HARP SEALS (Pagophilus groenlandicus) SOLVE TWO-CHOICE VISUAL DISCRIMINATIONS USING LEARNED OBJECT VALENCE AND A CONDITIONAL CUE

STEPHANIE J. WALSH

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisisitons et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-93069-6
Our file Notre référence
ISBN: 0-612-93069-6

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this dissertation.

While these forms may be included in the document page count, their removal does not represent any loss of content from the dissertation.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de ce manuscrit.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Harp Seals (*Pagophilus groenlandicus*) Solve Two-Choice Visual Discriminations Using Learned Object Valence and a Conditional Cue

by

© Stephanie J. Walsh, B. Sc. (Honours)

A thesis submitted to the School of Graduate Studies
in partial fulfillment of the requirements for the degree of
Master of Science

Cognitive and Behavioural Ecology Programme
Departments of Psychology and Biology
Memorial University of Newfoundland
June 2003

St. John's Newfoundland

Abstract

Five harp seals (*Pagophilus groenlandicus*) experienced behavioural training on several learning tasks. In Experiment 1, the seals were trained on six 2-choice visual discrimination tasks. The ability of the seals to transfer learned object valence (i.e., S+ and S-) to new tasks involving 1 or 2 previously experienced stimuli was investigated. All seals learned to solve 2-choice discriminations and also performed significantly better on tasks involving 1 or 2 objects that had attained positive or negative valence from previous discriminative training than tasks involving 2 novel stimuli. This finding supports the hypothesis that harp seals can transfer learned object valence. Experiment 2 explored the capacity of harp seals to use the tank they were in as a conditional cue to solve a 2-choice visual discrimination reversal task. Seals that experienced a switch to a different tank that coincided with a reversal in reward contingencies showed significantly more improvement across five reversals than seals that did not experience a change in context. The results suggest that harp seals may be sensitive to spatial cues, which supports field observations of their ability to orient and navigate despite a lack of other cues (Kovacs, 1995). The findings are discussed in terms of harp seals' adaptations to the pack-ice environment, the constraints of the learning tasks, the nature of the subjects who were raised in captivity, and the number of subjects involved in the experiment.

Acknowledgements

First and foremost, I want to say "Thank-you" to Oscar, Lenny, Deane, Tyler, Jamie and Babette for making this project possible, and for allowing me to learn from them by having them learn from me. (I don't thank them for each time I was soaked from head to toe in freezing salt water – but I forgive them.)

I owe much gratitude to my supervisor, Dr. Gerard Martin, for his guidance throughout this project. Gerard has spent many hours simply teaching me how to be a better "story-teller," as all good scientists must be, and to obey the law of parsimony in my writing (i.e., "Don't say 'marmalade', say 'jam'"). I credit Gerard with keeping me sane throughout the writing process. Each time I reached a point where something caused me to panic, Gerard always knew what to say to make it sound like no big deal. (Thank God he always turned out to be right!).

I also wish to thank my co-supervisor, Dr. Darlene Skinner, and my committee member, Dr. John Evans, for their encouragement, as well as helpful comments and criticisms, throughout the project. Also, Dr. Dave Schneider, Dr. Trevor Avery, and Dr. Kim Bell were very kind to offer their time to assist me with various aspects of the statistical analysis along the way.

During the data collection phase of my project, I spent each day with the Seal Lab, including Daryl Jones, Terri-Lynn Pinksen, Jodi Frye, and many, many others along the way. Those days provided some of the best experiences of my life. Daryl was wonderful to work with, and I owe him so much for all of the things he did to help the project run smoothly that were clearly beyond the call of duty. Daryl, Terri, and Jodi were invaluable in the process of designing the training procedures and apparatuses, and offered many useful ideas. But most of all, my friends and fellow "seal babes" made this project a huge amount of fun (despite the dead fish and poop patrol). Cheers!

I received encouragement throughout the project from both friends and family. Thanks, Mom and Dad, for never letting me believe that I could do any less. To Jay, and to Stacy, for letting me know they are proud each in their own way. To Steve, Homer, and Cooper, for feeding my intellectual ego when I needed a boost. And to Mr. and Mrs. Martin and Nan Martin, for treating me as their own and offering much encouragement. Finally, I want to thank Skye, Blue and Monty for keeping me company and listening intently to each and every draft version and presentation.

Financial support for this research was kindly provided by the School of Graduate Studies F. A. Aldrich Fellowship, a postgraduate scholarship from the Natural Sciences and Engineering Research Council of Canada, and a Student Award from the Association of Newfoundland Psychologists.

I dedicate this thesis to my grandparents, Joseph Frye, Violet Frye, Bridgett Walsh, and Peter Walsh, who never got to see me get this far, but always knew that I would.

Stephanie

Table of Contents

List of Tables

Page

List of Figures

Chapter 1: Introduction

The goal of the present study was to learn about the cognitive abilities of harp seals (*Pagophilus groenlandicus*) by examining their performance on various learning tasks. The study was carried out between May 2001 and January 2003, with the only captive harp seal population in North America, located at the Ocean Sciences Centre, Memorial University, Logy Bay, Newfoundland and Labrador. Given this very special population, the aim of the study was to develop and test several methods for training these seals that may ultimately allow us to draw some conclusions about how harp seals perceive and understand their environment.

