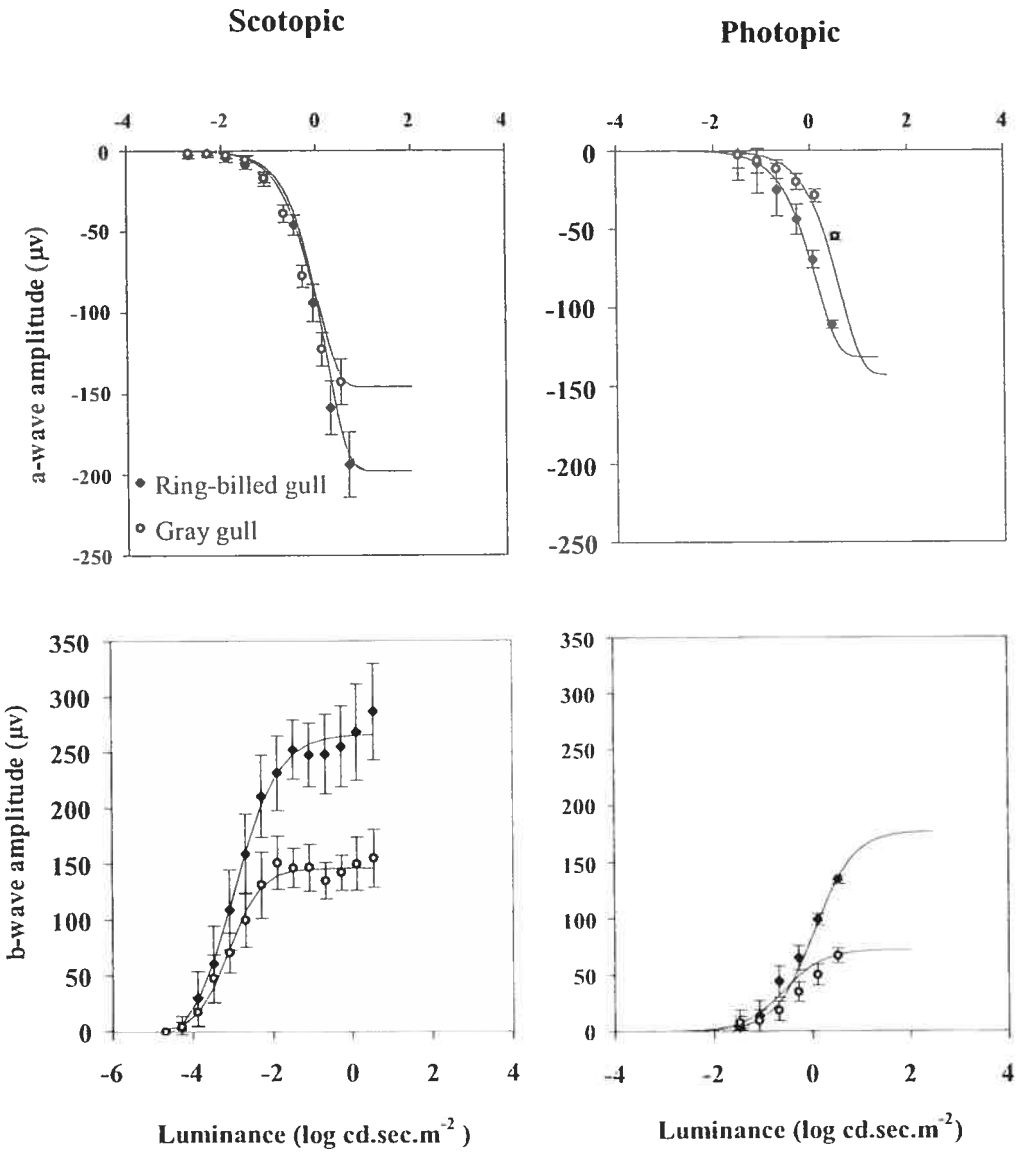
Scotopic
Photopic
a-wave amplitude (µv)
b-wave amplitude (µv)
Ring-billed gull
Gray gull
Luminance (log cd.sec.m-2)
Luminance (log cd.sec.m-2)

Figure 4

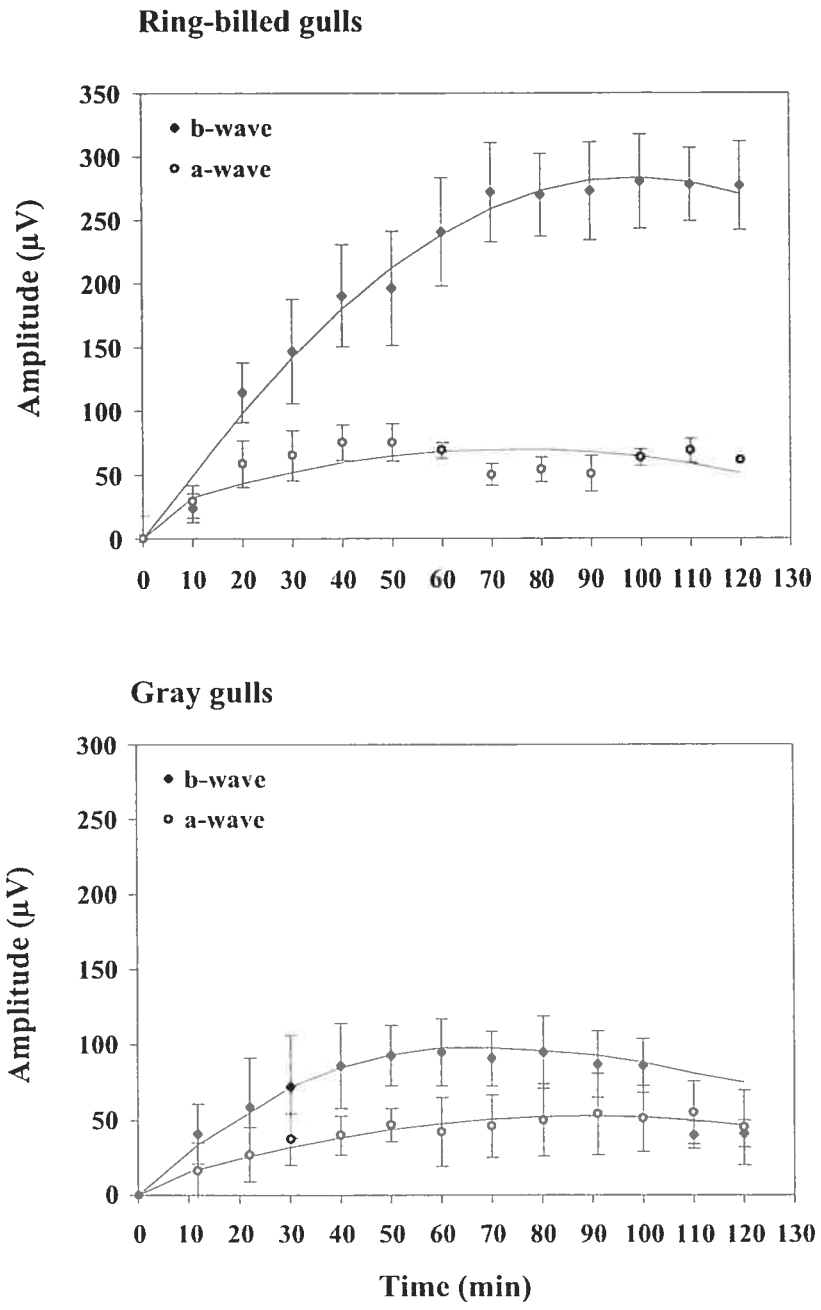
Ring-billed gulls
b-wave
a-wave
Amplitude (µV)
350
300
250
200
150
100
50
0
0 10 20 30 40 50 60 70 80 90 100 110 120 130
Gray gulls
b-wave
a-wave
Amplitude (µV)
300
250
200
150
100
50
0
0 10 20 30 40 50 60 70 80 90 100 110 120 130
Time (min)

Figure 5

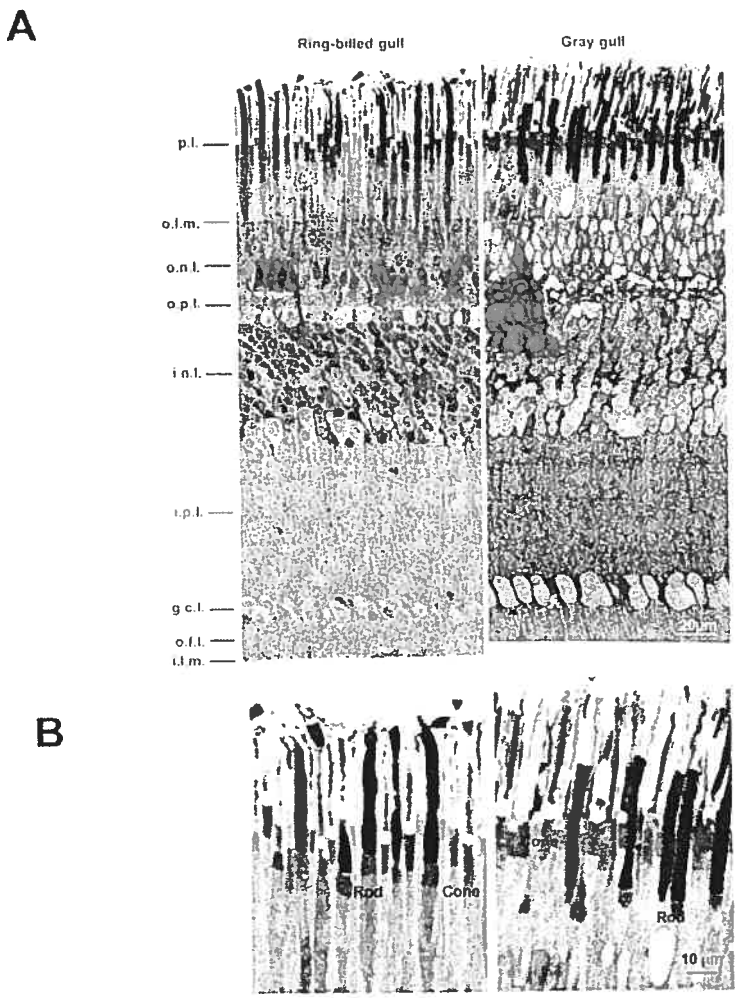
A
Ring-billed gull
Gray gull
p.l.
o.l.m.
o.n.l.
o.p.l.
i.n.l.
i.p.l.
g.c.l.
o.f.l.
i.l.m.
B
Rod
Cone
Rod
10 µm

Figure 6

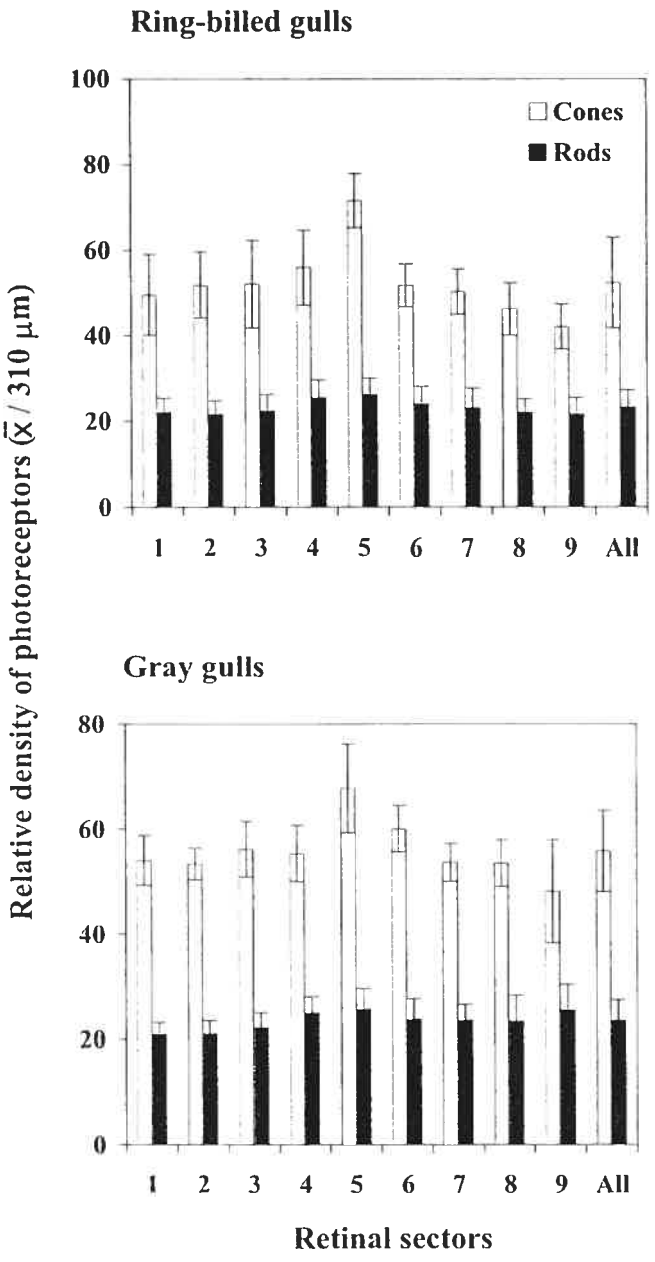
Ring-billed gulls
Cones
Rods
100
80
60
40
20
0
1 2 3 4 5 6 7 8 9 All
Gray gulls
80
60
40
20
0
1 2 3 4 5 6 7 8 9 All
Relative density of photoreceptors ($\bar{x}$ / 310 µm)
Retinal sectors

Figure 7

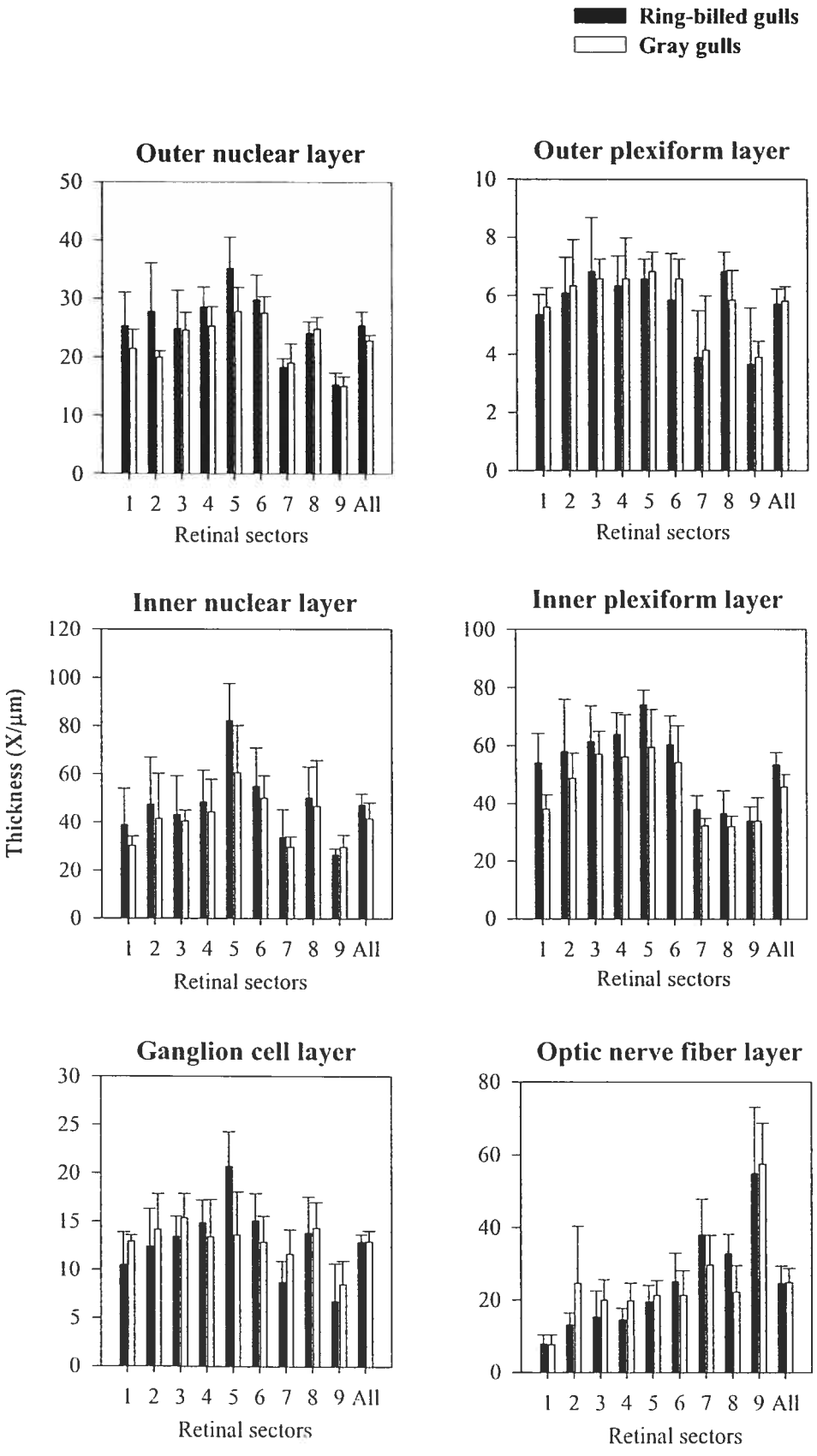
Ring-billed gulls
Gray gulls
Outer nuclear layer
Outer plexiform layer
Inner nuclear layer
Inner plexiform layer
Ganglion cell layer
Optic nerve fiber layer
Thickness (X/µm)
Retinal sectors
1 2 3 4 5 6 7 8 9 All

Figure 8

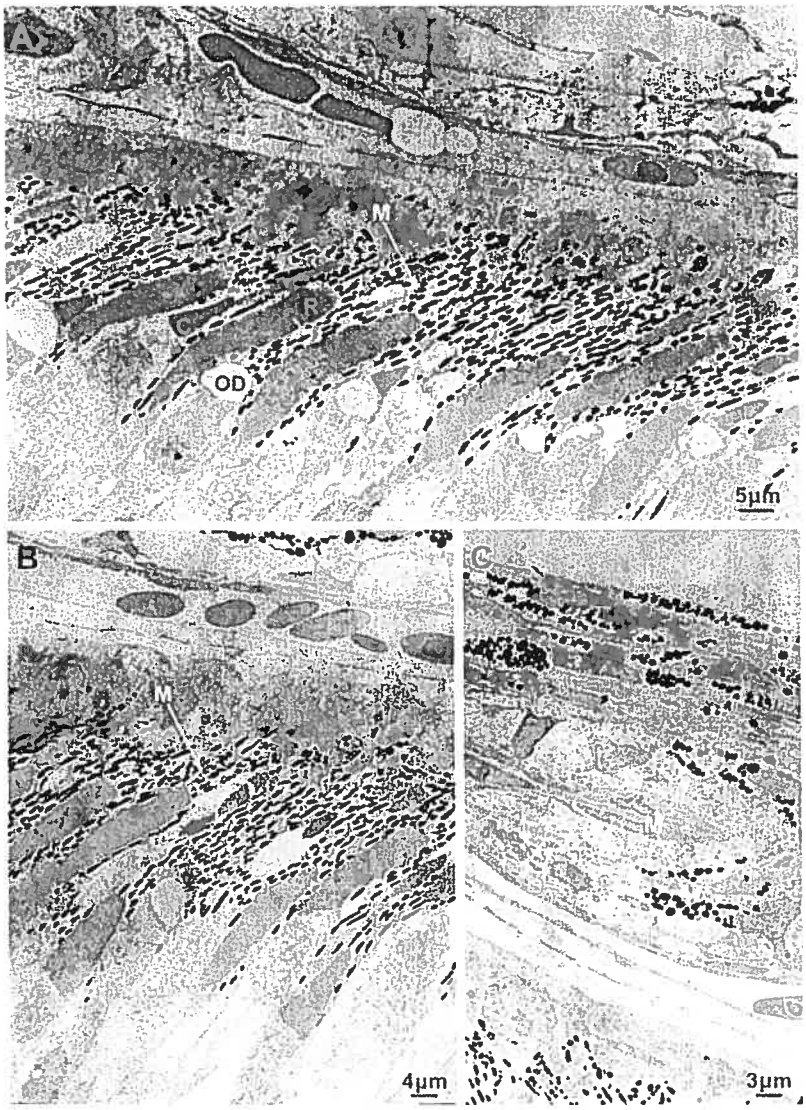

Figure 9

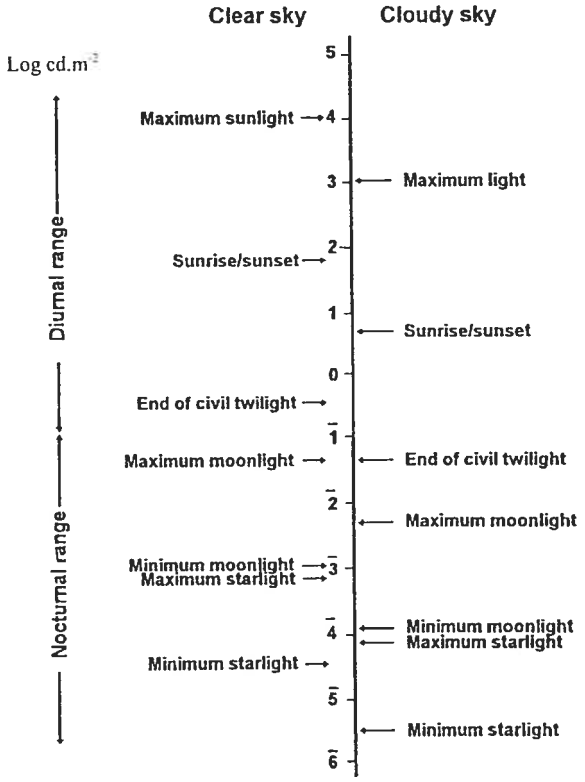
Clear sky
Cloudy sky
Log cd.m⁻²
Diurnal range
Nocturnal range
5
Maximum sunlight
4
3
Maximum light
Sunrise/sunset
2
1
Sunrise/sunset
0
End of civil twilight
1̄
Maximum moonlight
End of civil twilight
2̄
Maximum moonlight
Minimum moonlight
Maximum starlight
3̄
4̄
Minimum moonlight
Maximum starlight
Minimum starlight
5̄
Minimum starlight
6̄

Table 1
Mean values (± SD) of the parameters of the luminance-response function obtained from ring-billed-gulls and gray gulls.

Waves	Parameters [a]	Ring-billed gulls [b]	Gray gulls [b]
Scotopic			
a-wave	10 μv threshold	-1.32 ± 0.10	-1.24 ± 0.31
	R_{max}	-198.97 ± 34.21*	-146.29 ± 37.15
	LR_{max}	0.53 ± 0.06	0.48 ± 0.08
	S	-0.23 ± 0.11	-0.34 ± 0.23
b-wave	10 μv threshold	-4.21 ± 0.22	-4.25 ± 0.27
	V_{max}	261.78 ± 80.31*	149.84 ± 20.78
	LV_{max}	-0.81 ± 0.31	-0.81 ± 0.65
	σ	-2.75 ± 0.40	-3.00 ± 0.43
Photopic			
a-wave	10 μv threshold	-0.88 ± 0.31	-0.54 ± 0.20
	R_{max}	-131.03 ± 70.28	-143.31 ± 74.52
	LR_{max}	0.69 ± 0.33	1.19 ± 0.67
	S	-0.04 ± 0.44*	0.33 ± 0.38
b-wave	10 μv threshold	-1.22 ± 0.17	-1.36 ± 0.56
	V_{max}	177.47 ± 54.70*	72.05 ± 43.43
	LV_{max}	1.55 ± 0.32	2.00 ± 0.58
	σ	0.03 ± 0.39	-0.16 ± 0.26

[a] The parameters represent: threshold (log cd.sec.m^{-2}) which evokes a criterion response of 10 μv; R_{max} and V_{max}, the maximum responses (μv) estimated from Eqs (1) and (2) respectively; LR_{max} and LV_{max}, the luminances (log cd.sec.m^{-2}) at which R_{max} and V_{max} are obtained respectively; S and σ, the luminances (log cd.sec.m^{-2}) required to generate half the maximum responses (semi-saturation constant) estimated from Eqs (1) and (2). [b]Measurements obtained from 15 specimens. * Difference between species, $p < 0.05$.

