

**VISUAL ACUITY IN THE BOTTLENOSE DOLPHIN**

VISUAL ACUITY IN THE BOTTLENOSE DOLPHIN,

TURSIOPS TRUNCATUS (MONTAGU, 1821)

by

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TURSIOPS TRUNCATUS, (MONTAGU, 1821)

## ABSTRACT

Visual acuity was studied, for the first time, in the bottlenose dolphin, Tursiops truncatus. Two methods were used, one involving a series of black squares of graded sizes (Experiment 1), the other using gratings of parallel lines of different widths (Experiment 2). The brightness variable introduced by the first set of cues did not appear to disturb the correlation of response with visual angle. Thresholds were obtained at 1, 2 and 3 metres in water and air in Experiment 1. In water, the threshold decreased with distance, the lowest being 6 minutes at 3 metres. The reduction of threshold might be caused by passing the nearpoint of accommodation, or by an improved binocular visual field at greater distances. In air, the thresholds were similar for three distances, averaging 33 minutes. Comparative tests on a human subject produced a visual threshold between 48 seconds and 1.75 minutes in air or with a mask under water, and 12.5 minutes at 1 metre in water. Experiment 2 gave a threshold of 13 minutes in water and 25 minutes in air, for five combined distances between 1 and 3 metres. The results were not considered valid, however, due to the haste with which they were collected. The human results obtained by this method were comparable to those in Experiment 1. The 6-minute threshold obtained for Tursiops by Experiment 1 compares well with the 5.5-minute threshold obtained for the California sea lion, and the 6-minute threshold of the Pacific whitesided dolphin.

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## TABLE OF CONTENTS

|                                                 |        |
|-------------------------------------------------|--------|
| INTRODUCTION                                    | Page 1 |
| 1. Natural History of <u>Tursiops truncatus</u> | 1      |
| 2. Visual Acuity: Methods of study              | 1      |
| 3. Visual Studies of Cetacea                    | 3      |
| 4. Echolocation in Cetacea                      | 4      |
| 5. Other Senses in Cetacea                      | 5      |
| 6. Vision in Cetacea                            | 7      |
| 7. Summary                                      | 7      |
| PROCEDURE                                       | 9      |
| 1. Apparatus                                    | 9      |
| 2. Experimental Method                          | 12     |
| RESULTS                                         | 16     |
| 1. General Observations                         | 16     |
| 2. Experiment 1                                 | 18     |
| 3. Experiment 2                                 | 30     |
| 4. Obtained Thresholds                          | 30     |
| 5. Results for Human Subject                    | 34     |
| DISCUSSION                                      | 39     |
| 1. Experiment 1                                 | 39     |
| 2. Experiment 2                                 | 41     |
| 3. Thresholds for Dolphin Visual Acuity         | 42     |
| 4. Human Data                                   | 43     |
| 5. Overview                                     | 44     |
| CONCLUSION                                      | 49     |
| BIBLIOGRAPHY                                    | 51     |
| Appendices                                      | 54     |

## LIST OF FIGURES

|           |                                                         |          |
|-----------|---------------------------------------------------------|----------|
| Figure 1. | Apparatus - parts A and B.                              | Page 10. |
| Figure 2. | Research tank - position of apparatus<br>parts A and B. | 10       |

## LIST OF TABLES

|          |                                                                                                           |          |
|----------|-----------------------------------------------------------------------------------------------------------|----------|
| Table 1. | Parameters for cue pairs - Experiment 1.                                                                  | 19       |
| Table 2. | Visual angle subtended by linear differences<br>between black squares of cue pairs -<br>Experiment 1.     | 21       |
| Table 3. | Percentage correct responses for cue pairs<br>used in Experiment 1.                                       | 22       |
| Table 4. | Visual angle subtended by one unit line of<br>cue pattern (B) - Experiment 2.                             | 31       |
| Table 5. | Percentage of correct response for pattern<br>discrimination - Experiment 2.                              | 32       |
| Table 6. | Thresholds for dolphin visual acuity at 75%<br>criterion.                                                 | 34       |
| Table 7. | Reflected brightness and visual angles subtended<br>by one unit line of cue pattern (A) - Human<br>study. | 35       |
| Table 8. | Human visual acuity: A - Experiment 1;<br>B - Experiment 2.                                               | 37<br>38 |
| Table 9. | Thresholds for Dolphin Visual Acuity at 65%<br>criterion (in minutes).                                    | 43       |

## LIST OF GRAPHS

|          |                                                                                                     |         |
|----------|-----------------------------------------------------------------------------------------------------|---------|
| Graph 1. | Percentage of correct response versus cue size for given visual angles - water - Experiment 1.      | Page 24 |
| Graph 2. | Percentage correct response versus cue size for given visual angles - air - Experiment 2.           | 25      |
| Graph 3. | Percentage correct response versus visual angle for given brightness ratios - water - Experiment 1. | 27      |
| Graph 4. | Percentage correct response versus visual angle for given brightness ratios - air - Experiment 1.   | 28      |
| Graph 5. | Percentage correct response versus visual angle - water - Experiment 2.                             | 33      |
| Graph 6. | Percentage correct response versus visual angle - air - Experiment 2.                               | 33      |

## INTRODUCTION

### 1. Natural History of Tursiops truncatus

The subject of the study with which this paper is concerned is the Atlantic bottlenose dolphin, Tursiops truncatus (Montagu, 1821). This is a species of small toothed whale, seldom exceeding twelve feet in length, of the family Delphinidae, suborder Odontoceti, order Cetacea. It is most commonly found off the east coast of the United States, though it has been sighted on both sides of the Atlantic, and the genus as a whole is found in all the major oceans (Gunter, 1942). Schools are seldom sighted in the open ocean, except when groups follow ships out to sea. They tend to remain in shallow coastal waters and estuaries. Like most cetaceans the species is gregarious, generally travelling in schools numbering from a few individuals to a hundred or more. They feed upon a variety of fish species, as described by Gunter (1942). The bottlenose dolphin is a fast and agile swimmer, suggesting well-developed senses, which makes it a good subject for a visual acuity study.

### 2. Visual Acuity: Methods of Study

Visual acuity is defined by Riggs (in Graham, 1965) as "the capacity to discriminate the fine details of objects in the field of view. It is specified in terms of the minimum dimension of some critical aspects of a test object that a subject can correctly identify." Riggs describes four types of tasks designed to measure

visual acuity: detection, recognition, localization and resolution.

The first three types of task probably involve parameters other than visual acuity, such as visual sensitivity or central associative processes. Thus the fourth type of task, resolution, is generally considered to give the most reliable results and is therefore the most frequently used.

The resolution task requires a response to a separation between elements of a test pattern. The most acceptable patterns used are gratings of parallel lines or checkerboards. Sometimes a single pair of lines or a pair of dots are used, but these test patterns probably require a detection process involving visual sensitivity rather than a resolution process. In this task, visual acuity is defined as the reciprocal of the visual angle subtended by the distance between two elements of a test pattern. The visual angle, or minimum angular resolution (MAR) is the unit in which results are recorded as a rule.

Two approaches have frequently been used for resolution tasks. One is an involuntary optomotor response used to test some invertebrates (Hecht and Wolf, 1929; Hecht and Wald, 1934) and in one case to compare visual acuity in a variety of vertebrates (Warkentin, 1937). The other is the more common discrimination learning task, in which a simultaneous or successive discrimination of two test patterns is required. Generally, a parallel line grating is used against another grating of a different orientation or a uniform standard of the same brightness as the test pattern.

### 3. Visual Studies of Cetacea

The subject of vision has been relatively unexplored in Cetacea until recently. There is very little published work on this subject. Kellogg and Rice (1966) did some work on shape discrimination and visual problem solving in the bottlenose dolphin, and concluded that shape discrimination was excellent underwater. The observed behaviour of the animal during discriminations led them to suspect a lack of binocular vision in the animal, and they also discussed the possibility of an inability to accommodate. However, they did no direct work on visual acuity.

Spong and White (1969, 1971) did visual acuity studies on the killer whale, Arcinus orca, and the Pacific whitesided dolphin, Lagenorhynchus obliquidens. They used a two-way simultaneous discrimination procedure for a resolution task involving a single pair of parallel lines, and obtained an MAR of 6.0 minutes for Lagenorhynchus. This is roughly comparable to the result obtained for the sea lion, Zalophus californianus (Schusterman, 1970), using the more-accepted parallel-line grating.

More indirect observations on Cetacean vision have been made by various people. McBride and Hebb (1948) stressed the apparent dependence on vision shown by captive bottlenose dolphins. McBride and Kritzler (1951) and Essapian (1953) both observed that a dolphin's eyes are open at birth and vision appears to be good. Schevill and Lawrence (1956) observed a strong dependence on vision for food finding in captive Tursiops. There have also been observations on use of vision by a

captive pilot whale (Kritzler, 1952) and by the Amazon River dolphin (Layne and Caldwell, 1964; Caldwell, 1966). Most authors agree that there appears to be a good deal of dependance on vision during normal, diurnal activity.

#### 4. Echolocation in Cetacea

Contrasting with the reports of dependance on vision stated above are the more prolific reports on the use of echolocation by cetaceans, especially Tursiops. Kellogg (1953) specified three criteria for its existence in whales: a) whales must be able to hear well and in a suitable frequency range for detection of echoes; b). they must be able to emit sounds of suitable temporal and frequency patterns; and c) proof must be shown that they actually employ these abilities in a functional manner.

Schevill and Lawrence (1953) satisfied the first criterion with their audiogram of Tursiops, which showed a hearing range up to 120 Kc/sec. Kellogg (1953) recorded click vocalizations in this species, having a wide band frequency, ranging up to 120 Kc/sec or higher. Kellogg demonstrated the use of click emissions under poor visibility conditions (1958) and was supported by Norris (1961) who experimented with the use of visual and acoustic "blindfolds" in Tursiops. Norris (1964) also described various anatomical adaptations for the transmission and reception of echolocation signals, involving the bone structure of the skull and the presence of a fatty melon on the forehead, which he postulated acted as an acoustic lens.

## 5. Other Senses in Cetacea

Hearing thus appears to be extraordinarily useful in at least some cetaceans. The other senses as described by Slijper (1962), appear to be rather less well developed. Olfaction is totally absent, the entire system being absent in toothed whales and drastically reduced in baleen whales. Gustation has fared no better according to past reports on the absence of taste buds in most cetaceans. However, it is possible that modified sense organs exist on the tongue, or even on the body surface, which react to chemical stimuli. However, both taste and touch, which is admittedly responded to over most of the body surface, are contact senses and useful primarily over short distances.

Vertebrates, particularly mammals, do not generally depend on only one sense for their perception of the external world. Most species have selectively specialized two or three senses. Most herbivorous animals are inclined to depend on hearing and olfaction, whereas predators frequently have excellent vision and hearing. Most marine mammals, aside from Sirenia (sea cows) and Mysticetes (baleen whales) are carnivorous. It is interesting that these two groups show few anatomical adaptations for underwater vision, and are considered to have poor visual acuity. Most other marine mammals show much greater ocular adaptations for their amphibious, or totally aquatic, existence. The sea otter uses a lens-squeeze accommodation device, which is probably very efficient in both air and water (Walls, 1942), though no visual acuity studies have been performed on this animal. The sea lion has stenopaic vision in air, and the pinhole device appears to allow

good visual acuity in air (in good light), while accommodation of the lens by ciliary muscle control occurs underwater. Schusterman (1970) tested visual acuity in the California sea lion, and obtained an MAR of 5.5 minutes, both in air and in water.

#### 6. Vision in Cetacea

Among the Cetacea, Odontocetes (toothed whales) appear to be rather better adapted for underwater vision than Mysticetes (baleen whales). The anatomy of the Odontocete eye, as described by Walls (1942), is very similar to that of a fish. The cornea is small and ovoid, thickened at the periphery for greater refraction. The eyeball is horizontally ellipsoidal to extend the horizontal field, and flattened from front to back to allow a larger visual field without increasing the lens-to-retina distance. The lens is spherical and has a refractive index similar to that of fish. However, accommodation is accomplished by the use of powerful ciliary muscles, as in terrestrial mammals. A very thick sclera protects the eyeball from distortion due to sudden changes in pressure in the water.

Walls believed that mysticetes show regression due to loss of importance of vision for their sluggish, herbivorous mode of life. The primary adaptation is for visual sensitivity, rather than acuity. The retina has very long rod receptors which are assumed to be highly light-sensitive, probably to optimize use of vision during deep dives. Otherwise, the anatomy of the eyes remains more similar to that of terrestrial mammals than that of odontocetes.

Walls believed that whale eyes were immobile in the socket and canted downward, which would make aerial vision awkward. However, Slijper (1962) pointed out that captive whales have been observed to have very mobile eyes. He advanced the theory that the dorsal part of the retina, which is closer to the lens and backed by a tapetum, is used for underwater vision, and the ventral hemisphere is used for aerial vision, as it is lacking a tapetum and having a greater lens-to-retina distance. This would suggest useful vision in both media.

Barry Peers (1971) did a study on the histology of the retina of Tursiops. He also observed the dorsal distribution of the tapetum, but implied no significance to it. He found two types of receptors, typical rods and a few cone-like receptors. These were mostly found in a horizontal area centralis, which Peers suggested might function for orientation in the three dimensional aquatic environment. He concluded that the retina seemed to be adapted for light sensitivity, due to the large rod population and considerable summation onto ganglion cells, and indicated that vision could be a useful modality in this animal.

## 7. Summary

It would thus appear that Tursiops truncatus, as a fast, agile, carnivorous odontocete, inhabiting shallow, well lighted waters, and having an eye well adapted for underwater vision, should be a good subject for visual acuity studies. Although shown to have a

sophisticated echolocation system, many observations of this animal's dependence on vision have been made, and the paucity of formal studies of visual acuity in Cetacea strongly emphasizes the value of a systematic study of visual acuity in this species.

## PROCEDURE

The procedure employed in this study was a simultaneous two-choice discrimination. The two visual cues, made to be as similar as possible in all respects except that of the test parameter, were presented together to the subject, which was required to choose between them on the basis of particular, systematically varied parameters. The cues were presented in an apparatus designed to screen the experimenter from the subject during the experiment. Two experiments were run, each using a different type of visual cue.

### 1. Apparatus

Transparent plexiglass envelopes were fabricated to enclose the white plexiglass cues used in experiment 1. In experiment 2, the envelopes were modified to form frames for the laminated photographs used as cues. The envelopes were attached to a mobile bar, which could be adjusted in the vertical plane, allowing the envelopes to be held behind the screen, during the manipulation of the cues, or in two test positions just above and just below the water surface. The screen and the adjustable bar and envelopes formed part A of the apparatus, and is diagrammatically represented in Figure 1.

The subject's position was controlled by part B of the apparatus, a movable, horizontal bar held by two cross-planks in a position in front of and parallel to part A. Attached to this bar was a

Figure 1. Apparatus - parts A and B.

Figure 2. Research tank - position of apparatus, parts  
A and B.