1.1 A Note on Taxonomy

Harp seals belong to the Family *Phocidae* of the Suborder *Pinnipedia*, Order *Carnivora*, Class *Mammalia*. There is some inconsistency within the scientific literature as to their genus and species. One classification is *Pagophilus groenlandicus*, which places harp seals in a separate genus within the family *Phocidae* (e.g., Moulton, Miller & Ochoa-Acuna, 2000; Sergeant, 1973; Serrano, 2001). Another commonly used classification is that of *Phoca groenlandica*, which places harp seals in the same taxonomic genus as such species as harbour seals, *Phoca vitulina*, and ringed seals, *Phoca hispida* (e.g., Kovacs, 1995; Ronald & Dougan, 1982; Watkins & Schevill, 1979). However, Carr and Perry (1997) presented molecular evidence to suggest that harp seals are more closely related to hooded seals than to harbour seals. Given that hooded seals are in a separate genus (i.e., *Cystophora*) within the *Phocidae*, it would be incorrect to include harp seals in the genus *Phoca*, because this classification would suggest that they are more closely related to species outside of the genus than within it. Therefore, the placement of harp seals into a separate genus, *Pagophilus*, is appropriate (Perry, Carr, Barlett, & Davidson, 1995).

While some older texts refer to the *Pinnipedia* as an order separate from the *Carnivora* (e.g., Renouf, 1991), more recent modifications to their taxonomy now list them as a suborder within the Order *Carnivora*. The Suborder *Pinnipedia* is divided into three families: The *Phocidae* (i.e., earless or "true" seals), The *Otariidae* (i.e., furred seals and sea lions), and the *Odobenidae* (i.e., walruses). Carr and Perry (1997) explained that recent molecular evidence suggests that all three groups evolved from weasel-like ancestors, validating their separation as a suborder within the Order *Carnivora*.

1.2 Background on Harp Seals

Harp seals are one of the most abundant marine mammals in the north Atlantic and Arctic Oceans. Currently, their numbers are estimated to be in the range of 4-5 million in the Northwest Atlantic alone (Shelton, Stenson, Sjare, & Warren, 1996; Vikingsson & Kapel, 2000). There are two other major populations, the White Sea-Barents Sea stock, and the Greenland Sea stock, each with its own distinct breeding ground (Sergeant, 1976). Harp seals are a migratory species. Typically, the Northwest Atlantic population spends the summer months in the Canadian Arctic and Western Greenland, and migrates southward in late autumn (Sergeant, 1991; Stenson, Hammill, & Lawson, 1997). In late February and early March, this population forms large whelping patches off the coast of Newfoundland and Labrador or near the Magdalen Islands in the Gulf of St. Lawrence (Stenson, Hammill, & Lawson, 1997). Pups are cared for for up to two weeks (Kovacs & Lavigne, 1985), and then breeding takes place. The seals disperse for a brief period and then recongregate for a period of moulting, from mid-April to mid-May (Stenson, Hammill, & Lawson, 1997). Shortly afterwards, they begin their northward migration.

1.3 Spatial Orientation and the Five Senses

Harp seals tend be associated with the northern ice floes and pack ice (Kapel, 1995; Lawson & Stenson, 1995; Sergeant, 1973, 1991; Shelton, Stenson, Sjare, & Warren, 1996). Thus, unlike related species that associate with land, for example, harbour seals (*Phoca vitulina*; Wartzok, 1991), harp seals live in a constantly changing environment. Kovacs (1995) suggested that the structure of the landscape in the pack-ice environment varies on a daily basis. An oscillating sea of ice likely provides little in the way of visual landmarks useful for navigation. Given a lack of reliable visual cues, seals may have to rely on overall distance and direction in order to navigate within a specific spatial context, especially when that context changes in form on a short-term basis (Kovacs, 1995). The relative instability of both visual and spatial cues suggests that harp seals may have unique spatial capabilities that enable them to navigate within such an environment in order to locate other individuals, including their pups, on the ice, or to find foraging locations, or even breathing holes, from beneath the surface.

1.3.1 Vision

The pinniped eye is adapted to underwater vision, as well as for quick adaptation to scotopic (low light) conditions (Nagy & Ronald, 1975; Schusterman et al., 2000). Also, various adaptive properties of the cornea, pupil and lens allow for increased visual acuity in air despite astigmatism (Mass, 1997). Schusterman and Balliet (1970a, 1970b, 1971) report that the in-air (and in some cases, underwater) visual acuities of five pinniped species, including two marine seals (*Arctocephalus pusillus* and *A. australis*), ranged from 5.5 - 8.5 minutes of arc. Typical human acuity is 1 minute of arc (Task, 1992). Mass (1997) suggested that such evidence indicates that pinnipeds have reasonably good vision.

Levenson and Schusterman (1999) suggested that pinnipeds' enhanced sensitivity to light, and their ability to adapt rapidly to darkened conditions, makes them well suited for foraging during dives. They concluded that, because pinnipeds are so well adapted to function visually at significant depths, non-visual explanations of their underwater orientation ability are unnecessary.