Table 2
Mean values (± SD) of the parameters of the dark adaptation function obtained from ring-billed gulls and gray gulls.

Parameters [a]	Ring-billed gulls [b]	Gray gulls [b]
a-wave		
R_{max}	84.35 ± 24.12	57.97 ± 19.12
T_{Rmax}	52.24 ± 16.13	49.09 ± 13.11
T	13.38 ± 11.03	13.03 ± 12.83
b-wave		
V_{max}	246.44 ± 74.46*	87.64 ± 42.40
Tv_{max}	71.603 ± 16.32*	41.59 ± 13.04
T	31.38 ± 10.10*	16.58 ± 12.11

[a] The parameters represent: R_{max} and V_{max} , the maximum response (μv) for the a- and b-wave, respectively; T_{Rmax} and T_{vmax} the time (min) at saturation for the a- and b-wave respectively; T, the time (min) at half-saturation. [b] Measurements obtained from 14 ring-billed gulls and 10 gray gulls. * Difference between species, $p< 0.05$.

Table 3
Overall cone and rod measurements (± SD) of ring-billed gulls and gray gulls.

	Ring-billed gulls [a]		Gray gulls[a]	
	Length (μm)	Diameter (μm)	Length (μm)	Diameter (μm)
Single and principal cones				
Outer segment	18.25 ± 4.20	1.76 ± 0.23	17.91 ± 2.75	1.55 ± 0.25
Inner segment	38.74 ± 2.11	1.87 ± 0.52	38.66 ± 2.99	1.45 ± 0.43
Accessory cones				
Outer segment	21.35 ± 3.02	1.32 + 0.20	19.42 ± 2.54	1.75 ± 1.02
Inner segment	33.65 ± 4.00	4.89 ± 0.95	36.85 ± 3.20	4.75 ± 1.20
Rods				
Outer segment	32.08 ± 5.32	4.79 ± 0.62	33.24 ± 3.12	4.79 ± 0.66
Inner segment	31.66 ± 3.28*	4.99 ± 0.99	37.41 ± 3.05	4.47 ± 0.59

[a] Measurements obtained from five specimens. * Difference between species, $p < 0.05$.

CHAPITRE 3

Colour vision in ring-billed gulls (*Larus delawarensis*) and gray gulls (*Larus modestus*), two species partly active at night: an electroretinographic and morphologic study

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Article qui sera soumis à la revue

Journal of Comparative Physiology A

3.1. Abstract

Using corneal electroretinography (ERG), the spectral sensitivity of ring-billed gulls (*Larus delawarensis*) and gray gulls (*Larus modestus*), two species partly active at night, was characterised and correlated to the relative abundance and topographical distribution of cones studied histologically. ERG recordings obtained under photopic condition show that gray gulls and ring-billed gulls have respective sensitivity peak (λ_{max}) at 550 and 513 nm, and at 549 and 515 nm. Under scotopic condition, ring-billed gulls present a λ_{max} located at 556 nm, which is much broader than the rod photopigment absorption spectrum described in most other bird species. In gray gulls data are close to fit the rod absorption spectrum but there is also a small shift toward longer wavelengths, with a λ_{max} at 514 nm. Both species possess four types of single cones: long-wavelength-sensitive cones (LWS cones), medium-wavelength-sensitive cones (MWS cones), short-wavelength-sensitive cones (SWS cones), ultra-violet-wavelength-sensitive cones (UVS cones), and one type of double LWS cones identified histologically by their oil droplets. In the central retina, the number of double LWS cones is higher in gray gulls than in ring-billed gulls, but the opposite is true for the MWS cones. Despite their nocturnal activities ring-billed gulls and gray gulls possess retinas with spectral features typically encountered in diurnal species. The differences observed in the structural organisation of their retinas may reflect their particular visual ecology.

Key words: birds, cones, gray gulls, nocturnal behaviour, oil droplets, ring-billed gulls, spectral sensitivity.

3.2. Introduction

In diurnal birds, the ability to discriminate colours is mediated by four classes of single cones whose visual pigments are maximally sensitive to long (LWS cones; red: λ_{max} 543-571 nm), middle (MWS cones; green: λ_{max} 497-510 nm), short (SWS cones; blue: λ_{max} 430-463 nm) and ultra-violet (UVS cones; λ_{max} 362-426 nm) wavelengths, and one class of LWS double cones (Hart, 2001a,b). All five classes of cones contain oil droplets in the distal end of their inner segment, through which light must pass before reaching the visual pigment. These oil droplets contain lipids and, with the exception of the one contains within the UVS cones, different carotenoid pigments, which determine their spectral transmittance (Goldsmith et al., 1984). The different classes of cones are highly conserved across species and the type of oil droplet within each cone class is always the same. Thus, LWS double cones always contain a pale greenish droplet (P), LWS single cones a red droplet (R), MWS cones a yellow droplet (Y), SWS cones a clear colourless droplet (C) and UVS cones a transparent type droplet (T) (Bowmaker and Knowles, 1977; Bowmaker, 1991; Bowmaker et al., 1997). The pigmented oil droplets act as cut-off filters by blocking short wavelengths and shift the effective peak spectral sensitivities of the SWS, MWS and LWS single cones to wavelengths longer than the wavelengths of maximum absorbance of the visual pigment they contain. Consequently, they reduce the overlap of adjacent spectral cone classes, and thus enhance the discrimination of colours (Bowmaker, 1977, 1991; Bowmaker and Knowles, 1977; Martin and Muntz, 1978; Goldsmith et al., 1984; Partridge, 1989; Vorobyev et al., 2001). In contrast, the T-type oil droplets, which do not contain any carotenoid pigments, transmit UV light (Vorobyev, 2003).

It has been hypothesised that pigmented oil droplets have evolved in diurnal bird species to improve colour vision, and thus permit a finer discrimination of objects which may have some ecological significance for them (Barlow 1982; Govardovskii 1983; Goldsmith 1991; Robinson 1994). For instance, a theoretical study has shown that changes induce by oil droplets in spectral sensitivity improve

discrimination of plumage colours, which is an important feature in the process of recognition of sexual display in most bird species (Vorobyev et al., 1998).

The advantage of pigmented oil droplets for colour vision has however a cost. Thus, by absorbing the light they reduce the overall photons catch and increase photoreceptors signal noise, which consequently decrease the absolute sensitivity of the retina and impair colour discrimination under dim light conditions (Vorobyev, 2003; Osorio and Vorobyev, 2005). Therefore, we may expect that birds that live in dim-light environment have no, or less pigmented oil droplets in their retina and a less accurate colour vision than diurnal birds. In fact, this is supported by descriptive studies that show that in diurnal species, such as chickens (*Gallus gallus*) and pigeons (*Columba livia*), cones with pigmented oil droplets account for more than 80% of the total cone population (Bowmaker, 1977; Bowmaker and Knowles, 1977), while in nocturnal species, such as owls (Strigiforms) and goatsuckers (Caprimulgiforms), only about 10% of the cones contain pigmented oil droplets, while the remainder are colourless (Nicol and Arnott, 1974; Bowmaker and Martin, 1978; Braekevelt, 1993; Gondo and Ando, 1995; Brekevelt et al., 1996).

Ring-billed gulls (*Larus delawarensis*) and gray gulls (*Larus modestus*) are two Laridae, which are in different aspects of their life cycle partly active at night. Thus, ring-billed gulls have been reported to forage and fly frequently at night, and most of the reproductive behaviour, courtship and, to a lesser extent, foraging of gray gulls take place also at night (Howel et al., 1974; Guerra, 1987; Blokpoel et al., 1992; Burger and Staine, 1993; Hébert and McNeil, 1999). A previous study has shown that both species have evolved retinal adaptations that allow them to be sensitive to most light levels occurring at night in their environment. Thus, the proportion and the specific topographical distribution of their rods, appears sufficient to provide them vision at night (Emond et al., 2006a). Whether these specific retinal adaptations for nocturnal vision have evolved to the detriment of colour vision is however not known. This issue was explored in the present study. Using corneal electroretinography (ERG), the spectral sensitivity of these two species has been

characterised and compared. Moreover, an histological study has been carried to determine the proportions and the topographic distribution of their different cone oil droplets

3.3. Materials and Methods

3.3.1. Animals

Twelve (n = 12) adult ring-billed gulls (350-475g) were captured near Montréal (45°50'N, 73°58'W), Province of Québec, Canada and twelve (n = 12) adult gray gulls (325-400g) in Antofagasta (23°65'S, 70°40'W), Chile. The electroretinographic procedure not being invasive, the birds not used for histology were allowed to recover from anaesthesia and released in their natural habitat after experimentation. All the experiments were performed following the guidelines of the Canadian Council on Animal Care (1993).

3.3.2. Electroretinography

Birds were anaesthetised by injection of ketamine hydrochloride (50 mg/kg i.m.; Ketaset, Ayerst) and xylazine hydrochloride (5 mg/kg i.m.; Rompun, Bayer) and placed in a custom-made recording holder inside a Ganzfeld dome of 41 cm in diameter (LKC Ganzfeld-2503B) so that only the left eye was stimulated. The eyelids and nictitating membrane were retracted with a speculum, the cornea was anaesthetised with proparacaine hydrochloride 0.5%, and the pupil was fully dilated with drops of tropicamide 1%. A DTL electrode (X-static© nylon coated yarn, Sauquoit Industries, Scranton, PA, USA) was placed on the cornea as the active electrode. Reference and ground electrodes (Grass subdermal electrodes, Astro-med Inc., Warwick, RI, USA) were inserted under the scalp and the skin of the chest, respectively. Responses were evoked to white flashes of 0.52 log cd.sec.m^{-2} delivered with a photostimulator (Grass PS-22) through the Ganzfeld and the stimulus luminance was attenuated with Wratten neutral density (ND) filters (Kodak

Ltd, Rochester, NY, USA). Seven Lee interference filters (Andover, England), which have peak transmission at 450 (blue), 500 (blue-green), 525 (green), 550 (yellow), 600 (orange), 625 (light red) and 650 (dark red) nm, were inserted in front of the flash to produce monochromatic stimuli. A photometer-radiometer (Quantum; model L1-185B) was used to measure the luminance generated with each interference filter. Responses were recorded within a bandwidth of 0.3 to 500 Hz, amplified 10,000 X, averaged and stored on a hard disc using an EPIC-2000 computer-controlled electrodiagnostic system (LKC Technologies, Inc., Gaithersburg, MD).

The spectral sensitivity of both species was assessed relative to their sensitivity measured to white stimuli by the method of criterion response described by DeVoe et al. (1997). Birds were dark adapted for a 4-h period prior to experimentation. Scotopic responses were afterward obtained using white flash stimuli at luminances increasing in steps of 0.4 log unit, from -4.68 to 0.52 log cd.sec.m^{-2}, following which the seven monochromatic stimuli were used at a luminance of 1.31 log cd.sec.m^{-2}. For each monochromatic stimulus, the responses to 6 successive flashes presented at intervals of 10.1-sec were averaged. The birds were then light adapted to the white background of 1.55 log cd.m^{-2} for 15 min and photopic responses were obtained using white flash stimuli of increasing luminances from -1.48 to 0.52 log cd.sec.m^{-2} in steps of 0.4 log unit. Responses were then obtained using the same monochromatic test stimuli as under scotopic condition, except that 10 successive flashes were presented at intervals of 4.2-sec.

Luminance-response curves were constructed for the responses obtained with the white flash by plotting the amplitude of the ERG b-wave, measured from trough-to-peak, as a function of stimulus luminance. The curves were then fitted by a least-squares algorithm to the equation:

$$V/V_{max} = I^n / (I^n + \sigma^n) \qquad (1)$$

which models the activity of the inner retina (Naka and Rushton, 1966, 1967), and

where V represents the response to stimulus luminance I, V_{max} the maximum response, σ the luminance required to generate a response equal to ½ V_{max} (semisaturation constant), and n the slope of the function (SAS Information Delivery System for UNIX, Version 6.07.02; SAS Institutes Inc., Cary, NC).

For each wavelength tested, the luminance required to obtain a b-wave criterion response of 150 μV (scotopic condition) and 50 μV (photopic condition) was determined by displacing the luminance-response curves (fit of equation 1) obtained with the white stimuli on the luminance scale to coincide with response amplitudes measured at each wavelength. These criterion responses were chosen because they were consistently above noise level and always below response saturation, falling within the linear portion of the luminance response function at all stimulus wavelengths and for each subject. Since under photopic condition the amplitude of the ERG responses were smaller than in scotopic condition, a criterion response of 50 μV was chosen. Spectral-sensitivity curves were then constructed by plotting the reciprocal of the log stimulus luminance that yielded the criterion response at each wavelength tested. The method of criterion response is schematised in Fig. 1. Finally, the λ_{max} was evaluated by fitting the data to a general peak function (OriginPro for windows, version 7.5SR6, OriginLab Corporation, Northampton, MA).

3.3.3. Oil droplets

Following the ERG recordings, four (n = 4) individuals of each species were given a lethal dose of sodium pentobarbital. Their right eye was removed and hemisected along the equator. The retina, still attached to the choroid, was cut into nine sectors using the pecten as a landmark (Fig. 2), according to the procedure of Rojas de Azuaje et al. (1993). The nine sectors were then bathed in saline solution (pH = 7.2) for 30 to 60 minutes to further the detachment of the retina from the pigmented epithelium. The retina was afterwards gently separated from the choroid and mounted flat, photoreceptors side up, on glass slides. Each of the nine retinal

sectors was photographed at four different locations randomly chosen, using a light microscope (Axiomat NDC Zeiss; magnification of 500X) with a Kodak Ektachrome 160 film under bright-field illumination. The oil droplets were identified according to their colour and counted from projected slides using a 50 X 50 μm grid boundary, and their average numbers were calculated from the four locations photographed for each sector and converted to percentages.

3.3.4. Statistical analyses

Statistical analyses were performed using analysis of variance (ANOVA) to evaluate differences between the amplitude of the ERG responses obtained for each wavelength stimuli within each species and between species, and to compare the spectral sensitivities between species. Post hoc Holm-Sidak tests were applied for evaluation of significant differences between the groups (Statistica for Windows version 5.0; StatSoft Inc., Tulsa, Oklahoma). A multiway contingency table analysis was performed to compare the proportions of oil droplets of each colour between retinal sectors within each species and between species (Statistica for Windows version 5.0; StatSoft Inc., Tulsa, Oklahoma). Data are presented as means ± SD and in all cases the $p < 0.05$ level was used to determine statistical significance.

3.4. Results

3.4.1. ERG and spectral sensitivity

Representative example of ERG responses obtained under scotopic and photopic conditions in single ring-billed gull and gray gull to a range of white (left) and chromatic stimuli (450 nm blue, 500 nm blue-green, 525 nm green, 550 nm yellow, 600 nm orange, 625 nm light red and 650 nm dark red) (right) are presented in Fig. 3. The corresponding luminance-response curves used to define the 150 μV and 50 μV criterion responses are reported at the bottom of the figure. Overall, the general morphology of the ERG responses was similar in both species and for all

stimuli. With the range of white stimuli, it can be seen that under scotopic condition and at low stimulus intensities, a positive potential (b-wave) predominates the waveform and as the intensity increases a negative potential (a-wave) begins to dip below the baseline. The amplitude of the a-wave gradually augments with increasing stimulus intensities while that of the b-wave initially grow in amplitude with progressively brighter stimuli and then reach a plateau. Under photopic condition, the amplitude of both the a- and b-waves also increases with the stimulus intensities. Fig. 3 also shows that the amplitude of both the a- and b-waves varied with wavelength of the stimulus in both species (ANOVA, $p < 0.001$). Under scotopic condition, the lowest amplitude for both the a- and b-waves was obtained in response to the 650 nm stimulus in both species, while the 525 nm stimulus yielded the highest a- and b-waves amplitude in gray gulls as well as the highest a-wave amplitude in ring-billed gulls. Interestingly, in this later species, the highest b-wave amplitude was obtained with the 600 nm stimulus. Under photopic condition, the lowest amplitude of the a- and b-waves was obtained at 650 nm in gray gulls and at 650 and 450 nm, respectively in ring-billed gulls, while the 550 nm stimulus yielded the highest a- and b-waves amplitude in both species.

Spectral sensitivity curves obtained in ring-billed gulls and gray gulls under photopic and scotopic conditions are presented in Fig. 4. The data points represent the mean sensitivity values obtained for each species while the continuous lines represent the general peak function to which the data were fitted and by which the different λ_{max} were estimated. The dotted lines represent the standard rod template (Govardovskii et al. 2000). It can be seen that under scotopic condition, data obtained from ring-billed gulls do not fit adequately the standard rod pigment template measured in most bird species (λ_{max} = 506 nm; Hart, 2001), the λ_{max} being located at 556 nm. In gray gulls, data are more close to fit the standard rod pigment template but there is also a small shift toward longer wavelengths, the scotopic λ_{max} being located at 514 nm for this species. Under photopic condition, both species present two λ_{max}. In ring-billed gulls, one λ_{max} was measured at 515 nm and the other at 549 nm, while in gray gulls the two λ_{max} were measured at 513 and 550nm,

respectively. Note that the sensitivity measured at 450 nm is significantly lower in ring-billed gulls than in gray gulls (Holm-Sidak method, t = 9,295; p < 0.001). Moreover, a pronounced dip in sensitivity was observed around 525 nm in both species.

3.4.2. Oil droplets

Representative photomicrographs from the central retina (sector 5) of single ring-billed gull and a gray gull are shown in Fig. 5 (A and B). Five types of oil droplets were identified in both species (R, Y, P, C and T), but types T and C were difficult to distinguish from each other, and were merged as one type termed CT. The percentages of the different types of oil droplets in each of the nine sectors and in all sectors together are given in Table 1. The multiway contingency table analysis revealed that in ring-billed gulls, no significant variation was observed in the distribution of the R, P and CT types of droplets between retinal sectors, but the distribution of the Y type varied significantly, this type being more abundant in sectors 4 (dorso-nasal), 7 (nasal) and 8 (centro-nasal) (χ^2 = 320.40; df = 256; P < 0.01). In gray gulls, sectorial variations were observed for the R type, which predominates in sectors 1 (dorsal), 4 (dorso-nasal) and 8 (centro-nasal) (χ^2 = 339.00; df = 232; P < 0.01), the Y type, which predominates in sectors 3 (temporal), 6 (ventro-temporal) and 9 (ventro-nasal) (χ^2 = 316.50; df = 216; P < 0.01), and the P type, which predominates in sectors 5 (central) and 7 (nasal) (χ^2 = 122.70; df = 120; P < 0.01), but the CT droplets were evenly distributed across the retina. Only within the central retina (sector 5) did the proportion of some droplets vary significantly between species (χ^2 = 9.09; df = 3; P < 0.05), the P type being more abundant in gray gulls than in ring-billed gulls (χ^2 = 8.45; df = 1; P < 0.05) and the Y type less numerous in gray gulls than in ring-billed gulls (χ^2 = 7.81; df = 1; P < 0.05).

3.5. Discussion

The data obtained in this study show that, despite their nocturnal activities, ring-billed gulls and gray gulls possess retinas with spectral features typically encountered in diurnal species. Thus, in both species, oil droplets of types R, Y, P, C and T were observed at the light microscope, suggesting that their retinas contain four types of single cones: LWS cones, MWS cones, SWS cones, UVS cones and one type of double LWS cones (Hart, 2001a). Moreover, in both species, the single LWS cones containing the R droplets account for more than 30% of the total cone population, a proportion which is found in diurnal waterbirds such as common terns (*Sterna hirundo*) (Goldsmith et al., 1984; Hart, 2001b).

The ERG recordings obtained under photopic condition show that both species have two λ_{max}, one around 549-550 nm (λ_{max} of single LWS cones modified by the transmittance of the R-type droplet) and another one around 513-515 nm (λ_{max} of MWS cones modified by the transmittance of the Y-type droplet). These results resemble that obtained in chicken and pigeon, two species mainly diurnal. In these later two species, the photopic λ_{max} determined electroretinographically has been estimated to be around 540-550 nm (Armington and Thiede, 1956; Ikeda, 1965). These results differ from that obtained in two other gull species also partly active at night. Thus, Thompson (1971) reported that, herring gulls (*Larus argentatus*) and lesser black-backed gulls (*Larus fuscus*) photopic spectral sensitivity have a λ_{max} at around 600 nm. Interestingly, in nocturnal tawny owls (*Strix aluco*), the value of the photopic λ_{max} has also been reported to be around 600 nm (Martin and al., 1975). Some caution must be exercised here however, since the experimental procedures used in the present study differ from that of the other studies. For instance, in the study of Martin and al. (1975), they used flickering stimuli of specific frequencies in order to evaluate the photopic spectral sensitivity of tawny owls instead of single flashes like we used in the present study. This may explain the difference observed between species.

Interestingly, the ERG recordings reveal that under scotopic condition spectral sensitivity of ring-billed gulls and gray gulls differ, with respective λ_{max} being at 556 and 514 nm. Microspectrophotometric studies have shown that the rod visual pigment of most bird species absorbs maximally around 500-506 nm (Bowmaker, 1991; Bowmaker et al., 1997). In the present study, the scotopic spectral sensitivity function of ring-billed gulls appears much broader than the rod photopigment absorption spectrum described in most other bird species. In fact, the λ_{max} measured in this species approximates the absorption spectrum of red cones (λ_{max} = 570 nm), suggesting that LWS cones may somehow contribute to the ERG rod responses. In most vertebrate species possessing a duplex retina, rods and cones are coupled via gap junctions and it is known that their signals can mix at different level of retinal signal processing. This coupling is modulated in a circadian rhythmic manner by dopamine, a neurocatecholamine which is synthesis in amacrine cells. Thus, during the day and at low levels of light intensity (like at dawn in natural condition), rods activate the ON bipolar cells that in turn trigger the release of dopamine from the amacrine cells. Dopamine subsequently diffuses to the outer plexiform layer, where it activates the cone signals, and later on inhibits the rod signals (Nussdorf and Powers, 1988; Ribelayga et al., 2002). Overall, this might explain the results obtained in ring-billed gulls. In fact, in a recent study, we have already demonstrated that the scotopic spectral sensitivity of ring-billed gulls is modulated by circadian mechanisms, such that λ_{max} reaches a value around 500 nm during the night and shift to longer wavelenghts (550-600 nm) during the day, suggesting that during the day the red cone contribute to the dark-adapted ERG responses and that rods dominated the response during the night (Emond et al., 2006b).