FIGURE 1

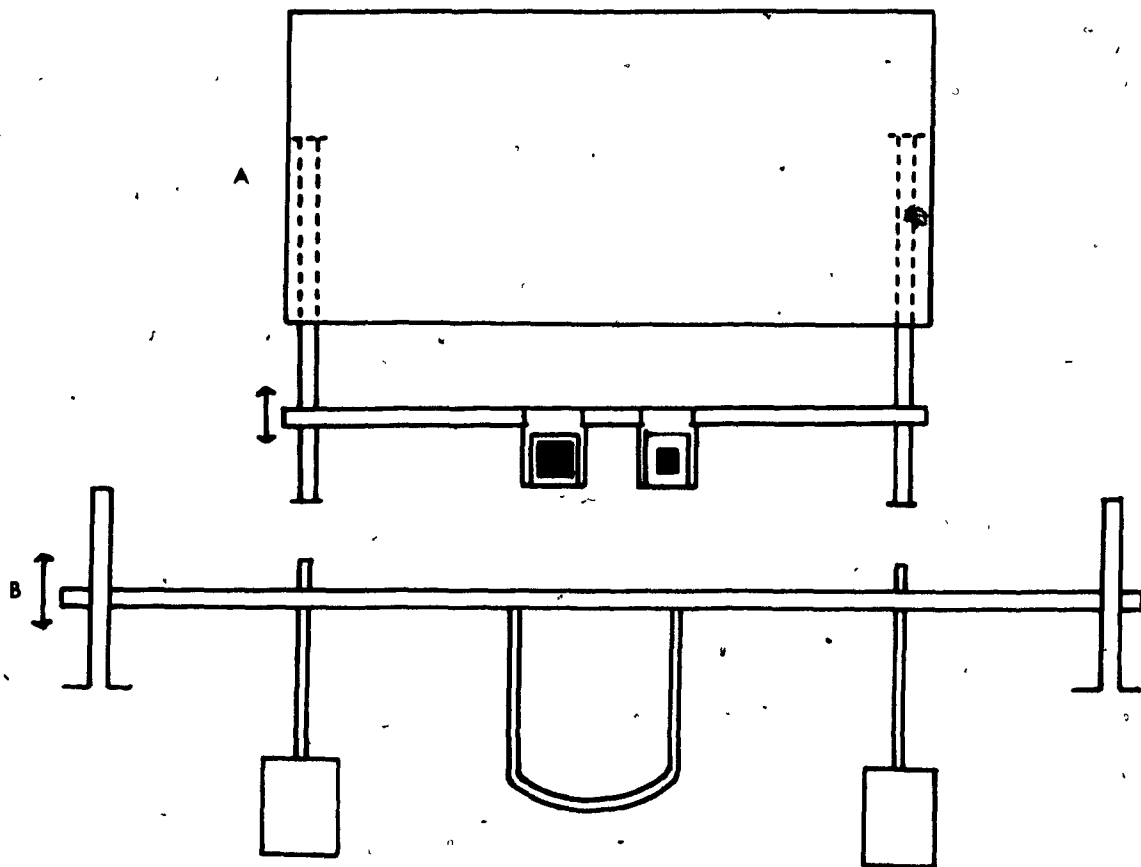
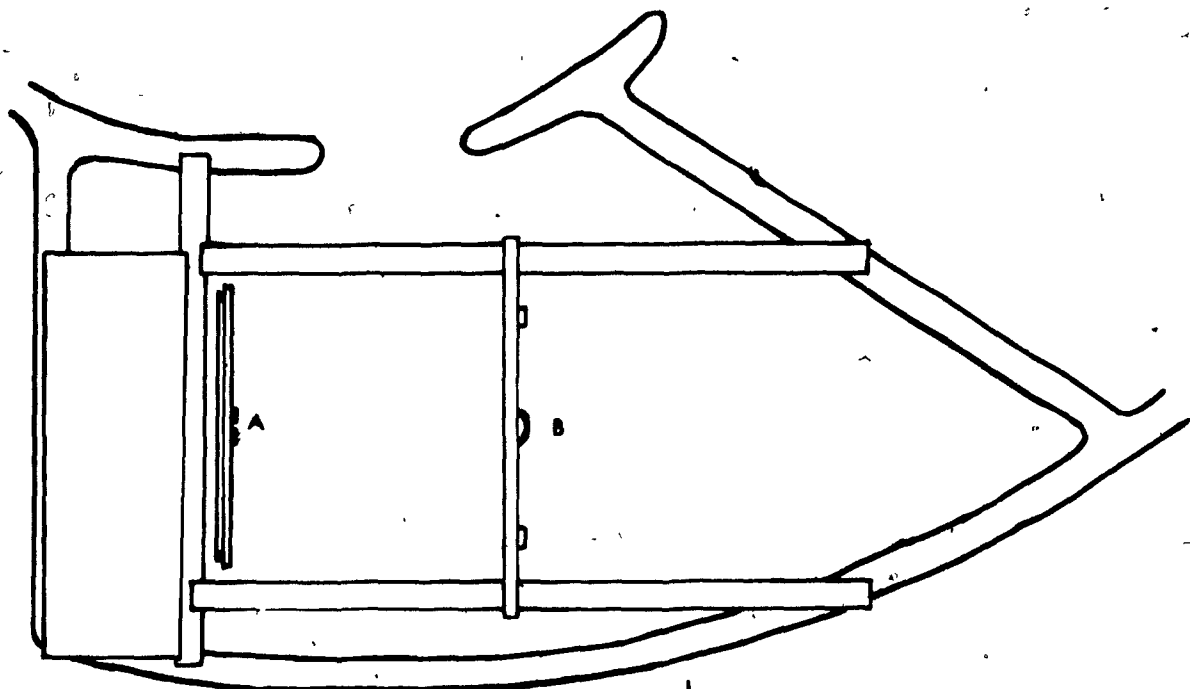


FIGURE 2



headrest in which the subject placed its head at the beginning of each trial. This held the animal at a known, but variable, distance from the cues during each trial. Two paddles were attached on either side of the headrest, and the subject signified its choice of cues by touching the paddle on the side of the chosen cue. The entire horizontal bar could be adjusted vertically so as to position the subject's head just above or just below the water surface during trials. It was also adjustable in the horizontal plane over a distance of 4 metres, as can be seen in Figure 2. The holding tank, diagrammed in Figure 2, was slightly curved, measuring 5 metres at its greatest length, 3 metres in width and 1.5 metres in depth. The distances between the subject and apparatus (A) chosen as the most practical for testing purposes were between 1 and 3 metres.

The set of cues used in experiment 1 were made of white plexiglass, 15 cm square, with superimposed squares of black, adhesive vinyl, varying from 1 to 10 cm square.

The set of cues used in experiment 2 were laminated photographs of a grating of parallel lines, 5.5 cm square, with a 2 cm wide white border, later replaced by gratings covering the entire photograph 9.5 cm square. The earlier set was produced partially from a Paratone sheet No. 236 (56 black lines per inch - series B). The remainder of the gratings were produced from photographs of a handmade pattern of black lines, consisting of three-quarter inch black vinyl tape, spaced three-quarters of an

inch apart on a white cardboard background. The first complete series was graded from a density of 0.73 lines/cm to 41.7 lines/cm. However, this series was used only to obtain results from a human subject under various conditions. The second series of gratings was produced entirely from a photographic reduction of the hand made pattern, ranging from 0.52 lines/cm to 2.32 lines/cm. All the recorded results from the dolphin subject were obtained using this series.

## 2. Experimental Method

Experiments 1 and 2 had certain behavioural techniques in common. In both cases, the desired response of choosing one cue as positive was 'shaped' by a trial-and-error training method. In experiment 1 a black-white discrimination was first trained, keeping white as the positive choice. The white cue was first presented alone, and the subject trained to touch it upon presentation. Both black and white cues were then presented simultaneously, with the subject required to respond only to white. When this response was performed reliably, the cues were transferred to the apparatus, which had not been used before. Direct contact with the cues was still the required response, but once the animal became familiar with the apparatus, the headrest and paddles were introduced, and the subject was taught to maintain position in the headrest and to transfer its response from the cues to the paddles. At the same time, the cues for experiment 1 were introduced and the

animal trained to choose the smaller of two simultaneously presented black squares. It was hoped that an errorless transfer would occur from the black-white discrimination to the large versus small square discrimination, but actually the animal learned the new discrimination by trial and error, with little facilitation of the second response by the first task learned.

Throughout both experiments, fish was used as a positive reinforcement for correct responses. The only negative reinforcement used was a 'time out'; i.e. the apparatus was withdrawn and the experimenter walked away from the tank for a period of one to five minutes. This withdrawal was an adequate punishment in most cases, and was used mostly when the animal refused to station or when it appeared to be responding indiscriminately to the cues, frequently showing a spatial preference for left or right instead.

The dolphin used in these experiments was fed 7 to 10 kg of fish a day, half herring and half smelt. The smelt were used most in the trial runs, due to their convenient size. Up to 300 trials were run a day, with a division of trials into two sessions, separated by a rest period of an hour or more. Experiment 1 was executed over a period of eleven months following nine months of preliminary training. Trial sessions were irregular, seldom exceeding three days a week. Experiment 2 was completed in three months, however, with more regular sessions, generally two a day, five days a week. Preliminary training occupied approximately half of this period, during which the subject learned to choose

a pattern of broad stripes over a pattern of narrow stripes, too fine to be resolved at the distances used. An unsuccessful attempt was made to 'fade in' this discrimination from the large versus small square discrimination of experiment 1, and was eventually abandoned in favour of a trial-and-error approach.

In both experiments the order of presentation of cues was randomized by the Gellerman (1933) procedure, thus minimizing the effect of position on the subject's choice of cues. If the animal formed a spatial preference for one side, a series of trials was run with the other side positive, until the animal broke its response pattern.

Two techniques for recording thresholds were used. In experiment 1, a method of descending limits was used, whereby the threshold was obtained by a gradual reduction of the difference between cues from a large and obvious difference (e.g. 10 cm square versus 1 cm square) to the threshold level. In experiment 2, however, time was more limited and a tracking technique was used to obtain the threshold, with a swift reduction of differences between cues to below threshold and then a tracking back and forth from just below to just above threshold.

The dolphin used in both experiments was an adult male, named Himself, which had been held in captivity at the Aquarium where the experiments were performed, for three years prior to the beginning of this study. This animal was trained, as part of a dolphin show, but had been removed from the show due to conflicts

with other animals and unpredictability in his own performance.

He was, however, returned to the show several times during the course of this study.

## RESULTS

### 1. General Observations

The entire project described in this paper occupied a period of 23 months. The first nine months were required for the preliminary training and modifications of the initial apparatus, which had been modelled after Kellogg and Rice (1966). Due to the forced irregularity of the experimental routine, training proceeded slowly, with many interruptions resulting in frequent regressions. Just prior to the beginning of recorded sessions for experiment 1, Himself was removed for use in the dolphin show for a month. This did not seriously affect his training, and recorded sessions began shortly after his return.

The results recorded for experiment 1 were obtained over a period of ten months, with a trial schedule generally occupying one session a day, three days a week. Each session might consist of 100 to 200 trials. The irregularity of this routine was unfortunate, as it almost certainly had a deleterious effect on the animal's conditioning. A further problem was the lack of isolation of the experimental tank. It was connected to other holding tanks containing dolphins, and also to the show basin, which contained four show animals. The routine work of the aquarium frequently interrupted trial sessions, and any activity in the other tanks distracted the test animal. However, the test dolphin's attention to the task was remarkable in view of the circumstances, although his performance was unpredictable. His attention was definitely more focussed on the

apparatus and the discrimination he had to make on some days than on others. A more regular routine would probably have permitted a better control of his behaviour.

The second experiment was initiated after a second withdrawal of Himself to the dolphin show. An attempt was made to shape a discrimination to the cue series A in Table 6, but this was abandoned in favour of the larger pattern used in series B, as described in the procedure. Preliminary training required two months or more, while the final results were over a period of approximately three weeks. The routine throughout this experiment was far more regular, with two sessions a day, five to seven days a week. At the end, 300 or more trials were being run a day, over a period of six to eight hours. The animal's behaviour became far more predictable at this time, and was further brought under control by frequent 'time outs' of up to ten minutes duration.

One of the most important external parameters which could not be brought under control was the ambient light level. This was provided from three sources, wall lamps, ceiling lamps and several large skylights. Most of the trials were conducted between mid-morning and mid-afternoon, and the skylight provided most of the illumination. To measure the variability of ambient illumination under different weather and daylight conditions, a series of readings were taken with a Pentax spotometer. The values were read from a 90% Kodak transmittance card placed in approximately the position of the cues for discrimination in air. The variation recorded was

between 300 lux, with lights on in rainy weather, and 3500 lux around noon on a sunny day. According to Pirenne (1948), human visual acuity reaches a plateau when plotted against log, of illumination, at 3 trolands, or 225 lux. If dolphin sensitivity is not inferior to human sensitivity, and there is reason to believe that it is at least as good (Peers, 1971), then ambient illumination should not be a limiting factor in the visual tests performed under the above lighting conditions.

## 2. Experiment 1

The use of squares as the visual cue in experiment 1 created certain difficulties for the study of visual acuity. Not only was there a difference in visual angle between cues, but the difference in ratio of white to black on each cue would produce a brightness difference as well. To attempt to study the effect of this difference, these parameters were calibrated for each of the 45 cue pairs tested. The three parameters were area difference between squares, area ratio of the two squares, and a quantity named the brightness ratio, which was determined by the ratio of areas of white on the two cues. The values of these parameters for each cue pair are given in Table 1. The visual angles encountered for the linear differences between squares at 1, 2 and 3 metres are given in Table 2.

The results obtained for experiment 1 are summarized in Table 3. Graphs were then drawn for given visual angle constants at 1, 2 and 3 metres in water and in air (Graphs 1 and 2). The abscissa consisted

7  
Table 1. Parameters for cue pairs in experiment 1.

| *Cue pair | Area difference | Area ratio | Brightness ratio |
|-----------|-----------------|------------|------------------|
| 10 x 9.8  | 3.96            | 1.04       | 1.032            |
| 10 x 9.7  | 5.91            | 1.06       | 1.047            |
| 9.8 x 9.7 | 4.95            | 1.05       | 1.015            |
| 10 x 9.5  | 8.75            | 1.10       | 1.078            |
| 10 x 9    | 19.00           | 1.24       | 1.152            |
| 10 x 8.5  | 27.75           | 1.38       | 1.222            |
| 8 x 7.5   | 7.75            | 1.14       | 1.048            |
| 8 x 7     | 15.00           | 1.32       | 1.093            |
| 6 x 7.5   | 20.25           | 1.56       | 1.126            |
| 6 x 7     | 13.00           | 1.36       | 1.074            |
| 6 x 6.5   | 6.25            | 1.17       | 1.033            |
| 6 x 6.3   | 3.79            | 1.11       | 1.020            |
| 6 x 6.2   | 2.44            | 1.07       | 1.012            |
| 6.3 x 6.2 | 1.25            | 1.03       | 1.007            |
| 5 x 6.5   | 17.25           | 1.69       | 1.094            |
| 5 x 6     | 11.00           | 1.44       | 1.058            |
| 5 x 5.5   | 5.25            | 1.21       | 1.027            |
| 4 x 5.5   | 24.25           | 2.52       | 1.077            |
| 4 x 5     | 9.00            | 1.56       | 1.045            |
| 4 x 4.5   | 4.25            | 1.27       | 1.021            |
| 3 x 6     | 27.00           | 4.00       | 1.143            |
| 3 x 5     | 16.00           | 2.78       | 1.080            |
| 3 x 4.5   | 11.25           | 2.25       | 1.055            |
| 3 x 4     | 7.00            | 1.77       | 1.033            |
| 3 x 3.5   | 3.25            | 1.36       | 1.015            |
| 3 x 3.3   | 1.89            | 1.21       | 1.009            |
| 3 x 3.2   | 1.24            | 1.14       | 1.006            |
| 3.3 x 3.2 | 0.65            | 1.06       | 1.002            |

Table 1 - continued

| *Cue pair | Area difference | Area ratio | Brightness ratio |
|-----------|-----------------|------------|------------------|
| 2 x 7     | 45.00           | 12.25      | 1.256            |
| 2 x 6.5   | 38.25           | 10.56      | 1.209            |
| 2 x 5     | 21.00           | 8.25       | 1.105            |
| 2 x 4.5   | 16.25           | 5.06       | 1.077            |
| 2 x 4     | 12.00           | 4.00       | 1.057            |
| 2 x 3.5   | 8.25            | 3.06       | 1.038            |
| 2 x 3     | 5.00            | 2.25       | 1.023            |
| 2 x 2.5   | 2.25            | 1.56       | 1.010            |
| 1 x 7     | 48.00           | 49.00      | 1.273            |
| 1 x 6.5   | 41.25           | 42.25      | 1.226            |
| 1 x 6     | 35.00           | 36.00      | 1.185            |
| 1 x 5.5   | 29.25           | 30.25      | 1.150            |
| 1 x 5     | 24.00           | 25.00      | 1.120            |
| 1 x 4.5   | 19.25           | 20.25      | 1.094            |
| 1 x 4     | 15.00           | 16.00      | 1.077            |
| 1 x 3.5   | 11.25           | 12.27      | 1.053            |
| 1 x 3     | 8.00            | 9.00       | 1.037            |
| 1 x 2.5   | 5.25            | 6.25       | 1.021            |
| 1 x 2     | 3.00            | 4.00       | 1.014            |
| 1 x 1.5   | 1.25            | 2.25       | 1.006            |
| 1 x 1.3   | 0.69            | 1.61       | 1.004            |
| 1 x 1.2   | 0.44            | 1.44       | 1.002            |
| 1.2 x 1.3 | 0.25            | 1.17       | 1.002            |

\*Note: A cue pair is symbolized by the size of the squares - e.g. 10 x 9.8 refers to a 10 cm square paired with a 9.8 cm square.