There has been much debate surrounding harp seals' spectral sensitivity (see Renouf, 1991). A study of the retinas of 24 harp seal eyes revealed that they possess two classes of photoreceptor cells: the typical class of rods, and an intermediate type thought to have some of the characteristics of both rods and cones (Nagy & Ronald, 1975). Lavigne and Ronald (1972) also found that harp seals experience a Purkinje shift, or change in maximum wavelength sensitivity (from approximately 550 nm to within 500-525 nm), when light conditions change from photopic (daylight vision) to scotopic (dark-adapted vision). This early finding offered some support for the possibility that harp seals may possess at least two types of photopigments. However, Lavigne and Ronald's findings were based on the data for a single immature female harp seal, and have yet to be replicated.

In a recent study of five other phocid species, it was reported that although all appear to have a green or "L"-cone photoreceptor spectral type, they all lack a second cone type (i.e., a blue, or "S"-cone) that is necessary for colour discrimination (Peichl, Behrmann, & Kroger, 2001). While this deficit has not been specifically determined in harp seals, it is very likely that their visual sensory systems have evolved in the same manner as those of other phocids. Thus, it remains unknown whether harp seals are colour-blind.

1.3.2 Hearing

Pinnipeds are often active at night, or in murky and turbid waters, where vision is reduced (Renouf, 1991). Schusterman, Kastak, Levenson, Reichmuth, and Southall (2000) suggested that pinnipeds may use hearing underwater to avoid predators and detect prey, as well as for navigation and orientation, in the absence of visual cues.

Harp seals communicate proficiently through both underwater and aerial vocalizations, particularly during the breeding season (e.g., Miller & Murray, 1995; Serrano & Terhune, 2002; Watkins & Schevill, 1979) and, to a lesser extent, outside the breeding season (Serrano, 2001). There is evidence to suggest that seals may make use of auditory cues from conspecifics when navigating underwater while in the vicinity of other individuals (Wartzok, 1991; Wartzok, Elsner, Stone, Kelly, & Davis, 1992). Such auditory cues may provide information about the spatial location of surface holes in the ice (Wartzok, 1991).

For harp seals and other pinniped species that require mother-pup recognition, many studies have demonstrated the importance of acoustic signalling between the mother and pup (e.g., Gisiner & Schusterman, 1991; Hanggi & Schusterman, 1990; Roux & Jouventin, 1987; Trillmich, 1981). Renouf (1985) found that a captive female harbour seal was able to discriminate between three different pairs of pup calls. This finding suggests that a mother should be able to recognize the calls of her own pup, in order to differentiate them from the calls of other pups. Thus, individual pup vocalizations likely aid in female pinnipeds' relocation of their pups.

In the past, there has been much controversy over whether pinnipeds possess the ability to use echolocation for navigation or location of prey (see Schusterman et al., 2000). However, the possibility of echolocation in pinnipeds has, for the most part, been ruled out (Oliver, 1978; Schusterman, 1967b; Scronce & Ridgway, 1980). Schusterman et al. (2000) argued that, because of the amphibious nature of pinnipeds, their auditory systems are adapted for hearing both in-air and underwater, and that this likely precluded the development of echolocation.

1.3.3 Mechanoreception (Taction)

Pinnipeds use their vibrissae as their primary means of gathering tactile information (Dehnhardt & Kaminski, 1995; Dehnhardt, Mauck, & Hyvarinen, 1998). Excellent shape and/or size discrimination abilities have been demonstrated in sea lions (Dehnhardt, 1990, 1994), walruses (Kastelein & van Gaalen, 1988), and harbour seals (Dehnhardt & Kaminski, 1995). Dehnhardt, Mauck, and Bleckmann (1998) demonstrated that blindfolded harbour seals could detect underwater vibrations similar (and, in fact, lower) in frequency to those generated by small fish, suggesting that, at fairly close range, seals may be able to use mechanoreception to detect and locate prey in the absence of visual cues (also see Davis, et al., 1999; Renouf, 1979). Wartzok et al. (1992) reported that, while blindfolded ringed seals could not use their vibrissae to find the location of a breathing hole farther than 1 m away, they did appear to use their vibrissae to centre themselves upon surfacing within the hole (also see Reidman, 1990). Thus, vibrissal sensation appears to be useful within a very limited spatial range.

1.3.4 Chemoreception (Taste and Olfaction)

Several fish species, such as Atlantic salmon (Sutterlin & Sutterlin, 1970) and catfish (Bardach, Todd, & Crickmer, 1967), have been shown to use salinity gradients as a means of orientation. Pinnipeds may also use chemosensory cues for orientation within their foraging ranges, as this would allow them to locate prey species that associate with various salinity layers within an oceanic basin or river plume front (Sticken & Dehnhardt, 2000). Evidence for this idea was reported by Sticken and Dehnhardt (2000), who demonstrated the ability of two harbour seals to discriminate between different water samples based on the level of salinity.