Our histological data also reveal a variation between the two gull species in the proportion and topographical distribution of the different cone classes. Thus, in central retinal sector 5, the number of double LWS cones is higher in gray gulls than in ring-billed gulls, but opposite is true for the MWS cones. Moreover, in ring-billed gulls, single LWS cones and double LWS cones as well as SWS cones are distributed uniformly across the retina, while in gray gulls double LWS cones predominate in the

central retina along an antero posterior gradient (sectors 7, 5 and 2), single LWS cones are more abundant in the dorsal retina (sectors 1 and 4) and the MWS cones dominate the ventral retina along an antero posterior gradient (sectors 3, 6 and 9). Double LWS cones are thought to play a role in movement detection and sensitivity, rather than in wavelength discrimination per see, and to be tuned to optimise spatial contrast within a given photic environment (Maier and Bowmaker, 1993; Campenhausen and Kirschfeld, 1998; Vorobyev and Osorio, 1998). Since, gray gulls have been reported to forage mainly at dawn (Guerra, 1987), the high proportion of double LWS cones found in the central retina (48% compared to 28% in ring-billed gulls) may be an adaptation for spotting fish swimming in low light intensity condition. Moreover, species which must look down into the water to catch food, like gray gulls, are known to have a higher proportion of single LWS cones in the dorsal half of the retina (Muntz, 1972; Goldsmith et al., 1984). It is assumed that the R-type droplets contained in single LWS cones help reduce glare from the water surface and improve prey detection (Muntz, 1972). In terrestrial species that do not have this visual constraint, single LWS cones are more uniformly distributed in the retina (Hart, 2001a,b). Ring-billed gulls inhabit different types of environment and forage on more varied sources of food, found either in the water or on the ground, day or night, using different foraging strategies (Burger and Staine, 1993). The uniform distribution of the different cone classes in their retina seems to reflect an adaptation for a more general lifestyle, in comparison to gray gulls.

In conclusion, the data presented in this study show that the retinas of ring-billed gulls and gray gulls possess spectral features typically encountered in diurnal species and that the differences observed in the structural organisation of their retinas seem to reflect their particular visual ecology.

Acknowledgements

This work was realised by MPE as partial requirement for the M.Sc. and Ph.D. degrees at the Université de Montréal and was supported by the Natural Sciences and

Engineering Research Council of Canada (NSERC) and the Université de Montréal (RM and TC) and by the Canadian Institutes of Health Research (CIHR) (PL). We thank Dr. Luz-Marina Rojas for the teaching of the ERG technique, and Alejandra Malinarich R and Consuelo Pastey for their invaluable assistance during the ERG recording in Antofagasta (Chile).

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Fig. 1. Schematic representation of the criterion method. A luminance-response curve was first obtained using white flash of 14 different luminances and fitted to equation 1. The curve was then slid along the intensity axis to coincide with response amplitudes measured at each wavelength but for only one luminance (dashed curves). The intensity needed for the criterion response was found by interpolation. The curves drawn for each wavelength were arbitrarily displaced along the abscissa in this figure for visual clarity.

Fig. 2. Schematic representation of the nine retinal sectors. D, N, T, and V correspond to dorsal, nasal, temporal and ventral sectors, respectively (From Emond et al., 2006).

Fig. 3. Representative ERG responses obtained from single ring-billed gull and gray gull under scotopic and photopic conditions to a range of white and chromatic stimuli with their corresponding luminance-response curves. Abbreviations: a = peak of the a-wave; b = peak of the b-wave.

Fig. 4. Spectral sensitivity curves obtained in ring-billed gulls and gray gulls under photopic and scotopic conditions at wavelengths ranging from 450 to 650 nm. Data points represent the average sensitivity of 12 birds ± SD. In A and C, the continuous lines represent the peak function to which the data have been fitted and by which the LWS, MWS and SWS cones λ_{max} were estimated. In B and D the dotted lines represent the rod template and the continuous lines the peak function to which the scotopic data have been fitted and by which λ_{max} was estimated.

Fig. 5. Light photomicrographs of flat mounted unfixed central retinas (sector 5) of a ring-billed gull (A) and a gray gull (B) showing the different types of oil droplets observed at the light microscope. R: red type; Y: yellow type; P: pale type and CT: clear and transparent type. The central retina contains more P-type droplets in gray gulls than in ring-billed gulls. Scale bars for A = 15 μm and for B = 12 μm.

Figure 1

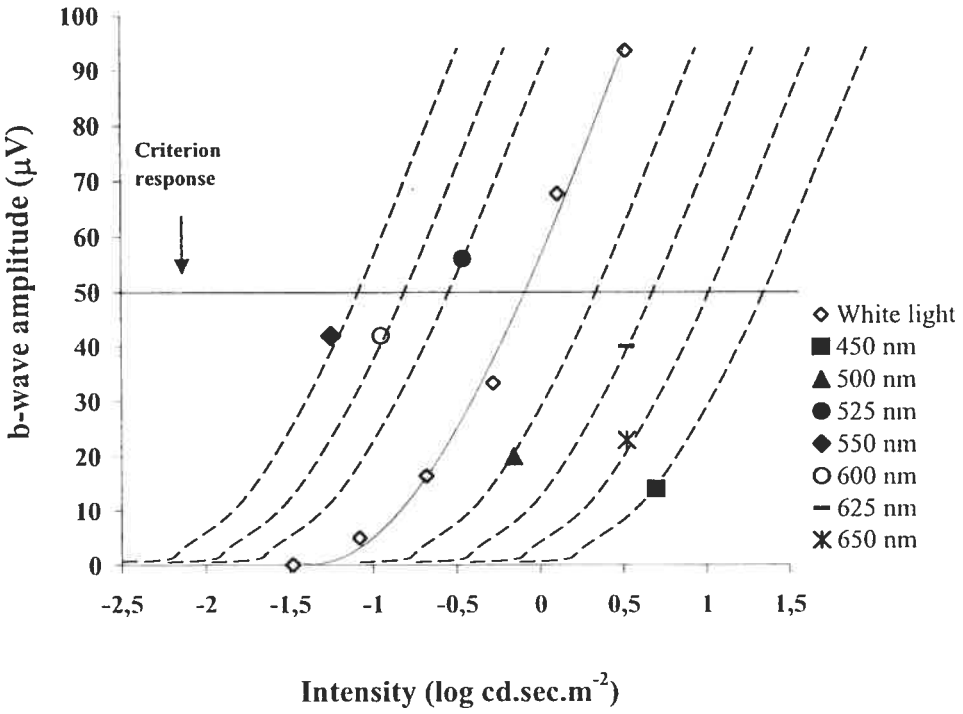

b-wave amplitude (μV)
100
90
80
70
60
50
40
30
20
10
0
Criterion response
-2,5
-2
-1,5
-1
-0,5
0
0,5
1
1,5
Intensity (log cd.sec.m-2)
White light
450 nm
500 nm
525 nm
550 nm
600 nm
625 nm
650 nm

Figure 2

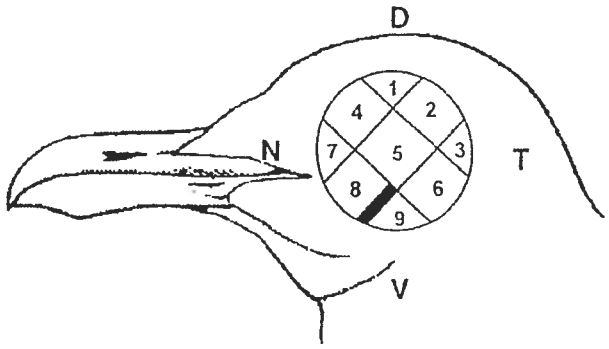
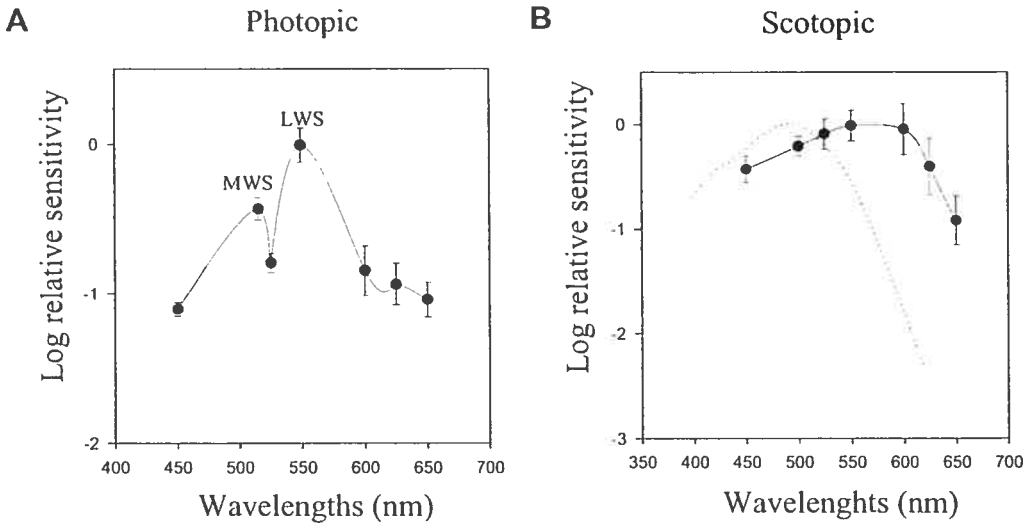


Figure 4

Ring-billed gulls



Gray gulls

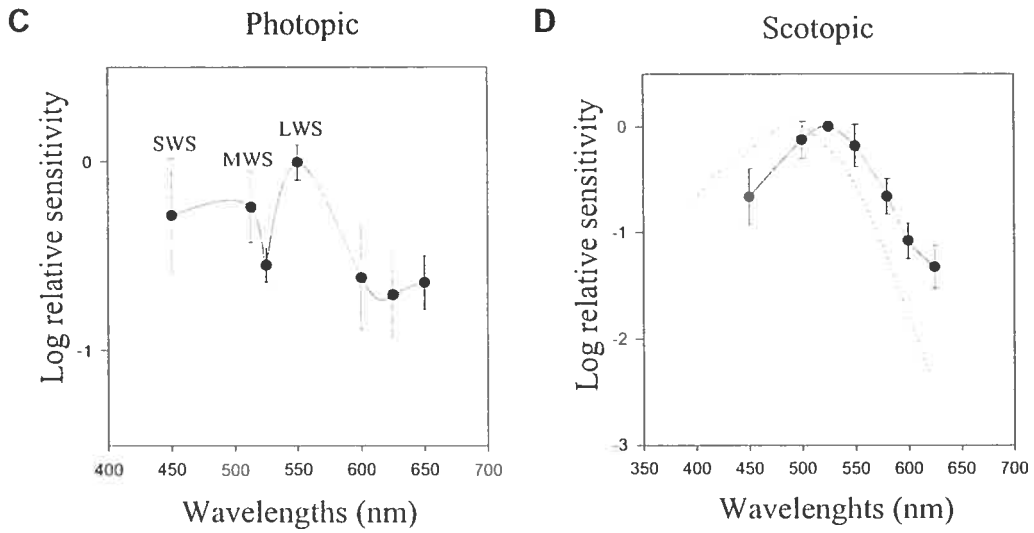


Figure 5

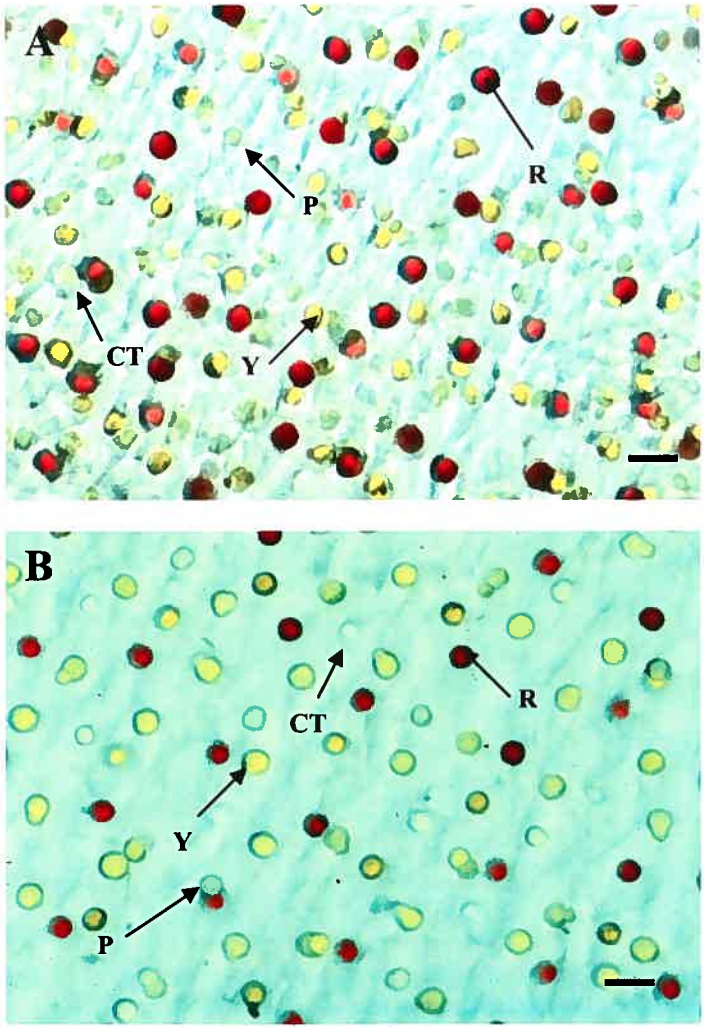


Table 1
Mean percentages of the different oil droplet types observed in cones of the nine retinal sectors in ring-billed gulls and gray gulls. Since the C and T oil droplets types were difficult to distinguish from each other, the two were merged as one type termed CT in this study.

Species	Retinal sectors	Oil droplet type (%)			
		P-type	R-type	Y-type	CT-type
Ring-billed gulls					
	1	37.5	41.9	18.6	2.0
	2	40.6	36.3	21.3	1.8
	3	41.3	34.9	22.0	1.7
	4	36.2	34.8	27.5	1.6
	5	28.5	43.7	26.2	1.7
	6	40.2	32.4	25.4	2.1
	7	31.6	39.2	26.9	2.3
	8	29.3	35.1	33.3	2.3
	9	47.9	32.5	15.7	4.0
	All	36.1	37.1	24.8	2.1
Gray gulls					
	1	32.9	41.4	24.3	1.5
	2	41.6	31.6	24.9	1.9
	3	38.7	31.4	27.1	2.7
	4	35.2	40.1	22.9	1.8
	5	48.7	32.2	17.0	2.1
	6	37.9	26.0	34.5	1.7
	7	50.0	26.3	20.7	3.1
	8	41.1	38.3	19.4	1.2
	9	41.9	29.4	27.6	1.2
	All	40.2	33.6	24.5	1.9

CHAPITRE 4

Different circadian patterns modulate the functional organisation of the retina of ring-billed gulls (*Larus delawarensis*) and gray gulls (*Larus modestus*)

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Article qui sera soumis à la revue

Visual Neuroscience

4.1. Abstract

Using corneal electroretinography (ERG) we have demonstrated that the retinal function of ring-billed gulls (*Larus delawarensis*) and gray gulls *(Larus modestus*) is modulated by circadian rhythms and that the functional organisation of these rhythms differs between the two species. In both species, retinal sensitivity obtained under scotopic condition (dark-adapted retina) and measured with broad spectrum light (white), fluctuates over the course of the day. An increase in retinal sensitivity of 0.46 log unit was measured from day to night in ring-billed gulls and of 0.30 log unit in gray gulls. Analysis of the scotopic ERGs recorded with light of different wavelengths shows that spectral sensitivity of ring-billed gulls reaches a maximum (λ_{max}) around 500 nm during the night and shifts to longer wavelengths (between 550 and 600 nm) during the day, suggesting that red cones contribute to the dark-adapted ERG responses during the day and that rods dominate the responses during the night. In gray gulls, rods dominate the dark-adapted ERG responses regardless of the time of day, λ_{max} being ~ 500 nm during both night and day. The results suggest that in ring-billed gulls the functional organisation of the retina is governed by circadian rhythmicity such that the cones contribute to the rod signals of the inner retina during the day but not at night, while in the gray gull circadian mechanisms seem not to be involved in changes of the retinal functional organisation. The difference observed between the two species may have resulted from adaptation to particular photopic environment in which the species have evolved.

Keywords: birds, circadian rhythms, electroretinogram (ERG), retina, spectral sensitivity, visual sensitivity.

4.2. Introduction

Accumulating evidence suggests that many retinal functions of vertebrates are modulated by circadian rhythms (Morin, 1994; Cahill and Besharse, 1995; Schantz et al., 2000). For instance, it is now well known that visual sensitivity (Manglapus et al., 1999; Li and Dowling, 2000), rod outer segment disc shedding (Besharse et al., 1988; Djamgoz and Wagner, 1992), coupling of rods and cones (Kramer, 1971; Bauer et al., 1980; Dearry and Burnside, 1989; Umino and Dowling, 1991; Krizaj et al., 1998, Krizaj, 2000) and expression of visual pigment genes (Zhang and Semple-Rowland, 2005) are modulated by circadian rhythms. The primary role of these rhythms is to adjust the retinal functions in anticipation of changes in light intensity occurring during the 24 h solar cycle (Underwood and Siopes, 1984; Underwood et al., 1988, 1990). These rhythms are generated by endogenous oscillators and have a period (duration) that matches approximately the 24 h solar cycle (Pittendrigh, 1981). In the absence of any environmental cues however, this period can drift from the solar cycle and may varies from 22 to 25 h (Aschoff, 1981). Synchronisation with the external environment is achieved by the daily resetting of the endogenous oscillators to daylight and it is believed that most species have evolved to use changes in light level during the twilight transition to synchronise their internal oscillators with the environment (Pittendrigh and Daan, 1976; Czeisler et al., 1995; Roenneberg and Foster, 1997). The process, by which the endogenous oscillators are resettled by light, is still not well understood. However, several lines of evidence indicate that the oscillators contain non visual photopigments which are involved in the resetting of the cycle (Foster and Hankins, 2002). Melanopsin seems to be the major component of the photoreceptive system for resetting circadian oscillators (Panda et al., 2002; Ruby et al., 2002; Hattar et al., 2003; Panda et al., 2003).

In birds, circadian oscillators have been found in the retina, the pineal gland and the hypothalamic suprachiasmatic nucleus (Cassone and Menaker, 1984; Underwood and Siopes, 1984; Ebihara et al., 1987; Gwinner, 1989; Oshima et al., 1989;

Yoshikawa and Oishi, 1998; Oishi et al., 2001). The contribution of each structure to the retinal circadian rhythms varies considerably among bird species, leading to different circadian organisations and types of rhythms (Cassone and Menaker, 1984; Cassone, 1990; Takahashi, 1991). For instance, in chickens, *Gallus domesticus*, retinal sensitivity, as measured by the electroretinogram (ERG), is higher during the day than during the night, and pinealectomy partly abolishes this rhythm (McGoogan and Cassone, 1999). In Japanese quails, *Coturnix coturnix japonica*, the ERG shows an increase at night and pinealectomy has no effect on this rhythm (Manglapus et al., 1998, 1999; Brandstätter, 2003). In nocturnal owls, *Strix uralensis*, the pineal gland is either atrophied or absent and the retina alone seems to modulate the retinal circadian rhythm (Taniguchi et al., 1993).

It has been hypothesised that the differences in retinal circadian organisation found among birds result from adaptations to the different photic environments into which they have evolved (Menaker et al., 1997; Gwinner and Brandstätter, 2001). Since the retinal circadian system has been shaped principally by light, we might expect that the differences in the natural light variation existing in different environments have contributed to the evolution of different retinal circadian organisations and types of rhythms in bird species. In the present study, we have tested this hypothesis in two species of gull of the same genus, ring-billed gulls *Larus delawarensis* and gray gulls *Larus modestus*, which are both partly active at night in different aspects of their life cycle, but which experience different light regime in their natural environment (Burger and Staine, 1993; Hébert and McNeil, 1999; Howell et al., 1974; Guerra, 1987; Blokpoel et al., 1992). Thus, ring-billed gulls live in temperate latitudes (between 40° and 60°N) where the light-dark cycle changes markedly throughout the year and where the twilight period is relatively long (Hébert and McNeil, 1999). In contrast, gray gulls live along the Pacific coast of South America in equatorial latitudes (between 0° and 24°S), where the light-dark cycle remains approximately the same every day of the year and where the twilight period is shorter (Howell et al., 1974). We therefore hypothesised that the functional

organisation of the retina of ring-billed gulls and gray gulls is modulated by different circadian pattern, which we have tested using corneal electroretinography (ERG).

4.3. Methods

4.3.1. Animals

Ring-billed gulls (n = 66) were captured between June and September near Montréal (45°50'N, 73°58'W), Province of Québec, Canada and gray gulls (n = 51) during the austral fall (April) in Antofagasta (23°65'S, 70°40'W), Chile. Birds were kept in their respective natural light-dark cycle (LD 14:10 for ring-billed gulls and LD 12:12 for gray gulls) prior to experimentation. Despite the two species were not tested during the same season, we expect that this will have no effect on the results. Near the equator (latitudes 0° to 20° S), the photoperiod is the same all over the year, therefore the retina function of gray gulls should not be affected by any changes of light regime from one season to the other. The ERG procedure not being invasive, the birds were allowed to recover from anaesthesia and were returned to their natural habitat after experimentation. All the experiments were conducted in accordance with the regulations of the Canadian Council on Animal Care (1993).

4.3.2. Electroretinography

The birds were dark adapted for a period of 4 h after which they were anaesthetised with an intramuscular injection of ketamine hydrochloride (50 mg/kg, i.m.; Ketaset, Ayerst) and xylazine hydrochloride (5 mg/kg, i.m.; Rompun, Bayer). Under dim red light illumination, they were placed on a custom-made recording holder inside a Ganzfeld dome of 41 cm in diameter (LKC Ganzfeld-2503B) so that only the left eye was stimulated. The eyelids and nictitating membrane were retracted with a speculum, the cornea was anaesthetised with proparacaine hydrochloride 0.5%, and the pupil was fully dilated with drops of tropicamide 1%. A DTL electrode (X-Static© conductive yarn, Sauquoit Industries, Scranton, PA, USA)

was placed on the cornea to act as the active electrode. Reference and ground electrodes (Grass subdermal electrodes, Astro-med Inc., Warwick, RI) were inserted under the scalp and under the skin of the chest, respectively. Responses were evoked to flashes of white light of 0.52 log cd.sec.m^{-2} in intensity, delivered with a photostimulator (Grass PS-22) through the Ganzfeld. Stimulus luminance was attenuated with Kodak Wratten neutral density (ND) filters (Kodak Ltd, Rochester, NY). Lee interference filters (Andover, England), with peak transmission at 450 (blue), 500 (blue-green), 525 (green), 550 (yellow), 600 (orange), 625 (light red) and 650 (dark red) nm, were inserted in front of the flash to produce monochromatic stimuli. A photometer-radiometer (Quantum; model L1-185B) was used to measure the luminance generated at the cornea. Photopic light adaptation was provided with a white background light of 1.55 log cd.m^{-2} in intensity. Responses were recorded within a bandwidth of 0.3 to 500 Hz, amplified 10,000 X, averaged and stored using an EPIC-2000 computer-controlled electrodiagnostic system (LKC Technologies, Inc., Gaithersburg, MD).

