

SYNCHRONY OF DOLPHIN EYE MOVEMENTS AND THEIR POWER DENSITY SPECTRA

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Abstract—1. In the laboratory, eye movements in the horizontal and vertical planes of a normal human and two adult dolphins, *Tursiops truncatus*, were analyzed and compared. Several of the visual conditions included structured, unstructured and moving stimulus fields.

2. Power spectral density analyses of the dolphin eye movements showed maximal power around 0.1 Hz, lower than the human counterpart.

3. Coefficients of determination (r^2) and correlation coefficients (r) derived from autocorrelation and crosscorrelation of dolphin eye signals produced typically small values scattered randomly around zero.

4. From 51,200 correlations, the greatest r^2 value indicated that movements of one dolphin eye predict no more than 30% of the movement variance of the fellow eye.

5. Although dolphin eyes are mobile at lower fundamental frequencies than in humans, there is a low level of synchrony between the two eyes.

INTRODUCTION

Important contributions are made to the synchrony of human eye movements by the balanced innervation and extraocular musculature. The resulting conjugate nature of human eye movements has been formalized as Hering's Law and is described in detail by Alpern (1969). Notwithstanding the lack of information on motor innervation, Walls (1963) considered the dolphin, *Tursiops truncatus* eye and the eyes of whales in general to be "immobile" and incapable of "binocular cooperation". While eye movements have never been measured, observations by Lilly have been described by Hedinger (1969) who claims that dolphins may sleep with one eye closed. McCormick (1969) also noticed eye independence to the extent that one eye might look forward and dorsal while the opposite eye might look to the rear and ventral. More recent observations on eye movements of dolphins in the laboratory (Dawson, in press) describe a relatively independent protractor-retractor function which provided for the retraction of the left eye of a *Tursiops* several cm into the head while the contralateral eye lid was open with the eye scanning the environment.

We have measured the electrical analog of eye movements in 2 adult dolphins, *T. truncatus*, under laboratory conditions and find, in comparison to a normal human subject, that dolphin eye movements are at frequencies lower than those of humans and are not conjugate.

METHODS AND MATERIALS

The experimental animals were 2 adult dolphins, *T. truncatus*, one male (animal JA) and one female (animal JE). On separate days, the dolphins were brought into the laboratory and rested in a special retaining sling with deep foam cushions for best weight distribution and were covered with wet toweling. All the exposed areas were kept cool and moist by frequent water sprayings. Controlled illumination in the laboratory provided 376 lx at eye level.

Walls were painted flat white and were at 2 m from the eyes.

Eye movement potentials were recorded bilaterally using bipolar Jelliff Alloy C wire (Ni, Cr, Fe alloy; Jelliff Metals, Inc., South Port, CN) electrodes in pairs on the horizontal axis 1.0 cm from the inner and outer canthus of the eye and vertically 2.5 cm above and below the eye's geometric center. The measuring technique takes advantage of the standing potential found along the axis of mammalian eyes and which presents a varying potential to electrodes placed in the horizontal and vertical planes when the eye moves in those planes (Alpern, 1969; Krogh, 1979). The procedures, measurement accuracies and variability associated with this type of recording and several others have been described by Young & Sheena (1975) and by Alpern (1969). Young & Sheena claim an accuracy of 1.5° for this recording technique following calibration. More recently, Connolly & Kleinman (1978) report accuracy of 1° or better in the measurement of eye movements. Several other techniques for the measurement of eye movements with greater accuracy and stability have been described (1969), but these sacrifice sensitivity for range which rarely exceeds 20°, require optical connections to the eye such as contact lenses, or are extremely expensive.

The anterior electrode of each pair was positive on the horizontal axis, and the dorsal electrodes were positive on the vertical. Consequently, the horizontal movement, gaze forward would produce a relative positive potential in the horizontal amplifier. A gaze-upward eye movement would produce a relative positive potential in the vertical amplifier. Two pairs of recording electrodes for each eye provided a vertical and horizontal data channel whose signals were amplified 10,000× by Grass model 78D polygraph amplifiers with a passband of 0.1–1000 Hz (3 dB points). The pre-amplified signals were recorded on 4 channels of an Ampex FR 100 FM tape recorder with voice annotation channel. Records of the electrical signals produced by movements in the horizontal and vertical planes were made from both animals under several visual conditions. These were: illumination of the environment without stimulus manipulation; total darkness; one eye illuminated with the fellow eye covered by an opaque suction cup; vertically or horizontally oriented high contrast grating (1.9 cm black and 1.5 cm white alternating stripes)