Table 2: Visual angles subtended by linear differences between black squares of cue pairs (experiment 1).

| Linear difference (cm) | Visual angle (degrees minutes)* |          |          |
|------------------------|---------------------------------|----------|----------|
|                        | 1 metre                         | 2 metres | 3 metres |
| 7.0                    | 4° 1                            | 2° 0.5   | 1° 20    |
| 6.5                    | 3° 43                           | 1° 51.5  | 1° 14.5  |
| 6.0                    | 3° 26                           | 1° 43    | 1° 8.5   |
| 5.5                    | 3° 9                            | 1° 34.5  | 1° 3.0   |
| 5.0                    | 2° 52                           | 1° 26    | 57.5     |
| 4.5                    | 2° 34.5                         | 1° 17.5  | 51.5     |
| 4.0                    | 2° 17.5                         | 1° 8.5   | 45.5     |
| 3.5                    | 2° 0.5                          | 1° 0.0   | 40.5     |
| 3.0                    | 1° 43                           | 51.5     | 34.5     |
| 2.5                    | 1° 26                           | 43       | 28.5     |
| 2.0                    | 1° 8.5                          | 34.5     | 23       |
| 1.5                    | 51.5                            | 25.5     | 17.5     |
| 1.0                    | 34.5                            | 17.5     | 11.5     |
| 0.5                    | 17.5                            | 8.5      | 6        |
| 0.3                    | 10.5                            | 5.0      | 3.5      |
| 0.2                    | 7.0                             | 3.5      | 2.5      |
| 0.1                    | 3.5                             | 1.5      | 1.0      |

\*Approximated to the nearest half-minutes.

Table 3. Percentage correct response for cue pairs used in experiment 1.

| Cue pair | Water |     |     | Air |     |     |
|----------|-------|-----|-----|-----|-----|-----|
|          | 1 m.  | 2 m | 3 m | 1 m | 2 m | 3 m |
| 10 x 9.8 | 46    | 54  | 50  | 50  | 50  | -   |
| 10 x 9.7 | 59    | 63  | 54  | 50  | 52  | 53  |
| 10 x 9.5 | 69    | 65  | 68  | 57  | 53  | 57  |
| 10 x 9   | 76    | 85  | 81  | 65  | 70  | 70  |
| 10 x 8.5 | -     | -   | -   | 74  | 83  | 86  |
| 8 x 7.5  | 68    | 71  | 72  | 63  | 59  | 50  |
| 8 x 7    | 93    | 90  | 82  | 71  | 70  | 68  |
| 6 x 7.5  | -     | -   | -   | 90  | 88  | 88  |
| 6 x 7    | 80    | 88  | 81  | 75  | 72  | 59  |
| 6 x 6.5  | 70    | 79  | 70  | 61  | 59  | 50  |
| 6 x 6.3  | 58    | 61  | 54  | -   | -   | -   |
| 6 x 6.2  | 55    | 56  | 54  | -   | -   | -   |
| 5 x 6.5  | -     | -   | -   | -   | 75  | 69  |
| 5 x 6    | 82    | 93  | 91  | 76  | 68  | 56  |
| 5 x 5.5  | 74    | 76  | 74  | 55  | 57  | 52  |
| 4 x 5.5  | -     | -   | 100 | 85  | -   | 69  |
| 4 x 5    | 82    | 88  | 98  | 83  | 68  | 62  |
| 4 x 4.5  | 71    | 80  | 70  | 63  | 56  | 50  |
| 3 x 5    | 100   | 100 | 100 | 93  | 86  | 73  |
| 3 x 4.5  | 100   | 100 | 100 | 82  | 72  | 55  |
| 3 x 4    | 80    | 87  | 96  | 76  | 60  | 59  |
| 3 x 3.5  | 75    | 72  | 80  | 63  | 58  | 56  |
| 3 x 3.3  | 58    | 62  | 58  | -   | -   | -   |
| 3 x 3.2  | 50    | 54  | 61  | -   | -   | -   |
| 2 x 7    | -     | -   | -   | -   | -   | 90  |
| 2 x 6.5  | -     | -   | -   | -   | -   | 90  |

Table 3 - continued

| Cue pair | Water |     |     | Air |     |     |
|----------|-------|-----|-----|-----|-----|-----|
|          | 1 m   | 2 m | 3 m | 1 m | 2 m | 3 m |
| 2 x 5    | -     | -   | -   | -   | 80  | -   |
| 2 x 4.5  | -     | 100 | 100 | 100 | 80  | 74  |
| 2 x 4    | 96    | 100 | 100 | 87  | 76  | 64  |
| 2 x 3.5  | -     | -   | -   | 80  | 57  | 55  |
| 2 x 3    | 80    | 88  | 90  | 74  | 58  | -   |
| 2 x 2.5  | 66    | 74  | 66  | 60  | 58  | -   |
| 1 x 7    | -     | -   | -   | -   | -   | 98  |
| 1 x 6.5  | -     | -   | -   | -   | -   | 89  |
| 1 x 6    | -     | -   | -   | -   | -   | 85  |
| 1 x 5.5  | -     | -   | -   | -   | -   | 85  |
| 1 x 5    | 100   | -   | -   | -   | 97  | 83  |
| 1 x 4.5  | -     | -   | -   | -   | 95  | 67  |
| 1 x 4    | 91    | 100 | 100 | 100 | 85  | 71  |
| 1 x 3.5  | 100   | 100 | 100 | 88  | 84  | 65  |
| 1 x 3    | 75    | -   | 90  | -   | 50  | 56  |
| 1 x 2.5  | 75    | 98  | 85  | 74  | 58  | 54  |
| 1 x 2    | 66    | 76  | 62  | 61  | 56  | 59  |
| 1 x 1.5  | 50    | 66  | 53  | 59  | 54  | 54  |
| 1 x 1.3  | 54    | 61  | 48  | -   | -   | -   |
| 1 x 1.2  | 52    | 54  | -   | -   | -   | -   |

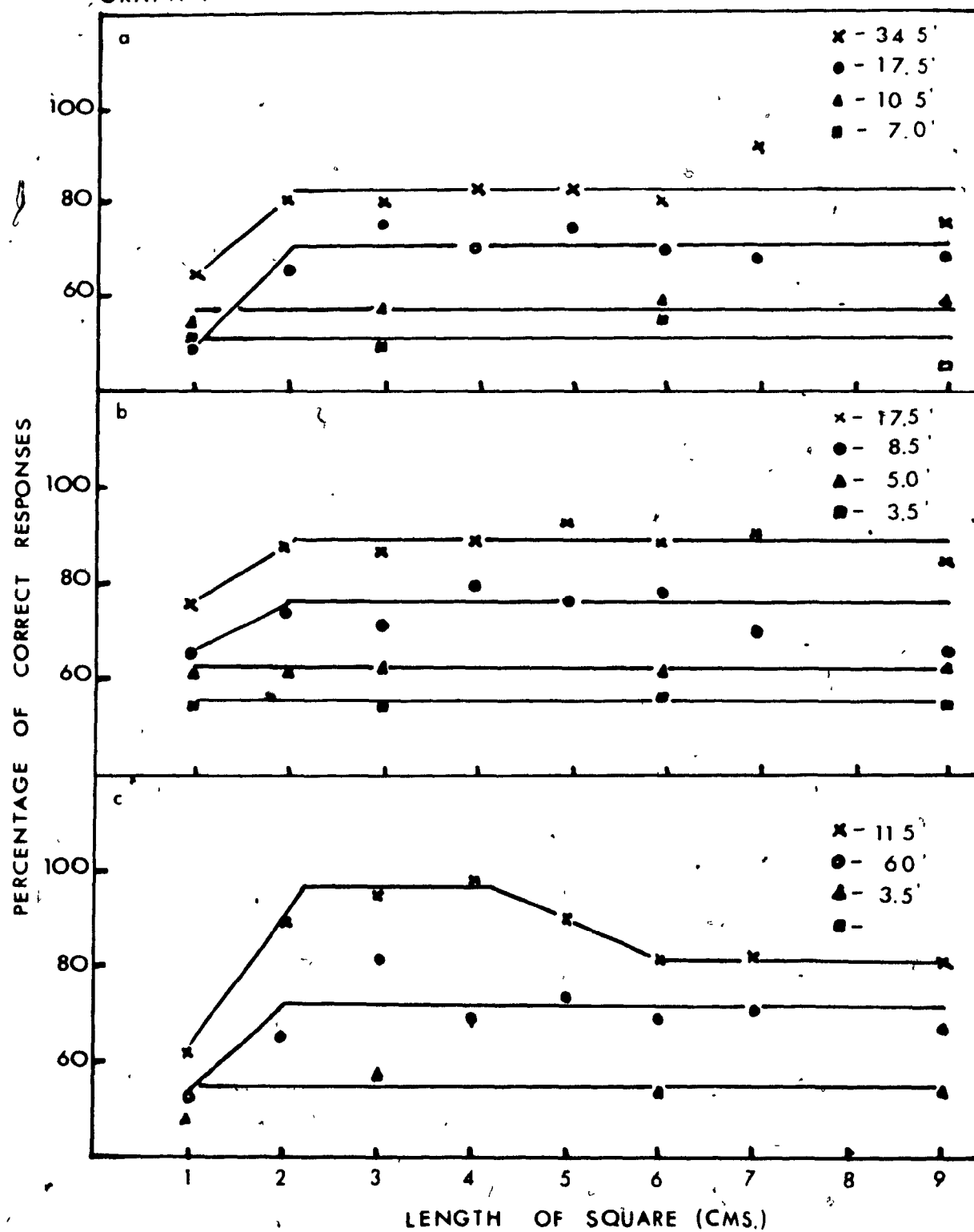
Note: The percentage values shown in the above table were based on varying numbers of trials, from as few as 20-50 where the response was consistent to 200 trials where the response showed much variability. The actual results of the separate trial runs with these cue pairs are presented in Appendix A, of which Table 3 is a summary.

Graph 1. Percentage of correct responses versus cue size  
for given visual angles in water.

a. 1 metre; b. 2 metres; c. 3 metres.

Experiment 1.

GRAPH 1

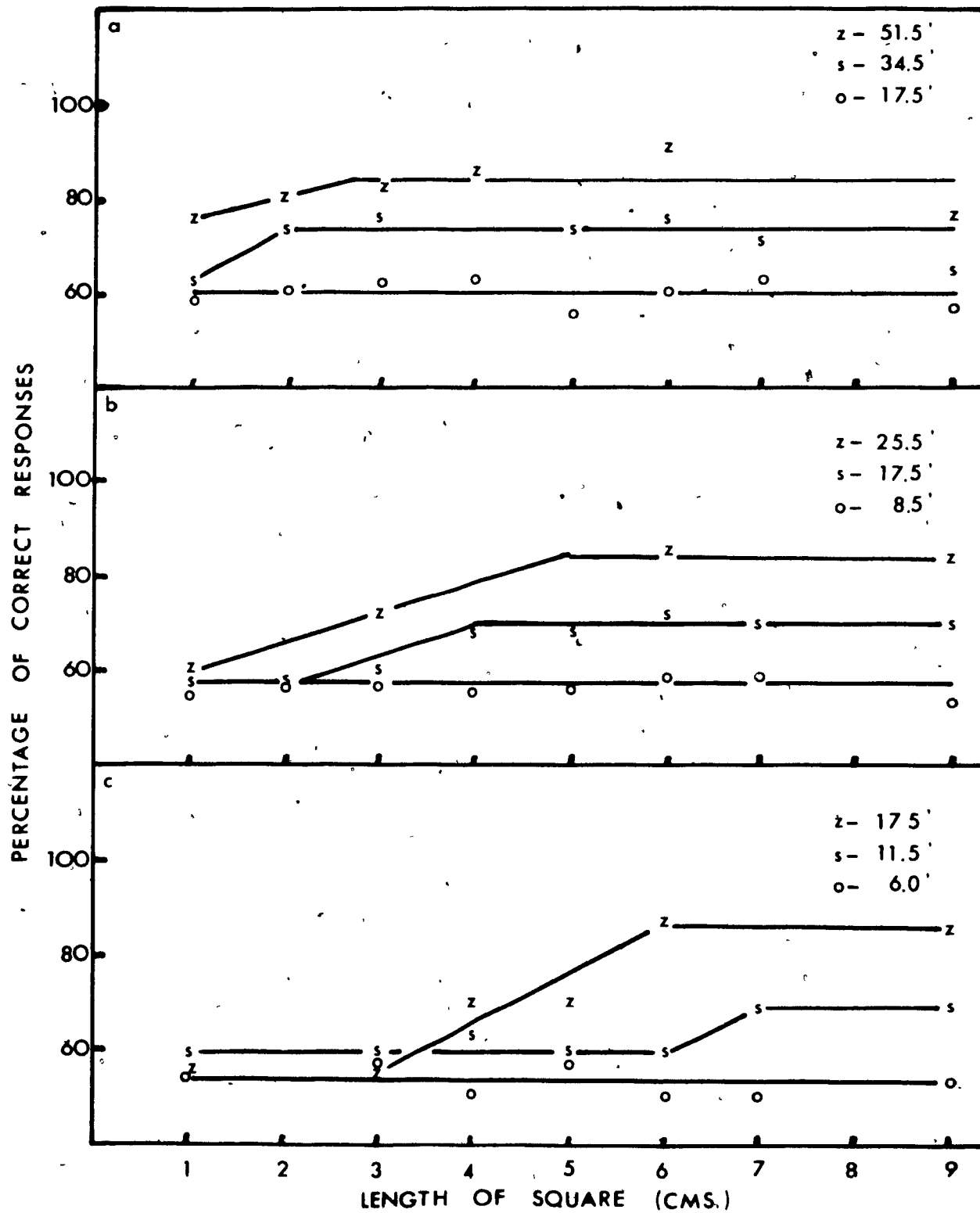


Graph 2. Percentage of correct responses versus cue size  
for given visual angles in air.

a. 1 metre; b. 2 metres; c. 3 metres.

Experiment 1.

GRAPH 2



of the absolute size of the smaller of the two squares in a pair (1 to 9 cm squares). The ordinate was the percentage correct response, as in all the graphs. As can be seen by looking at graphs 1 and 2, the result is a straight line for each visual angle constant, dropping off below a particular absolute size level. In water this size was between 1 and 2 cm squares, but in air the level was higher at 2 and 3 metres, and the overall response percentage was lower than for water. The irregularity of the upper lines in Graph 1c is surprising in view of the general regularity of the other lines, and will be discussed later. T-tests performed between 1 cm values and their lines were significant at the 5% level, as were the two levels of values in 1c for 11.5 minutes.