Scotopic responses were first obtained using white flash stimuli at increasing luminances ranging from -4.68 to 0.52 log cd.sec.m^{-2} in steps of 0.4 log unit following which the seven monochromatic stimuli were used. For each luminance, responses to 6 consecutive flashes, presented at an inter-stimulus interval of 10.1 sec were averaged. The birds were then light adapted to the white background light for 15 min, following which photopic responses were evoked using flashes of white light of increasing luminances ranging from -1.48 to 0.52 log cd.sec.m^{-2} in steps of 0.4 log unit. Responses were then recorded using the same monochromatic light stimuli as above. For each luminance, responses to 10 consecutive flashes presented at an inter-stimulus interval of 4.2 sec were averaged.

ERGs were recorded every 4 h over a 24 h cycle using different individuals for each time point in order to prevent the possible compounding effects of repeated anaesthesia. Therefore, for each species, five individuals were tested for assessment

of visual and spectral sensitivities at each of the following time: 0000h, 0400h, 0800h, 1200h, 1600h and 2000h. Ten additional ring-billed gulls were used to test if the daily variation observed in the retinal functions is controlled by endogenous mechanisms. To allow the expression of the endogenous (free-running) circadian rhythm of retinal functions, the birds were kept in constant darkness (DD) for a period of 48 h before experimentation, after which five of them were tested as previously described at 0000h and five others at 1200h. Because of time and specimen limitations in Chili, only four gray gulls were tested in DD, two at 0000h and two at 1200h.

4.3.3. Data analysis

The amplitude of the ERG a-wave was measured from baseline to trough, and that of the b-wave, from trough of the a-wave to peak of the b-wave. Luminance-response curves were obtained by plotting the amplitude of these waves as a function of the stimulus luminance. The scotopic and photopic a-wave luminance-response curves were then fitted to equation (1) (Matlab, MathWorks, Natick, MA):

$$P_3(I,t) \cong \{1 - \exp[-I \cdot S \cdot (t - t_d)^2]\} \cdot R_{max\,(P3)} \text{ for } t > t_d \qquad (1)$$

which describes the transduction mechanisms of photoreceptors in vertebrates according to the Lamb and Pugh (1992) model, and where P_3 represents the sum of the photoreceptor responses as a function of flash energy I and time t after the occurrence of a short flash. S is a sensitivity parameter that scales the intensity of the flash required to generate a response equal to ½ R_{max} (semisaturation constant), R_{max} the maximum response amplitude, and t_d a brief delay (see Hood and Birch, 1990, 1993, 1997). Likewise, the scotopic and photopic b-wave luminance-response curves were fitted to equation (2) (SAS Information Delivery System for UNIX, Version 6.07.02; SAS Institutes Inc., Cary, NC):

$$V/V_{max} = I^n / (I^n + \sigma^n) \quad (2)$$

which models the activity of the inner retina in vertebrates, and where V represents the response to stimulus luminance I, V_{max} the maximum response, σ the luminance required to generate a response equal to ½ V_{max} (semisaturation constant) and n the slope of the function (Naka and Rushton, 1966, 1967).

Spectral sensitivity of both species was assessed relative to their sensitivity measured to white stimuli by the method of criterion response (DeVoe et al., 1997). For each wavelength tested; the luminance required to obtain a b-wave criterion response of 150 μV (scotopic condition) and 60 μV (photopic condition) was determined by displacing the luminance-response curves (fit of equation 2) obtained with the white stimuli on the luminance scale to coincide with response amplitudes measured at each wavelength. These criterion responses were chosen because they were consistently above noise level and always below response saturation, falling within the linear portion of the luminance response function at all stimulus wavelengths and for each subject. Since under photopic condition the amplitude of the ERG responses were smaller ($V_{max} \leq 100$ μV in the gray gull) than in scotopic condition, a criterion response of 60 μV was chosen. Spectral-sensitivity curves were then constructed by plotting the reciprocal of the log stimulus luminance that yielded the criterion response at each wavelength.

Analysis of variance (ANOVA) was performed to evaluate the difference within and between species in their physiological responses at different time of the day. Post hoc Holm-Sidak tests were applied for evaluation of significant differences between the groups. The data are presented as mean ± SD and in all cases the $p < 0.05$ level was used to determine statistical significance.

4.4. Results

Fig. 1 shows representative ERG responses obtained in single ring-billed gull and gray gull during the day (1200h) and the night (0000h) to a range of white flash stimuli presented under scotopic and photopic conditions when they were maintained in their natural LD cycle. Note that different individuals were used for each time point. In both species, the amplitude of the a-wave showed no daily variation. In the ring-billed gull, it can be seen that under scotopic condition and for luminances between –2.68 and –1.08 log cd.sec.m^{-2}, the amplitude of the b-wave varied such that it was about 20% higher at 0000h than at 1200h, while no difference was observed at lower (below –2.68 log cd.sec.m^{-2}) and higher (above –1.08 log cd.sec.m^{-2}) luminances. In the gray gull, daily variations in the amplitude of the b-wave were observed between -3.88 and –1.88 log cd.sec.m^{-2}. Under photopic condition and at the highest luminances (0.12 to 0.52 log cd.sec.m^{-2}), a difference between the day (1200h) and the night (0000h) was also observed in the amplitude of the b-wave in both species, such that it was more than 20% higher at 1200h than at 0000h. As under scotopic condition, in both species the amplitude of the photopic a-wave showed no daily variation. Moreover, the same daily variations in the b-wave amplitude were observed in both species when they were maintained in DD cycle for 48 hours (not shown).

Fig. 2 presents the luminance-response curves derived from the ERGs obtained in the same individuals of Fig. 1. The lines represent the least-squares fit of equations 1 and 2 to the amplitude of the a- and b-waves, respectively. It can be seen that in both species the scotopic luminance-response function of the b-wave obtained at 0000h shifted to the left along the horizontal axis compared to that obtained during the day at 1200h. This shift indicates a change in retinal sensitivity such that it was higher at 0000h than at 1200h. Note that in both species, and under both scotopic and photopic conditions, the amplitude of the a-wave never reached saturation value. The highest flash intensity (0.52 log cd.sec.m^{-2}) used in this study was probably not high

enough to provoke saturation of the photoreceptors. However, since the equation (1) significantly fitted the data points in all subjects, the values of the scotopic and photopic R_{max} obtained can be considered a good estimation of the values that could have been measured with a higher flash intensity. The mean values of the parameters of the luminance-response function obtained at different hours are presented in Table 1. In both species, the sensitivity parameter σ exhibited daily variations (for ring-billed gulls: ANOVA: $F = 4.42$; $p = 0.005$ and for gray gulls: ANOVA: $F = 3.23$; $p = 0.020$). This is further evidenced at Fig. 3. It can be seen that in ring-billed gulls, the lowest value of σ was obtained at 2000h and the highest value at 1200h (Holm-Sidak test: $t = 3.85$, $p = 0.001$), while in gray gulls, σ was at its lowest value at 0400h and highest at 1200h (Holm-Sidak test: $t = -2.96$, $p = 0.018$). No daily variation was observed for the sensitivity parameter S, or in the saturated response of the a- and b-waves ($R_{max}$and V_{max}) in either species. Under photopic condition, no significant daily variation was found however the parameter σ tended to be lower during the afternoon and higher early in the morning in both species, a peak of sensitivity being observed at 0800h in ring-billed gulls, and at 0400h in gray gulls. The daily variation of σ that was observed in LD persisted in DD in both species, suggesting that these variations are driven by an endogenous circadian rhythm. Thus, in both species, the mean value of σ was lower during the night (0000h) than during the day (1200h) (Holm-Sidak test: ring-billed gulls: $t = 5.22$, $p < 0.001$ and gray gulls: $t = -21.97$, $p = 0.002$)

Fig. 4 shows representative spectral sensitivity curves obtained in single ring-billed gull and gray gull during the day (1200h) and the night (0000h) under scotopic and photopic conditions. The continuous lines represent rod template with $\lambda_{max} = 506$ nm (Govardovskii et al., 2000) and the dotted lines correspond to the red cone template with $\lambda_{max} = 570$ nm to which data have been fitted (Hart, 2001). It can be seen that in the ring-billed gull, the scotopic spectral sensitivity curve shifts from day to night, from longer wavelengths (between 550-600 nm) at 1200h to shorter

wavelengths (between 500-525 nm) at 0000h. This shift was not observed in the gray gull. In the latter species, the spectral sensitivity curves peak around 500 nm during both the day (1200h) and the night (0000h). Under photopic condition, the spectral sensitivity curves peak between 550 and 600 nm in both species. The mean values of spectral sensitivity obtained under scotopic and photopic conditions and at different hours are given in Table 2 and Table 3, respectively. In Table 2 it can be seen that, under scotopic condition, spectral sensitivity of ring-billed gulls exhibited daily variations (ANOVA: $F = 8.75$, $p < 0.001$) such that $\lambda_{max} \sim 500$ nm between 0000 and 0400h and shift near 550-600 nm between 0800h and 1600h. No such daily variation was observed in gray gulls, λ_{max} being ~ 500-525 nm for every hour. Under photopic condition, $\lambda_{max} \sim$ 550-600 nm in both species, regardless the time of day (Table 3).

4.5. Discussion

The results obtained in the present study demonstrate that in ring-billed gulls and gray gulls retinal function is modulated by circadian rhythm and that the organisation of this rhythm differs between the two species. Thus, analysis of the ERGs recorded with broad spectrum light (white light) shows that in both species retinal sensitivity, as measured with the parameter σ, fluctuates over the course of the day such that it increases at approximately the time of sunset, remains high throughout the night, decreases near dawn and remains low during the day (see Fig. 3). An increase of 0.46 log unit was measured from day to night in ring-billed gulls and of 0.30 log unit in gray gulls. Moreover, when the birds were maintained under constant darkness (DD) for 48 hours, the daily variations in retinal sensitivity persisted, suggesting that these variations are driven by an endogenous circadian rhythm.

Analysis of the ERGs recorded with light of different wavelengths shows that the functional organisation of the retina of each species is modulate by different circadian patterns. Thus, in ring-billed gulls, when the ERGs were obtained at night

and under scotopic condition (dark adapted retina), the spectral sensitivity reached a maximum (λ_{max}) around 500 nm, which corresponds to the rods' absorption spectrum (λ_{max} = 506 nm) measured in almost all bird species, while during the day, λ_{max} shifted to longer wavelengths between 550 and 600 nm, approximating the absorption spectrum of red cones (λ_{max} = 570 nm) (Hart, 2001). This suggests that rods contributed to the ERG responses during the night and that red cones dominated the dark-adapted responses during the day. During the day, we did not observe any significant decrease of sensitivity, as would be expected if the cones were the only photoreceptors involved in the responses. In fact, the sensitivity was approximately identical whether measured during the night or the day, indicating that rods may also contribute to the scotopic ERG responses during the day. Under photopic condition (light adapted retina) the spectral sensitivity of ring-billed gulls exhibited a λ_{max} between 550-600 nm during both night and day, indicating that cones dominate the retinal responses regardless of the time of the day in this condition. In gray gulls, under scotopic condition, a different pattern emerged. Thus, in this species λ_{max} was around 500 nm during both day and night, suggesting that rods are the only photoreceptors involved in the dark-adapted responses. Under photopic condition, as for ring-billed gulls, the cones dominated the retinal responses both at day and at night, λ_{max} being between 550 and 600 nm.

Therefore, spectral sensitivity of ring-billed gulls seems to be under control of a circadian mechanism that changes the organisation of the retina such that under scotopic condition the rod system responds during the night and the cone system during the day. In gray gulls, such changes in functional organisation do not seem to occur. The changes observed in ring-billed gulls resemble the phenomenon called the Purkinje shift, which refers to changes occurring in spectral sensitivity as a function of availability of light (Sjostrand, 2003). Thus, as the eyes adapt to higher light levels, the part of the spectrum to which they are most sensitive shifts toward longer wavelengths, while dark-adapted eyes are most sensitive to shorter wavelengths. In

the case of ring-billed gulls, a circadian mechanism would generate a Purkinje-like shift that adapts the retina for dim light vision at night and for bright light vision during the day.

The results obtained in ring-billed gulls are consistent with the reports of Schaeffel et al. (1991) and Manglapus et al. (1998, 1999), who have demonstrated that the functional organisation of the retina of chickens (*Gallus gallus*) and Japanese quails (*Coturnix coturnix*) changes over the course of the day such that the scotopic ERG b-wave is dominated by rods at night and by cones during daylight. The mechanisms by which the functional organisation of the retina changes over the course of the day are however not well understood. It has been hypothesised that the neurocatecholamine dopamine might play an important role in this effect (Manglapus et al, 1998, 1999; Li and Dowling, 2000; Ribelayga et al., 2002).

In the retina, dopamine is principally found in the amacrine and/or the interplexiform cells, depending on the species, and it modulates several retinal functions such as photoreceptor disc shedding (Besharse et al., 1988; Djamgoz and Wagner, 1992), retinomotor movements (Hillman et al., 1995; Kolbinger et al., 1996), retinal sensitivity (Manglapus et al., 1999; Li and Dowling, 2000), melatonin biosynthesis (Cahill and Besharse, 1991; Zawilska, 1994) and the coupling of rods and cones (Kramer, 1971; Bauer et al., 1980; Dearry and Burnside, 1989; Umino and Dowling, 1991; Krizaj et al., 1998, Krizaj, 2000). The release of dopamine is regulated both by light and by circadian oscillators, and two different dopaminergic systems have been described in the retina of vertebrates (Nowak and Zurawska, 1989; Kolibinger and Weiler, 1993; Boelen et al., 1998; Manglapus et al. 1998, 1999; Li and Dowling, 2000; Nir et al., 2000; Pozdeyev and Lavrikova, 2000; Witkovsky et al., 2000; Ribelayga et al., 2002; Ribelayga and Mangel, 2003). The light-controlled system activates D_1-like receptors located on cone-horizontal cells and the one modulated by circadian oscillators activates D_2-like receptors found on the photoreceptors (Ribelayga et al., 2002; Ribelayga and Mangel, 2003). It has been

demonstrated in Japanese quails that at dawn rods activate the ON bipolar cells that trigger the release of dopamine from the amacrine cells, and in turn dopamine activates D_2-like receptors, which increase rod-cone coupling such that the rod signals are blocked at the outer retina and the cone signals are transmitted to the inner retina (Manglapus et al., 1998, 1999; Li and Dowling, 2000). Therefore, dopamine seems to turn on the photopic state at dawn and thus to shorten the duration of the mesopic state. This may explain why in quails the ERGs recorded during the day and under scotopic condition are dominated by cones. It may also explain the results obtained in ring-billed gulls, but not why the scotopic ERGs obtained during the day seem to be dominated only by rods in gray gulls.

Near the equator (latitudes 0° to 20°S), the length of day and night, as well as twilight varies little over a year, sunset and sunrise occurring almost at the same time every day. Therefore, birds like gray gulls that live near the equator experience the same light regime day after day over a year, and changes in light intensity are thus highly predictable for these birds. In contrast, birds like ring-billed gulls living at higher latitudes (40° to 60°N) cope with a highly variable light: dark cycle and longer twilight. Therefore, their retinal circadian organisation may have evolved to favour activation of the cones system early during the twilight transition period, which may have behavioural and ecological significance during foraging. Note also that gray gulls are known to forage mainly along the shoreline in the wave washed littoral zone, in a manner similar to that of sandpipers (Blokpoel et al., 1992). Therefore, the time of this activity seems to be governed by tidal cycle, rather than by night-day cycle, and this species probably do not need such an adaptation

Acknowledgements

This work was performed by MPE as partial requirement for the M.Sc. and Ph.D. degrees at the Université de Montréal and was supported by the Natural

Sciences and Engineering Research Council of Canada and the Université de Montréal (RM and TC) and by the Canadian Institutes of Health Research (PL). We thank Dr Luz-Marina Rojas for the teaching of the ERG and histology techniques, Dr. Vincent Ferretti for the mathematical advice for the analysis of the data and the programming of the models, Alejandra Malinarich and Consuelo Pastey for their invaluable assistance during the ERG recording in Antofagasta (Chile).

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Fig. 1. Representative ERG waveforms obtained in ring-billed gulls and gray gulls to a range of flash stimuli presented under scotopic and photopic conditions recorded during the day (1200h) and the night (0000h). For this example, the birds were maintained in their natural LD cycle.

Fig. 2. Luminance-response curves of the a- and b-waves derived from the ERGs of fig. 1. The lines represent the least-squares fit of equations (1) and (2) to the amplitudes of the a- and b-waves, respectively.

Fig. 3. Visual sensitivity measured at different times of the day in ring-billed gulls and gray gulls maintained in their natural LD cycle. The data points represent the mean values (± SD) of the parameter σ devrived from equation 2. The black horizontal line at the bottom of the figure represents night hours and the white one day hours.

Fig. 4. Representative spectral sensitivity curves obtained in one ring-billed gull and one gray gull under scotopic and photopic conditions during the day (1200h) and the night (0000h). The continous lines represent rod template with λ_{max} = 500 nm and the dotted lines correspond to the red-cone template with λ_{max} = 570 nm to which data have been fit.

Figure 1

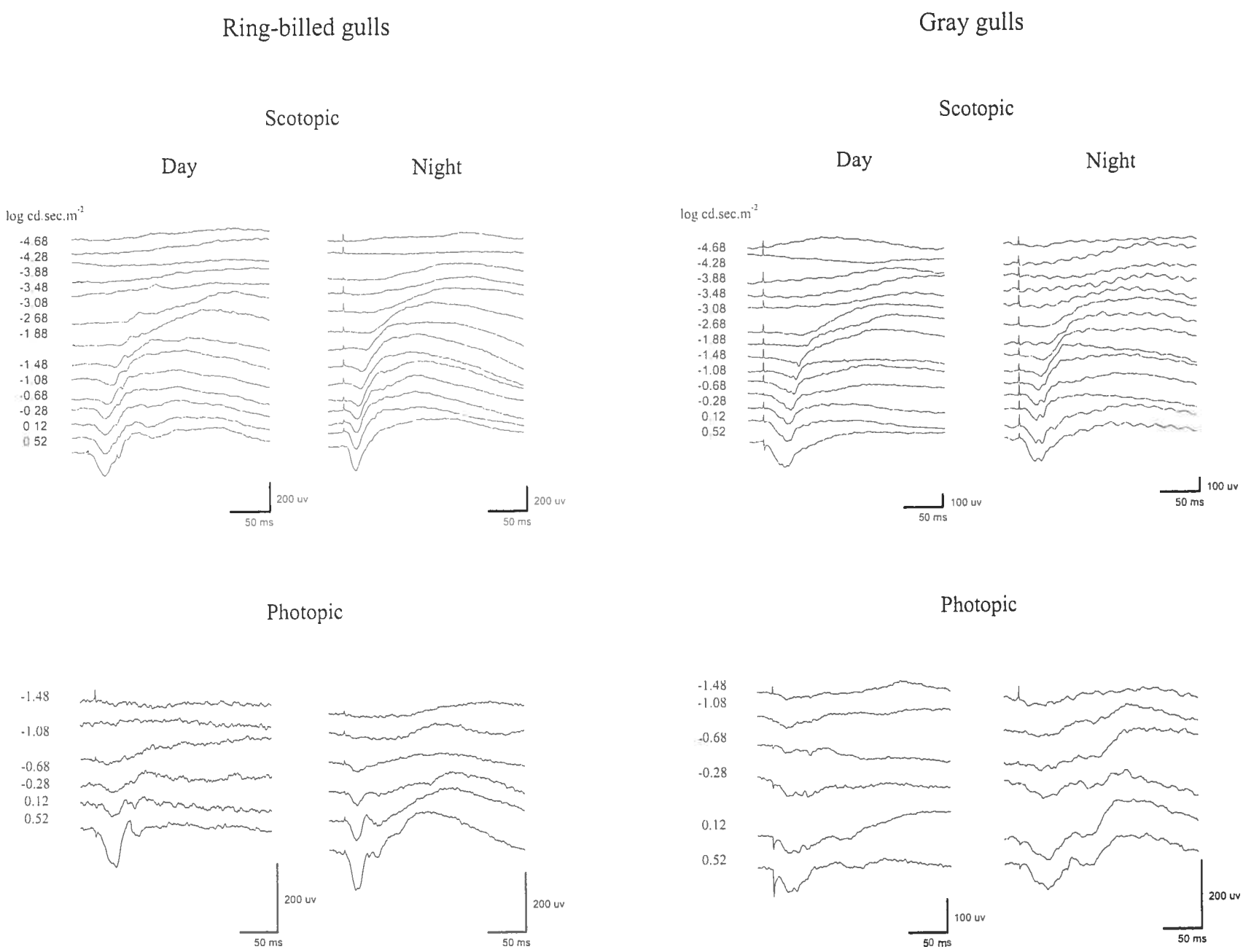
Ring-billed gulls
Scotopic
Day
Night
log cd.sec.m-2
-4.68
-4.28
-3.88
-3.48
-3.08
-2.68
-1.88
-1.48
-1.08
-0.68
-0.28
0.12
0.52
200 uv
50 ms
200 uv
50 ms
Photopic
-1.48
-1.08
-0.68
-0.28
0.12
0.52
200 uv
50 ms
200 uv
50 ms
Gray gulls
Scotopic
Day
Night
log cd.sec.m-2
-4.68
-4.28
-3.88
-3.48
-3.08
-2.68
-1.88
-1.48
-1.08
-0.68
-0.28
0.12
0.52
100 uv
50 ms
100 uv
50 ms
Photopic
-1.48
-1.08
-0.68
-0.28
0.12
0.52
100 uv
50 ms
200 uv
50 ms

Figure 2

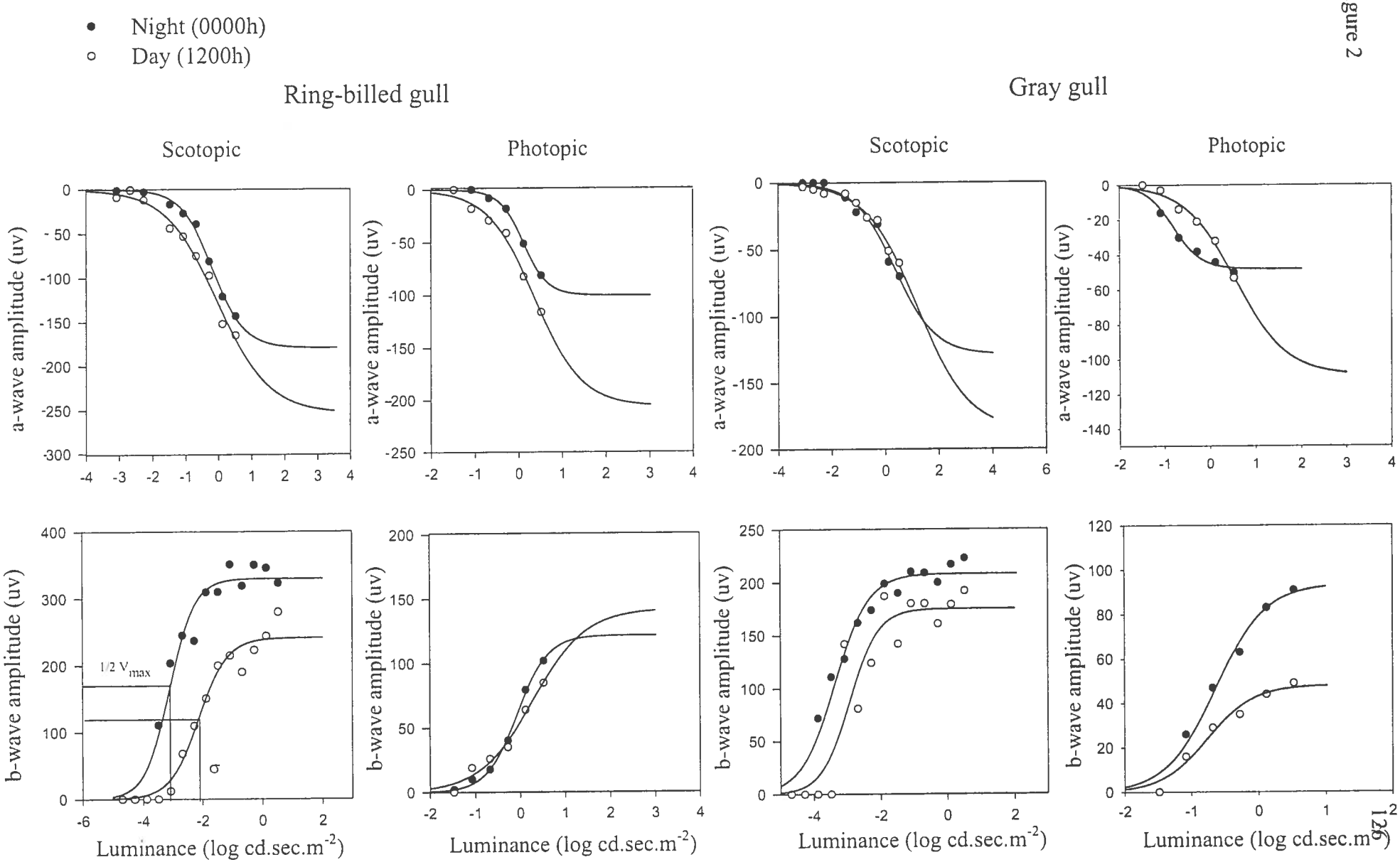
Night (0000h)
Day (1200h)
Ring-billed gull
Gray gull
Scotopic
Photopic
Scotopic
Photopic
a-wave amplitude (uv)
b-wave amplitude (uv)
1/2 V max
Luminance (log cd.sec.m-2)