Olfaction is thought to play a substantial role in pinniped behaviour, especially in terms of social interactions (Hanlan, 1998; Renouf, 1991). There appears to be general agreement that, at close range, olfaction is an important cue for pup-recognition by females (e.g., Bowen, 1991; Kovacs, 1995, 1986; Terhune, Terhune, & Ronald, 1979). Kovacs (1986) reported that harp seal mothers sniffed and touched their pups with their noses very frequently during the first few hours after birth, and also did so after returning from the water, as a final means of identification. More recently, Hanlan (1998) reported high levels of olfactory-based affiliative behaviours in a group of captive harbour seals

(*Phoca vitulina*). Hanlan suggested that the various forms of nose contact observed between the seals might serve as a way for the seals to monitor social or environmental cues. Such affiliative behaviours are thought to promote maintenance of the group (Hanlan, 1998).

1.3.5 Spatial Orientation

While evidence is limited, field observations of harp seal behaviour from several different investigators (e.g., Bowen, 1991; Kovacs, 1995; Lydersen & Kovacs, 1993) have produced some speculation that harp seals may have good spatial abilities.

Kovacs (1995) observed that female harp seals were able to return to pups that were either sleeping or dead, suggesting that the mothers did not need auditory cues to locate their pups. In addition, Kovacs (1995) noted that the pups were often not visible to the females from the origin of the return path taken. Contrary to Terhune, Terhune and Ronald (1979), who reported that females returned and searched in a random manner in the absence of visual or auditory cues, Kovacs (1995) observed that the females oriented toward and approached their pups in a non-random manner. Kovacs' observation would suggest that, at long distances, and when visual cues are not available, harp seal mothers may be able to use spatial cues, such as distance travelled and orientation, in order to return to their pups in the pack-ice environment.

The pups of many pinniped species, in particular, the Otariids, are mobile, and tend to aggregate in close spatial proximity (Bartholomew; 1952; Bonner, 1968; Gentry, 1970, 1975; McNab & Crawley, 1975; Stirling, 1971;Trillmich, 1981). Such aggregation tendencies likely make the task of differentiating pups difficult for females, and also, rule out the possibility of demonstrating an ability to use spatial location for pup relocation. Only three Otariid species (i.e., the south American fur seal, Northern fur seal, and Australian sea lion) do not form these social "pods" (Higgins & Gass, 1993; Riedman, 1990). In contrast, the pups of many Phocid species have been reported to display preferences for a specific limited area and do not aggregate to the same degree. Kovacs (1986) found that pre-weanling harp seal pups spend most of their time asleep, and are generally idle more than 60% of the time. Such immobility likely makes them easier to find. Bowen (1991) reported that harp seal mothers are discriminating in their nursing of pups, and mistakes rarely occur, despite the fact that females typically spend up to several hours in the water between bouts of nursing (Kovacs, 1987). Because harp seal pups are relatively immobile, females may be able to use spatial information, (e.g., the structural layout of the ice pans) on a short-term basis to relocate their pups (Bowen, 1991; Kovacs, 1995). While the structure of the pack-ice landscape changes on a daily basis, Kovacs (1995) suggested that a female may be able to adjust her spatial map accordingly during each bout of nursing, or each time she emerges to check on the pup. (Harp seal mothers have been reported to visually monitor their pups intermittently between nursing sessions; Kovacs, 1987; Stewart, 1987).

Lydersen and Kovacs (1993) found that harp seals typically do not exceed their aerobic dive limit, which they had calculated for a sample of lactating females as approximately 10.4 min. This finding suggests that the seals must be able to keep track of how far they have gone and their orientation in order to be able to return to their breathing hole before running out of air. The lack of visual cues beneath the ice surface suggests that harp seals may use kinaesthetic information about their speed and direction of locomotion to navigate. Seals may also obtain information about their location from changes in water salinity (Sticken & Dehnhardt, 2000) or currents (Wartzok, 1991).

Renouf (1991) pointed out that there are many instances where pinnipeds appear to operate without much conventional sensory information. Renouf suggests that, in order to compensate for this lack of sensory information, pinnipeds may continually record a cognitive map of their own locomotion within their environment, and then refer to this map for orientation and navigation. Thus, there appears to be some evidence that harp seals do possess a good "spatial sense".

1.4 Learning in Pinnipeds

There has been very little research designed specifically to test the learning abilities of harp seals. However, indirectly, the results of the above studies on harp seals' ability to navigate in a structurally unstable environment, as well as to locate their pups after relatively long separations, suggests that harp seals are, indeed, very good at certain types of learning. Also, Serrano and Terhune (2002) noted that social learning (i.e., observation and imitation) is thought to be one factor influencing the transmission of harp seals' vocal repertoires.

Some of the few behavioural studies on harp seals involved a series of experiments on harp seal spectral sensitivity and dark-adaptation (Lavigne, 1973; Lavigne & Ronald, 1972a, 1972b). The seals were first trained to press a start lever to initiate a trial. On "stimulus present" trials, the harp seals were trained to indicate the presence of a light on a screen by pressing a "yes" response lever, and were rewarded with a piece of herring. If the seal failed to detect the light on a stimulus trial, it pressed a "no" lever. This incorrect response resulted in a loud click and no reward. On "catch trials", no light was present, and the seal was rewarded for pressing the "no" response lever. A "yes" response was not rewarded. In one experiment, a harp seal took approximately 3 months[1] to learn this task to a criterion of 90% correct responses when presented with an equal number of above-threshold stimulus presentations and "catch" trials (Lavigne & Ronald, 1972a). Only a few other studies demonstrating learning in harp seals exist. In addition to those listed above, the remaining studies used a similar technique of training the seals to touch one of two paddles or levers in the presence or absence of an auditory stimulus in order to determine hearing thresholds in air (Terhune & Ronald, 1971) and underwater (Møhl & Ronald, 1975; Terhune & Ronald, 1972). Because the focus of those studies was on the perceptual abilities of the harp seals, and not their learning *per se*, the authors typically do not report the number of trials it took the seals to acquire the learned behavioural response.