presented to one or both eyes, moving (0.5–1.5 Hz; 45° sinusoidal displacements) and stationary. The striped fields subtended $54 \times 61^\circ$ visual angles at 15 cm from the eye. Both animals were tested under all visual conditions. More records and repetitions with an unorganized visual environment were made from dolphin JE while those records from dolphin JA tend to emphasize grating stimuli. The duration of each visual condition was long enough to assure a 2-min data sample after eliminating some tape regions which contained large electrical artifacts caused by blinks and gross body movements. Sixteen complete records were available from JE and 34 records from JA. Each record consisted of a horizontal signal from the right (OD) and left (OS) eyes and a vertical signal from OS and OD, respectively.

Each of these 4 signals from FM tape was digitized and stored on disc by a general purpose computer. Power density spectra (mW by frequency) were calculated on each record in order to better understand the frequency characteristics of the movements of the dolphin eye under the various conditions. Then, crosscorrelograms were calculated for either the horizontal or vertical signal components. Briefly, a horizontal movement crosscorrelogram was calculated by loading both horizontal signals into core. Each record occupied 1024-core addresses. Under a subroutine, a 512 address window was defined beginning with address 0 in the first signal block and ending with address 511 in that signal block. Those addresses contained in the window were then correlated to produce a single Pearson r value with respect to the first 512 addresses in the second signal, in the upper core memory block. The r value calculated in this fashion would be designated as " τ_0 " ($\tau = 0$) and indicative of 0 temporal shift between the two correlated data blocks. The second Pearson r was calculated similarly except that the "window" was shifted to the right (117 msec or one address) in data block No. 1. The coefficient r calculated at this time represented τ_1 . Subsequently, 510 other r values were calculated to characterize the similarity of these two signals. It may be seen that similarities in the signals, offset in time (phase shifted) would be represented in the crosscorrelogram as a high correlation for the appropriate τ value. The majority of the data comparing movements of the two eyes was analyzed by crosscorrelation technique. Some signals were autocorrelated. Autocorrelation provides an excellent method of detecting "rhythmicity" in a signal. A brief theoretical discussion of the analytic methods is provided by Gaskill (1978).

As a methodological "calibration" and for comparison purposes, several of the measures and analyses were performed on data from a single human male volunteer. The volunteer was 28 yr of age, was in good health, and had normal corrected vision with no history of eye disease. The recording parameters were identical to those described for dolphins JE and JA. The positive electrode OD was placed at the temporal canthus rather than anteriorly for dolphin. Consequently, movements of the human subject's eyes to the right produced a positive signal in the horizontal plane electrodes while moving the dolphin's eyes forward produced a positive signal in the horizontal electrodes. Human records were made in total darkness or during viewing a white field with an illumination of approximately 175 lx. Stimuli were provided to evoke following eye movements of 10° at a rate of 0.5 Hz. Analyses for human and dolphin data were similar.

For the dolphins, there were 50 record sets resulting in 2 crosscorrelations each and totaling 100 crosscorrelations. A power density spectrum was calculated for each of the 4 signals in every record totaling 200 power density spectra. Finally, each crosscorrelogram consisted of 512 correlations made between two 512 data point records. There was a total of 51,200 such correlations. For the human subject, there were three visual conditions from which 12

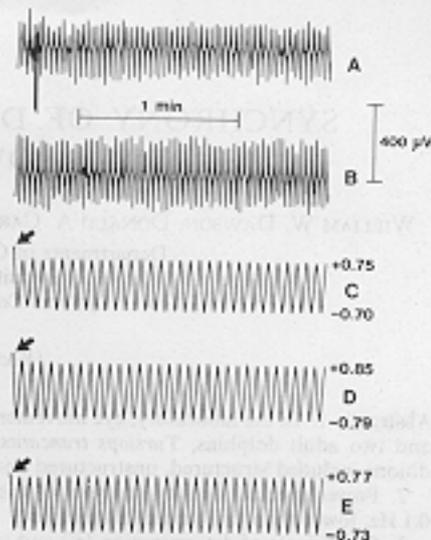


Fig. 1. Eye signal during human saccadic movements evoked by horizontal 10° target shifts at a 0.5 Hz rate. A, right eye signal in the horizontal plane. B, corresponding left eye signal. C, D, E, decimal values are correlation coefficient r . C, autocorrelation function of signals A. D, autocorrelation function of signals B. E, the crosscorrelation function of A, B. Arrows mark ± 0.5 shifts.

power density spectra were calculated for horizontal and vertical signals. Six crosscorrelograms and 4 autocorrelograms were calculated resulting in a total of 5120 Pearson r coefficients.