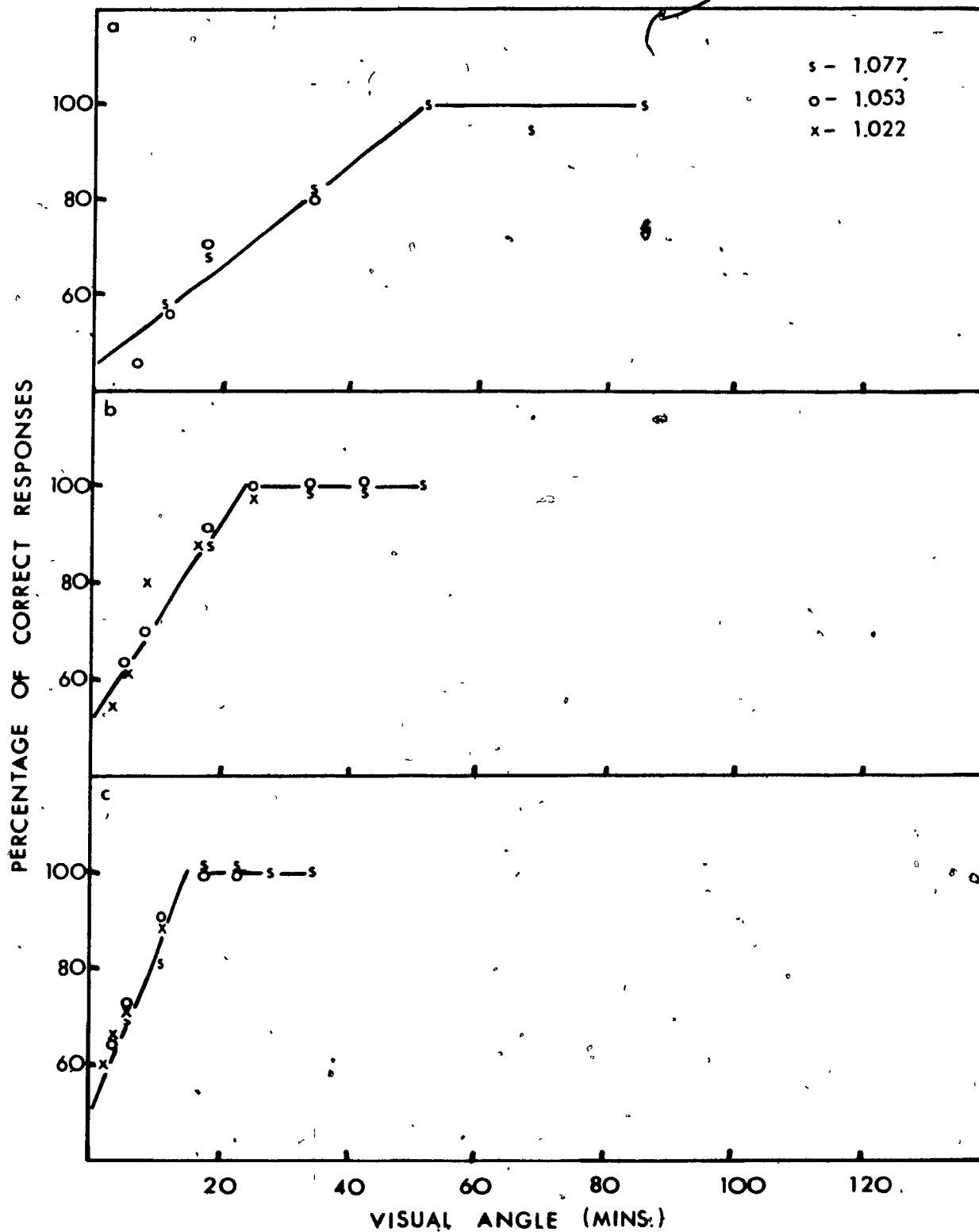
Graphs 3 and 4 were based on the same set of results from experiment 1. In this case the abscissa is visual angle and given brightness ratio constants were used. It is immediately obvious that there is a systematic variation of response with visual angle that is unaffected by brightness ratio. The values for 1 cm square were omitted in these graphs, due to their systematic variance from the other values in Graphs 1 and 2. Multiple regression analysis produced a highly significant (at 1% level) straight line fit of all the lines except 3a. However, it can be seen that the values at 1 metre in both water and air appear to be slightly curvilinear, which suggests the imposition of another variable on the response pattern.

Graph 3. Percentage correct response versus visual  
angle for given brightness ratio - water.

a. 1 metre; b. 2 metres; c. 3 metres.

Experiment 1.

GRAPH 3

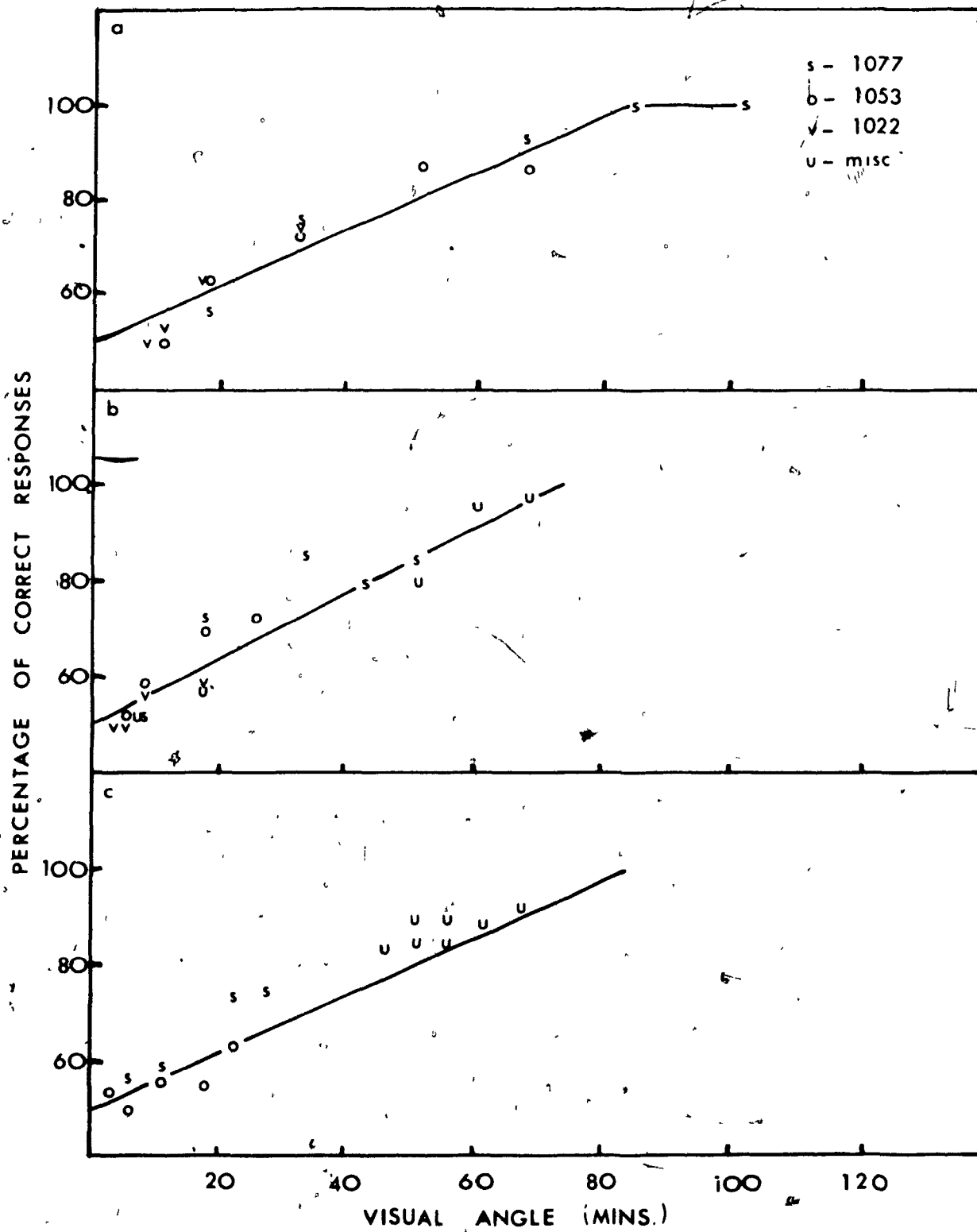


Graph 4. Percentage correct response versus visual  
angle for given brightness ratios - air.

a. 1 metre; b. 2 metres; c. 3 metres.

Experiment 1.

GRAPH 4



LEAF 29 OMITTED IN PAGE NUMBERING.

### 3. Experiment 2

In experiment 2, the brightness difference was supposed to be eliminated by use of gratings of black and white parallel lines of equal width and number. Unfortunately, it was impossible to totally remove brightness differences with the photographic techniques used to produce the cues. The differences were small, however, and were controlled for by the use of duplicate sets of cues. A grating of 2.32 lines/cm could not be discriminated by the subject against a uniform standard of the same approximate brightness, after training, so this grating was used as the standard during actual testing. The larger grids were positively reinforced for the subject. The visual angles for each of the grids at the five test distances are given in Table 4.

The summarized results for experiment 2 are given in Table 5. Linear regression analysis showed no significant differences between the values for each of the five test distances, so one line was fitted for all five distances by linear regression, and was found to be significant at the 5% level. It is probable that the limited time allowed for final tests in experiment 2 led to a recording of results before the animal's response was fully shaped. This might have affected the quality of the results to the extent of masking distance differences.

### 4. Obtained Thresholds

Thresholds are usually taken at the 75% level of response in

Table 4. Visual angle subtended by one unit line of cue pattern  
(B). Experiment 2.

| Cue | Visual Angle (Minutes) |       |      |       |      |
|-----|------------------------|-------|------|-------|------|
|     | 1 m                    | 1.5 m | 2 m  | 2.5 m | 3 m  |
| 5*  | 38                     | 25    | 19   | 15    | 12.5 |
| 6   | 30.5                   | 20    | 15.5 | 12.5  | 10   |
| 7   | 26                     | 17    | 13   | 10    | 8.5  |
| 8   | 22                     | 15    | 11.5 | 9     | 7.5  |
| 9   | 20                     | 13.5  | 10   | 8     | 6.5  |
| 10  | 17.5                   | 12    | 9.5  | 7     | 6    |
| 11  | 16                     | 11    | 8    | 6     | 5    |
| 12  | 15                     | 10    | 7.5  | 6     | 5    |
| 13  | 13.5                   | 9     | 7    | 5     | 4.5  |
| 15  | 11                     | 8     | 6    | 4.5   | 4    |
| 17  | 10                     | 7     | 5    | 4     | 3.5  |
| 20  | 8.5                    | 5.5   | 4.5  | 3.5   | 3    |
| 22  | 8                      | 5     | 4    | 3     | 2.5  |

\*Numbers refer to number of black lines on the 9.5 cm x 9.5 cm square.

Table 5. Percentage correct response for pattern discrimination in Experiment 2.

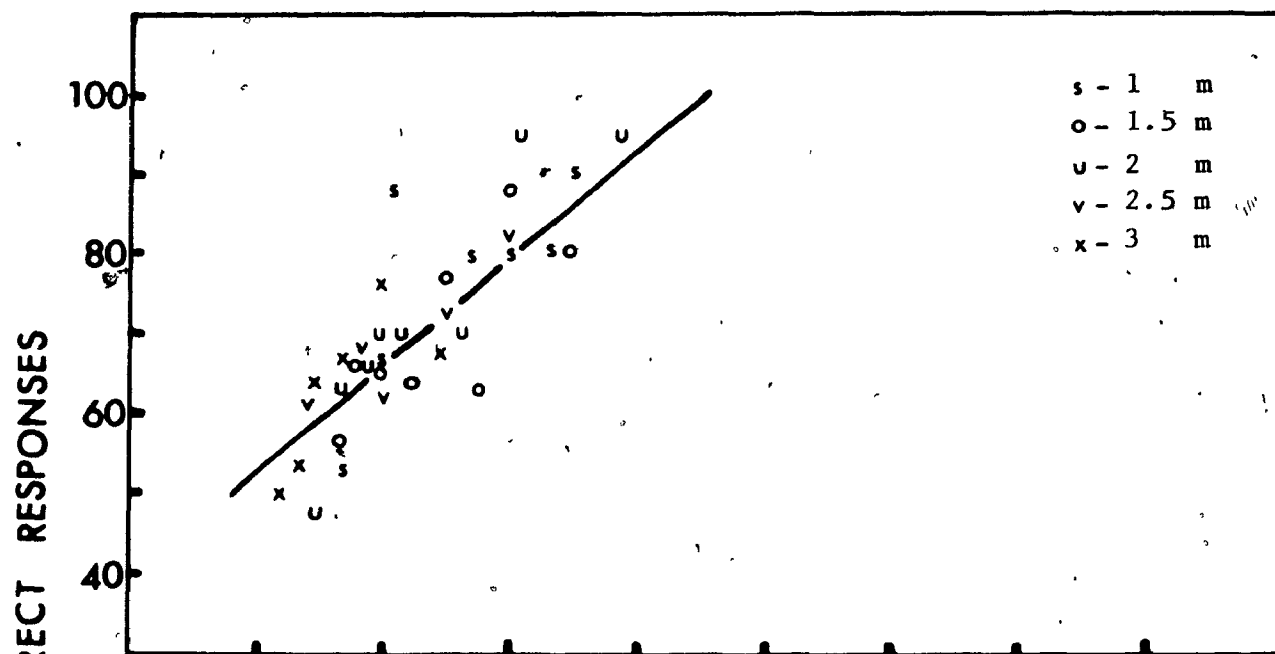
| Cue | Water |       |     |       |     |
|-----|-------|-------|-----|-------|-----|
|     | 1 m   | 1.5 m | 2 m | 2.5 m | 3 m |
| 5   | -     | -     | 95  | 82    | 67  |
| 6   | -     | -     | 95  | 68    | 76  |
| 7   | -     | 80    | 70  | 62    | 66  |
| 8   | -     | 88    | 70  | 67    | 64  |
| 9   | -     | 63    | 70  | 65    | 59  |
| 10  | 90    | 77    | 66  | 61    | 50  |
| 11  | 80    | 64    | 63  | -     | -   |
| 12  | 80    | 66    | 46  | -     | -   |
| 13  | 80    | 66    | -   | -     | -   |
| 15  | 81    | 56    | -   | -     | -   |
| 17  | 67    | -     | -   | -     | -   |
| 20  | 53    | -     | -   | -     | -   |
|     | Air   |       |     |       |     |
|     | 1 m   | 1.5 m | 2 m | 2.5 m | 3 m |
| 5   | 90    | 67    | 73  | 65    | 67  |
| 6   | 75    | 71    | 70  | 65    | 61  |
| 7   | 72    | 83    | 65  | 67    | 56  |
| 8   | 73    | 73    | 67  | 50    | -   |
| 9   | 66    | 70    | 59  | -     | -   |
| 10  | 66    | 63    | 48  | -     | -   |
| 11  | 73    | 56    | -   | -     | -   |
| 12  | 63    | 45    | -   | -     | -   |
| 13  | 51    | -     | -   | -     | -   |
| 15  | -     | -     | -   | -     | -   |
| 17  | -     | -     | -   | -     | -   |
| 20  | -     | -     | -   | -     | -   |

Note: The results of the separate trial runs, which are summarised in this table, are presented in Appendix B.

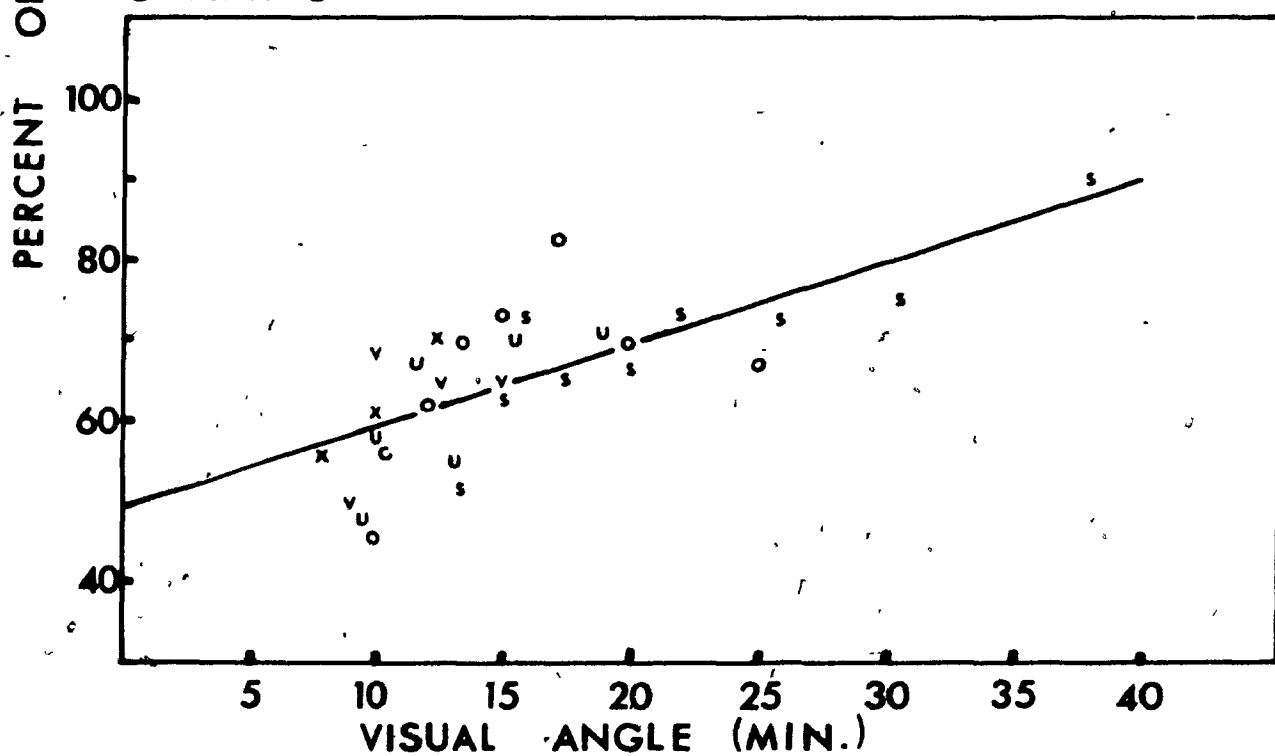
Graph 5. Percentage correct response versus visual angle -  
water. Experiment 2.