In a review of the relative trainability of various pinnipeds, Schusterman (1981) cited Lavigne's (1973) study as evidence that the potential for taming and training harp seals is excellent, although very few researchers have since undertaken the task. However, there is a wealth of literature on the learning abilities of other pinnipeds. On a cautionary note, it is important to keep in mind that even the more closely related phocids, such as harbour seals, have very different life history traits and very different behaviour patterns. For example, while harp seals associate with pack ice, are migratory,

---

[1] The number of trials was not provided by the authors.

and spend the majority of their time in the water (Lydersen & Kovacs, 1993), harbour seals are a coastal species, relatively sedentary, and tend to haul out onto land much more frequently (Lavigne & Ronald, 1976; Moulton, Miller, & Ochoa-Acuna, 2000). These two species have been shown to have different spectral sensitivity, attributed to their different environments (Lavigne & Ronald, 1976). While harp seal pups are relatively immobile (Kovacs, 1987), harbour seal pups have been described as unusually precocial (Renouf, 1985). Thus, although I must base my predictions about the learning behaviour of harp seals on the research of other pinnipeds, I cannot be sure just how different they may be. Nevertheless, the abundance of literature on the learning abilities of various other pinnipeds does provide a good starting point from which to hypothesize about the abilities of harp seals.

A final note of caution is required relating to the differences that exist between the population of five captive harp seals in the present study, and the entire population of several million feral harp seals. These two populations are exposed to very different spatial and visual contexts, which may have differential effects on their behaviour. The issue of generalization from a captive population is addressed in detail in the discussion.

1.4.1 Discrimination Learning in Pinnipeds

The ability to recognize and discriminate between various objects in terms of their potential to harm or benefit an animal would likely be a very useful adaptation in any environment. In the case of pinnipeds, Hobson (1966) suggested that these animals use visual pattern recognition to distinguish between rewarding and non-rewarding stimuli. While in the water at night, pinnipeds are reported to view objects from below. They use surface light to distinguish the size and shape of the object, in order to recognize it. This ability allows them to quickly make a decision to approach or avoid the object, while minimizing their chance of being detected (Hobson, 1966). Pinnipeds have demonstrated such an ability (in particular, to solve two-choice discriminations) using several sensory modalities.

1.4.1.1 Visual discriminations

Schusterman (1969, unpublished data; cited in Schusterman, 1981) exposed one California sea lion (*Zalophus californianus*), one Steller sea lion (*Eumetopias jubatus*) and one harbour seal to 20 pairs of two-dimensional visual stimuli. The pairs of stimuli had each been presented for only one trial until all pairs had been cycled through, and the seals were exposed to the entire list of pairs several times. The seals were required to choose one of the two stimuli by touching it, and were rewarded for correct choices only. Remarkably, all animals were able to learn and remember the correct choices for the entire series of 20 stimulus pairs, without a single error. Schusterman (1968) also reported on two experiments where, in each, a different California sea lion was conditioned to make a "click" vocalization when presented with a "large" stimulus (i.e., 736 cm^2) and to make no click in the presence of a small stimulus (i.e., 16 cm^2), as a means of discrimination. After 1500 trials, both sea lions were performing with nearly 100% accuracy.

1.4.1.2 Auditory Discriminations

Auditory cues also appear to be salient to pinnipeds in their ability to make discriminations. For example, Renouf (1985) trained a female harbour seal to open one feeder box to receive a fish when she heard one pup vocalization, and to open a second door when she heard a vocalization from a different pup. The seal was able to perform this auditory discrimination for three different pairs of stimuli to a criterion of 16/20 correct trials on three consecutive days. Renouf (1980) also trained two harbour seals to discriminate between the presence and absence of a pure tone by having them swim to and touch a paddle to their left when they detected a tone, and to swim to a paddle to their right when they did not detect a tone. Both animals learned to perform with 95% accuracy on both "stimulus present" and catch trials.

1.4.1.3 Tactile Discriminations

Pinnipeds are reported to be very efficient at using their mystacial vibrissae to detect and investigate objects at close range. For example, Dehnhardt, Mauck, and Bleckmann (1998) trained two harbour seals to perform a texture discrimination task while blindfolded. Dehnhardt (1990) also demonstrated the ability of a California sea lion to discriminate between five different shapes using its vibrissae alone. Similarly, Dehnhardt and Kaminski (1995) trained two harbour seals to tactually discriminate between pairs of circular disks of different sizes. Kastelein and van Gaalen (1988) demonstrated that a walrus was capable of using its mystacial vibrissae to discriminate between two different shapes, a circle and a triangle, when the areas of the two stimuli were as small as 0.4 cm^2.