RESULTS

Figures 1–4 describe human data and its analysis which will be used as perspective for results from the dolphins where signals were taken under similar conditions and analyzed in a similar fashion. Signals (Fig. 1) were produced by horizontal eye movements (saccades) from the left (B) and right (A) eyes following

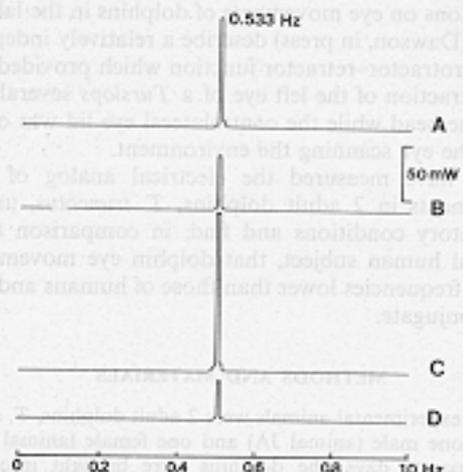


Fig. 2. A, C, power density spectra of signals in Fig. 1A, B. D were calculated from the vertical signals recorded simultaneously with signals Fig. 1A, B. Axis calibrations refer to A–D.

10° target shifts in the horizontal plane which occurred at a rate of approximately 0.5 Hz. The 10° movement gave about a $350 \mu\text{V}$ (peak-peak) analog potential. Irregularities embedded within the raw data signals (A and B) are indicative of small eye movements and jerks. The extent to which there is consistency in the repeating of a signal in record A is indicated by the autocorrelogram (C) in which A was correlated with itself. The expected $r = +1.0$ peak at τ_0 is marked by the arrow to the left. Values for the correlation coefficient r are to the right and indicate the high degree of signal consistency within A. As in other analyses which will be presented, the r values to the right of the autocorrelogram are r for $\tau = 511$ and for the preceding negative minimum where the tau shift had provided a 180° phase shift condition. Autocorrelogram (D) indicates a somewhat higher internal consistency in the horizontal signal components on the left eye. This is probably due to the early transients recorded in Fig. 1A. The extent to which the right and left eyes track one another in the horizontal plane is indicated by the crosscorrelogram result presented in E. The value at τ_0 in this case indicates the r value achieved when records A and B were correlated in the phase relations shown. Shifts of A with respect to B (τ_0 to 511) are indicated by the remainder of E. The uniformity of the positive and negative correlation peaks indicates no failure in agreement throughout two records. Calculation of power density spectra for the horizontal eye movement data (Fig. 1) yields the power densities shown in A and C (Fig. 2). Power density (mW) of vertical signals recorded simultaneously is shown in B and D. While the power density peak is shown to reflect the frequency of the eye movement-inducing stimuli, there was a harmonic (not shown) at just greater than 1 Hz.

It is valuable to compare Fig. 2 directly with the power densities produced by eye movements which occurred in the absence of a structured visual field. Fig. 3 represents the power densities at various movement frequencies produced by "wanderings" of the unstimulated human eye in light adaptation. There was very little power at frequencies above 1 Hz. Figure 4 demonstrates that in the absence of an organized visual field, the human eyes continue to track one another with high accuracy in the light (C and D) and with somewhat reduced accuracy in the dark (A and B). The lower correlation values at times other than τ_0 indicate that the movements are not repetitive and have no single fundamental frequency. Observation of spontaneous dolphin eye movements during recording indicated that the potential produced by a 10° movement is of the same order of magnitude as in human (Fig. 1). No direct measures of the eye standing potential of a dolphin have been made.

Figures 5-9 describe the findings and analyses of results on animal JA. Animals JE and JA final analyses are presented in Figs 10 and 11. There were no notable differences in the eye movement results from the 2 animals. Figure 5 shows raw signals produced by eye movements from the right (A) and left (B) eyes of dolphin JA during a period when vertical black and white bars were moved horizontally before the right eye. The left eye was covered with an opaque suction cup. Autocorrelation of the signal A in record C suggests a very weak repeating element within A.