Figure 3

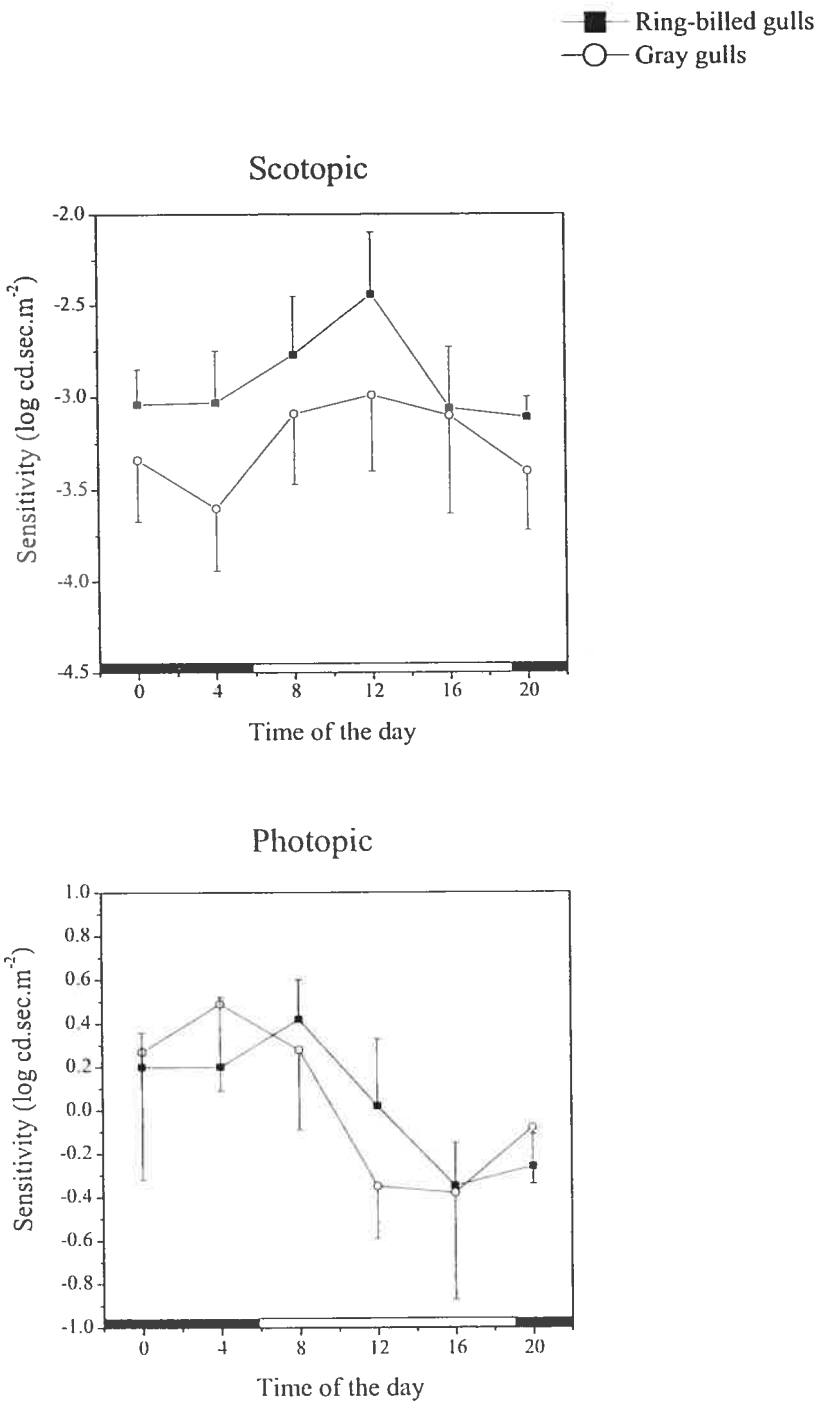
Ring-billed gulls
Gray gulls
Scotopic
Sensitivity (log cd.sec.m-2)
-2.0
-2.5
-3.0
-3.5
-4.0
-4.5
0
4
8
12
16
20
Time of the day
Photopic
Sensitivity (log cd.sec.m-2)
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
0
4
8
12
16
20
Time of the day

Figure 4

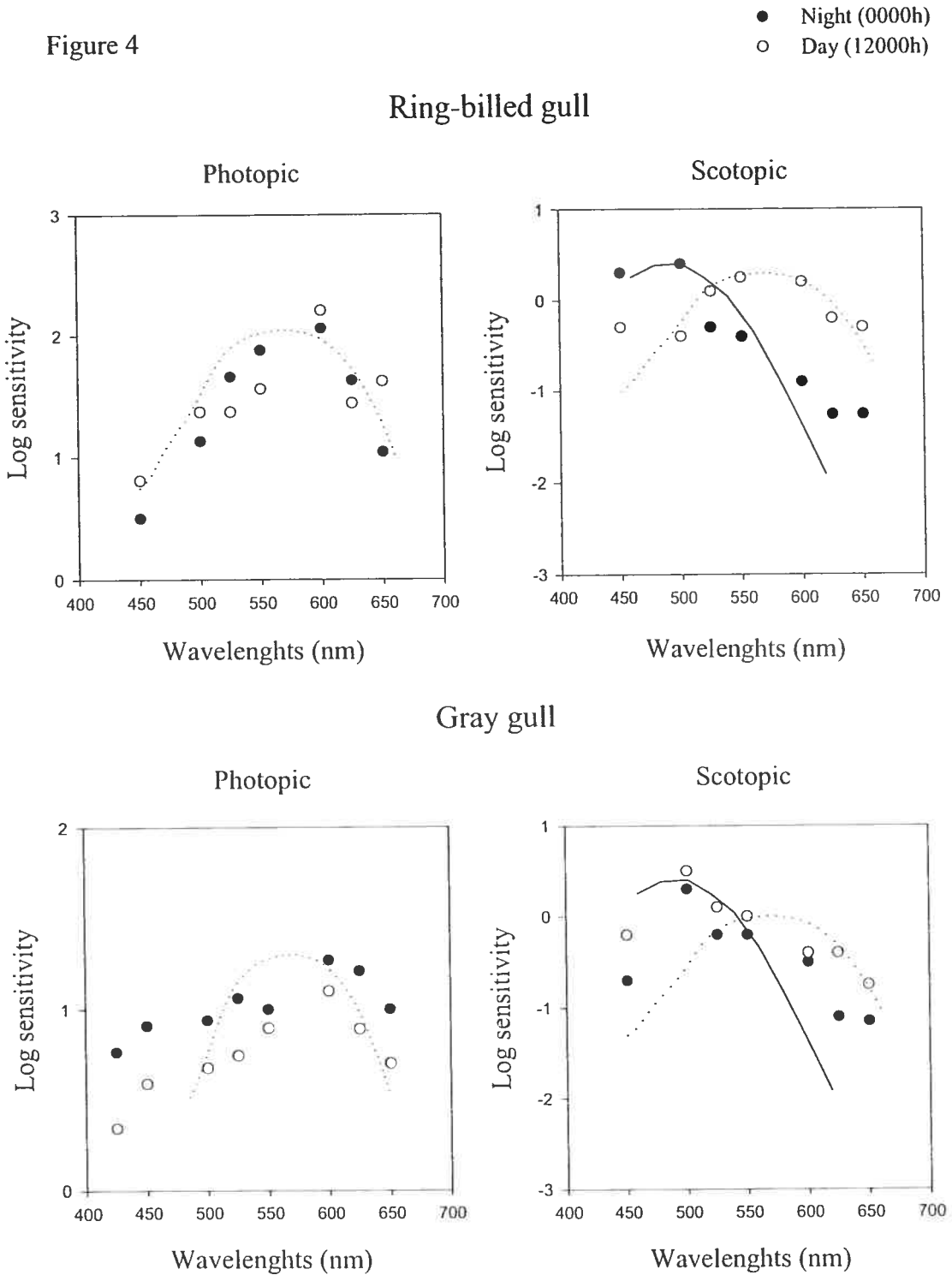
Night (0000h)
Day (12000h)
Ring-billed gull
Photopic
Scotopic
Log sensitivity
Wavelenghts (nm)
Gray gull
Photopic
Scotopic
Log sensitivity
Wavelenghts (nm)

Table 1
Mean values (± SD) of the parameters of the luminance-response function obtained from ring-billed gulls and gray gulls at different time of the day. R_{max} and V_{max} represent the saturated responses of the a- and b-waves respectively and S and σ the parameters of sensitivity evaluated from the a- and b-waves.

Species	Time of recording	Scotopic				Photopic			
		R_{max} (μv) a-wave	V_{max} (μv) b-wave	S (log cd.s.m^{-2}) a-wave	σ (log cd.s.m^{-2}) b-wave	R_{max} (μv) a-wave	V_{max} (μv) b-wave	S (log cd.s.m^{-2}) a-wave	σ (log cd.s.m^{-2}) b-wave
Ring-billed gulls	00: 00	-187.65 ± 36.30	299.84 ± 57.21	-0.29 ± 0.12	-3.04 ± 0.19	-115.82 ± 22.04	154.87 ± 47.28	-0.30 ± 0.37	0.29 ± 0.16
LD[1]	04: 00	-197.26 ± 41.64	311.39 ± 78.10	-0.44 ± 0.33	-3.03 ± 0.28	-136.90 ± 25.55	155.12 ± 80.70	0.03 ± 0.27	0.20 ± 0.32
	08: 00	-195.61 ± 9.05	206.52 ± 44.78	-0.23 ± 0.12	-2.77 ± 0.32	-108.35 ± 21.06	194.35 ± 68.36	-0.08 ± 0.33	0.42 ± 0.18
	12: 00	-208.87 ± 48.61	293.83 ± 69.06	-0.26 ± 0.10	-2.44 ± 0.34	-178.96 ± 85.28	170.08 ± 61.57	0.16 ± 0.45	0.02 ± 0.31
	16: 00	-214.79 ± 64.21	296.05 ± 97.85	-0.48 ± 0.11	-3.06 ± 0.33	-105.78 ± 38.06	167.99 ± 38.36	-0.22 ± 0.49	-0.35 ± 0.20
	20: 00	-197.30 ± 11.35	258.34 ± 48.13	-0.23 ± 0.19	-3.11 ± 0.11	-135.54 ± 32.18	121.20 ± 34.80	0.00 ± 0.28	-0.26 ± 0.15
DD[2]	Day (n=5)	-217.42 ± 39.99	382.44 ± 99.34	-0.25 ± 0.17	-2.43 ± 0.20	-76.03 ± 14.57	171.53 ± 43.44	-0.06 ± 0.34	0.30 ± 0.21
	Night (n=5)	-214.14 ± 38.37	351.56 ± 63.22	-0.33 ± 0.13	-3.00 ± 0.14	-82.69 ± 29.00	218.54 ± 85.89	-0.05 ± 0.22	0.06 ± 0.30
Gray gulls	00: 00	-122.91 ± 22.71	167.60 ± 27.16	-0.29 ± 0.26	-3.34 ± 0.33	-108.41± 53.47	142.74 ± 82.43	-0.07 ± 0.42	0.27 ± 0.59
LD[1]	04: 00	-151.62 ± 8.99	160.36 ± 45.13	-0.45 ± 0.45	-3.60 ± 0.34	-102.31 ± 35.32	120.36 ± 47.25	-0.12 ± 0.12	0.49 ± 0.4
	08: 00	-116.10± 44.10	145.01 ± 20.80	-0.47 ± 0.39	-3.09 ± 0.38	-141.12 ± 23.95	122.82 ± 25.43	0.40 ± 0.30	0.28 ± 0.37
	12: 00	-168.65 ± 29.28	151.25 ± 30.77	-0.31 ± 0.19	-2.99 ± 0.41	-128.89 ± 42.34	41.91 ± 15.73	0.26 ± 0.33	-0.35 ± 0.24
	16: 00	-148.67 ± 25.79	152.30 ± 37.11	-0.27 ± 0.08	-3.10 ± 0.53	-159.48 ± 25.65	55.53 ± 19.04	0.33 ± 0.43	-0.38 ± 0.49
	20: 00	-159.09 ± 16.78	130.00 ± 28.28	-0.19 ± 0.12	-3.40 ± 0.32	-91.17 ± 36.11	57.08 ± 29.31	-0.40 ± 0.50	-0.08 ± 0.26
DD[2]	Day (n=2)	-124.51 ± 28.51	129.33 ± 19.78	-0.24 ± 0.33	-3.10 ± 0.33	-103.21 ± 60.18	66.10 ± 44.53	0.38 ± 0.33	-0.15 ± 0.19
	Night (n=2)	-137.42 ± 29.52	161.44 ± 28.38	-0.22 ± 0.23	-3.15 ± 0.23	-80.45 ± 22.80	102.74 ± 37.50	-0.30 ± 0.24	0.29 ± 0.45

[1] Birds were kept before experimentation in their natural light-dark cycle (LD: 14-10) or [2] in constant darkness (DD) for 48 hours.

Table 2

Mean values of spectral sensitivity (± SD) obtained from ring-billed gulls and gray gulls under scotopic condition at different time of the day.

Species	Time of recording	Wavelengths (nm)						
		450	500	525	550	600	625	650
Ring-billed gulls	00: 00	-0.43 ± 0.44	-0.02 ± 0.33	-0.25 ± 0.20	-0.28 ± 0.16	-0.48 ± 0.22	-0.79 ± 0.24	-1.03 ± 0.10
	04: 00	-0.57 ± 0.30	0.27 ± 0.38	-0.05 ± 0.28	-0.32 ± 0.12	-0.60 ± 0.25	-1.00 ± 0.16	-1.12 ± 0.10
	08: 00	-0.35 ± 0.16	-0.35 ± 0.10	-0.11 ± 0.25	0.13 ± 0.21	0.13 ± 0.14	-0.30 ± 0.17	-0.69 ± 0.19
	12: 00	-0.44 ± 0.24	-0.18 ± 0.16	-0.10 ± 0.17	-0.04 ± 0.18	0.13 ± 0.49	-0.18 ± 0.37	-0.98 ± 0.38
	16: 00	-1.22 ± 0.36	-0.77 ± 0.26	-0.82 ± 0.26	0.85 ± 0.39	-1.30 ± 0.36	-1.61 ± 0.20	-1.83 ± 0.19
	20: 00	-0.43 ± 0.23	-0.20 ± 0.17	0.10 ± 0.30	0.10 ± 0.19	-0.10 ± 0.32	-0.50 ± 0.27	-0.65 ± 0.30
Gray gulls	00: 00	-0.46 ± 0.18	0.13 ± 0.43	-0.05 ± 0.21	-0.16 ± 0.15	-0.40 ± 0.17	-1.03 ± 0.22	-1.62 ± 0.31
	04: 00	-1.00 ± 0.23	0.28 ± 0.36	0.12 ± 0.22	-0.41 ± 0.34	-0.51 ± 0.12	-0.70 ± 0.35	-1.19 ± 0.34
	08: 00	-0.30 ± 0.33	0.29 ± 0.21	0.16 ± 0.15	0.13 ± 0.41	-0.05 ± 0.34	-0.18 ± 0.22	-0.35 ± 0.30
	12: 00	-0.10 ± 0.12	0.20 ± 0.22	0.26 ± 0.13	0.05 ± 0.16	-0.16 ± 0.36	-0.44 ± 0.28	-0.66 ± 0.34
	16: 00	-0.21 ± 0.23	0.00 ± 0.11	0.33 ± 0.12	0.22 ± 0.22	-0.13 ± 0.28	-0.43 ± 0.28	-0.68 ± 0.31
	20: 00	-0.10 ± 0.10	0.18 ± 0.19	0.25 ± 0.17	0.11 ± 0.22	-0.11 ± 0.34	-0.30 ± 0.41	-0.35 ± 0.21

Table 3
Mean values of spectral sensitivity (± SD) obtained from ring-billed gulls and gray gulls under photopic condition at different time of the day.

Species	Time of recording	Wavelengths (nm)						
		450	500	525	550	600	625	650
Ring-billed gulls	00: 00	0.79 ± 0.11	1.19 ± 0.17	1.70 ± 0.23	2.02 ± 0.36	1.92 ± 0.30	1.44 ± 0.19	1.13 ± 0.40
	04: 00	0.74 ± 0.19	1.10 ± 0.17	1.31 ± 0.24	1.61 ± 0.18	1.30 ± 0.19	1.00 ± 0.23	0.83 ± 0.26
	08: 00	0.51 ± 0.14	0.99 ± 0.26	1.64 ± 0.28	1.84 ± 0.20	1.60 ± 0.42	1.45 ± 0.25	0.91 ± 0.22
	12: 00	0.65 ± 0.09	1.06 ± 0.22	1.72 ± 0.20	1.66 ± 0.44	1.94 ± 0.18	1.70 ± 0.16	0.93 ± 0.15
	16: 00	0.80 ± 0.39	1.20 ± 0.41	1.89 ± 0.34	2.07 ± 0.40	2.16 ± 0.61	1.91 ± 0.63	1.34 ± 0.55
	20: 00	0.68 ± 0.31	0.97 ± 0.25	1.58 ± 0.48	2.01 ± 0.25	1.55 ± 0.38	1.24 ± 0.52	0.95 ± 0.41
Gray gulls	00: 00	0.80 ± 0.06	1.06 ± 0.10	1.40 ± 0.11	1.31 ± 0.24	1.31 ± 0.38	0.93 ± 0.14	1.09 ± 0.22
	04: 00	1.60 ± 0.28	1.38 ± 0.27	1.25 ± 0.15	1.20 ± 0.28	1.61 ± 0.27	1.44 ± 0.21	1.28 ± 0.27
	08: 00	1.40 ± 0.22	1.18 ± 0.14	1.17 ± 0.16	1.39 ± 0.21	1.51 ± 0.14	1.58 ± 0.27	1.33 ± 0.14
	12: 00	1.12 ± 0.44	1.25 ± 0.24	1.37 ± 0.19	1.49 ± 0.45	1.84 ± 0.34	1.65 ± 0.29	1.20 ± 0.41
	16: 00	0.38 ± 0.43	0.25 ± 0.38	1.10 ± 0.02	0.92 ± 0.41	0.72 ± 0.36	0.44 ± 0.40	0.61 ± 0.12
	20: 00	0.88 ± 0.43	0.90 ± 0.01	1.01 ± 0.17	1.46 ± 0.07	1.19 ± 0.06	0.94 ± 0.51	0.88 ± 0.34

CHAPITRE 5

Comparative study of the retinal function and structure of nocturnal Leach's storm-petrels (*Oceanodroma leucorhoa*) and diurnal Atlantic puffins (*Fratercula arctica*)

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Article en preparation

5.1. Abstract

The function and structure of the retina of the Leach's storm-petrels *(Oceanodroma leucorhoa)* and Atlantic puffins (*Fratercula arctica*) were characterised and compared in order to identify possible correlations between their retinal organisation and visual ecology. The retina of Atlantic puffins possess histological features typically encountered in diurnal species with 77% of cones and 23% of rods, while the retina of Leach's storm petrels contains 48% of cones and 52% of rods, which are proportions typically found in nocturnal species. Corneal electroretinography (ERG) analysis revealed no significant difference in sensitivity as measured by the a- and b-waves between the two species, neither in scotopic nor in photopic conditions. Moreover, even if the overall rod density is significantly higher in Leach's storm-petrels than in Atlantic puffins, the scotopic dynamic range as measured by the a-wave is larger in the latter species; while in Leach's storm-petrels the scotopic dynamic range measured by the b-wave is just slightly larger than in Atlantic puffins. Overall, the results suggest that both species are functionally equally efficient for night vision.

Keywords: Atlantic puffins, birds, cones, electroretinogram (ERG), Leach's storm petrels, nocturnal and diurnal behaviours, retina, rods.

5.2. Introduction

Leach's storm-petrels *(Procellariidea; Oceanodroma leucorhoa)* and Atlantic puffins (*Alcidea*; *Fratercula arctica*) are two pelagic seabirds that breed in nesting burrows dug into the ground (Beck and Brown, 1972; Bradstreet and Brown, 1985). In order to avoid predation from gulls, Leach's storm-petrels visit their nests exclusively at night and are more active on dark nights than on bright ones (Watanuki, 1986; Bretagnolle, 1990; Bryant, 1993). This predator avoidance strategy implies that Leach's storm-petrels return to their nests with reduced visual cues. At sea, Leach's storm-petrels are surface feeders and are known to forage on a variety of plankton, fish, krill and squid (Brown, 1988; Grubb, 1972; Haney, 1987). Nocturnal foraging is suspected in this species, since many types of prey found in their stomach migrate vertically to the surface during the night (Vermeer and Devito, 1988). It has been argued that Leach's storm-petrels may use olfactory cues to return to their burrows or to locate food at night but this is unclear (Grubb, 1974, 1979). Anatomically, these birds have among the largest olfactory bulbs of any bird (Bang, 1966; Bang and Cobb, 1968; Bang, 1971). Moreover, behavioural observations suggest that, while visual cues may be used to locate aggregation of food, odour cues seem to aid these birds in locating preys (Grubb, 1972). In contrast, Atlantic puffins visit their burrows during the day when the nest site can be easily located visually (Bradstreet and Brown, 1985). This species forages exclusively during the day on small fish, mollusks, crustaceans and zooplankton by diving from the surface and swimming underwater with wings (Bradstreet and Brown, 1985).

These different behavioural strategies presumably impose different demands on the visual system and more specifically on the retina of these two species. We therefore expected that these behavioural differences be reflected in their retinal structural organisation and function. If Leach's storm petrels used visual cues to localise their nests or to forage at night, they must have a rod-dominated retina sensitive to light of low intensities, while in Atlantic puffins the retina may be cone-

dominated and designed for diurnal vision. Using corneal electroretinography (ERG), we have characterised and compared the retinal function of Leach's storm-petrels and Atlantic puffins and have also studied the structural organisation of their retinas.