1.4.1.4 Chemosensory discriminations

Pinnipeds are thought to be able to make discriminations based on chemosensory cues obtained from taste and olfaction as well. In one study, Sticken and Denhardt (2000) trained harbour seals to discriminate between water samples having different salinity concentrations. The seals' ability to discriminate actually increased as the level of salinity increased. Sticken and Denhardt (2000) reported that, at 30% salinity, the seals were able to detect differences in salinity as small as 4%, which is far beyond the ability of humans.

1.5 Learning Set Formation

Many early studies focused on the question of whether animals are capable of learning a simple rule or heuristic in one context that they can transfer to other tasks, as if by analogy. Harlow (1949, cited in Schusterman, 1968) termed this type of learning "learning-set formation". Essentially, it refers to a problem-solving strategy that animals use when exposed to a series of similar tasks. Schusterman (1968) identified two types of learning set formation. One type of learning set formation occurs when an animal shows improvement on a discrimination task after having learned a series of similar discrimination tasks. Another type of learning set formation occurs when an animal learns to solve a discrimination reversal task. In this type of task, the animal must not only learn that touching the correct object results in a reward; it must also learn what is known as a "win-stay, lose-shift" strategy (Restle, 1958; cited in Mackintosh, 1969), so that, when the reward contingencies are reversed, the animal learns to immediately shift its response to the other object. The occurrence of these two types of learning to learn will be discussed separately in Experiments 1 and 2.

1.6 The Present Study

In the present study, various types of behavioural training and testing were employed in order to find a way of assessing certain aspects of harp seal learning and cognition. Initially, several different pilot studies were carried out, on a trial-and-error basis at first, in order to determine the method of training to which the seals would best respond. During the initial pilot studies, seals were first trained to recognize and remain stationed at individual shapes. They were then trained on a two-choice, two-dimensional panel discrimination using black and white panels as stimuli. An unsuccessful attempt was made to train the seals to come out of the tank on command in order to separate them for training (see Appendix A). The seals were then habituated to a transparent plastic box that was suspended in the tank. Later, objects were placed inside the box, and the seals were habituated to these as well. Finally, in Experiments 1 and 2, the seals were exposed to a series of two-choice visual discriminations using three-dimensional stimuli presented inside two transparent boxes.

In Experiment 1, I explored the ability of the seals to transfer information they had learned about familiar objects (i.e., whether they were associated with a reward or with the absence of a reward) to new discriminations involving these familiar stimuli. In Experiment 2, I explored the seals' ability to use different tanks as a conditional cue to solve a discrimination reversal task. The seals were trained to discriminate between a single pair of objects. When they reached a criterion of 18/20 consecutive trials correct, the reward contingencies were reversed, such that S+ became S-, and vice versa. For two of the seals, this reversal coincided with a change in context, i.e., a switch to a different tank. Two other seals experienced both acquisition and subsequent reversal trials in a single tank.

Several hypotheses were formulated throughout the course of the study. It was first hypothesized that harp seals would be able to solve a two-choice visual discrimination, on the basis that various other pinnipeds have demonstrated such an ability (e.g., Renouf & Gaborko, 1988, 1989; Schusterman, 1967a, 1968). Secondly, it was hypothesized that, after the harp seals had learned several two-choice discriminations, they would require significantly fewer trials to solve discriminations involving pairings of familiar objects (i.e., objects which they had previously learned to be rewarded or unrewarded) with novel objects. It was hypothesized that harp seals would be able to solve a visual, two-choice discrimination reversal task when the tank they were in was used as a conditional cue. It was also hypothesized that, across the series of discrimination tasks, some learning set formation would occur, such that the seals would require fewer trials to solve later discriminations than earlier ones, as was previously demonstrated with sea lions (Schusterman, 1968) and harbour seals (Renouf & Gaborko, 1989).

Chapter 2: Experiment 1

2.1 Introduction

Animal discrimination learning has been studied extensively for over a century (see Gilbert & Sutherland, 1969; Mackintosh, 1974, 1983; Maier & Schneirla, 1935). Discrimination learning relies on the basic process of association learning, whereby animals come to associate an originally neutral stimulus with a biologically significant stimulus (i.e., classical conditioning; Pavlov, 1927) or with a certain response (i.e., operant conditioning; Skinner, 1938). In an operantly conditioned two-choice discrimination, animals are thought to learn two pieces of information: 1) they learn that responding to one of the stimuli results in reinforcement; 2) they also learn that the other stimulus is associated with the absence of reinforcement (Komischke, Giurfa, Lachnit, and Malun, 2002). These two stimuli are typically referred to as S+ and S-, respectively (e.g., Honig, 1969; Thomas, 1969). In a discrimination task, animals are usually trained to a certain chosen criterion, such as 4/4 correct choices on two successive days (Chiszar & Spear, 1969); learning the task is defined in terms of reaching the specified criterion.

2.1.1 Transfer of Learned Associations

In addition to learning specific associations between a choice and a reinforcement (or absence thereof) in the context of a single two-choice discrimination, researchers have also looked at the ability of animals to carry over these learned associations (i.e., S+ and S-) to new discriminations involving one or more familiar stimuli (i.e., stimuli with which the animals have come to associate a valence).