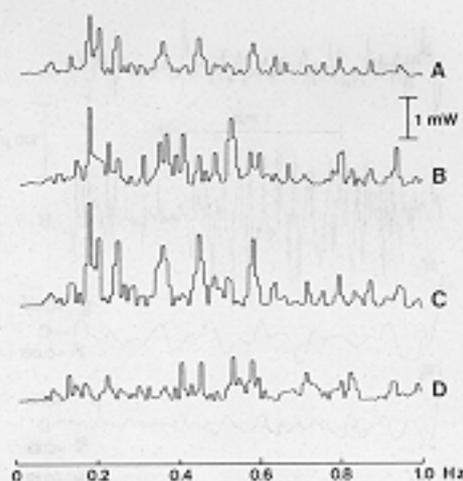


Fig. 3. Power density spectra for human eye movements in the horizontal and vertical planes when viewing a featureless illuminated surface. A, B, horizontal and vertical right eye. C, D, horizontal and vertical left eye.

Similar results were obtained and are presented in record D for the left eye. Crosscorrelation of records A and B indicate very low interrelationships, particularly at τ_0 (record E). Analysis of records A and B for power spectral density and for the simultaneously recorded vertical components are presented in Fig. 6. Peak power spectral densities for the dolphin records were in lower regions of the frequency domain than those of the human subject (Fig. 3) and were found

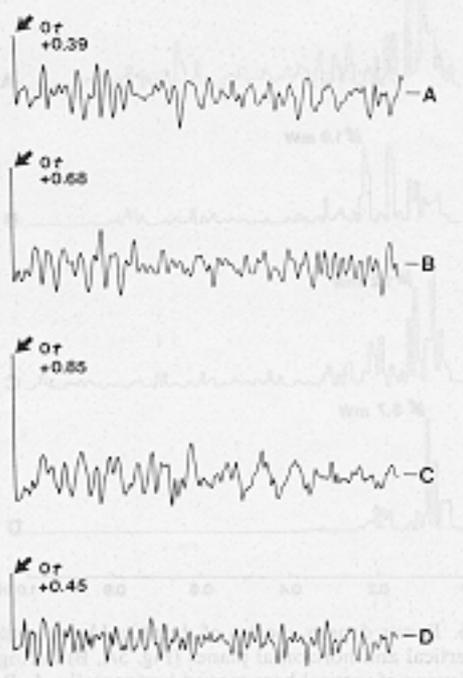


Fig. 4. Crosscorrelation functions for signals produced by the left and right human eyes viewing a featureless surface in darkness (A, B) and in light (C, D). A, C, horizontal signals crosscorrelograms. B, C, vertical signal crosscorrelograms. Each correlogram represents 512 τ shifts.

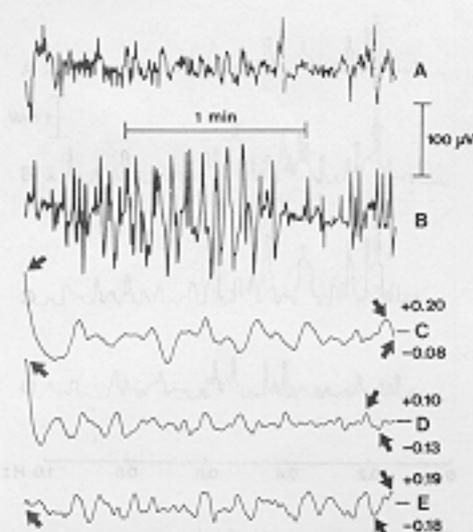


Fig. 5. Horizontal eye movement signals from dolphin JA during right eye stimulation by vertical bars moved horizontally, left eye covered. A, right eye. B, left eye. C, autocorrelation function of record A. D, autocorrelation function of record B. Crosscorrelation function of records A, B. Arrows to the left indicate $r(0)$ (C, D, E). Arrows to right mark points at which $\pm r$ values (shown) were measured. Lines at ends of C, D, E indicate $r = 0$. Time shifts for $\tau = 511$.

where peak power was approximately 0.2 Hz. All records from "stimulated" dolphin eyes produced power spectral densities like those shown in Fig. 6.