5.3. Methods

5.3.1. Animals

Experiments were performed on six (n = 6) adult Leach's storm-petrels (70-85 g) and six (n = 6) adult Atlantic puffins (400-450 g) following the guidelines of the Canadian Council on Animal Care (1993). Leach's storm-petrels were captured in Corossol Island (50°20'N, 66°12'W) and Atlantic puffins in Sainte-Marie Island (50°36'N, 59°21'W) (Golf of Saint-Laurence, Province of Québec, Canada).

5.3.2. Electroretinography

After a 4 h period of dark adaptation, the birds were anaesthetised with an injection of ketamine hydrochloride (40-100 mg/kg i.m.; Ketaset, Ayerst) and xylazine hydrochloride (4-5 mg/kg; i.m. Rompun, Bayer). They were placed in a custom-made recording holder inside a Ganzfeld dome of 41 cm in diameter (LKC Ganzfeld-2503B) and their head positioned so that only the left eye was stimulated. The eyelids and nictitating membrane were retracted with a speculum, the cornea was anaesthetised with 0.5% proparacaine hydrochloride and the pupil was fully dilated with 1% Tropicamide. A DTL electrode (X-static© nylon coated yarn, Sauquoit Industries, Scranton, PA, USA) was placed on the cornea to act as the active electrode. Reference and ground electrodes (Grass subdermal electrodes, Astro-med Inc., Warwick, RI, USA) were inserted under the scalp and the skin of the chest, respectively. Responses were evoked to flashes of white light of 0.52 log cd.sec.m^{-2} and 20 µs duration delivered with a photostimulator (Grass PS-22) through the

Ganzfeld and the stimulus luminance was attenuated with Kodak Wratten neutral density (ND) filters (Kodak Ltd, Rochester, NY, USA). Responses were recorded within a bandwidth of 0.3 to 500 Hz, amplified 10,000 X, averaged and stored on hard disc using an EPIC-2000 computer-controlled electrodiagnostic system (LKC Technologies, Inc., Gaithersburg, MD). All the manipulations described above were performed under dim red light illumination.

Scotopic responses were first obtained using increasing flash luminance from -4.68 to 0.52 log cd.sec.m^{-2} in steps of 0.4 log unit. For each luminance, the responses to six successive flashes presented at intervals of 10.1 sec were averaged. Afterwards, the birds were light adapted to a white background light of 1.55 log cd.m^{-2} for 15 min and photopic responses were obtained using increasing flash luminance of -1.48 to 0.52 l log cd.sec.m^{-2} in steps of 0.4 log unit. For each luminance the responses to 10 successive flashes presented at intervals of 4.2 sec were averaged.

5.3.3. Histology

Immediately after the ERG recordings the birds were given a lethal dose of sodium pentobarbital. Their eyes were removed under this photopic illumination and the axial length (AL), equatorial diameter (ED) and maximal entrance pupil were measured (Martin, 1986). The left eye was injected with 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH = 7.2) and bathed in this fixative for 30 min. The anterior part of the eye was removed at the equator and the retina, still attached to the choroid, was cut into nine sectors using the pecten as a landmark (Fig. 1), according to the procedure of Emond et al. (2006a). Each sector was further subdivided into smaller portions and kept in the fixative for 3-h. The retinal portions were washed with phosphate buffer for 10 min, postfixed in 1% OsO_4 in 0.1 M phosphate buffer for 1 h, rinsed again in phosphate buffer followed by distilled water, 10 min each, and finally dehydrated in graded ethanol and propylene oxide. The tissues were then infiltrated with a 1:1 mixture of propylene oxide and epon resin for 12 h and with pure epon

resin for another 2 h. Four retinal portions were selected randomly from each sector and were embedded in silicone rubber moulds filled with epon resin and polymerised in an oven at 60°C for 48 h. Semithin (0.7 µm) sections were cut transversally through the retina with an ultramicrotome. They were mounted onto glass slides, stained with toluidin blue and examined with the light microscope. The rods and cones were counted in a field of 310µm and their respective average densities were calculated from 15 sections randomly selected for each sector. The length and diameter of the outer and inner segments as well as the thickness of each retinal layer were measured using a calibrated graticule and were averaged from the same sections.

In order to observe the oil droplets contained in cones, the right eye of both species was hemisected along the equator axis and the retina was cut into nine sectors as described previously (Emond et al., 2006b). The nine sectors were bathed in saline solution (pH = 7.2) for 30 to 60 min to assess the detachment of the retina from the pigment epithelium. The retina was then gently removed from the choroid and mounted flat, photoreceptors side up, on glass slides. The oil droplets were observed with a light microscope (Axiomat NDC Zeiss; magnification of 500X).

5.3.4. Data analysis

Analysis of the ERG included peak time and amplitude measurements of the a- and b-waves. Peak times were measured from flash onset to the peak of each wave. The amplitude of the a-wave was measured from baseline to trough, and that of the b-wave from the trough of the a-wave to the peak of the b-wave or, when no a-wave was present, from baseline to peak. Luminance-response curves were then constructed for the scotopic and photopic a- and b-waves by plotting their amplitudes as a function of the stimulus luminance.

The thresholds of the scotopic and photopic a- and b-waves were obtained by

extrapolating from the luminance-response curves the luminance that produced a criterion response of 10 μV, which was the response amplitude just above the average amplitude of the baseline in all the animals tested.

The scotopic and photopic a-wave luminance-response curves were fitted by a least-squares algorithm (Matlab, MathWorks, Natick, MA) to the equation:

$$P_3(I,t) \cong \{1 - \exp[-I \cdot S \cdot (t - t_d)^2]\} \cdot R_{max\,(P3)} \text{ for } t > t_d \qquad (1)$$

which describes the transduction mechanisms of the photoreceptors in vertebrates, and where P_3 represents the sum of the individual photoreceptor responses as a function of flash energy I and time t after the occurrence of a short flash. S is a sensitivity parameter that scales the intensity of the flash required to generate a response equal to ½ R_{max} (semisaturation constant), R_{max} the maximum response amplitude, and t_d a brief delay (see Hood and Birch, 1990, 1993, 1997). Similarly, the scotopic and photopic b-wave luminance-response curves were fitted by a least-squares algorithm to the equation (SAS Information Delivery System for UNIX, Version 6.07.02; SAS Institutes Inc., Cary, NC):

$$V/V_{max} = I^n / (I^n + \sigma^n) \qquad (2)$$

which models the activity of the inner retina in vertebrates, and where V represents the response to stimulus luminance I, V_{max} the maximum response, σ a parameter of sensitivity which scales the luminance required to generate a response equal to ½ V_{max} (semisaturation constant) and n the slope of the function (see Naka and Rushton, 1966, 1967).

ANOVA analysis was performed to evaluate the difference in the physiological responses between species. Morphological differences retinal sectors within each species and between species were tested by two-way ANOVA. Post hoc Holm-Sidak

tests were applied for evaluation of significant differences between the groups. Data fitting a non-parametric distribution were tested for significance using the Kuskal-Wallis ANOVA by ranks test with Dunn's post hoc comparison when comparing groups (Statistica for Windows version 5.0; StatSoft Inc., Tulsa, Oklahoma). Data are presented as mean ± SD and in all cases the $p < 0.05$ level was used to determine statistical significance.

5.4. Results

5.4.1. Electroretinography

Representative ERG waveforms obtained from single Leach's storm-petrel and Atlantic puffin under scotopic and photopic conditions to a range of white flash intensities are presented in Fig. 2. Overall, the morphology of the ERG a-wave appears different in both species. Thus, under scotopic condition, the a-wave is barely profiled in Leach's storm petrels, while in Atlantic puffins this wave presents a more frofiled form. The same pattern is observed under photopic condition. Under scotopic condition, at low stimulus intensities, a positive potential (b-wave) predominates the waveform and as the intensity increases a negative potential (a-wave) begins to dip below the baseline in both species. The amplitude of the a-wave gradually augments with increasing stimulus intensities while that of the b-wave initially grow in amplitude with progressively brighter stimuli and then reach a plateau. Under photopic condition, the amplitude of both the a- and b-waves also increases with the stimulus intensities. In all instance and for both species, an increase in the intensity of the flash resulted in faster scotopic and photopic a-wave (Fig.3). In comparison, in Leach's storm petrels, the peak time of the scotopic b-wave first shortens gradually (until around -0.28 log cd.sec.m^{-2}) with progressively brighter flashes, and than lengthens (up to intensities of 0.52 log cd.sec.m^{-2}) with the brightest stimuli. This pattern was not observed in Atlantic puffins; in this species the peak time of the scotopic b-wave shorten with increasing flash intensities as for

the scotopic a-wave. For almost all flash intensities, the peak time of the scotopic b-wave of Leach's storm petrels was slower than in Atlantic puffins (ANOVA, $p < 0.001$). No significant difference was observed between species for the other timing parameters.

Fig. 4 presents the luminance-response curves derived from the ERGs obtained from the same individuals of Fig. 2. The lines represent the least-squares fit of equations 1 and 2 to the amplitude of the a- and b-waves, respectively. The mean values of the parameters of the luminance-response function obtained under scotopic and photopic conditions are given in Table 1, where it can be seen that the scotopic a-wave 10 μV criterion threshold is higher in Leach's storm-petrels than in Atlantic puffins (Holm-Sidak method, $t = 6.22$; $p < 0.001$), while the luminance at which the a-wave saturates is approximately the same in both species. Consequently, the scotopic dynamic range, as measured by the a-wave, reaches a value of 4.49 log cd.sec.m^{-2} in Atlantic puffins and of 2.73 log cd.sec.m^{-2} in Leach's storm-petrels. On the other hand, the scotopic dynamic range, as measured by the b-wave, is slightly higher in Leach's storm-petrels (4.64 log cd.sec.m^{-2}) than in Atlantic puffins (4.29 log cd.sec.m^{-2}).

ANOVA tests reveal that under scotopic condition the saturated response of the a-wave (R_{max}) is higher in Atlantic puffins than in Leach's storm-petrels (Holm-Sidak method, $t = 4.80$; $p < 0.001$), but there is no significant difference between species for the luminance at which R_{max} is reached, nor in the sensitivity parameter S (Table 1). The saturated response of the scotopic b-wave V_{max} and σ show no significant difference between species (Table 1). Under photopic condition, the parameters R_{max} (Holm-Sidak method, $t = 11.15$; $p < 0.001$) and V_{max} (Holm-Sidak method, $t = 15.69$; $p < 0.001$) are higher in Atlantic puffins than in Leach's storm-petrels. However, there is no difference between species in the luminance at which R_{max} and V_{max} are reached (Table 1).

5.4.2. Eye and pupil measurements

The eyes of Atlantic puffins are bigger than those of Leach's storm-petrels, with an average equatorial diameter (ED) and axial length (AL) of 15.6 ± 1.8 mm and 13.5 ± 1.3 mm, respectively, in the former (AL: ED = 0.87), and an average ED and AL of 7.5 ± 0.5 mm (Holm-Sidak method, $t = 10.62$; $p < 0.001$) and 6.2 ± 0.7 mm (Holm-Sidak method, $t = 12.11$; $p < 0.001$), respectively, in the latter (AL: ED = 0.82). The pupil of puffins reaches a maximum diameter of 3.8 ± 0.4 mm and that of Leach's storm-petrels 3.2 ± 0.4 mm.

5.4.3. Retinal layers

Light photomicrographs from the central retina (sector 5) of Atlantic puffins and Leach's storm-petrels are presented in Fig. 5. A significant difference was observed in the thickness of the inner nuclear layer and the ganglion cell layer between the two species (Fig. 6). Overall, the inner nuclear layer of Atlantic puffins was about 39% thicker than in Leach's storm petrels (Holm-Sidak method, $t = 5.15$; $p < 0.001$), while the ganglion cell layer was 24% thicker in Atlantic puffins than in Leach's storm petrels (sector 9) (Holm-Sidak method, $t = 3.98$; $p = 0.003$).

5.4.4. Photoreceptors

In both species, single cones, double cones (comprising of a principal cone closely linked to an accessory one) and rods are found. Cones and rods are easily differentiated by the length and diameter of their outer segment, which are smaller in cones and by the presence of an oil droplet in the apical portion of the cone inner segment. In Atlantic puffins, the cones outnumber the rods, comprising about 77% of the total photoreceptors, while in Leach's storm-petrels the rods outnumber the cones and comprise 52% of the total photoreceptors (Fig. 7). The overall relative cone density is slightly higher in Atlantic puffins (62.86/310 µm ± 5.92) than in Leach's

storm-petrels (47.42/310 µm ± 10.67) (Holm-Sidak method, $t = 3.10$; $p = 0.01$), while the overall relative rod density is much lower in Atlantic puffins than in Leach's storm-petrels (18.26/310 µm ± 1.93 vs 52.21/310 µm ± 9.23) (Holm-Sidak method, $t = 8.82$; $p < 0.001$). The topographical distribution of the photoreceptors varies across the retina in approximately the same pattern in both species. Thus, the relative density of cones reaches a peak in the central retina (sector 5) and declines towards the ventral retina where the lowest density is attained in sector 9 (Fig.7), whereas the rods are evenly distributed across the entire retina. The rods and cones are therefore not complementary in their distribution, i.e. the increase in cones in the central retina is not compensated by a decrease in rod number. In Atlantic puffins the cone: rod ratio is 5:1 in the central retina and 3:1 in all other sectors. In Leach's storm-petrels the cone: rod ratio is 0:9 in the central retina and 0:8 in all other sectors (Table 2).

5.4.5. Oil droplets

Photomicrographs from the central retina (sector 5) of single Atlantic puffin and a Leach's storm-petrel are shown in Fig. 8 A and B respectively. In Atlantic puffins, red (R), yellow (Y), pale (P), clear (C) and transparent (T) oil droplets were identified. In Leach's storm-petrels only Y, P and C oil droplets were distinguished. Table 3 gives the percentage of the different types of oil droplets evaluated in each sectors. In both species, no significant variation was observed in the distribution of the different types of droplets between retinal sectors. The P type were the more abundant in both species compared to the other types and the CT type the less numerous.

5.5. Discussion

The histological results presented in this study show that Atlantic puffins possess a retina with features typically encountered in diurnal species, while the retina of Leach's storm-petrels resemble more that of nocturnal species. Thus, in

Atlantic puffins, 77% of the total photoreceptors are cones and 23% rods, a proportion similar to what is found in strictly diurnal marine species such as herring gulls (*Larus novaehollandiae*) and common terns (*Sterna hirundo*) (Hart, 2001). The retina of Atlantic puffins is also characterised by an inner nuclear layer twice thicker than the external nuclear layer, which is also a structural feature typically encountered in diurnal species (Ali and Klyne, 1986). Moreover, five types of oil droplets i.e.: red (R), yellow (Y), pale (P), clear (C) and transparent (T) were distinguished under the light microscope in this species, indicating the presence of four classes of single cones: long (LWS cones with λ_{max} = 543-571 nm), middle (MWS cones with λ_{max} = 497-510 nm), short (SWS cones with λ_{max} = 430-463 nm) and ultra-violet (UVS cones with λ_{max} = 362-426 nm), and one class of LWS double cones. The presence of these five classes of cones suggests that Atlantic puffins have at least a tetrachromatic colour vision (Hart, 2001). Comparatively, 52% of the photoreceptors of the retina of Leach's storm-petrels are rods and 48% cones, which are proportions found in nocturnal species (Roze et al., 1990). The retina of Leach's storm-petrels is also characterised by an inner nuclear layer that is of the same thickness than the external nuclear layer, which is typical of nocturnal species (Walls, 1967; Roze and al., 1990). Moreover, our histological study revealed that only cones with oil droplets of type P (double LWS cones), Y (single MWS cones) and C (single SWS cones) are present in the retina of this species and that the proportion of double cones is relatively high. Although the role of double cones is still not well understood, accumulating evidence suggests that these photoreceptors optimise space contrasts when the light intensities are low (Maier and Bowmaker, 1993; Vorobyev and Osorio, 1998; Campenhausen and Kirschfeld, 1998). Therefore, the abundance of double cones observed in Leach's storm-petrels might allow a better detection of preys under condition of low light intensities (Hart, 2001). Here, the absence of single LWS cones (with type R droplet) in Leach's storm petrel is surprising. It was assumed that R droplets would help to reduce glare from water surface and improve prey detection (Muntz, 1972), a theory supported by the high percentage of R droplets found in the retina of kingfishers which is a surface feeder like Leach's storm petrels (Walls, 1967; Hart

2001). However, it has been also argued that R droplets would make it harder to look trough the water surface, because at long wavelengths, the surface reflections are relatively brighter than the upwelling illumination (Austin, 1974). Therefore, the functional significance of enhanced long-wavelength sensitivity in surface-feeding aquatic birds remains to be determined.

Surprisingly and contrary to our prediction, the parameters of the luminance-response function measured in both species do not correlate with their respective histological data. Thus, despite the retina of Leach's storm-petrels presents a higher number of rods than Atlantic puffins, the value of the scotopic parameter R_{max}, which can be related to the overall number of rods (Hood and Birch, 1993), is higher in Atlantic puffins than in Leach's storm-petrels. Moreover, the scotopic sensitivity parameter σ, which can be used as an index for nocturnal vision, showed no significant difference between species, indicating that the retinas of both species are equally sensitive under scotopic condition. Interestingly, our results show that the scotopic dynamic range, as measured by the a-wave, is larger in Atlantic puffins (4.49 log cd.sec.m^{-2}) than in Leach's storm-petrels (2.73 log cd.sec.m^{-2}), suggesting that photoreceptors of puffins are sensitive within a larger range of scotopic light intensities than petrels. On the other hand, the scotopic dynamic range, as measured by the b-wave, is just slightly larger in Leach's storm-petrels (4.64 log cd.sec.m^{-2}) than in Atlantic puffins (4.29 log cd.sec.m^{-2}). The huge difference observed between the a- and b-wave scotopic dynamic ranges measured in Leach's storm-petrels, may result from a high number of rods converging on bipolar cells within the inner retina. In mammals, it is well known that rods convergence on bipolar cells increases by 20 times the signals between rods and bipolar cells and by the way, enhances the capacity of the retina to respond over a larger range of light intensities (Bloomfiels and Dacheux, 2001). According to these results, the retina of Leach's storm-petrels seems to have evolved to maximise the efficiency of the inner retina in order to respond to the visual challenge imposed by the night. Our results also show that both species have a similar scotopic b-wave threshold, which corresponds approximately

to the light level occurring just before the end of the twilight period under clear sky (Martin, 1990). Again, this result suggests that both species are equally effective for night vision.

Acknowledgements

This work was realised by MPE as partial requirement for the M.Sc. and Ph.D. degrees at the Université de Montréal and was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Université de Montréal (RM and TC) and by the Canadian Institutes of Health Research (CIHR) (PL). We thank Dr. Luz-Marina Rojas for the teaching of the ERG and histology techniques, Dr. Vincent Ferretti for the mathematical advice for the analysis of the data and the programming of the models.

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Fig. 1. Schematic representation of the nine retinal sectors. D, N, T, and V correspond to dorsal, nasal, temporal and ventral sectors, respectively.

Fig. 2. Representative ERG waveforms obtained in one Leach's storm-petrel and one Atlantic puffin to a range of flash stimuli presented under scotopic and photopic conditions. Abbreviations: a = peak of the a-wave; b = peak of the b-wave.

Fig. 3. A- and b-wave peak time (± SD) luminance-response functions obtained in Leach's storm petrels and Atlantic puffins under scotopic and photopic conditions.

Fig. 4. Representative examples of luminance-response curves of the a- and b-waves obtained under scotopic and photopic conditions from one Leach's storm-petrel and one Atlantic puffin. The solid lines represent the least-squares fit of equations 1 and 2 to the amplitudes of the a- and b-wave, respectively.

Fig. 5. Light photomicrographs of the central retina (sector 5) of one Leach's storm-petrel and one Atlantic puffin. p.l. = photoreceptor layer; o.l.m. = outer limiting membrane; o.n.l. = outer nuclear layer; o.p.l. = outer plexiform layer; i.n.l. = inner nuclear layer; i.p.l. = inner plexiform layer; g.c.l. = ganglion cell layer; o.f.l. = optic nerve fiber layer; i.l.m. = inner limiting membrane. Scale bar = 15 μm

Fig. 6. Mean thickness (μm) of retinal layers in each retinal sector of Leach's storm-petrels and Atlantic puffins, as well as in all sectors averaged. Columns represent the means ± SD. The number of birds is 6 in each case.

Fig. 7. Mean cone and rod densities (± SD) in Leach's storm-petrels and Atlantic puffins in each of the nine retinal sectors.

Fig. 8. Light photomicrographs of flat mounted unfixed central retina (sector 5) of a Atlantic puffin (A) and a Leach's storm petrel (B) showing the different types of oil

droplets observed at the light microscope. Abbreviations: R: red type; Y: yellow type; P: pale type and CT: clear and transparent type. Scale bars = 15 μm.