In one early study, originally designed to test for colour vision in Game Bantam cocks, Lashley (1916) trained chicks to choose to enter one of two compartments based on the spectral illumination provided through a window at the end of each compartment. The stimuli used were red (650 nm) and green (520 nm) lights. One chick was rewarded for choosing red only; the other, for choosing green only. After a clear preference had been established, each stimulus was separately paired with a white light, and the chicks were again given a choice. Lashley (1916) found that when the previously rewarded colour (S+) was available, the birds continued to choose that stimulus. As well, when the chicks were given a choice between the previously unrewarded colour (S-) and a white light, they chose the white light. Lashley (1916) obtained similar results despite controlled modifications to the brightness and intensity of each of the stimuli, as well as when blue versus yellow lights were used.

Klüver (1933) trained a squirrel monkey to perform a two-choice colour discrimination, where the correct stimulus (S+) was violet-red and the unrewarded stimulus (S-) was yellow. When the violet-red stimulus was then separately paired with either a black stimulus or a white stimulus, the animal chose the violet-red panel 90% of the time. However, the squirrel monkey avoided the yellow stimulus when it was paired with either black or white. Klüver's (1933) results suggest that the monkey had learned something about the value of the yellow and violet-red stimuli (in terms of their associations with reward or no reward), and this information later influenced its behaviour in subsequent tasks involving these stimuli.

Lashley's (1916) and Klüver's (1933) results demonstrate the ability of animals to learn associations both in the presence and absence of reinforcement. Similarly, DiGello, Brown and Affuso (2002) showed that rats were able to use information about the presence or absence of a food reward placed atop vertical poles in order to solve a spatial problem that required the rats to find the baited poles. The baited poles were always aligned in a linear fashion within a matrix of poles. Once a rat learned this pattern, it could use information about the presence or absence of food on top of particular poles to figure out the direction of the line of baited poles. This is an example of animals' ability to make use of negative information within a task; it also demonstrates the ability of rats to learn a general pattern or rule in order to solve a problem.

2.1.2 Learning Set Formation for Discriminations

The first type of learning set identified by Schusterman (1968) occurs when animals show improvement across a series of similar discrimination tasks. Schusterman (1968) reported significant improvement on a series of visual pattern discriminations by both a California sea lion and a harbour seal. Across a series of 12 two-choice discriminations, the sea lion never required more than approximately 110 trials to reach a criterion of 12 consecutive trials correct. While on the first two tasks, the sea lion made approximately 55 errors, by the end of the twelfth task, it was able to solve the problem with only six errors. Over a series of 16 tasks, the harbour seal dropped from nearly 140 errors to less than 20. Schusterman (1968) also trained one California sea lion on a series of 220 six-trial discrimination tasks, where the seal was presented with a pair of objects for only six trials before being moved on to the next pair. The correct object was always the stimulus that was not chosen on the first trial, so that the seal was never reinforced on Trial 1 of a six-trial set. At the end of this training, the sea lion had reached a level of performance of 90% correct on Trials 2 to 6 of each set. In both of these examples, the improved performance provides evidence for the formation of a learning set for two-choice discriminations.

Another example of this type of acquired learning strategy is presented in a study by Slotnick, Hanford and Hodos (2000), who trained two groups of rats on two-odour discrimination tasks. The experimental group was trained on a series of novel two-choice discriminations, whereas the control group was continually trained to discriminate between the same two odours. Each group was then tested with a final novel discrimination. The rats that had previous experience solving several different discriminations immediately performed well on the final discrimination, suggesting strong positive transfer across problems, whereas the control rats performed at chance on initial trials of the novel discrimination. Slotnick et al.'s (2000) results demonstrated that rats are capable of forming a learning set for odour discriminations.

Many species have demonstrated an ability to learn a simple rule, and then use this rule to solve analogous problems. For example, Révész (1924) trained hens to peck food from the smaller of two figures, for a series of pairs. The hens were then exposed to a stimulus consisting of two identical arches, one positioned above the other to give the illusion that the bottom arch was larger. The purpose of Révész's experiment was to demonstrate that birds perceive optical illusions in the same manner as humans. Révész showed that hens trained to choose the smallest of a pair of objects chose the apparently smaller stimulus, despite the fact that the two novel stimuli were identical. While not the focus of Révész's experiment, Révész demonstrated that hens are capable of learning a simple rule (i.e., "choose the smaller stimulus"), which can be carried over to discriminations involving novel objects. Schusterman (1968) trained a California sea lion to choose the larger of two circles. Once the sea lion could do this, it easily transferred to a size discrimination task involving squares. Schusterman was able to train the sea lion to learn to choose the longer of two vertical lines by progressively narrowing the width and increasing the length of the square stimuli. The animal learned to choose the longer line with 100% accuracy.