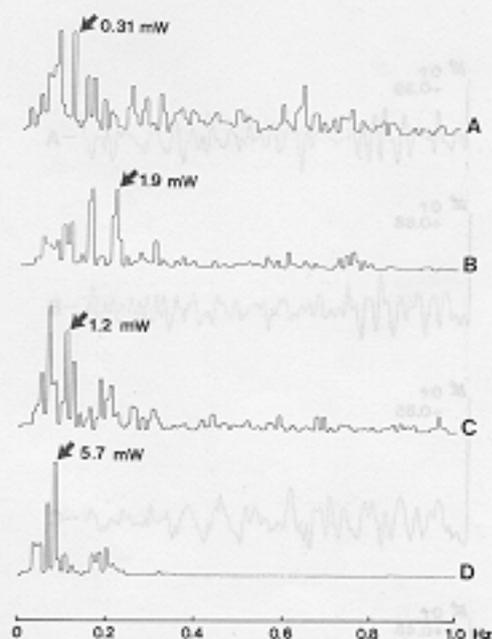


Fig. 6. Power density spectra of dolphin JA eye signals in the vertical and horizontal planes (Fig. 5A, B) during right eye viewing of vertical bars moved horizontally. A, B, from right and left eye signals, horizontal electrode orientation. C, D, from right and left eye, vertical electrode orientation. Arrows mark points of power density measurement indicating vertical scale magnification. Vertical axis scaling is not equal between records.

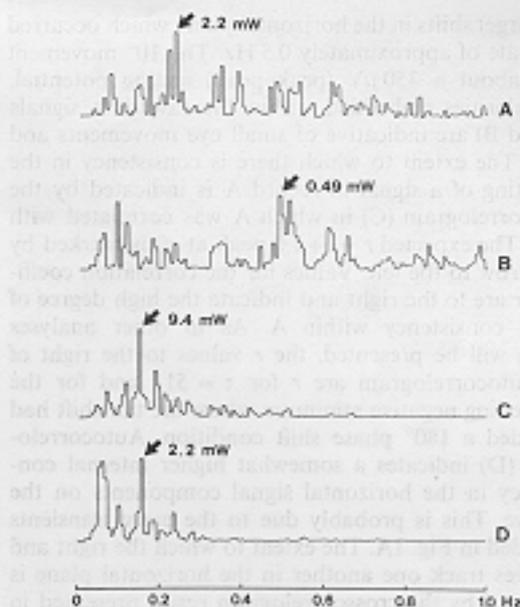


Fig. 7. Power density spectra of dolphin JA eye signal recorded in darkness. A and B are right eye horizontal and vertical, respectively. C and D are left eye horizontal and vertical, respectively. Otherwise as Fig. 6.

These results contrast sharply with the power spectral density calculated from the human stimulated eye data (Fig. 2). They bear more resemblance to the unstimulated human results (Fig. 3). However, when the dolphin eyes are completely unstimulated as in darkness, the power density spectra appear to "spread" to include higher frequencies such as in Fig. 7. Binocular

It is valuable to compare Fig. 7 directly with the power densities produced by eye movements which occurred in the absence of a structured visual field. Fig. 7 represents the power densities at various movement frequencies produced by eye movements of the unstimulated human eye in light and dark. Their was very little power at frequencies above 0.2 Hz. Figure 8 shows the power densities of the human eye in the dark. The human eye in the dark (A) and with somewhat reduced accuracy in the light (B) and with somewhat reduced accuracy in the light (C) and D). The lower correlation values and other than to indicate that the movements are not driven by a single fundamental frequency. Observation of spontaneous dolphin eye movements during recording indicated that the potential peak of a 10° movement is of the same order of magnitude as in human. The findings and analyses of the potential of a dolphin have been made. Figures 2-9 describe the findings and analyses of results on animal JA. Animal JA. A full analysis is presented in Fig. 10 and the results are no notable differences in the eye movements from the 10° movements. The eye movements produced by eye movements from the right (A) and left (B) eye of dolphin JA were moved horizontally below black and white bars moved horizontally below.

Fig. 8. Power density spectra of dolphin JA eye signals recorded in light binocularly viewing a featureless surface. Otherwise as Fig. 7.