Graph 6. Percentage correct response versus visual angle -  
air. Experiment 2.

GRAPH 5



GRAPH 6



visual acuity studies. At this level, the threshold obtained in experiments 1 and 2 for the dolphin were as follows:

Table 6. Thresholds for dolphin visual acuity - .75% criterion.

| Experiment 1. | Water | Air |
|---------------|-------|-----|
| 1 m           | 25'   | 34' |
| 2 m           | 8'    | 31' |
| 3 m           | 6'    | 34' |
| Experiment 2. | Water | Air |
| 1-3 m         | 13'   | 25' |

#### 5. Results for Human Subject

A brief replication of both experiments 1 and 2 was done with a human subject who had 20-20 vision. The same set of cues was used for experiment 1, but the series A cues, which were replaced in experiment 2 by series B for the dolphin study, were used in experiment 2 for the human study. The series A cues showed greater brightness differences than series B, and these were measured under controlled light conditions with a Pentax spotometer. The readings are given in Table 7, together with the equivalent lux values. The greatest differences were between the cues produced with the Paratone sheet (67-115) and the lighter cues produced with the hand-made grid (4-55). This difference was eliminated in series B.

Table 7. Reflected brightness and visual angles subtended by one unit line of cue patterns (A) - human study.

| Cue | Reflected Brightness |      | Visual Angle (min., sec.) |      |     |     |
|-----|----------------------|------|---------------------------|------|-----|-----|
|     | Spotometer reading   | Lux  | 1 m                       | 2 m  | 3 m | 4 m |
| 4*  | 8.2                  | 11.1 | 27.0                      | 13.5 | 9.5 | 6.8 |
| 5   | 8.1                  | 11.1 | 21.0                      | 10.5 | 7.0 | 5.3 |
| 6   | 8.25                 | 11.1 | 17.5                      | 9.0  | 6.0 | 4.5 |
| 7   | 8.1                  | 11.1 | 14.5                      | 7.5  | 4.5 | 3.8 |
| 8   | 8.1                  | 11.1 | 12.5                      | 6.5  | 4.0 | 3.3 |
| 9   | 7.9                  | 10.9 | 11.0                      | 5.5  | 3.5 | 2.8 |
| 10  | 8.0                  | 11.0 | 9.5                       | 4.8  | 3.0 | 2.4 |
| 11  | 8.0                  | 11.0 | 8.8                       | 4.3  | 3.0 | 2.2 |
| 12  | 7.9                  | 10.9 | 7.8                       | 4.0  | 2.6 | 2.0 |
| 13  | 8.0                  | 11.0 | 7.2                       | 3.5  | 2.4 | 1.8 |
| 14  | 7.95                 | 11.0 | 7.0                       | 3.3  | 2.2 | 1.7 |
| 16  | 7.92                 | 10.9 | 5.8                       | 3.0  | 2.0 | 1.5 |
| 19  | 7.92                 | 10.9 | 5.0                       | 2.5  | 1.5 | 1.3 |
| 22  | 8.2                  | 11.1 | 4.2                       | 2.2  | 1.5 | 1.1 |
| 23  | 7.9                  | 10.9 | 4.0                       | 2.0  | 1.2 | 1.0 |
| 30  | 7.95                 | 11.0 | 3.0                       | 1.5  | 1.0 | 45" |
| 35  | 8.4                  | 11.2 | 2.5                       | 1.3  | 1.0 | 39" |
| 40  | 7.84                 | 10.9 | 2.3                       | 1.2  | 46" | 36" |
| 49  | 7.82                 | 10.9 | 2.0                       | 56"  | 37" | 28" |
| 55  | 7.84                 | 10.9 | 1.7                       | 50"  | 34" | 25" |
| 67  | 7.42                 | 10.6 | 1.3                       | 41"  | 28" | 20" |
| 73  | 7.38                 | 10.6 | 1.3                       | 38"  | 26" | 19" |
| 79  | 7.40                 | 10.6 | 1.2                       | 35"  | 24" | 17" |
| 96  | 7.42                 | 10.6 | 1.1                       | 34"  | 23" | 17" |
| 97  | 7.32                 | 10.5 | 1.0                       | 28"  | 19" | 14" |
| 115 | 7.60                 | 10.7 | 48"                       | 24"  | 16" | 12" |

\*Numbers refer to number of black lines on the 5.5 cm x 5.5 cm square.

The differences in brightness did not affect the results in the human study, because a single cue discrimination was required for experiment 2, the subject simply identifying which cues he could resolve into a pattern. The visual angles of the cues in series A at 1, 2, 3 and 4 metres are given in Table 7.

The results of both experiments are recorded in Table 8. An abbreviated number of results were recorded for tests in water, with and without a mask, and in air. The conditions were otherwise the same as in the dolphin study. For experiment 1, it can be seen that in air, or with a mask in water, the subject approached threshold at about 1.0', being able to discriminate 48" at some sizes but not at others. Without a mask, the subject appeared to be responding in part to absolute size, as the dolphin did, and in part perhaps to visual angle. His best discrimination was 8.5' at 2 metres.

The results for experiment 2 tend to support the results for experiment 1. In water without a mask the subject was able to discriminate a 12.5' angle at 1 metre, as opposed to 17.5' at 1 metre in experiment 1. With a mask in water, or in air, the threshold at 1 to 3 metres varied between 46" and 64". A further set of results obtained in an artificially lighted corridor were slightly lower, between 42" and 48" at 1 to 4 metres. This is similar to other people's results for human visual acuity (e.g. Johnson, 1914; Weinstein, 1940), which is generally accepted as ranging between 30" and 60".

Table 8. Visual acuity of human subject, showing threshold responses at different distances.

A. Experiment 1.

| Conditions          | 1 m       |           |  | 2 m       |           |  | 3 m       |           |  | 4 m                |           |  |
|---------------------|-----------|-----------|--|-----------|-----------|--|-----------|-----------|--|--------------------|-----------|--|
|                     | Cue pair  | Vis. ang. |  | Cue pair  | Vis. ang. |  | Cue pair  | Vis. ang. |  | Cue pair           | Vis. ang. |  |
| Water without mask. | 1 x 1.5   | 17.5'     |  | 1 x 5.5   | 1° 17.5'  |  | 1 x 6     | 57.5'     |  | could not see cues |           |  |
|                     | 3 x 3.5   | 17.5'     |  | 3 x 4     | 17.5'     |  | 3 x 6     | 34.5'     |  |                    |           |  |
|                     | 6 x 6.5   | 17.5'     |  | 6 x 6.5   | 8.5'      |  | 6 x 7     | 11.5'     |  |                    |           |  |
|                     | 10 x 9.5  | 17.5'     |  | 10 x 9.5  | 8.5'      |  | 10 x 9    | 11.5'     |  |                    |           |  |
| Water with mask.    | 1.2 x 1.3 | 3.5'      |  | 1.2 x 1.3 | 1.5'      |  | 1.2 x 1.3 | 1.0'      |  | 1.2 x 1.3          | 48"       |  |
|                     | 3.2 x 3.3 | 3.5'      |  | 3.2 x 3.3 | 1.5'      |  | 3.2 x 3.3 | 1.0'      |  | 3.2 x 3.3          | 48"       |  |
|                     | 6.2 x 6.3 | 3.5'      |  | 6.2 x 6.3 | 1.5'      |  | 6.2 x 6.3 | 1.0'      |  | 6.2 x 6            | 1.75'     |  |
|                     | 9.7 x 9.8 | 3.5'      |  | 9.8 x 10  | 3.5'      |  | 9.7 x 9.8 | 1.0'      |  | 9.7 x 9.8          | 48"       |  |
| Air                 | 1.2 x 1.3 | 3.5'      |  | 1.2 x 1.3 | 1.5'      |  | 1.2 x 1.3 | 1.0'      |  | 1.2 x 1.3          | 48"       |  |
|                     | 3.2 x 3.3 | 3.5'      |  | 3.2 x 3.3 | 1.5'      |  | 3.2 x 3.3 | 1.0'      |  | 3.2 x 3.3          | 48"       |  |
|                     | 6.2 x 6.3 | 3.5'      |  | 6.2 x 6.3 | 1.5'      |  | 6.2 x 6   | 2.5'      |  | 6.2 x 6            | 1.75'     |  |
|                     | 9.7 x 9.8 | 3.5'      |  | 9.7 x 9.8 | 1.5'      |  | 10 x 9.8  | 2.5'      |  | 9.8 x 10           | 1.75'     |  |

Note: In this table are shown the minimal-difference cue pairs which could be distinguished. Since 1 mm was the minimal difference available between cues, the detection of such a difference indicates a lower threshold MAR than the calculated angular differences indicated in the table.

Table 8 - continued

B. Experiment 2

| Conditions                    | 1 m    |              | 2 m            |              | 3 m   |              | 4 m   |              |
|-------------------------------|--------|--------------|----------------|--------------|-------|--------------|-------|--------------|
|                               | Cue    | Visual angle | Cue            | Visual angle | Cue   | Visual angle | Cue   | Visual angle |
| Water without<br>mask.        | 8      | 12.5'        | 115<br>[10 cm] | 16'          |       |              |       |              |
| Water with<br>mask.           | 97-115 | 54"          | 40-49          | 64"          | 30-35 | 60"          |       |              |
| Air                           | 97-115 | 54"          | 55             | 50"          | 40    | 46"          |       |              |
| Air in<br>lighted<br>corridor | 115    | 48"          | 73-55          | 42"          | 49-40 | 43"          | 35-23 | 45"          |

## DISCUSSION

## 1. Experiment I.

The results for experiment 1 are inevitably brought into question by the presence of an experimental variable other than visual angle. It has generally been assumed that visual cues differing in area, and therefore in overall brightness, cannot be used in a visual acuity task, because the extra variable would contaminate the results. In order to test the effect of this extra variable, a series of squares of different sizes and areas were used in this experiment. Squares of varying sizes between 1 and 10 cm were combined in a variety of ways to produce some series with the same visual angles and others with the same 'brightness ratios'. The results were recorded and graphed so as to study the relationships of values having the same visual angle or brightness ratio.

In Graphs 1 and 2, it is very apparent that there is a constant relationship for values with the same visual angle under a given set of conditions. Not all the values fit this constant relationship well. Almost all of the responses for discriminations with a 1 cm square are lower than the general trend. In air, this drop-off occurs at larger sizes, the size threshold increasing with distance. In water, there is a further irregularity in the results at 3 metres. The exceptionally high response at 11.5 mins drops off at larger sizes. It could be that these particular sizes are of particular significance to a dolphin; it is hard to see why, however. The

difference was significant as were most of the drop-offs at 1 cm. The latter can be explained as an absolute size threshold; the dolphin is probably unable to identify, or rather resolve, a square in that size range. The aberration in Graph 1c remains a mystery, however.

It is probable that much of the variance in results for experiment 1, as depicted by Graphs 1 and 2, is a matter of experimental variability and the irregularity of sample size for different data points. Sample size varied from as few as 20 trials, when response was perfect, to 200 trials, when response showed much variability.

In producing Graphs 3 and 4, the data for the 1 cm square was dropped, as it was considered aberrant. The remaining points fitted remarkably well into a straight line curve for each set of conditions. The different brightness ratios had little or no effect on the relationship between visual angle and response level. Graphs 3a and 4a did, however, show a tendency to fit a curved line. The response was also consistently lower at 1 metre in water. It thus seems likely that another variable was affecting response at 1 metre. It is highly possible that the dolphin eye is incapable of accommodation at this point; its nearpoint may be somewhere near 2 metres. In this case resolution would be greatly reduced at 1 metre. The animal might include the brightness or size difference in its effort to discriminate.

If 2 metres is the approximate nearpoint for visual accommodation, it would explain the difference in the slopes of the lines a, b and c in

Graph 3. Assuming further that the dolphin cannot accommodate in air at all would explain why there is little difference in the slopes of lines a, b and c in Graph 4. It would also explain why the response is much poorer than in water.

Considering graphs 1 to 4, it is apparent that visual angle was strongly correlated with response level, above the absolute size threshold, in water and air. Brightness ratio showed no consistent relationship with response, and there was even less correlation with area ratio or simple difference in areas. The variability which did occur seemed much more related to linear differences in size than to area differences, and suggested an absolute size threshold, below which the dolphin could not distinguish the squares.

## 2. Experiment 2

The limited time available for execution of experiment 2 forced a hasty collection of results. Recording began as soon as the animal showed a reasonably dependable response to the cue pattern. It is probable that Himself had not yet reached his optimal performance level when the results were taken. In view of the low criterion of performance accepted, it is not surprising that results at each of the five subject-to-cue distances were rather irregular and did not differ significantly from one another. When all were lumped together, straight line fits were obtained as shown in Graphs 5 and 6. The tracking technique which was used placed great emphasis on the lower range of data points, close to the

threshold. The other values depended on relatively few trials. If there had been time to collect more data points and to perform more trials for each value, it is likely that the linear fit would have been different. Possibly, the values for the five distances would have showed some difference.

### 3. Thresholds for Dolphin Visual Acuity

If 75% response is taken as the criterion for positive discrimination of cues, it would seem that the results of experiments 1 and 2 do not compare well. According to Table 6, there are distinct differences in threshold visual angle (or MAR) at 1, 2 and 3 metres. Only ~~one~~ value was obtained in experiment 2. However, it is interesting to observe that the average of the three threshold values in experiment 1 is identical to that for experiment 2. Disappointingly, if one looks at the data points closest to 75% for each of the five distances in water in Table 5, it is seen that the visual angles increase from 1 to 3 metres, instead of decreasing. This completely contradicts the results for experiment 1 and challenges the reasoning that loss of accommodation causes the higher threshold at closer distances.

In view of the fact that data was collected before the dolphin reached optimal performance, it is tempting to study the effect of lowering the criterion response for discrimination to 65%. A look at Table 5 will show that the threshold tends to drop with increasing distance in both water and air. This proves nothing, of course, except perhaps that the data is not totally reliable when the

distances are studied separately with such limited data. If the criterion is lowered to 65% in experiment 1, all the thresholds are lowered, but their relationship to one another is unchanged.

Table 9. Thresholds for dolphin visual acuity at 65% criterion (in minutes).

| Experiment 2 | Water | (75%) | Air  |
|--------------|-------|-------|------|
| 1 m          | 10    | 10.5  | 15.5 |
| 1.5 m        | 9     | 12    | 13   |
| 2 m          | 9     | 13    | 11.5 |
| 2.5 m        | 8     | 14    | 10   |
| 3 m          | 8     | -     | 11   |
| Experiment 1 |       |       |      |
| 1 m          | 14    |       | 26   |
| 2 m          | 7     |       | 24   |
| 3 m          | 5     |       | 27   |

#### 4. Human Data

The human data shows better correspondence between the two methods than the dolphin data. In experiment 1, the subject discriminated the finest resolution available down to between 1.75' and 48" in air and in water when wearing a mask. In water without a mask, the best resolution was 8.5' at 2 metres. Absolute size

seemed to play an important role when the subject was no longer able to accommodate. It will be remembered that the dolphin showed a similar reliance on size in air.