Figure 1

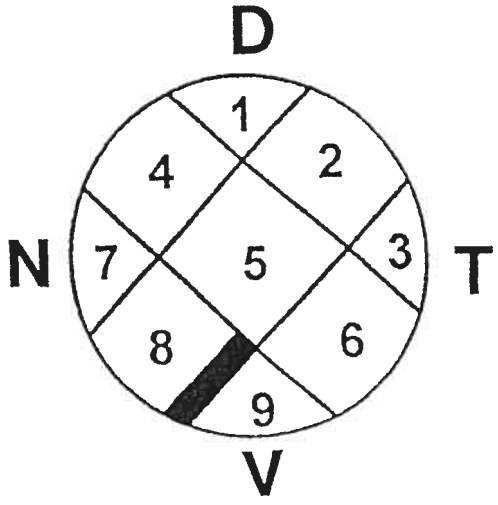

Figure 2

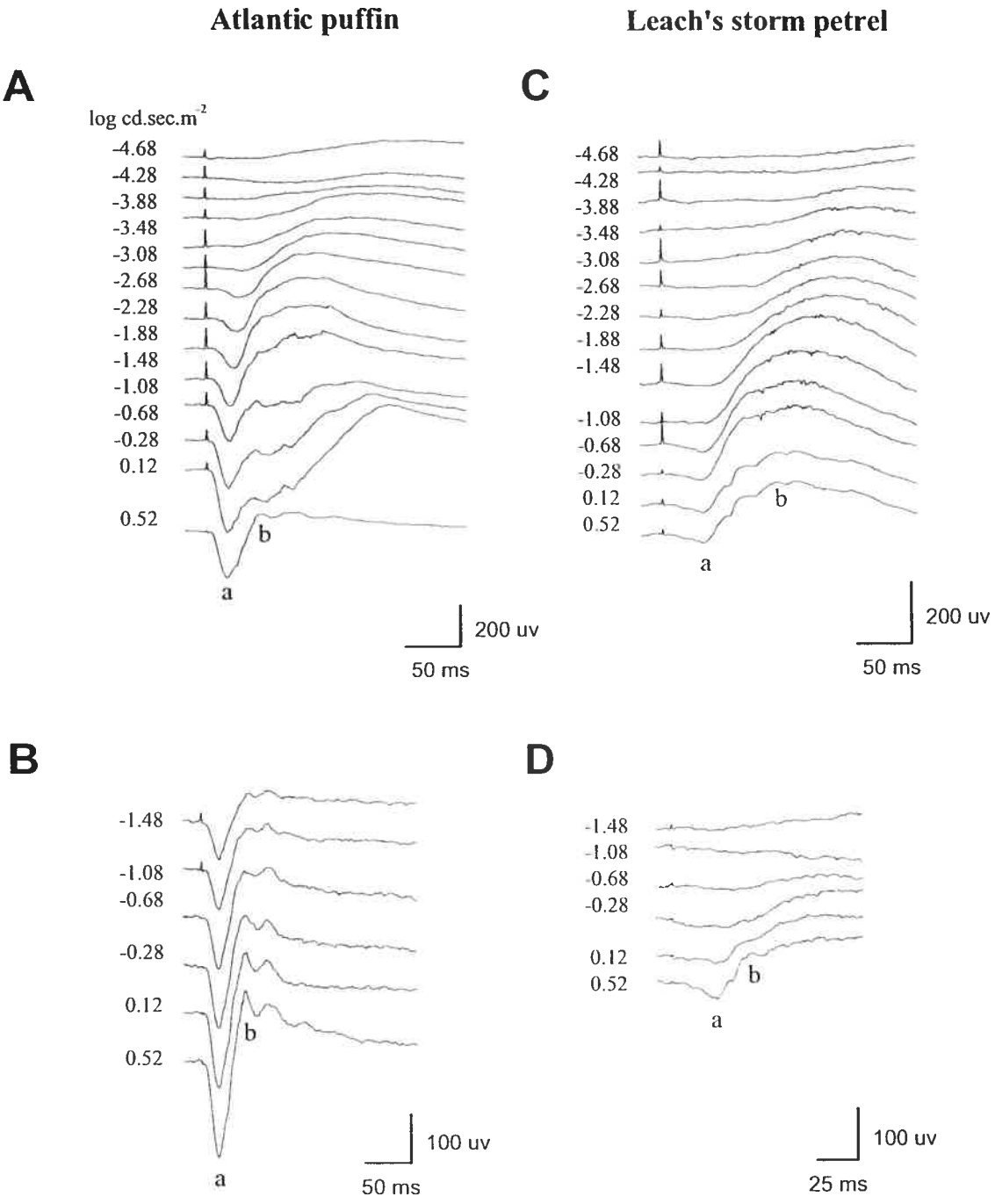
Atlantic puffin
Leach's storm petrel
A
log cd.sec.m-2
-4.68
-4.28
-3.88
-3.48
-3.08
-2.68
-2.28
-1.88
-1.48
-1.08
-0.68
-0.28
0.12
0.52
b
a
200 uv
50 ms
C
-4.68
-4.28
-3.88
-3.48
-3.08
-2.68
-2.28
-1.88
-1.48
-1.08
-0.68
-0.28
0.12
0.52
b
a
200 uv
50 ms
B
-1.48
-1.08
-0.68
-0.28
0.12
0.52
b
a
100 uv
50 ms
D
-1.48
-1.08
-0.68
-0.28
0.12
0.52
b
a
100 uv
25 ms

Figure 3

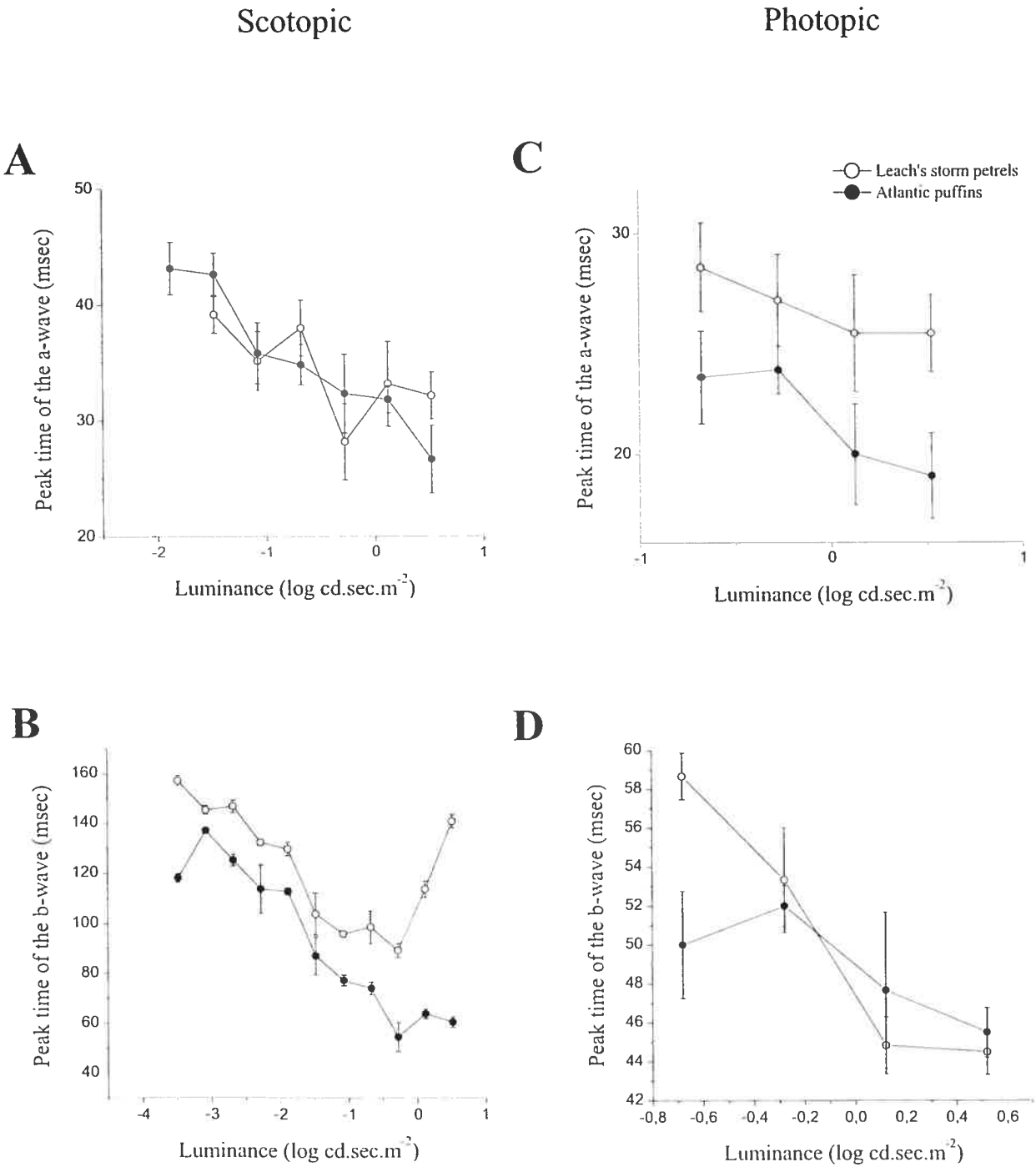
Scotopic
Photopic
A
B
C
D
Leach's storm petrels
Atlantic puffins
Peak time of the a-wave (msec)
Peak time of the b-wave (msec)
Luminance (log cd.sec.m-2)

Figure 4

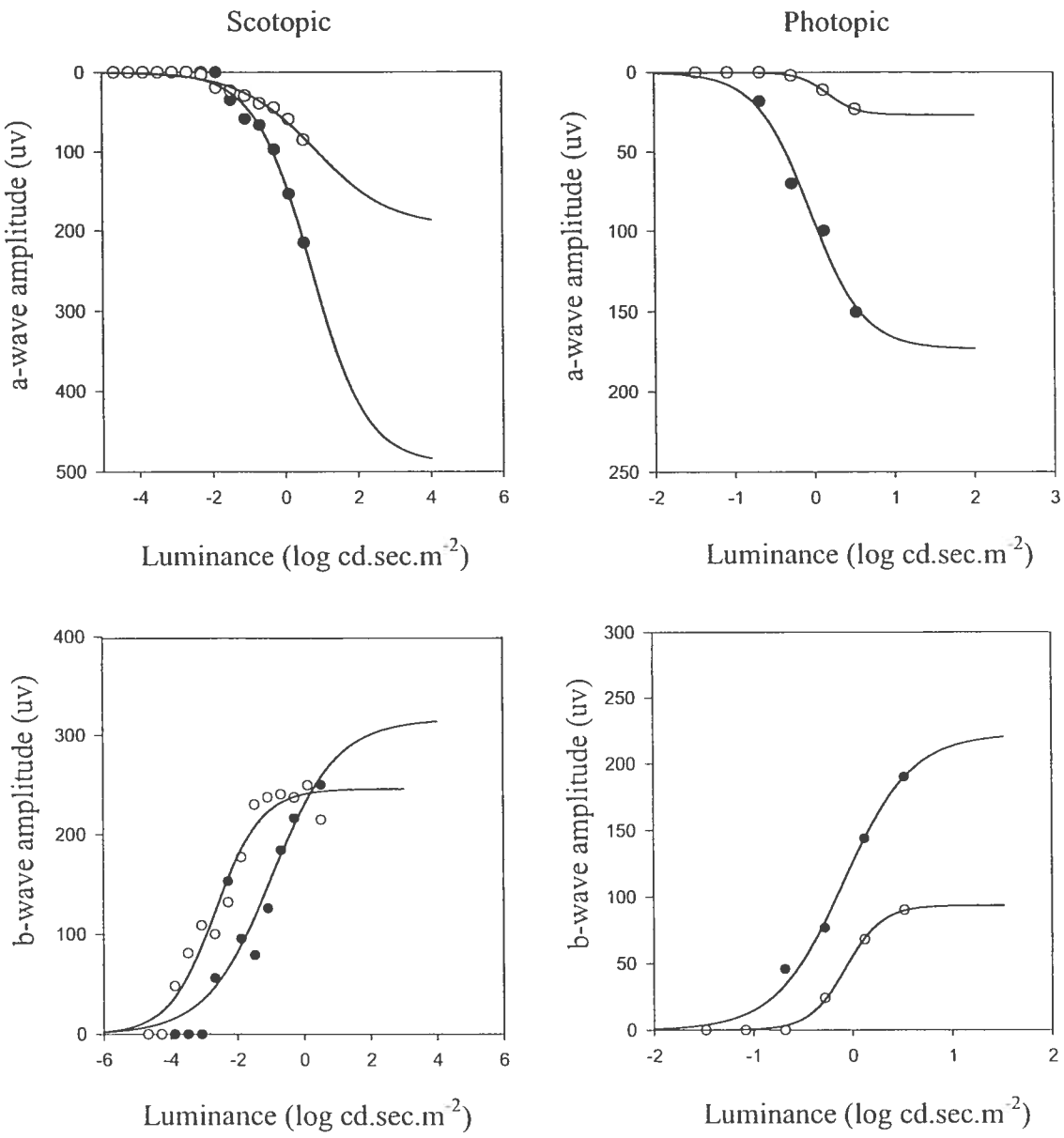
Atlantic puffins
Leach's storm-petrels
Scotopic
Photopic
a-wave amplitude (uv)
b-wave amplitude (uv)
Luminance (log cd.sec.m-2)
Luminance (log cd.sec.m-2)
Luminance (log cd.sec.m-2)
Luminance (log cd.sec.m-2)

Figure 5

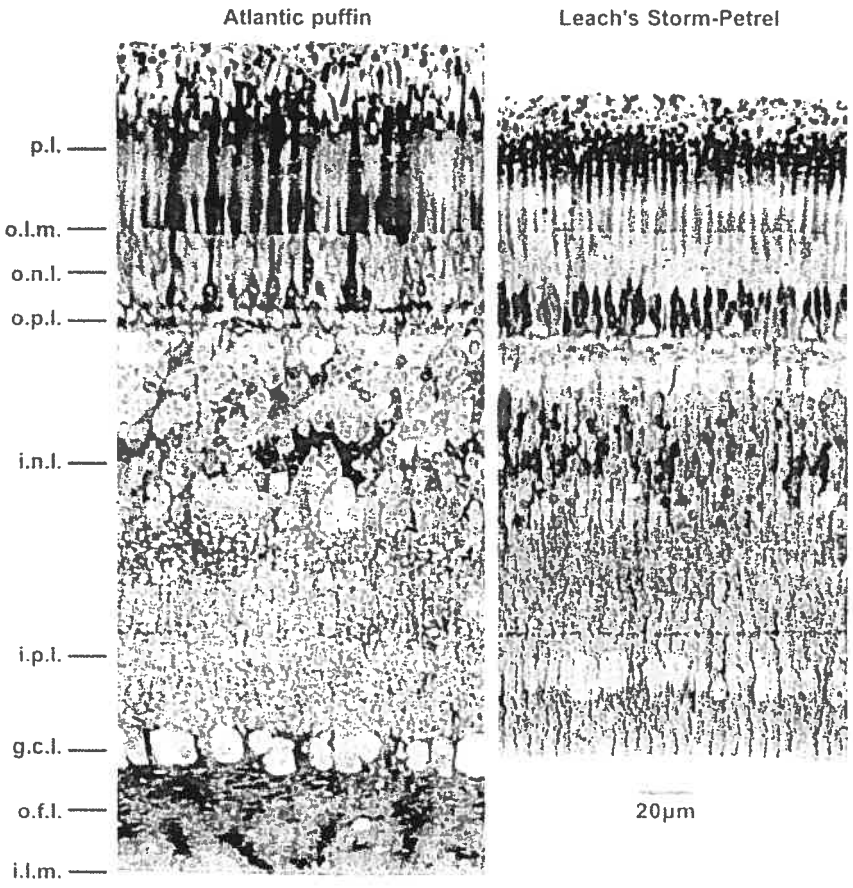
Atlantic puffin
Leach's Storm-Petrel
p.l.
o.l.m.
o.n.l.
o.p.l.
i.n.l.
i.p.l.
g.c.l.
o.f.l.
i.l.m.
20µm

Figure 6

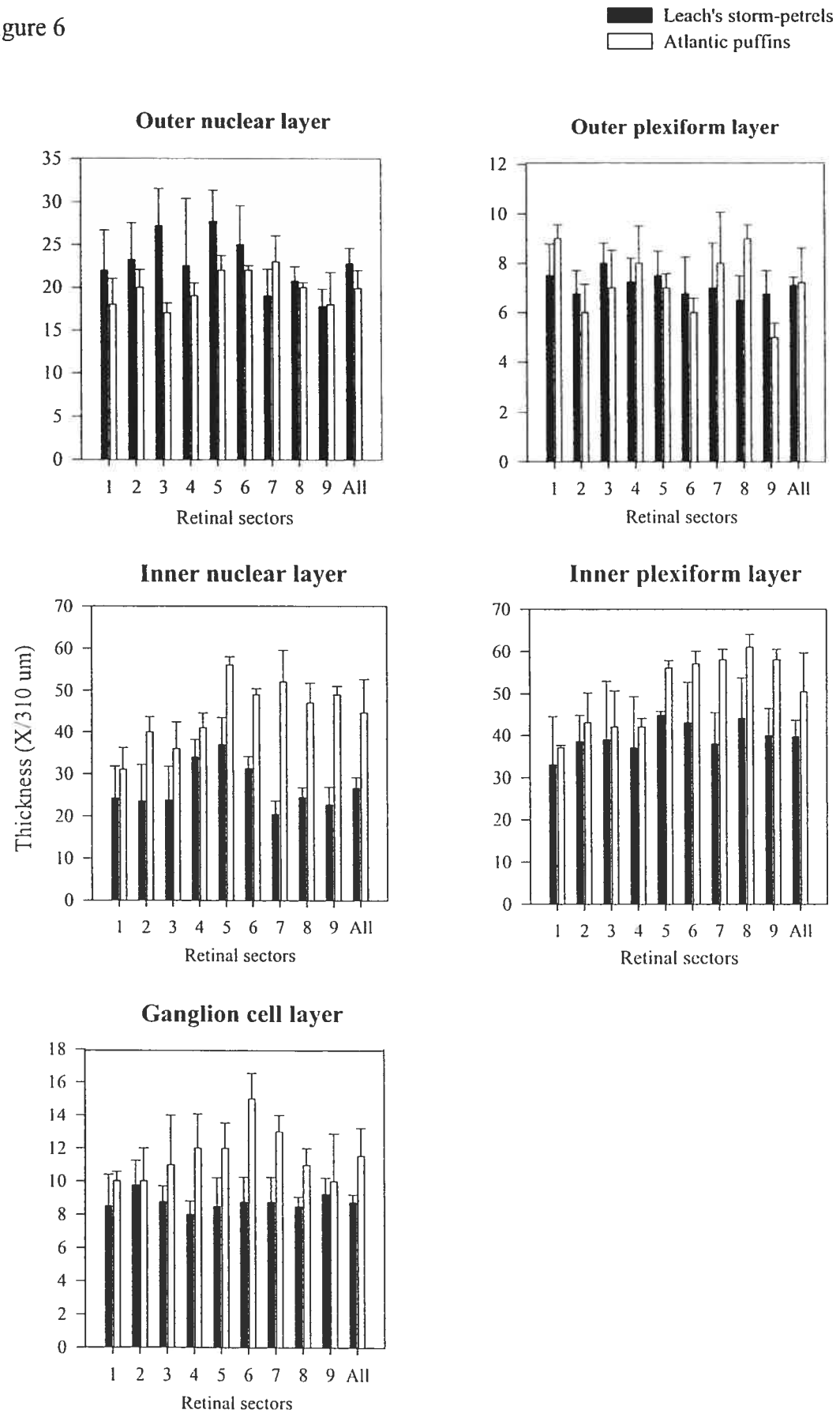
Leach's storm-petrels
Atlantic puffins
Outer nuclear layer
Outer plexiform layer
Inner nuclear layer
Inner plexiform layer
Ganglion cell layer
Thickness (X/310 um)
Retinal sectors
1 2 3 4 5 6 7 8 9 All

Figure 7

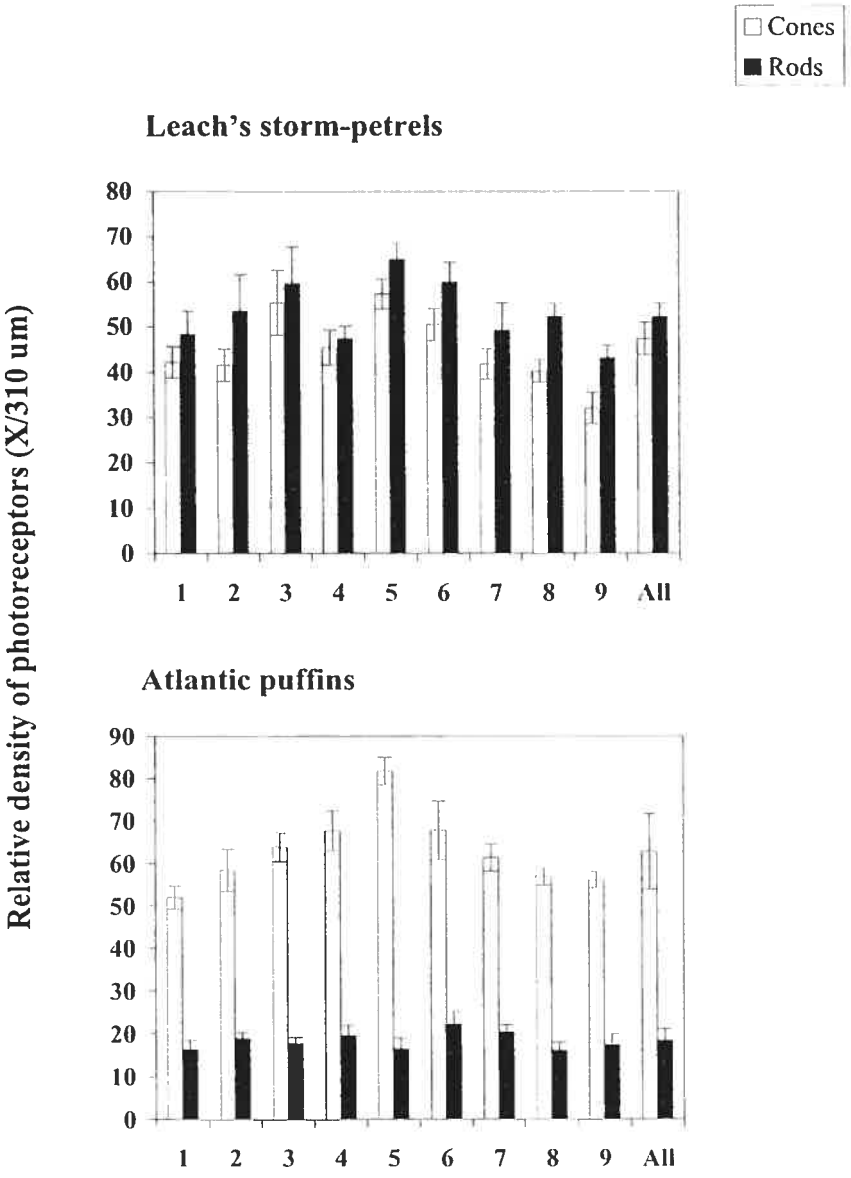
Cones
Rods
Leach's storm-petrels
Relative density of photoreceptors (X/310 um)
80
70
60
50
40
30
20
10
0
1 2 3 4 5 6 7 8 9 All
Atlantic puffins
90
80
70
60
50
40
30
20
10
0
1 2 3 4 5 6 7 8 9 All

Figure 8

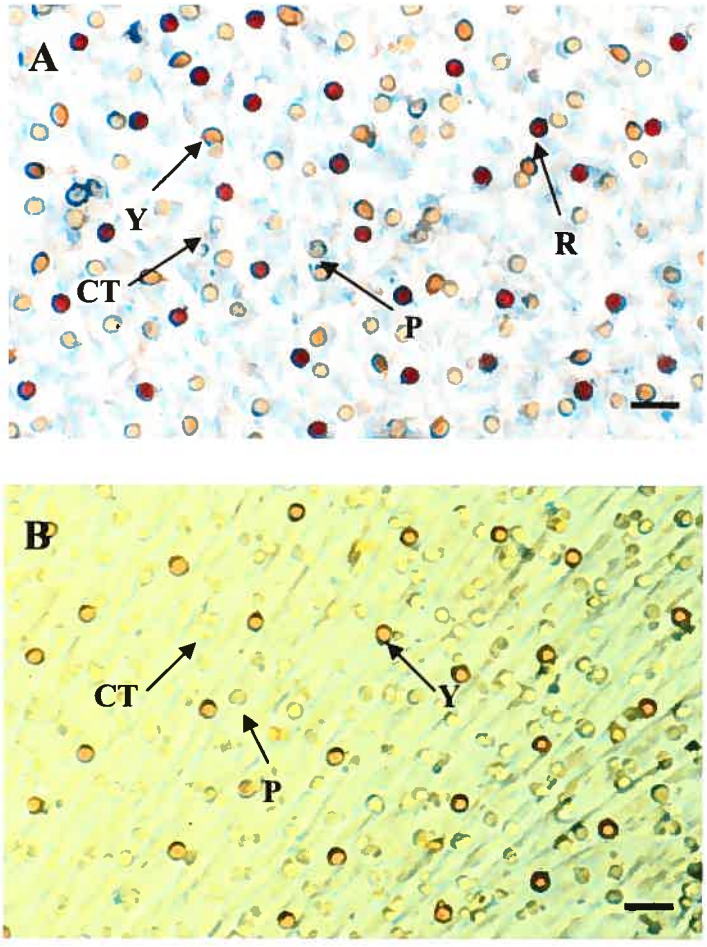

Table 1
Mean values (± SD) of the parameters of the luminance-response function obtained from Atlantic puffins and Leach's storm-petrels.