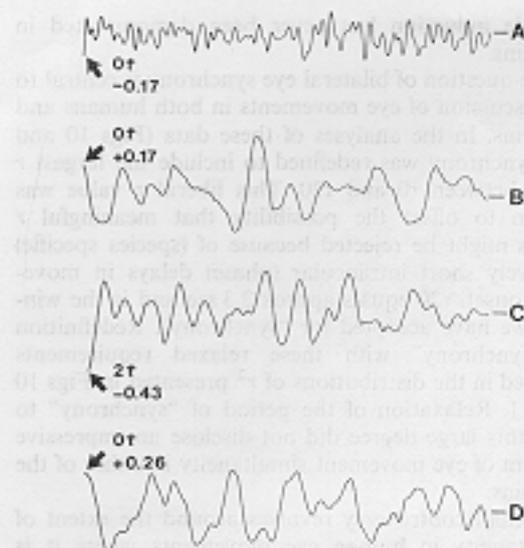


Fig. 9. Crosscorrelation functions of dolphin JA left and right eye signals in darkness (A, B) and in light binocularly viewing a featureless surface (C, D). Values of τ near τ_0 provide vertical axis calibrations. A and C represent horizontal plane. C and D represent vertical plane. Otherwise as Fig. 5C-E.

light adaptation of the dolphin produces power density spectra (Fig. 8) which are not distinctly different from those which are recorded when one or both eyes are viewing stationary or moving stripes (Fig. 6).

There is very little synchrony in either the horizontal or vertical eye movements of the dolphin in darkness (Fig. 9A and B). However, there is a slight increase in eye movement synchrony in light adaptation (Fig. 9C and D). These results do not compare well with the human cross correlations (Fig. 4) for similar conditions.

Data from animals JA and JE provided 50 records containing four sets of eye movement data each. These data and the resulting 100 crosscorrelograms and 200 power density spectra are in good agreement with the data sample which has been provided in Figs. 5-9. The human data in comparison with it are important because the correlation coefficient (r) becomes difficult to interpret when the number of observations contributing to it becomes very large as it has in these analyses (for $N = 511$, $P = 0.01$ when $r = 0.086$) (2). Thus, almost any similarities between data sets will provide a statistically significant r value when the number of data sets producing the r value is very large. A more useful statistic is the coefficient of determination (r^2) which is an estimate of the predictive value of variable x for variable y after the two have been correlated. $r^2 = 0.5$ would indicate that 50% of x variance could be predicted from y .

Figures 10 and 11 summarize data from dolphins JE and JA pooled into five general conditions: (1) illumination of both eyes in the absence of visual features in the fields seen by either eye; (2) both eyes in darkness; (3) one eye in featureless illumination with the other eye covered; (4) one or both eyes presented with horizontal stripes; and (5) one or both eyes presented with vertical stripes. r^2 conversions of the peak correlation coefficient r (between τ_0 and τ_{20})

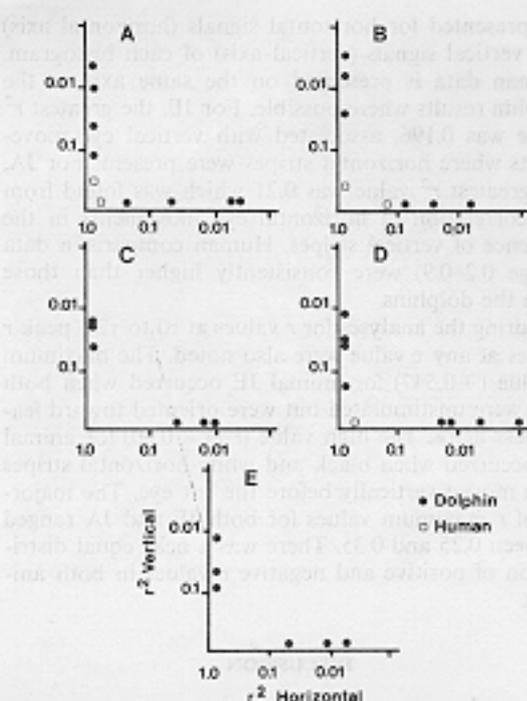


Fig. 10. r^2 values for the peak crosscorrelation (between τ_0 and τ_{20}) of eye movement signals in the horizontal and vertical planes. Animal JE. Data from five general conditions. A, both eyes illuminated with no organized near-field content. B, both eyes in darkness. C, one eye illuminated. D, one or both eyes viewing horizontally oriented stripes. E, one or both eyes viewing vertically oriented stripes. Comparable human results are in A, B, D.