In experiment 2, the subject again had a threshold of about 1' in water with a mask, but the threshold was closer to 50" in air. The difference might be due to distortion in the water producing a lower threshold although it did not appear in experiment 1. Without a mask, the subject had a threshold of 12.5' at 1 metre and 16' at 10 cm. This was in the same range as the results from experiment 1.

Overall, the results from the tests with the human subject suggest that the two methods for studying visual acuity might both be valid, and compare favourably with one another under suitable conditions. The human threshold in air is in the normal accepted range for human vision. In water, it compares somewhat to dolphin visual acuity, a great deal less acute than normal human vision but still useful for general discriminations.

## 5. Overview

In determining how large a role vision is likely to play in a dolphin's normal perception, it is necessary to consider what functions it would have and whether these could be replaced by other senses. There are several major functions of perception: detection and identification of objects, orientation and navigation, and communication with other individuals. Under the first two categories are such activities as food finding, predator avoidance, normal swimming and obstacle avoidance, and long distance navigation, as in

migration. Communication introduces complex activities such as aggression, courtship and mating, protective and care-giving behaviour, group play, schooling, and so on.

In terrestrial species, navigation is generally accomplished by vision, perhaps aided by olfaction and passive echolocation. Active echolocation is rare, though it has been demonstrated in bats and some species of birds. Detection may involve vision, olfaction or hearing, or any combination of the three, and the same is true of identification. Vision and/or olfaction are most frequently used in the latter activity. Orientation of the animal with respect to the area requires a response to stable environmental conditions rather than to changes, as in orientation to a novel stimulus. Both may involve the use of any or all of the above senses. Contact may also be involved in some of the above activities, and more frequently in the third major category, communication. In species which vocalize seldom, visual shape, pattern and colouring are generally important for identification of conspecifics or other species, while postures, touch and scent play a large role in communication as well as identification.

Since olfaction has been eliminated in cetaceans, the burden of perception is thrown on the other three senses. Touch is primarily involved in communicatory behaviour. Chemical sense, if one exists, and temperature sense may play some role in long distance navigation and perhaps in the other activities as well. However, nothing is known of these senses as yet, and it seems likely that

hearing and vision would dominate in most activities. The influence of hearing in vocal communication, which is very active in many cetacean species, and in echolocation, is irrefutable. How important, then, is vision in these activities?

The striking shapes and colour patterns of many cetaceans suggests a definite role of vision in species identification (Evans and Bastian, 1969). Furthermore, a variety of stereotyped postures and activities are performed by cetaceans during communication. It is possible, of course, that these visual signals are vestigial, but it seems highly unlikely.

The degree of dependence on vision for activities such as detection, identification, orientation and navigation has been studied very little. However, the observations of the various authors mentioned in the introduction suggest a strong reliance on vision for food finding, orientation and various social activities. Schevill and Lawrence (1956) suggested that echolocation was replaced by vision at close range. Norris (1969) pointed out that at distances closer than 1 metre, the click frequency necessary for echolocation ( $> 400/\text{sec}$ ) was too fast for the dolphin to be capable of separating clicks from echos.

It seems probable then, that echolocation is used for long range detection, localization and homing in on objects, and for navigation, particularly in turbid, coastal water. However, echolocation is probably replaced by vision at close range, although this has been seen to be less efficient under 1 metre in Tursiops. Possibly, the

enforced head-on position of Himself in the head rest created difficulty in seeing the cues, as binocular vision, if it exists at all, would not be possible at this distance, and monocular vision was impeded by the position of the head. In this case, vision might be better at a close distance when the dolphin is free to view an object from any angle it wishes. Of course this hypothesis again disputes the theory that accommodation is reduced at this distance, a theory which Kellogg and Rice (1966) also suggested. Until more work is done, neither theory has any foundation, and cannot really be supported or disproved.

It also seems reasonable to assume the use of vision in shallow water, especially where the substrate provides poor acoustics. At the surface or in shallow water and obviously in air, vision would be a distinct asset and require less expenditure of energy on the dolphin's part. It is known that dolphins kept in isolation tend to stop vocalizing (Lilly, 1962) unless novel stimuli are introduced. The animal does not rely on echolocation in water of good visibility, but uses it to supplement the visual evidence when studying novel stimuli. Although the results of my study do not suggest very outstanding visual acuity in the dolphin, it would be sufficient to give a good deal of information under water, and impressions of objects and movement in air.

Most toothed whales are hunters. They require alertness and acute senses in order to capture their prey. Of course some members of the group have a mode of life which discourages the use of vision. The Ganges dolphin roots in the substrate for its food, spending its

life in an extremely turbid environment. It is totally blind and its eyes are vestigial. At the opposite extreme, the sperm whale inhabits the open ocean, sounding to great depths in search of squid which form the main part of its diet. It requires sensitivity to light more than acute vision and has probably sacrificed the latter for the former. In between these extremes are a wide range of dolphins, porpoises and beaked whales, which occupy widely varying habitats. Many of these are shallow water, coastal environments, such as that of Tursiops. Here the need for acute senses can frequently be satisfied by use of vision as well as hearing. Where the water is turbid and where acoustics are good, echolocation probably takes precedence, but vision is doubtless used under conditions of good visibility, either alone or in combination with echolocation for maximum efficiency.

## CONCLUSION

In conclusion, I would like to reassert my belief that vision is a useful and commonly used mode of perception in some species of cetaceans. Anyone who has observed dolphins is impressed by their obvious attention to objects and movement in air, where their echolocation is impossible. In dolphin shows, the animals are trained to perform certain responses to visual signals, and have no difficulty in forming such associations. Under water, objects are frequently observed, investigated and handled without any audible click-creakings being emitted. As a form of negative evidence, I have seen several animals frightened and bewildered by transparent plexiglass sheets, which they had located by use of sonar but were unable to see.

The visual acuity thresholds obtained in this study show a far better adaptation to underwater vision than to air. This was predictable from Walls' (1942) description of the anatomy of the odontocete eye. Animals as completely adapted to water as cetaceans have relatively little use for aerial perception any longer. But vision in water is not much less acute than that of the sea lion, as recorded by Schusterman (1970), which was specified as 5.5 minutes. Spong and White (1971) obtained 6 minutes for the Pacific whitesided dolphin in water. Experiment 1 gave a value of 6 minutes at 3 metres in water for the bottlenose dolphin. The results are rather poorer by experiment 2 (13 minutes) but they are

questionable because of the haste with which they were collected. The amphibious sea lion has far better acuity in air (5.5. minutes as opposed to 33 minutes by experiment 1 or 25 minutes by experiment 2), but this is to be expected, as Tursiops is totally aquatic.

It is predicted that more complete visual acuity studies using a method similar to that of experiment 2 will provide a threshold for Tursiops close to that yielded by experiment 1 in this study, and by Spong and White for Lagenorhynchus.

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Appendix A. Table of proportion of correct responses for separate runs  
of trials with cue pairs - Experiment 1

% = percentage correct response;

N = number of trials; X = number of correct trials.

| Cue pair  | Water     |    |           |    |          |    | Air      |    |          |    |          |    |
|-----------|-----------|----|-----------|----|----------|----|----------|----|----------|----|----------|----|
|           | 1 m       |    | 2 m       |    | 3 m      |    | 1 m      |    | 2 m      |    | 3 m      |    |
|           | %         | N  | %         | N  | %        | N  | %        | N  | %        | N  | %        | N  |
| 10 x 9.8  | 50        | 10 | 60        | 20 | 53       | 30 | 30       | 10 | 50       | 30 |          |    |
|           | 50        | 10 | 57        | 30 | 40       | 10 | 60       | 20 |          |    |          |    |
|           | 60        | 20 | 57        | 30 |          |    |          |    |          |    |          |    |
|           | 10        | 10 | 40        | 20 |          |    |          |    |          |    |          |    |
| Total X:N | 23 : 50   |    | 54 : 100  |    | 20 : 40  |    | 15 : 30  |    | 15 : 30  |    |          |    |
| 10 x 9.7  | 40        | 30 | 70        | 40 | 50       | 40 | 40       | 10 | 50       | 30 | 57       | 30 |
|           | 60        | 30 | 70        | 30 | 60       | 30 | 53       | 15 | 55       | 20 | 70       | 10 |
|           | 70        | 80 | 80        | 10 | 50       | 10 |          |    |          |    | 50       | 10 |
|           | 53        | 30 | 60        | 20 |          |    |          |    |          |    | 50       | 20 |
|           | 50        | 10 | 50        | 10 |          |    |          |    |          |    | 47       | 30 |
|           |           |    | 53        | 40 |          |    |          |    |          |    |          |    |
| Total X:N | 107 : 180 |    | 95 : 150  |    | 43 : 80  |    | 12 : 25  |    | 26 : 50  |    | 53 : 100 |    |
| 10 x 9.5  | 85        | 20 | 60        | 10 | 66       | 50 | 45       | 20 | 30       | 20 | 70       | 40 |
|           | 60        | 10 | 75        | 20 | 70       | 20 | 50       | 30 | 60       | 10 | 43       | 40 |
|           | 80        | 20 | 65        | 60 | 66       | 50 | 60       | 10 | 55       | 20 | 50       | 10 |
|           | 60        | 10 | 60        | 10 | 50       | 10 | 70       | 10 | 70       | 10 | 70       | 10 |
|           | 75        | 20 | 70        | 30 | 100      | 10 | 60       | 10 | 58       | 40 |          |    |
|           | 50        | 20 | 100       | 10 |          |    | 70       | 20 |          |    |          |    |
|           | 70        | 40 | 40        | 10 |          |    |          |    |          |    |          |    |
|           | 75        | 20 | 40        | 10 |          |    |          |    |          |    |          |    |
|           | 50        | 10 | 63        | 40 |          |    |          |    |          |    |          |    |
| Total X:N | 118 : 170 |    | 130 : 200 |    | 95 : 140 |    | 57 : 100 |    | 53 : 100 |    | 57 : 100 |    |

## Appendix A - continued

| Cue pair  | Water    |    |          |    |          |    | Air       |    |          |     |          |    |
|-----------|----------|----|----------|----|----------|----|-----------|----|----------|-----|----------|----|
|           | 1 m      |    | 2 m      |    | 3 m      |    | 1 m       |    | 2 m      |     | 3 m      |    |
|           | %        | N  | %        | N  | %        | N  | %         | N  | %        | N   | %        | N  |
| 10 x 9.0  | 90       | 20 | 70       | 20 | 100      | 10 | 80        | 20 | 66       | 50  | 68       | 40 |
|           | 77       | 30 | 80       | 20 | 70       | 30 | 90        | 10 | 75       | 20  | 80       | 20 |
|           | 73       | 30 | 90       | 10 | 90       | 10 | 90        | 10 | 70       | 30  | 55       | 20 |
|           | 65       | 20 | 100      | 10 | 70       | 10 | 45        | 20 | 70       | 10  | 70       | 10 |
|           | 80       | 10 | 60       | 10 | 85       | 40 | 60        | 30 | 75       | 20  | 90       | 10 |
|           | 80       | 10 | 40       | 10 |          |    | 30        | 10 |          |     |          |    |
|           |          |    | 80       | 20 |          |    | 63        | 30 |          |     |          |    |
|           |          |    |          |    |          |    | 64        | 50 |          |     |          |    |
|           |          |    |          |    |          |    | 80        | 10 |          |     |          |    |
| Total X:N | 95 : 120 |    | 85 : 100 |    | 81 : 100 |    | 123 : 190 |    | 91 : 130 |     | 70 : 100 |    |
| 10 x 8.5  |          |    |          |    |          |    | 80        | 10 | 100      | 10  | 90       | 10 |
|           |          |    |          |    |          |    | 73        | 15 | 90       | 10  | 80       | 20 |
|           |          |    |          |    |          |    | 80        | 15 | 70       | 10  | 90       | 10 |
|           |          |    |          |    |          |    | 70        | 10 | 90       | 10  | 90       | 10 |
|           |          |    |          |    |          |    | 60        | 10 | 70       | 10  |          |    |
|           |          |    |          |    |          |    | 60        | 40 | 80       | 20  |          |    |
|           |          |    |          |    |          |    | 75        | 20 |          |     |          |    |
|           |          |    |          |    |          |    | 80        | 20 |          |     |          |    |
|           |          |    |          |    |          |    | 95        | 20 |          |     |          |    |
| Total X:N |          |    |          |    |          |    | 118 : 160 |    | 58 : 70  |     | 43 : 50  |    |
| 8 x 7.5   | 68       | 50 | 85       | 20 | 73       | 30 | 67        | 30 | 70       | 20  | 45       | 20 |
|           |          |    | 67       | 30 | 70       | 10 | 60        | 10 | 60       | 10  | 53       | 30 |
|           |          |    | 50       | 10 | 70       | 10 | 60        | 20 | 50       | 10  |          |    |
|           |          |    | 75       | 20 |          |    |           |    | 70       | 10  |          |    |
|           |          |    |          |    |          |    |           |    | 50       | 20  |          |    |
|           |          |    |          |    |          |    |           |    | 53       | 30  |          |    |
| Total X:N | 34       | 50 | 57       | 80 | 36       | 50 | 38        | 60 | 59       | 100 | 25       | 50 |

## Appendix A - continued

| Cue pair  | Water    |    |          |    |          |    | Air       |     |          |    |          |    |
|-----------|----------|----|----------|----|----------|----|-----------|-----|----------|----|----------|----|
|           | 1 m      |    | 2 m      |    | 3 m      |    | 1 m       |     | 2 m      |    | 3 m      |    |
|           | %        | N  | %        | N  | %        | N  | %         | N   | %        | N  | %        | N  |
| 8 x 7     | 100      | 10 | 80       | 20 | 90       | 20 | 67        | 30  | 60       | 20 | 80       | 20 |
|           | 90       | 20 | 100      | 10 | 77       | 30 | 70        | 100 | 90       | 10 | 63       | 60 |
|           |          |    | 95       | 20 |          |    | 100       | 10  | 70       | 20 |          |    |
| Total X:N | 28 : 30  |    | 45 : 50  |    | 41 : 50  |    | 100 : 140 |     | 35 : 50  |    | 54 : 80  |    |
| 6 x 7.5   |          |    |          |    |          |    | 87        | 30  | 93       | 15 | 70       | 10 |
|           |          |    |          |    |          |    | 90        | 20  | 85       | 20 | 100      | 10 |
|           |          |    |          |    |          |    | 100       | 10  | 93       | 15 | 90       | 10 |
|           |          |    |          |    |          |    |           |     | 80       | 10 | 90       | 20 |
| Total X:N |          |    |          |    |          |    | 54 : 60   |     | 53 : 60  |    | 44 : 50  |    |
| 6 x 7     | 65       | 20 | 60       | 10 | 90       | 10 | 76        | 70  | 90       | 20 | 80       | 20 |
|           | 80       | 20 | 90       | 30 | 80       | 10 | 70        | 10  | 60       | 10 | 50       | 10 |
|           | 90       | 20 | 80       | 10 | 80       | 10 | 90        | 10  | 65       | 20 | 55       | 20 |
|           | 90       | 20 | 90       | 10 | 80       | 20 |           |     | 72       | 25 | 64       | 50 |
|           | 50       | 10 | 100      | 10 | 80       | 40 |           |     | 76       | 25 | 35       | 20 |
|           | 90       | 10 | 80       | 10 |          |    |           |     | 60       | 20 |          |    |
|           | 80       | 20 | 100      | 20 |          |    |           |     |          |    |          |    |
| Total X:N | 96 : 120 |    | 88 : 100 |    | 73 : 90  |    | 60 : 90   |     | 86 : 120 |    | 71 : 120 |    |
| 6 x 6.5   | 75       | 40 | 80       | 10 | 70       | 30 | 60        | 40  | 55       | 20 |          |    |
|           | 60       | 20 | 60       | 10 | 50       | 10 | 60        | 10  | 53       | 30 |          |    |
|           |          |    | 90       | 20 | 78       | 40 | 65        | 20  | 65       | 40 |          |    |
|           |          |    | 83       | 40 | 65       | 20 |           |     |          |    |          |    |
|           |          |    | 60       | 10 |          |    |           |     |          |    | 55       | 20 |
|           |          |    | 80       | 10 |          |    |           |     |          |    | 47       | 30 |
| Total X:N | 42 : 60  |    | 79 : 100 |    | 70 : 100 |    | 43 : 70   |     | 53 : 90  |    | 25 : 50  |    |
| 6 x 6.3   | 50       | 10 | 80       | 10 | 53       | 30 |           |     |          |    |          |    |
|           | 55       | 40 | 70       | 10 | 40       | 10 |           |     |          |    |          |    |
|           | 50       | 10 | 58       | 50 | 55       | 20 |           |     |          |    |          |    |
|           | 65       | 40 | 50       | 10 | 60       | 20 |           |     |          |    |          |    |
|           |          |    | 70       | 10 |          |    |           |     |          |    |          |    |
| Total X:N | 58 : 100 |    | 61 : 100 |    | 43 : 80  |    |           |     |          |    |          |    |