Waves	Parameters [a]	Atlantic puffins [b]	Leach's storm-petrels [b]
Scotopic			
a-wave	10 μv threshold	-2.46 ± 0.33*	-1.20 ± 0.37
	R_{max}	-392.29 ± 103.93*	-185.73 ± 20.0
	LR_{max}	2.03 ± 0.15	1.53 ± 0.75
	S	0.72 ± 0.36	0.24 ± 0.65
b-wave	10 μv threshold	-4.08 ± 0.36	-4.15 ± 0.40
	V_{max}	339.27 ± 76.53	270.89 ± 115.67
	LV_{max}	0.21 ± 0.43	0.49 ± 0.31
	σ	-2.11 ± 0.29	-2.57 ± 0.36
Photopic			
a-wave	10 μv threshold	-0.91 ± 0.06	0.13 ± 0.08
	R_{max}	-172.04 ± 27.45*	-25.97 ± 16.63
	LR_{max}	1.16 ± 0.41	1.07 ± 0.02
	S	0.13 ± 0.19	0.29 ± 0.22
b-wave	10 μv threshold	-0.89 ± 0.16	-0.42 ± 0.16
	V_{max}	273.28 ± 25.12*	79.22 ± 16.93
	LV_{max}	0.88 ± 0.31	0.99 ± 0.09
	σ	0.05 ± 0.36	0.08 ± 0.17

[a] The parameters represent: Threshold (log cd.sec.m^{-2}) which evokes a criterion response of 10 μv; R_{max} and V_{max}, the maximum responses (μv) estimated from Eqs. (1) and (2) respectively; LR_{max} and LV_{max}, the luminances (log cd.sec.m^{-2}) at which R_{max} and V_{max} are obtained respectively; S and σ, the luminances (log cd.sec.m^{-2}) required to generate half the maximum responses (semisaturation constant) estimated from the Eqs. (1) and (2). [b] Measurements obtained from six birds. * Difference between species, $p < 0.05$.

Table 2
Cone: rod ratio of Atlantic puffins and Leach's storm-petrels for each retinal sector and for whole retina

Retinal sectors	Atlantic puffins[a]	Leach's storm-petrels[a]
1	3:1	0.87:1
2	3:1	0.77:1
3	4:1	0.93:1
4	3:1	0.95:1
5	5:1	0.88:1
6	3:1	0.84:1
7	3:1	0.84:1
8	4:1	0.77:1
9	3:1	0.74:1
All	3:1	0.91:1

[a] Measurements obtained from six birds.

Table 3
Mean percentages of the different oil droplet types observed in cones of the nine retinal sectors in Atlantic puffins and Leach's storm petrels. Since the C and T oil droplets types were difficult to distinguish from each other, the two were merged as one type termed CT in this study.

Species	Retinal sectors	Oil droplet type (%)			
		P-type	R-type	Y-type	CT-type
Atlantic puffins					
	1	39.5	25.6	19.6	15.8
	2	38.4	26.5	17.9	17.2
	3	39.8	24.5	21.0	15.2
	4	36.9	26.7	22.0	14.6
	5	36.8	28.0	23.0	12.1
	6	35.4	25.3	25.0	14.4
	7	39.9	25.2	21.9	13.5
	8	37.0	26.9	22.5	14.2
	9	37.0	24.9	23.8	15.1
	All	37.8	25.9	21.8	14.6
Leach's storm-petrels					
	1	44.8	0.0	31.7	23.8
	2	42.8	0.0	30.7	26.8
	3	42.7	0.0	29.9	27.8
	4	42.8	0.0	29.8	27.6
	5	39.9	0.0	33.3	27.4
	6	40.9	0.0	31.8	27.7
	7	43.0	0.0	32.3	25.5
	8	42.3	0.0	29.8	26.3
	9	44.0	0.0	29.8	26.0
	All	42.6	0.0	30.0	26.5

CHAPITRE 6

Discussion

Dans le cadre de la présente thèse, nous avons caractérisé et comparé les structures et fonctions rétiniennes de deux espèces aviaires côtières partiellement nocturnes, soit le goéland à bec-cerclé et le goéland gris, d'une espèce marine principalement nocturne, l'océanite cul-blanc et d'une espèce marine diurne, le macareux moine. Cette étude nous a fourni des éléments d'appréciation des adaptations rétiniennes chez les oiseaux côtiers et marins à un mode de vie nocturne. D'une façon générale, les résultats que nous avons présentés dans le cadre de cette thèse ont démontré que chez les oiseaux côtiers et marins les activités nocturnes, qu'elles soient partielles ou qu'elles se manifestent de façon plus systématique et régulière, s'accompagnent d'adaptations du système visuel et plus particulièrement du système rétinien.

Premièrement, l'analyse histologique des rétines des espèces étudiées a mis en évidence l'existence d'une variation dans l'organisation structurelle de celles-ci en fonction du degré d'activité nocturne manifestée. Ainsi, cette analyse a permis de distinguer trois types différents d'organisation structurelle.

Le premier type est celui du macareux moine. Chez cette espèce, la rétine se caractérise par une densité élevée des cônes comparativement à celle des bâtonnets (77% de cônes pour 23% de bâtonnets pour l'ensemble de la rétine), avec un rapport cônes : bâtonnets de 3:1 pour l'ensemble de la rétine et de 5:1 pour la rétine centrale. De plus, elle se distingue par l'abondance de gouttelettes lipidiques colorées. Ainsi, nous avons pu distinguer des gouttelettes rouge (R), jaune (Y), pâle (P), claire (C) et transparente (T), ce qui indique la présence de cinq types de cônes chez cette espèce, soit les cônes simples L (associés aux gouttelettes R et avec un λ_{max} : 541-571 nm), les cônes doubles L (associés aux gouttelettes P), les cônes M (associés aux gouttelettes Y et avec un λ_{max} : 497-510 nm), les cônes S (associés aux gouttelettes C et avec un λ_{max} :430-463 nm) et les cônes UV (associés aux gouttelettes T et avec un λ_{max} : 362-426 nm) (Bowmaker, 1991; Thompson et al, 1992; Bowmaker et al., 1997). La présence de ces cinq types de cônes laisse donc supposer que cette espèce

possède au moins une vision tétrachromatique des couleurs et qu'elle possède peut-être également une capacité de vision des ultraviolets. Il faut cependant noter ici que sans une analyse microspectrophotométrique des pigments contenus dans les cônes qui possèdent des gouttelettes de type T, la vision des ultraviolets ne peut-être que suspectée chez cette espèce. En fait, le λ_{max} des pigments contenus dans ce type de cône varie considérablement en fonction des espèces. Ainsi, chez les anseriformes et les galliformes la valeur du λ_{max} de ces cônes se situe entre 415 et 426 nm, ce qui se rapproche plus du spectre du violet que de l'ultraviolet. En comparaison, chez les passeriformes et les psittaciformes le λ_{max} varie entre 355 et 380 nm, ce qui correspond plus au spectre des ultraviolets (Hart, 2001). La rétine du macareux moine se caractérise également par une couche nucléaire interne deux fois plus épaisse que la couche nucléaire externe. Cette organisation structurelle est typique des rétines qui sont constituées principalement de cônes et indique que les connections synaptiques entre les cônes et les cellules bipolaires sont de type linéaires. Chaque cône fait synapse avec une seule cellule bipolaire. Ce type d'organisation permet une meilleure acuité visuelle (capacité de distinguer de fins détails), car chaque signal transmis est unique et n'est pas transformé par d'autres signaux qui peuvent se superposer (Ali et Klyne, 1986). La couche plexiforme interne et celle des fibres nerveuses sont également très épaisses chez cette espèce. De façon générale, ce type d'organisation se compare à celle d'autres oiseaux essentiellement diurnes comme le goéland argenté (*Larus novaehollandiae*) et la sterne commune (*Sterna hirundo*) et marque une adaptation à un mode de vie diurne (Hart, 2001).

Le deuxième type correspond à la rétine de l'océanite cul-blanc. Celle-ci possède une densité de bâtonnets plus élevée que celle des cônes (52% de bâtonnets pour 48% de cônes), avec un rapport cônes : bâtonnets de 0:8 pour l'ensemble de la rétine et de 0:9 pour la rétine centrale et une très faible proportion de gouttelettes lipidiques colorées. En fait, l'analyse histologique a révélé que seul les cônes associés aux gouttelettes lipidiques de type P, Y et C, soit les cônes doubles L, les

cônes M et les cônes S, sont présents dans la rétine de l'océanite cul-blanc. L'abondance de cônes doubles observée chez cette espèce permettrait une meilleure détection de proies dans des conditions de faibles intensités lumineuses (Hart, 2001). En effet, bien que le rôle des cônes doubles soit encore mal définie, de plus en plus d'évidences indiquent que ces photorécepteurs optimisent les contrastes spatiaux dans des environnements lumineux où les contrastes ne sont pas marqués, comme par exemple dans les environnements où les intensités lumineuses sont faibles (Maier and Bowmaker, 1993; Vorobyev and Osorio, 1998; Campenhausen and Kirschfeld, 1998; Hart, 2001). La rétine de l'océanite cul-blanc se caractérise également par une couche nucléaire interne de même épaisseur que la couche nucléaire externe. Ce qui est généralement caractéristique des rétines composées principalement de bâtonnets et indique un certain degré de convergence des bâtonnets sur les cellules bipolaires (Ali et Klyne, 1986). L'ensemble de ces caractéristiques structurelles se rencontrent chez plusieurs espèces nocturnes, comme certains rapaces et marque une adaptation à un mode de vie nocturne (Walls, 1967; Roze et al., 1990).

Les rétines du goéland à bec-cerclé et du goéland gris représentent le troisième type. Chez ces deux espèces, les cônes prédominent sur l'ensemble des photorécepteurs (70% de cônes pour 30% de bâtonnets), tout comme chez le macareux moine, cependant le rapport cônes : bâtonnets est beaucoup plus petit que chez cette dernière espèce. Ainsi, pour l'ensemble de la rétine ce rapport est de 2:1 et de 3:1 pour la rétine centrale. La densité de bâtonnets est donc presque deux fois plus élevée dans la rétine centrale chez ces deux espèces que chez le macareux moine, ce qui leur confère une plus grande sensibilité en condition de faibles intensités lumineuses. De plus, chez ces deux espèces, les bâtonnets se distribuent de façon homogène sur l'ensemble de la rétine, ce qui pourrait favoriser une sensibilité uniforme de la rétine. Tout comme chez le macareux moine nous avons pu observer chez les deux espèces de goélands la présence de cinq types de gouttelettes lipidiques. Ainsi, nous avons pu distinguer des gouttelettes de type R, Y, P, C et T, ce qui indique la présence de cônes L simples et doubles, de même que de cônes M, S et

UV. Tout comme pour le macareux moine la présence de ces cinq types de cônes laisse supposer que les deux goélands possèdent au moins une vision tétrachromatique des couleurs et peut-être une vision dans le spectre de l'ultraviolet. Cette organisation rétinienne marque donc une adaptation à un mode de vie diurne, mais présente également, par la densité et la distribution des bâtonnets, des éléments adaptatifs à un mode de vie partiellement nocturne.

Il est intéressant de souligner ici la différence qui existe entre les deux espèces de goélands quant aux proportions et distributions topographiques des différents types de cônes. Ainsi, dans le troisième article nous avons vu que la rétine centrale du goéland gris contient une plus grande proportion de cônes doubles que celle du goéland à bec-cerclé (48% comparativement à 28%). Le goéland gris se nourrissant presque exclusivement à l'aube (Guerra, 1987), la proportion élevée de cônes doubles dans la rétine centrale faciliterait la quête alimentaire dans des conditions de faibles intensités lumineuses et représente très certainement un élément adaptatif supplémentaire à un mode de vie nocturne. De plus, nous avons pu observer que chez le goéland gris les cônes simples L sont plus abondants dans la rétine dorsale (les secteurs 1 et 4) et les cônes M plus nombreux dans la rétine ventrale (selon un axe antério-postérieur ; secteurs 3, 6 et 9), alors que chez le goéland à bec-cerclé ces deux types de cônes sont distribués de façon uniforme. Chez le goéland gris, cette distribution topographique permettrait de mieux percevoir les proies à travers l'eau. Les gouttelettes lipidiques R associées au cônes simples L réduisent en effet les reflets lumineux à la surface de l'eau en agissant comme des filtres (Muntz, 1972; Goldsmith and al., 1984; Hart, 2001). D'une façon générale, ces résultats suggèrent que les deux espèces subissent des contraintes visuelles différentes dans leur environnement lumineux respectif.

Enfin, soulignons que l'observation au microscope électronique de la rétine du goéland gris à permis de confirmer que cette espèce ne possède pas de *tapetum lucidium*. En effet, bien que certains auteurs aient rapporté que l'œil de cette espèce

luit dans la nuit, aucune étude histologique n'avait jusqu'à ce jour documenté la présence d'une telle structure chez cette espèce. Cette membrane que l'on retrouve chez plusieurs espèces de vertébrés nocturnes, réfléchit et renvoie une partie de la lumière vers les photorécepteurs et permet par le fait même d'augmenter la sensibilité rétinienne (Walls, 1967). Elle représente donc une adaptation à un mode de vie nocturne. Chez les oiseaux, cette membrane a été observée uniquement chez quelques espèces de Caprimulgidae (Nicol et Arnott, 1974).

Au niveau fonctionnel nous avons également pu observer une variation entre les différentes espèces étudiées, cependant les résultats que nous avons obtenus ne permettent pas d'établir de corrélation nette entre cette variation, les variations structurelles observées et le mode de vie nocturne ou diurne.

Ainsi, bien que les deux espèces de goélands possèdent une structure rétinienne identique (70% de cônes et 30% de bâtonnets chez les deux espèces), nous avons montré qu'il existe entre ces deux espèces une différence dans l'organisation fonctionnelle de leur rétine. Le tableau 1 présenté dans le premier article montre en effet que les paramètres d'amplitude maximale des ondes scotopiques *a* et *b* de l'ERG, soit les paramètres R_{max} et V_{max}, ont des valeurs moyennes plus élevées chez le goéland à bec-cerclé que chez le goéland gris. Nous avons également vu dans le quatrième article (voir tableau 1) que chez le macareux moine la valeur moyenne de R_{max} est nettement supérieure a celle mesurée chez l'océanite cul-blanc. Ici, nous nous attendions à ce que la valeur de ce paramètre soit supérieure chez l'océanite cul-blanc comparativement au macareux moine, puisque la rétine de l'océanite est majoritairement composée de bâtonnets (52% de l'ensemble des photorécepteurs chez cette espèce sont des bâtonnets) et que l'amplitude d'un signal est généralement considérée comme étant proportionnelle au nombre et à la densité des récepteurs stimulés (Armington, 1974; Hood et Birch, 1993). De plus, la comparaison des valeurs moyennes des paramètres de sensibilité rétinienne scotopique S et σ montre qu'il n'y a pas de différence significative entre le macareux moine et l'océanite cul-

blanc. Encore une fois, nous nous attendions à ce que l'espèce la plus nocturne, soit l'océanite présente une plus grande sensibilité rétinienne scotopique que l'espèce essentiellement diurne puisque la densité relative de bâtonnets est plus grande chez le l'océanite que chez le macareux moine.

L'analyse des enregistrements d'ERG a également montré qu'il existe une différence entre les deux espèces de goélands dans l'organisation des mécanismes qui régissent le processus d'adaptation à l'obscurité. Ainsi, dans le premier article nous avons montré que chez le goéland à bec-cerclé le processus d'adaptation à l'obscurité se caractérise par deux mécanismes qui procèdent de façon différente à la baisse du seuil de sensibilité de la rétine. Le premier mécanisme, tel que mesuré par l'onde *a*, étant relié à la régénération de la rhodopsine, et le deuxième, tel que mesuré par l'onde b, étant relié à un phénomène nerveux intrinsèque au circuit nerveux rétinien (Rushton and Cohen, 1954; Dowling, 1963; Fain et al., 2001). Chez le goéland gris, aucun mécanisme nerveux post-récepteurs n'a été identifié lors de nos expériences ce qui suggèrent que l'organisation des circuits nerveux rétiniens des deux goélands diffère considérablement, bien que les deux espèces aient des densités relatives de cônes et de bâtonnets identiques. De plus, nous avons vu que chez le goéland gris, le seuil de sensibilité de la rétine (niveau de saturation) était atteint beaucoup plus rapidement (approximativement 30 minutes plus rapidement) que chez le goéland à bec-cerclé, ce qui confère au goéland gris un certain avantage écologique. En effet, à l'équateur, la transition entre le jour et la nuit est plus rapide que dans les zones tempérées (Almanac astronomique, 1996), la capacité d'atteindre rapidement le seuil maximal de sensibilité rétinienne semble donc être très avantageux pour le goéland gris qui est particulièrement active pendant ces périodes de transition (Guerra, 1987) et représente certainement une adaptation à son environnement lumineux particulier.

Nos résultats ont également pu mettre en évidence que la sensibilité rétinienne des deux goélands est modulée par des rythmes circadiens mais que l'organisation fonctionnelle de ces rythmes diffère entre les deux espèces. Ainsi, nous avons montré

que chez le goéland à bec-cerclé, les cônes dominent les réponses scotopiques pendant le jour, alors que chez le goéland gris les bâtonnets dominaient les réponses scotopiques, la nuit les bâtonnets dominant les réponses d'ERG chez les deux espèces. Ces résultats suggèrent que chez le goéland à bec-cerclé l'organisation fonctionnelle de la rétine est régie par un rythme circadien où les cônes bloquent la transmission de signaux des bâtonnets au niveau de la rétine interne, tandis que chez le goéland gris des mécanismes circadiens ne semblent pas être impliqués dans les changements de l'organisation fonctionnelle de la rétine. La différence que nous avons observée entre les deux espèces semble s'expliquer par une adaptation à l'environnement lumineux particulier dans lequel chacune des deux espèces ont évoluées.

Finalement, nos données d'ERG ont également montré que les deux goélands possèdent une sensibilité spectrale différente. Ainsi, chez le goéland à bec cerclé, la courbe de sensibilité spectrale scotopique atteint un pic de sensibilité entre 550 et 600 nm, alors que chez le goéland gris ce pic se situe entre 500 et 525 nm. Les résultats obtenus chez le goéland à bec-cerclé laisse supposer que chez cette espèce, les cônes simples L contribuent aux réponses scotopiques d'ERG. En fait, plusieurs études ont montré que chez certaines espèces de vertébrés, les bâtonnets et les cônes simples L font synapses sur les mêmes cellules bipolaires et qu'en condition scotopique les signaux des deux récepteurs empruntent les mêmes voies nerveuses (Nussdorf et Powers, 1988 ; Ribelayga et al., 2002). Encore une fois les résultats que nous avons obtenus pour la sensibilité spectrale suggèrent que les deux goélands bien qu'ayant une densité relative de cônes et de bâtonnets identiques possèdent une organisation de leurs réseaux nerveux rétiniens très différente.

Selon Martin (1990), malgré sa grande plasticité, le système visuel possède ses limites et ne peut guider à lui seul l'ensemble des comportements nocturnes manifestés par les différentes espèces aviaires. Ainsi, chez plusieurs espèces nocturnes on observe, parallèlement à une spécialisation du système visuel, la présence d'autres adaptations. Plusieurs espèces ont en effet développé au cours de

leur évolution une spécialisation de certains autres systèmes sensoriels de même que des stratégies comportementales qui leur permettent de maximiser leurs chances de survie et de reproduction, tout en occupant des niches écologiques nocturnes.

Ainsi, chez plusieurs espèces nocturnes de l'ordre des Strigiformes, on observe un élargissement des structures du tympan, de l'oreille interne et de la cochlée, comparativement aux espèces diurnes. Cet élargissement permettrait une meilleure perception des sons et faciliterait la capture de proies la nuit (Martin, 1990). L'audition semble également jouer un rôle important chez plusieurs espèces nocturnes d'Alcidés. Ainsi, lors des visites nocturnes des aires de nidification, la reconnaissance entre individus, de même qu'entre partenaires d'un même couple, semble se faire essentiellement par des vocalisations de fréquences et d'amplitudes très spécifiques (Jones et al.,1989). De façon similaire, chez certaines espèces de puffins, de fulmars et de pétrels nocturnes l'olfaction semble jouer un rôle important lors de la quête alimentaire nocturne. L'élargissement des structures olfactives permettrait à ces espèces de localiser la nuit, grâce à des signaux olfactifs, leurs aliments ainsi que leurs sites de quête alimentaire et de nidification (Grubb, 1972, 1974; Hutchinson et Wenzel, 1980; Bang et Cobb, 1968; Bang, 1971; Lequette et al., 1989). Aussi, chez plusieurs autres espèces d'oiseaux aquatiques on retrouve au niveau du bec et de la langue de nombreux récepteurs tactiles (Berkhoudt, 1980; Gottschaldt, 1985). Chez un bon nombre de Scolopacidés nocturnes (*Limnodromus, Gallinago, Calidris*, etc.), la présence de ces récepteurs favoriserait la quête alimentaire nocturne (McNeil et al., 1996).

Plusieurs autres espèces ont quant à elles développé au cours de leur évolution des stratégies comportementales leur permettant d'occuper des niches écologiques diurnes et/ou nocturnes. C'est le cas du grand chevalier (*Tringa melanoleuca*) et du chevalier a pattes jaunes (*T. flavipes*) qui utilisent deux types de stratégies de quête alimentaire selon qu'ils sont actifs de jour ou de nuit. Ainsi, ils acquièrent leurs aliments soit visuellement de jour soit tactilement de nuit (Gross-Custard, 1970;

Rojas et al., 1993). De même, l'avocette (*Himantopus himantopus*), bien que principalement visuelle, elle s'alimente de façon tactile lors des nuits sans lune (McNeil et Robert, 1988, 1992; Robert et McNeil, 1989).

Finalement, différents facteurs environnementaux peuvent également favoriser l'occupation de niches écologiques nocturnes. Selon Martin (1990), dans les milieux ouverts, comme les milieux marins, l'intensité lumineuse ambiante mesurée la nuit est suffisante pour induire des réponses visuelles chez les espèces qui possèdent des adaptations visuelles qui leur confèrent une bonne capacité de vision nocturne. De même, les espèces territoriales semblent avoir plus de facilité à se repérer la nuit du fait qu'ils connaissent bien leur territoire (Martin, 1990). Il devient donc impératif de considérer tous ces facteurs écologiques lorsque l'on aborde le phénomène de la nocturnalité chez les oiseaux.

Au point de vue purement méthodologique, l'utilisation de la technique d'ERG pour caractériser et comparer les fonctions rétiniennes des quatre espèces côtières et marines étudiées, a permis d'établir qu'il existe d'importantes différences fonctionnelles entre ces espèces, cependant ces résultats ont monté une certaine disparité avec les données histologiques. Cette disparité peut s'expliquer par le fait que les différentes ondes de l'ERG ainsi que leurs caractéristiques varient en fonction de la proportion de bâtonnets et de cônes contenus dans la rétine mais aussi en fonction de l'organisation du réseau nerveux rétinien, cette organisation variant considérablement d'une espèce à l'autre. Très peu d'études se sont intéressées à étudier dans une perspective comparative l'organisation rétinienne de différentes espèces aviaires. De telles études pourraient être une prochaine étape dans la compréhension de vison chez les oiseaux et représenteraient un complément à la présente thèse.

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