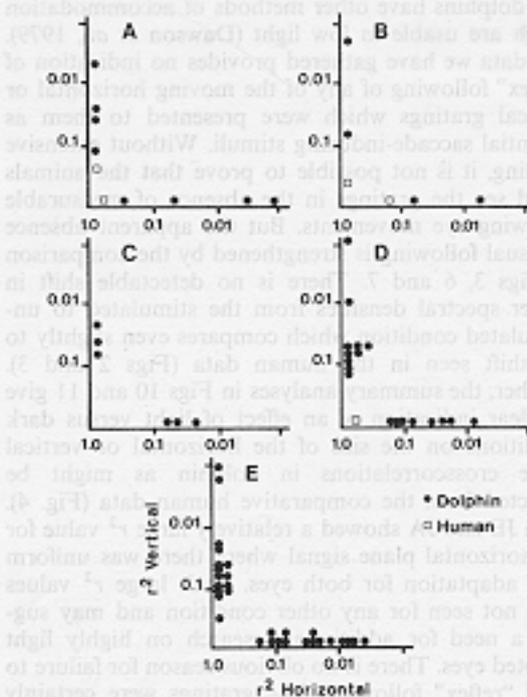


Fig. 11. r^2 values for crosscorrelations. Animal JA. Otherwise as Fig. 10.

are presented for horizontal signals (horizontal axis) and vertical signals (vertical axis) of each histogram. Human data is presented on the same axis as the dolphin results where possible. For JE, the greatest r^2 value was 0.196, associated with vertical eye movements where horizontal stripes were present. For JA, the greatest r^2 value was 0.21 which was found from the correlation of horizontal eye movements in the presence of vertical stripes. Human comparison data (range 0.2–0.9) were consistently higher than those from the dolphins.

During the analyses for r values at $\tau 0$ to $\tau 20$, peak r values at any τ value were also noted. The maximum r value (+0.547) for animal JE occurred when both eyes were unstimulated but were oriented toward featureless fields. The high value ($r = -0.60$) for animal JA occurred when black and white horizontal stripes were moved vertically before the left eye. The majority of r maximum values for both JE and JA ranged between 0.25 and 0.35. There was a near equal distribution of positive and negative r values in both animals.

DISCUSSION

There is agreement between laboratories that the optical condition of the dolphin's eye deteriorates toward a high myopia when the eye is out of the water (Dawson *et al.*, 1972; Dral, 1972). Behavioral research (Herman *et al.*, 1975) indicates that a mechanism exists for the correction of the high aerial myopia in very bright daylight conditions. Herman *et al.* (1975) postulated that the mechanism is the slit (stenopaic) pupil. However, that mechanism may not be effective under laboratory conditions where the typical ambient illumination is reduced by at least 2 log units (Dawson, in press). Further, there is evidence that dolphins have other methods of accommodation which are usable in low light (Dawson *et al.*, 1979). The data we have gathered provides no indication of "reflex" following of any of the moving horizontal or vertical gratings which were presented to them as potential saccade-inducing stimuli. Without extensive training, it is not possible to prove that the animals could see the gratings in the absence of measurable following eye movements. But the apparent absence of visual following is strengthened by the comparison of Figs 3, 6 and 7. There is no detectable shift in power spectral densities from the stimulated to unstimulated condition which compares even slightly to the shift seen in the human data (Figs 2 and 3). Further, the summary analyses in Figs 10 and 11 give no clear indication of an effect of light versus dark conditions on the size of the horizontal or vertical plane crosscorrelations in dolphin as might be expected from the comparative human data (Fig. 4). Both JE and JA showed a relatively large r^2 value for the horizontal plane signal where there was uniform light adaptation for both eyes. Such large r^2 values were not seen for any other condition and may suggest a need for additional research on highly light adapted eyes. There is no obvious reason for failure to elicit "reflex" following. The gratings were certainly outside the near point of the dolphin eye in air. Yet the "failure" is based on expectations consistent with visual motor control in terrestrial mammals. Reflex

saccade induction has never been demonstrated in dolphins.

The question of bilateral eye synchrony is central to the discussion of eye movements in both humans and dolphins. In the analyses of these data (Figs 10 and 11), synchrony was redefined to include the largest r value between $\tau 0$ and $\tau 20$. This liberal τ value was chosen to offset the possibility that meaningful r values might be rejected because of (species specific) relatively short intraocular (phase) delays in movement onset. $\tau 20$ equals approx 2.3 sec and is the window we have accepted for "synchrony". Redefinition of "synchrony" with these relaxed requirements resulted in the distributions of r^2 presented in Figs 10 and 11. Relaxation of the period of "synchrony" to even this large degree did not disclose an impressive amount of eye movement simultaneity in either of the dolphins.