## Appendix A - continued

| Cue pair  | Water    |    |          |    |          |    | Air     |    |          |    |          |    |
|-----------|----------|----|----------|----|----------|----|---------|----|----------|----|----------|----|
|           | 1 m      |    | 2 m      |    | 3 m      |    | 1 m     |    | 2 m      |    | 3 m      |    |
|           | %        | N  | %        | N  | %        | N  | %       | N  | %        | N  | %        | N  |
| 6 x 6.2   | 60       | 10 | 60       | 10 | 60       | 30 |         |    |          |    |          |    |
|           | 57       | 30 | 60       | 20 | 50       | 10 |         |    |          |    |          |    |
|           | 70       | 10 | 66       | 50 | 53       | 30 |         |    |          |    |          |    |
|           | 50       | 50 | 60       | 10 | 50       | 20 |         |    |          |    |          |    |
|           |          |    | 50       | 40 |          |    |         |    |          |    |          |    |
|           |          |    | 35       | 20 |          |    |         |    |          |    |          |    |
| Total X:N | 55 : 100 |    | 84 : 150 |    | 49 : 90  |    |         |    |          |    |          |    |
| 5 x 6.5   |          |    |          |    |          |    |         |    | 80       | 10 | 60       | 20 |
|           |          |    |          |    |          |    |         |    | 80       | 30 | 60       | 30 |
|           |          |    |          |    |          |    |         |    |          |    | 74       | 80 |
|           |          |    |          |    |          |    |         |    |          |    | 70       | 20 |
| 5 x 6     | 65       | 20 | 90       | 10 | 90       | 10 | 60      | 20 | 68       | 40 | 53       | 40 |
|           | 75       | 20 | 90       | 10 | 95       | 20 | 90      | 10 | 50       | 30 | 50       | 10 |
|           | 90       | 10 | 93       | 30 | 60       | 10 | 75      | 20 | 60       | 10 | 65       | 20 |
|           | 80       | 20 | 95       | 20 | 100      | 10 | 85      | 20 | 80       | 20 | 43       | 30 |
|           | 97       | 30 |          |    | 97       | 30 |         |    | 85       | 20 | 77       | 30 |
| Total X:N | 82 : 100 |    | 65 : 70  |    | 73 : 80  |    | 53 : 70 |    | 81 : 120 |    | 73 : 130 |    |
| 5 x 5.5   | 90       | 20 | 75       | 20 | 85       | 20 | 40      | 20 | 50       | 30 | 53       | 40 |
|           | 75       | 20 | 75       | 20 | 50       | 10 | 30      | 10 | 60       | 10 | 50       | 10 |
|           | 80       | 10 | 80       | 10 | 100      | 20 | 75      | 20 | 50       | 10 |          |    |
|           | 88       | 50 |          |    | 58       | 40 | 60      | 30 | 70       | 20 |          |    |
|           | 70       | 20 |          |    | 90       | 10 |         |    |          |    |          |    |
| Total X:N | 89 : 120 |    | 38 : 50  |    | 74 : 100 |    | 44 : 80 |    | 40 : 70  |    | 26 : 50  |    |
| 4 x 5.5   |          |    |          |    | 100      | 20 | 100     | 10 |          |    | 70       | 20 |
|           |          |    |          |    |          |    | 90      | 10 |          |    | 70       | 30 |
|           |          |    |          |    |          |    | 83      | 30 |          |    | 65       | 20 |
|           |          |    |          |    |          |    | 70      | 10 |          |    |          |    |
| Total X:N |          |    |          |    | 20 : 20  |    | 51 : 60 |    |          |    | 48 : 70  |    |

## Appendix A - Continued

| Cue Pair  | Water     |     |         |    |         |    | Air      |    |         |    |          |    |
|-----------|-----------|-----|---------|----|---------|----|----------|----|---------|----|----------|----|
|           | 1 m       |     | 2 m     |    | 3 m     |    | 1 m      |    | 2 m     |    | 3 m      |    |
|           | %         | N   | %       | N  | %       | N  | %        | N  | %       | N  | %        | N  |
| 4 x 5     | 70        | 50  | 90      | 10 | 90      | 10 | 90       | 20 | 60      | 10 | 67       | 30 |
|           | 85        | 20  | 88      | 40 | 100     | 40 | 80       | 20 | 60      | 10 | 60       | 50 |
|           | 100       | 20  | 90      | 10 |         |    | 70       | 10 | 73      | 30 |          |    |
|           | 95        | 20  |         |    |         |    | 80       | 10 |         |    |          |    |
|           |           |     |         |    |         |    | 85       | 40 |         |    |          |    |
| Total X:N | 91 : 110  |     | 53 : 60 |    | 49 : 50 |    | 83 : 100 |    | 34 : 50 |    | 50 : 80  |    |
| 4 x 4.5   | 68        | 50  | 80      | 20 | 68      | 40 | 65       | 20 | 80      | 10 | 43       | 30 |
|           | 71        | 100 | 70      | 10 | 60      | 10 | 65       | 40 | 30      | 10 | 55       | 20 |
|           | 77        | 30  | 83      | 30 | 77      | 30 | 50       | 10 | 60      | 50 | 55       | 20 |
|           |           |     |         |    |         |    |          |    | 45      | 20 |          |    |
| Total X:N | 128 : 180 |     | 48 : 60 |    | 56 : 80 |    | 44 : 70  |    | 50 : 90 |    | 35 : 70  |    |
| 3 x 5     | 100       | 5   | 100     | 10 | 100     | 10 | 80       | 15 | 100     | 5  | 100      | 10 |
|           | 100       | 20  | 100     | 20 | 100     | 10 | 100      | 10 | 85      | 20 | 70       | 20 |
|           |           |     |         |    |         |    | 100      | 20 | 88      | 25 | 70       | 10 |
|           |           |     |         |    |         |    |          |    | 80      | 20 | 60       | 10 |
|           |           |     |         |    |         |    |          |    |         |    | 80       | 10 |
|           |           |     |         |    |         |    |          |    |         |    | 65       | 20 |
| Total X:N | 25 : 25   |     | 30 : 30 |    | 20 : 20 |    | 42 : 45  |    | 60 : 70 |    | 58 : 80  |    |
| 3 x 4.5   | 100       | 10  | 100     | 30 | 100     | 10 | 85       | 20 | 72      | 25 | 48       | 40 |
|           | 100       | 20  |         |    | 100     | 10 | 90       | 20 | 72      | 25 | 50       | 10 |
|           |           |     |         |    | 100     | 10 | 60       | 10 |         |    | 56       | 50 |
|           |           |     |         |    |         |    |          |    |         |    | 70       | 20 |
| Total X:N | 30 : 30   |     | 30 : 30 |    | 30 : 30 |    | 41 : 50  |    | 36 : 50 |    | 66 : 120 |    |

## Appendix A - Continued

| Cue pair  | Water     |    |          |    |           |    | Air      |    |          |    |          |    |
|-----------|-----------|----|----------|----|-----------|----|----------|----|----------|----|----------|----|
|           | 1 m       |    | 2 m      |    | 3 m       |    | 1 m      |    | 2 m      |    | 3 m      |    |
|           | %         | N  | %        | N  | %         | N  | %        | N  | %        | N  | %        | N  |
| 3 x 4     | 90        | 20 | 90       | 20 | 100       | 10 | 70       | 20 | 57       | 30 | 50       | 10 |
|           | 80        | 10 | 75       | 20 | 100       | 10 | 80       | 20 | 70       | 10 | 57       | 30 |
|           | 60        | 10 | 90       | 10 | 90        | 10 | 80       | 10 | 52       | 25 | 63       | 30 |
|           | 85        | 20 | 70       | 10 | 100       | 10 |          |    | 57       | 25 | 60       | 30 |
|           | 70        | 10 | 100      | 10 | 100       | 10 |          |    |          |    |          |    |
|           |           |    | 95       | 20 | 93        | 30 |          |    |          |    |          |    |
|           |           |    |          |    | 95        | 20 |          |    |          |    |          |    |
|           |           |    |          |    | 100       | 10 |          |    |          |    |          |    |
| Total X:N | 56 : 70   |    | 78 : 90  |    | 106 : 110 |    | 38 : 50  |    | 54 : 90  |    | 59 : 100 |    |
| 3 x 3.5   | 80        | 20 | 75       | 40 | 85        | 20 | 50       | 20 | 50       | 10 | 50       | 10 |
|           | 77        | 30 | 60       | 20 | 83        | 30 | 60       | 10 | 60       | 35 | 50       | 20 |
|           | 80        | 10 | 80       | 10 | 100       | 10 | 80       | 30 | 60       | 25 | 70       | 50 |
|           | 75        | 20 | 70       | 10 | 90        | 10 | 70       | 20 | 43       | 30 | 40       | 20 |
|           | 70        | 10 | 70       | 10 | 75        | 20 | 45       | 20 |          |    | 45       | 20 |
|           | 85        | 20 | 65       | 20 | 100       | 10 |          |    |          |    |          |    |
|           | 73        | 40 | 85       | 20 | 67        | 30 |          |    |          |    |          |    |
|           |           |    |          |    | 75        | 20 |          |    |          |    |          |    |
| Total X:N | 113 : 150 |    | 74 : 130 |    | 121 : 150 |    | 63 : 100 |    | 75 : 100 |    | 67 : 120 |    |
| 3 x 3.3   | 80        | 10 | 80       | 10 | 73        | 40 |          |    |          |    |          |    |
|           | 63        | 40 | 50       | 10 | 70        | 10 |          |    |          |    |          |    |
|           | 50        | 30 | 73       | 30 | 40        | 30 |          |    |          |    |          |    |
|           | 50        | 20 | 52       | 50 | 75        | 20 |          |    |          |    |          |    |
|           |           |    |          |    | 43        | 30 |          |    |          |    |          |    |
| Total X:N | 58 : 100  |    | 62 : 100 |    | 76 : 130  |    |          |    |          |    |          |    |
| 3 x 3.2   | 70        | 10 | 50       | 10 | 60        | 40 |          |    |          |    |          |    |
|           | 40        | 20 | 55       | 40 | 80        | 20 |          |    |          |    |          |    |
|           | 50        | 20 |          |    | 50        | 20 |          |    |          |    |          |    |
|           |           |    |          |    | 60        | 20 |          |    |          |    |          |    |
|           |           |    |          |    | 70        | 20 |          |    |          |    |          |    |
|           |           |    |          |    | 53        | 30 |          |    |          |    |          |    |
| Total X:N | 25 : 50   |    | 27 : 50  |    | 92 : 150  |    |          |    |          |    |          |    |

## Appendix A - Continued

| Cue Pair  | Water |    |     |    |     |    | Air |    |     |     |     |    |
|-----------|-------|----|-----|----|-----|----|-----|----|-----|-----|-----|----|
|           | 1 m   |    | 2 m |    | 3 m |    | 1 m |    | 2 m |     | 3 m |    |
|           | %     | N  | %   | N  | %   | N  | %   | N  | %   | N   | %   | N  |
| 2 x 7     |       |    |     |    |     |    |     |    |     |     | 90  | 20 |
| 2 x 6.5   |       |    |     |    |     |    |     |    |     |     | 90  | 20 |
| 2 x 5     |       |    |     |    |     |    |     |    | 75  | 20  |     |    |
|           |       |    |     |    |     |    |     |    | 90  | 10  |     |    |
| Total X:N |       |    |     |    |     |    |     |    | 24  | 30  |     |    |
| 2 x 4.5   |       |    | 100 | 10 | 100 | 10 | 100 | 10 | 76  | 25  | 75  | 20 |
|           |       |    | 100 | 10 | 100 | 10 | 100 | 15 | 65  | 60  | 73  | 30 |
|           |       |    |     |    | 100 | 10 |     |    | 92  | 25  |     |    |
|           |       |    |     |    |     |    |     |    | 98  | 40  |     |    |
| Total X:N |       |    | 20  | 20 | 30  | 30 | 25  | 25 | 120 | 150 | 37  | 50 |
| 2 x 4     | 80    | 10 | 100 | 5  | 100 | 35 | 100 | 5  | 53  | 15  | 70  | 30 |
|           | 100   | 10 | 100 | 10 |     |    | 83  | 35 | 75  | 20  | 55  | 20 |
|           | 90    | 10 | 100 | 10 |     |    | 90  | 20 | 100 | 15  |     |    |
|           | 100   | 20 |     |    |     |    |     |    |     |     |     |    |
|           | 100   | 30 |     |    |     |    |     |    |     |     |     |    |
| Total X:N | 77    | 80 | 25  | 25 | 35  | 35 | 52  | 60 | 38  | 50  | 32  | 50 |
| 2 x 3.5   |       |    |     |    |     |    | 80  | 10 | 65  | 20  | 55  | 20 |
|           |       |    |     |    |     |    | 80  | 40 | 53  | 40  |     |    |
| Total X:N |       |    |     |    |     |    | 40  | 50 | 34  | 60  | 11  | 20 |
| 2 x 3     | 73    | 30 | 100 | 15 | 85  | 20 | 65  | 20 | 55  | 20  |     |    |
|           | 100   | 10 | 76  | 25 | 95  | 20 | 80  | 20 | 50  | 10  |     |    |
|           |       |    | 100 | 10 | 90  | 10 | 80  | 10 | 50  | 20  |     |    |
|           |       |    |     |    |     |    |     |    | 67  | 30  |     |    |
| Total X:N | 32    | 40 | 44  | 50 | 45  | 50 | 37  | 50 | 46  | 80  |     |    |

## Appendix A - continued

| Cue pair  | Water   |    |         |    |         |    | Air     |    |          |    |          |    |
|-----------|---------|----|---------|----|---------|----|---------|----|----------|----|----------|----|
|           | 1 m     |    | 2 m     |    | 3 m     |    | 1 m     |    | 2 m      |    | 3 m      |    |
|           | %       | N  | %       | N  | %       | N  | %       | N  | %        | N  | %        | N  |
| 2 x 2.5   | 80      | 20 | 75      | 40 | 66      | 50 | 60      | 20 | 60       | 10 |          |    |
|           | 40      | 10 | 70      | 10 |         |    | 60      | 10 | 70       | 10 |          |    |
|           | 65      | 20 |         |    |         |    | 57      | 30 | 53       | 30 |          |    |
| Total X:N | 33 : 50 |    | 37 : 50 |    | 33 : 50 |    | 35 : 60 |    | 29 : 50  |    |          |    |
| 1 x 7     |         |    |         |    |         |    |         |    |          |    | 95       | 20 |
|           |         |    |         |    |         |    |         |    |          |    | 100      | 20 |
| Total X:N |         |    |         |    |         |    |         |    |          |    | 39 : 40  |    |
| 1 x 6.5   |         |    |         |    |         |    |         |    |          |    | 85       | 20 |
|           |         |    |         |    |         |    |         |    |          |    | 92       | 25 |
| Total X:N |         |    |         |    |         |    |         |    |          |    | 40 : 45  |    |
| 1 x 6     |         |    |         |    |         |    |         |    |          |    | 85       | 20 |
| 1 x 5.5   |         |    |         |    |         |    |         |    |          |    | 85       | 20 |
| 1 x 5     | 100     | 25 |         |    |         |    |         |    | 90       | 10 | 70       | 40 |
|           |         |    |         |    |         |    |         |    | 100      | 10 | 75       | 20 |
|           |         |    |         |    |         |    |         |    | 100      | 10 | 53       | 30 |
|           |         |    |         |    |         |    |         |    |          |    | 85       | 20 |
| Total X:N | 25 : 25 |    |         |    |         |    |         |    | 29 : 30  |    | 78 : 110 |    |
| 1 x 4.5   |         |    |         |    |         |    |         |    | 90       | 20 | 50       | 15 |
|           |         |    |         |    |         |    |         |    | 100      | 20 | 60       | 30 |
|           |         |    |         |    |         |    |         |    |          |    | 68       | 25 |
|           |         |    |         |    |         |    |         |    |          |    | 80       | 30 |
| Total X:N |         |    |         |    |         |    |         |    | 38 : 40  |    | 67 : 100 |    |
| 1 x 4     | 91      | 55 | 100     | 10 | 100     | 15 | 100     | 15 | 100      | 15 | 80       | 15 |
|           |         |    | 100     | 20 | 100     | 15 | 100     | 10 | 67       | 35 | 55       | 20 |
|           |         |    |         |    |         |    |         |    | 90       | 50 | 60       | 20 |
|           |         |    |         |    |         |    |         |    |          |    | 90       | 20 |
| Total X:N | 50 : 55 |    | 30 : 30 |    | 30 : 30 |    | 25 : 25 |    | 85 : 100 |    | 53 : 75  |    |