A small controversy revolves around the extent of simultaneity in human eye movements where it is generally accepted that intraocular delays in human are rarely greater than 2 msec. Williams & Fender (1977) have reviewed the asynchrony controversy and together with new data conclude that binocular voluntary tracking in humans is nearly exact and exhibits mean errors less than ± 0.8 msec. Any significant departure from almost perfect synchrony in human eye movements has been interpreted in recent years to indicate the presence of central nervous system abnormality (Goldstein & Gupta, 1976; Kimm & MacLean, 1975; Mastaglia *et al.*, 1976).

The numerous "significant" correlations obtained from our dolphin records are probably a consequence of the very large sample size and similarities in intrinsic rhythmicities which might be expected in eyes innervated by the same central nervous system and with similar physical and motor characteristics. But there were very few similarities between dolphin and human eye movements whether binocular or monocular. The human eye movements typically contained higher signal power at higher frequencies. Eye signals crosscorrelated very highly in the human data when the movements were visually stimulated, somewhat less well in featureless light, and relatively poorly in darkness. The dolphin eye movements signal power peaked typically in lower regions of the frequency spectrum and showed little binocular agreement regardless of plane or condition of visual stimulation. We conclude that Walls' (1963) view of cetacean eye immobility was incorrect, but his estimated failure of "binocular cooperation" of eye movements seems consistent with our quantitative measurements.

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REFERENCES

- ALPERN M. (1969) Movements of the eye. In *The Eye*, Vol. 3 (Edited by DAWSON H.), p. 106. Academic Press, New York.
- BEYER W. (1969) *Handbook of Tables for Probability and Statistics*, p. 391. Chemical Rubber Company, Cleveland.
- CONNOLLY J. & KLEINMAN K. (1978) A single channel method for recording vertical and lateral eye movements. *EEG Clin. Neurophysiol.* **45**, 128–129.

- DAWSON W. W. (1980) The cetacean eye. In *Cetacean Behavior* (Edited by HERMAN L.), pp. 53-100. Wiley Interscience, New York.
- DAWSON W. W., ADAMS C. K., BARRIS M. C. & LITZKOW C. A. (1979) Static and kinetic properties of the dolphin pupil. *Am. J. Physiol.* **237**, R301-R305.
- DAWSON W. W., BIRNDORF L. & PEREZ J. (1972) Gross anatomy and optics of the dolphin eye (*Tursiops truncatus*). *Cetology* **10**, 1-12.
- DAWSON W. W. & PEREZ J. (1973) Unusual retinal cells in the dolphin eye. *Science* **181**, 747-749.
- DRAL A. D. G. (1972) Aquatic and aerial vision in the bottle-nosed dolphin. *Netherlands J. Sea Res.* **5**, 510-518.
- GASKILL J. (1978) *Linear Systems, Fourier Transforms and Optics*. Wiley, New York.
- GOLDSTEIN J. & GUPTA M. (1976) Abnormal eye movements in rubella syndrome. *J. Ped. Ophthalmol.* **14**, 281-283.
- HEDIGER H. (1969) Comparative observations on sleep. *Proc. R. Soc. Med.* **62**, 153.
- HERMAN L., PEACOCK M., YUNKER M. & MADSON C. (1975) Bottlenosed dolphin: double slit pupil yields equivalent under water diurnal acuity. *Science* **189**, 650-652.
- KELLY T. (1947) *Fundamentals of Statistics*. Harvard University Press, Cambridge.
- KIMM J. & MACLEAN J. (1975) Disconjugate eye movements during electronstagnographic testing in patients with known central nervous system lesions. *Ann. Otol.* **84**, 368-373.
- KROGH E. (1979) The corneofundal potential and the electrooculogram: aspects of normal physiology and variability. *Acta ophthalmol., Suppl.* **140**, 1-69.
- MASTAGLIA F., BLACK J. & COLLINGS D. W. R. (1976) Saccadic velocities in multiple sclerosis. *The Lancet* (December), 1359.
- MCCORMICK J. (1969) Relationship of sleep, respiration and anesthesia in the porpoise: a preliminary report. *Proc. natn. Acad. Sci. U.S.A.* **62**, 697-703.
- WALLS G. (1963) *The Vertebrate Eye and Its Adaptive Radiation*, pp. 412-413. Hafner, New York.
- WILLIAMS R. & FINDER D. (1977) The synchrony of binocular saccadic eye movements. *Vision Res.* **17**, 303-306.
- YOUNG L. & SHEENA D. (1975) Eye-movement measurement techniques. *Am. Psychol.* (March), 314-330.