## Appendix A - continued

| Cue pair  | Water    |    |          |    |           |    | Air      |    |          |    |          |    |
|-----------|----------|----|----------|----|-----------|----|----------|----|----------|----|----------|----|
|           | 1 m      |    | 2 m      |    | 3 m       |    | 1 m      |    | 2 m      |    | 3 m      |    |
|           | %        | N  | %        | N  | %         | N  | %        | N  | %        | N  | %        | N  |
| 1 x 3.5   | 100      | 25 | 100      | 25 | 100       | 30 | 75       | 20 | 80       | 10 | 70       | 40 |
|           |          |    |          |    |           |    | 100      | 20 | 100      | 10 | 60       | 30 |
|           |          |    |          |    |           |    |          |    | 85       | 20 | 75       | 20 |
|           |          |    |          |    |           |    |          |    | 80       | 10 | 50       | 10 |
|           |          |    |          |    |           |    |          |    | 80       | 20 |          |    |
| Total X:N | 25 : 25  |    | 25 : 25  |    | 30 : 30   |    | 35 : 40  |    | 59 : 70  |    | 65 : 100 |    |
| 1 x 3     | 75       | 40 |          |    | 90        | 30 |          |    | 50       | 40 | 48       | 40 |
|           |          |    |          |    |           |    |          |    |          |    | 90       | 10 |
| Total X:N | 30 : 40  |    |          |    | 27 : 30   |    |          |    | 20 : 40  |    | 28 : 50  |    |
| 1 x 2.5   | 75       | 40 | 100      | 10 | 95        | 20 | 67       | 55 | 60       | 10 | 35       | 20 |
|           | 60       | 10 | 95       | 20 | 85        | 20 | 90       | 10 | 58       | 40 | 50       | 30 |
|           | 90       | 10 | 100      | 20 | 87        | 15 | 84       | 25 |          |    | 75       | 20 |
|           |          |    |          |    | 93        | 30 |          |    |          |    |          |    |
| Total X:N | 45 : 60  |    | 49 : 50  |    | 77 : 85   |    | 67 : 90  |    | 29 : 50  |    | 37 : 70  |    |
| 1 x 2     | 67       | 30 | 70       | 20 | 63        | 40 | 75       | 20 | 53       | 30 | 60       | 50 |
|           | 50       | 10 | 84       | 25 | 75        | 20 | 45       | 20 | 40       | 10 | 57       | 30 |
|           | 70       | 20 | 55       | 20 | 40        | 10 | 90       | 10 | 55       | 40 | 60       | 20 |
|           | 90       | 10 | 80       | 10 | 50        | 20 | 57       | 30 | 60       | 20 |          |    |
|           | 58       | 40 | 80       | 10 | 70        | 10 | 50       | 10 | 65       | 20 |          |    |
|           | 75       | 20 | 93       | 15 | 62        | 50 |          |    |          |    |          |    |
|           |          |    |          |    | 60        | 10 |          |    |          |    |          |    |
| Total X:N | 86 : 130 |    | 76 : 100 |    | 104 : 160 |    | 55 : 90  |    | 67 : 120 |    | 59 : 100 |    |
| 1 x 1.5   | 60       | 30 | 75       | 20 | 50        | 20 | 67       | 30 | 50       | 20 | 67       | 30 |
|           | 40       | 10 | 60       | 20 | 80        | 10 | 60       | 20 | 58       | 30 | 60       | 10 |
|           | 45       | 20 | 50       | 20 | 45        | 20 | 50       | 10 |          |    | 50       | 10 |
|           | 50       | 10 | 80       | 10 | 50        | 10 | 60       | 20 |          |    | 50       | 20 |
|           | 40       | 20 | 70       | 40 |           |    | 50       | 10 |          |    | 40       | 20 |
|           | 50       | 10 |          |    |           |    | 50       | 10 |          |    |          |    |
|           | 55       | 20 |          |    |           |    |          |    |          |    |          |    |
| Total X:N | 60 : 120 |    | 73 : 110 |    | 32        | 60 | 59 : 100 |    | 27 : 50  |    | 49 : 90  |    |

## Appendix A - continued

| Cue Pair  | Water   |    |          |    |         |    | Air |   |     |   |     |   |
|-----------|---------|----|----------|----|---------|----|-----|---|-----|---|-----|---|
|           | 1 m     |    | 2 m      |    | 3 m     |    | 1 m |   | 2 m |   | 3 m |   |
|           | %       | N  | %        | N  | %       | N  | %   | N | %   | N | %   | N |
| 1 x 1.3   | 40      | 10 | 60       | 10 | 50      | 10 |     |   |     |   |     |   |
|           | 55      | 20 | 64       | 50 | 47      | 30 |     |   |     |   |     |   |
|           | 65      | 20 | 80       | 15 |         |    |     |   |     |   |     |   |
|           | 50      | 20 | 62       | 50 |         |    |     |   |     |   |     |   |
|           | 55      | 20 | 51       | 35 |         |    |     |   |     |   |     |   |
| Total X:N | 49 : 90 |    | 97 : 160 |    | 19 : 40 |    |     |   |     |   |     |   |
| 1 x 1.2   | 60      | 10 | 50       | 10 |         |    |     |   |     |   |     |   |
|           | 50      | 40 | 58       | 30 |         |    |     |   |     |   |     |   |
|           |         |    | 50       | 10 |         |    |     |   |     |   |     |   |
| Total X:N | 26 : 50 |    | 27 : 50  |    |         |    |     |   |     |   |     |   |

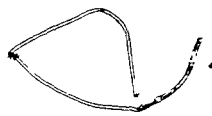
Appendix B. Table of proportion of correct responses for separate runs of Trials with cues - Experiment 2.

I. WATER - % = percentage of correct trials; N = number of trials;  
X = number of correct trials.

| Distance   | Visual Angle (Minutes) |    |         |    |         |    |          |    |           |     |           |    |           |     |          |     |
|------------|------------------------|----|---------|----|---------|----|----------|----|-----------|-----|-----------|----|-----------|-----|----------|-----|
|            | 17.5'                  |    | 16'     |    | 15'     |    | 13.5'    |    | 11'       |     | 10'       |    | 8.5'      |     | 8'       |     |
| 1 metre    | %                      | N  | %       | N  | %       | N  | %        | N  | %         | N   | %         | N  | %         | N   | %        | N   |
|            | 90                     | 10 | 80      | 10 | 70      | 20 | 73       | 30 | 82        | 50  | 81        | 80 | 54        | 70  | 43       | 30  |
|            |                        |    | 80      | 10 | 100     | 10 | 100      | 10 | 80        | 10  | 63        | 70 | 54        | 100 | 50       | 40  |
|            |                        |    |         |    |         |    |          |    | 78        | 50  | 80        | 50 | 50        | 80  |          |     |
|            |                        |    |         |    |         |    |          |    | 83        | 30  | 75        | 20 |           |     |          |     |
| Total X:N  | 9 : 10                 |    | 16 : 20 |    | 24 : 30 |    | 32 : 40  |    | 113 : 140 |     | 148 : 220 |    | 132 : 250 |     | 33 : 70  |     |
| 1.5 metres | 17'                    |    | 15'     |    | 13.5'   |    | 12'      |    | 11'       |     | 10'       |    | 9'        |     | 8'       |     |
|            | 90                     | 10 | 90      | 20 | 60      | 40 | 70       | 40 | 50        | 40  | 61        | 70 | 57        | 30  | 56       | 160 |
|            | 75                     | 20 | 80      | 10 | 60      | 30 | 90       | 20 | 73        | 30  | 62        | 60 | 69        | 110 |          |     |
|            | 80                     | 20 | 90      | 10 | 75      | 20 | 77       | 30 | 90        | 10  |           |    |           |     |          |     |
| Total X:N  | 40 : 50                |    | 35 : 40 |    | 57 : 90 |    | 69 : 90  |    | 51 : 80   |     | 86 : 130  |    | 93 : 140  |     | 90 : 160 |     |
| 2 metres   | 19'                    |    | 15.5'   |    | 13'     |    | 11.5'    |    | 10'       |     | 9.5'      |    | 8'        |     | 7.5'     |     |
|            | 90                     | 10 | 90      | 10 | 73      | 30 | 72       | 50 | 63        | 110 | 65        | 60 | 60        | 30  | 50       | 30  |
|            | 100                    | 10 | 100     | 10 | 80      | 10 | 80       | 10 | 70        | 20  | 68        | 40 | 60        | 50  | 44       | 50  |
|            |                        |    |         |    | 65      | 40 | 66       | 50 | 80        | 10  | 80        | 10 | 70        | 50  |          |     |
| Total X:N  | 19 : 20                |    | 19 : 20 |    | 56 : 80 |    | 77 : 110 |    | 139 : 200 |     | 99 : 150  |    | 101 : 160 |     | 37 : 80  |     |

Appendix B - continued

| Distance   |           | Visual Angle (Minutes) |           |           |           |          |  |  |  |  |  |
|------------|-----------|------------------------|-----------|-----------|-----------|----------|--|--|--|--|--|
| 2.5 metres | 15'       | 12.5'                  | 10'       | 9'        | 8'        | 7'       |  |  |  |  |  |
|            | 40 40     | 67 70                  | 53 90     | 62 130    | 56 100    | 61 100   |  |  |  |  |  |
|            | 70 10     | 68 100                 | 70 90     | 82 40     | 71 130    |          |  |  |  |  |  |
|            | 60 20     |                        |           |           |           |          |  |  |  |  |  |
| Total X:N  | 41 : 50   | 115 : 170              | 111 : 180 | 114 : 170 | 149 : 230 | 61 : 100 |  |  |  |  |  |
| 3 metres   | 12.5'     | 10'                    | 8.5'      | 7.5'      | 6.5'      | 6'       |  |  |  |  |  |
|            | 71 80     | 71 100                 | 65 130    | 57 150    | 48 50     | 43 30    |  |  |  |  |  |
|            | 70 20     | 85 20                  | 66 90     | 68 90     | 59 90     | 53 70    |  |  |  |  |  |
|            | 65 20     | 90 20                  | 66 50     | 80 50     | 68 60     |          |  |  |  |  |  |
|            | 58 30     |                        |           |           |           |          |  |  |  |  |  |
| Total X:N  | 101 : 150 | 106 : 140              | 177 : 270 | 186 : 290 | 118 : 200 | 50 : 100 |  |  |  |  |  |



Appendix B. Table of proportion of correct responses for separate runs of trials with cues - Experiment 2.

II. AIR - % = percentage response; N = number of trials;  
X = number of correct trials.

| Distance   | Visual Angle (Minutes) |    |         |    |         |    |          |    |           |     |           |    |          |    |          |    |
|------------|------------------------|----|---------|----|---------|----|----------|----|-----------|-----|-----------|----|----------|----|----------|----|
|            | %                      | N  | %       | N  | %       | N  | %        | N  | %         | N   | %         | N  | %        | N  | %        | N  |
| 1 metre    | 38'                    |    | 30.5'   |    | 26'     |    | 22'      |    | 20'       |     | 17.5'     |    | 16'      |    | 15'      |    |
|            | 90                     | 10 | 70      | 10 | 75      | 20 | 80       | 10 | 85        | 20  | 75        | 20 | 85       | 20 | 65       | 60 |
|            |                        |    | 80      | 10 | 70      | 20 | 77       | 30 | 60        | 60  | 57        | 30 | 68       | 60 | 60       | 60 |
|            |                        |    |         |    | 70      | 20 | 68       | 40 | 75        | 40  | 68        | 40 |          |    |          |    |
| Totals X:N | 9 : 10                 |    | 15 : 20 |    | 43 : 60 |    | 58 : 80  |    | 79 : 120  |     | 59 : 90   |    | 58 : 80  |    | 75 : 120 |    |
| 1.5 metres | 25'                    |    | 20'     |    | 17'     |    | 15'      |    | 13.5'     |     | 12'       |    | 11'      |    | 10'      |    |
|            | 75                     | 20 | 100     | 10 | 100     | 10 | 90       | 10 | 80        | 10  | 72        | 60 | 54       | 90 | 40       | 30 |
|            | 63                     | 40 | 70      | 20 | 78      | 40 | 73       | 30 | 65        | 110 | 64        | 70 | 57       | 80 | 50       | 30 |
|            | 70                     | 10 | 65      | 40 | 83      | 30 | 70       | 70 | 83        | 40  | 56        | 80 |          |    |          |    |
| Totals X:N | 47 : 70                |    | 50 : 70 |    | 66 : 80 |    | 80 : 110 |    | 112 : 160 |     | 133 : 210 |    | 95 : 170 |    | 27 : 60  |    |

Appendix B - continued

|            | Visual Angle (Minutes) |     |          |     |          |     |         |     |          |     |         |     |
|------------|------------------------|-----|----------|-----|----------|-----|---------|-----|----------|-----|---------|-----|
| Distance   | %                      | N   | %        | N   | %        | N   | %       | N   | %        | N   | %       | N   |
| 2 metres   | 19'                    |     | 15.5'    |     | 13'      |     | 11.5'   |     | 10'      |     | 9.5'    |     |
|            | 72                     | 50  | 67       | 110 | 62       | 100 | 55      | 40  | 50       | 30  | 48      | 120 |
|            | 75                     | 20  | 78       | 40  | 68       | 70  | 73      | 80  | 60       | 160 |         |     |
|            | 70                     | 10  |          |     |          |     |         |     |          |     |         |     |
|            | 73                     | 30  |          |     |          |     |         |     |          |     |         |     |
| Total X:N  | 80 :110                |     | 105 :150 |     | 110 :170 |     | 80 :120 |     | 112 :190 |     | 58 :120 |     |
| 2.5 metres | 15'                    |     | 12.5'    |     | 10'      |     | 9'      |     |          |     |         |     |
|            | 65                     | 110 | 64       | 130 | 68       | 130 | 48      | 100 |          |     |         |     |
|            | 80                     | 10  | 66       | 70  | 50       | 10  | 52      | 50  |          |     |         |     |
|            | 63                     | 80  | 65       | 20  | 70       | 40  |         |     |          |     |         |     |
| Total X:N  | 130 :200               |     | 143 :220 |     | 120 :180 |     | 74 :150 |     |          |     |         |     |
| 3 metres   | 12.5'                  |     | 10'      |     | 8.5'     |     |         |     |          |     |         |     |
|            | 67                     | 140 | 60       | 140 | 56       | 110 |         |     |          |     |         |     |
|            | 67                     | 30  | 63       | 60  | 54       | 50  |         |     |          |     |         |     |
| Total X:N  | 114 :170               |     | 122 :200 |     | 89 :160  |     |         |     |          |     |         |     |