Renouf and Gaborko (1988) trained two harbour seals on a series of five match-to-sample problems. For four of the tasks, the correct choice could be made based on spatial cues. Both seals experienced three of the four spatial tasks. These were labelled "above/below", "left/right", and "near/far", and involved manipulation of objects based on each spatial dimension. (For example, in the "left/right" task, the sample was a buoy suspended either to the left or right of a vertical pole, and the comparison stimuli were two buoys, one to the left and one to the right of the pole). One seal also experienced an "up/down" task, the other, an "in/out" task. The fifth task required the seals to use a visual cue to solve the problem. The seals were shown either a black or white buoy, and then given a choice between a black buoy and a white buoy. The seals required an average of 482 trials to solve the spatial tasks to a criterion of 27/30 correct trials. However, the seals showed no evidence of transfer of a learning rule in terms of improvement across tasks. Neither of the two seals had completed the visual task after 1725 and 1800 trials. Thus, while the seals were able to solve each of the spatial tasks, they were unable to transfer a general learning rule to the visual match-to-sample problem. Constantine (1981; cited in Renouf and Gaborko, 1988) similarly reported an inability of harbour seals to learn a match-to-sample rule. These reports are not surprising, given that only a handful of other species have demonstrated acquisition of a "match-to-sample" concept (e.g., dolphins, Herman, Hovancik, Gory, & Bradshaw, 1989; sea lions, Kastak & Schusterman, 1994; primates, Colombo & D'Amato, 1986; Shyan, Wright, Cook, & Jitsumori, 1987; parrots, Pepperberg, 1987).

In a second experiment, Renouf and Gaborko (1989) trained another two harbour seals on a series of spatial and visual two-choice discriminations. On the spatial tasks, the correct response common to all tasks required the seals to perform some action on the spatial dimension of "above" versus "below". On the visual tasks, the correct response common to all tasks involved manipulating an object that was either black or white. Renouf and Gaborko (1989) found that the harbour seals learned the spatial tasks quickly, while only one of them was able to solve the visual tasks. They reported that the seals appeared to show "insight learning" or use of a simple rule (e.g., act on the object that is "above" the other) on later spatial tasks, while no such learning set appeared to evolve for the visual tasks.

Schusterman and Thomas (1966) demonstrated that two sea lions learned to discriminate between pairs of shapes, and continued to perform with high accuracy when either the rewarded or unrewarded stimulus (or both) was rotated either 45°, 90°, or 180°. In a further exploration of learning to learn in three species of pinnipeds (i.e., California seal lion, Stellar sea lion, and harbour seal), Schusterman (1968) presented the animals with a series of acquisition and retraining tasks in which they were exposed to 12 pairs of visual stimuli. On the acquisition trials, the seals were trained to discriminate between a pair of two-dimensional shapes that were the same size and colour. Once the seals were performing with near 100% accuracy, they were again presented with the same pair of stimuli. This time, however, one of the objects was rotated either 45°, 90°, or 180°. Once the seals reached an accuracy of 90%, they were moved on to the next pair of objects. The results were inconclusive as to whether any of the three species showed improvement across tasks. Schusterman suggested that some of the later pairs of objects might have been less easily differentiated than earlier pairs, which may have resulted in the lack of improvement. Schusterman also noted that the animals appeared to solve the orientation problems more quickly when the negative, or unrewarded, stimulus was manipulated than when the positive stimulus was reoriented. This finding may be interpreted in terms of learned object valence. It is possible that the seal and sea lions did not recognize the rotated stimuli, and yet, were still able to solve these problems quickly because they remembered the valence of the unmanipulated object. Mauck and Dehnhardt (1997) have since demonstrated mental rotation in a California sea lion. Mauck and Dehnhardt showed that response time increased as the degree of rotation of the stimulus increased. Thus, using previously learned object valence may have facilitated the animals' solution of the problem in Schusterman's (1968) experiment.

Schusterman (1968) also pointed out that, across the pinniped genera tested, there appeared to be a considerable amount of consistency in their manner of responding to this type of shape reorientation discrimination problem (i.e., they showed similar performance patterns). This observation provides substantiation for my use of the studies of learning behaviours in other pinnipeds to make predictions about learning in harp seals.

2.1.3 The Present Experiment

Only a handful of studies have demonstrated any sort of learning in harp seals (Lavigne, 1973; Lavigne & Ronald, 1972a, 1972b; Møhl & Ronald, 1975; Terhune & Ronald, 1971, 1972), and all of them simply required the animal to report the presence or absence of a stimulus in the interest of determining perceptual thresholds of vision and audition. The present experiment directly investigates the learning of harp seals in a behavioural training context. My first goal is to confirm that harp seals are capable of solving a two-choice visual discrimination. If successful, I also wish to determine whether they can transfer learned information about S+ and S- to new tasks involving these stimuli, as has been demonstrated in other species (Klüver, 1933; Lashley, 1916).

In this experiment, the seals were trained to solve a series of two-choice visual discriminations. The first two tasks each involved a pair of novel objects. The third task involved a pairing of two familiar objects, i.e., the rewarded object from the first task, and the unrewarded object from the second task. In the fourth and fifth tasks, the remaining familiar objects from Tasks 1 and 2 were each paired with a novel object. Finally, the sixth task involved a third pair of novel objects. My hypothesis was that information the seals learned about whether an object was associated with a reward (S+) or no reward (S-) would improve their performance on later tasks involving these previously reinforced objects, in comparison to tasks in which both objects were novel. I also hypothesized that the seals would show improvement across the three novel tasks in that they would require fewer trials to solve later novel tasks than earlier ones.

2.2 Method

2.2.1 Subjects

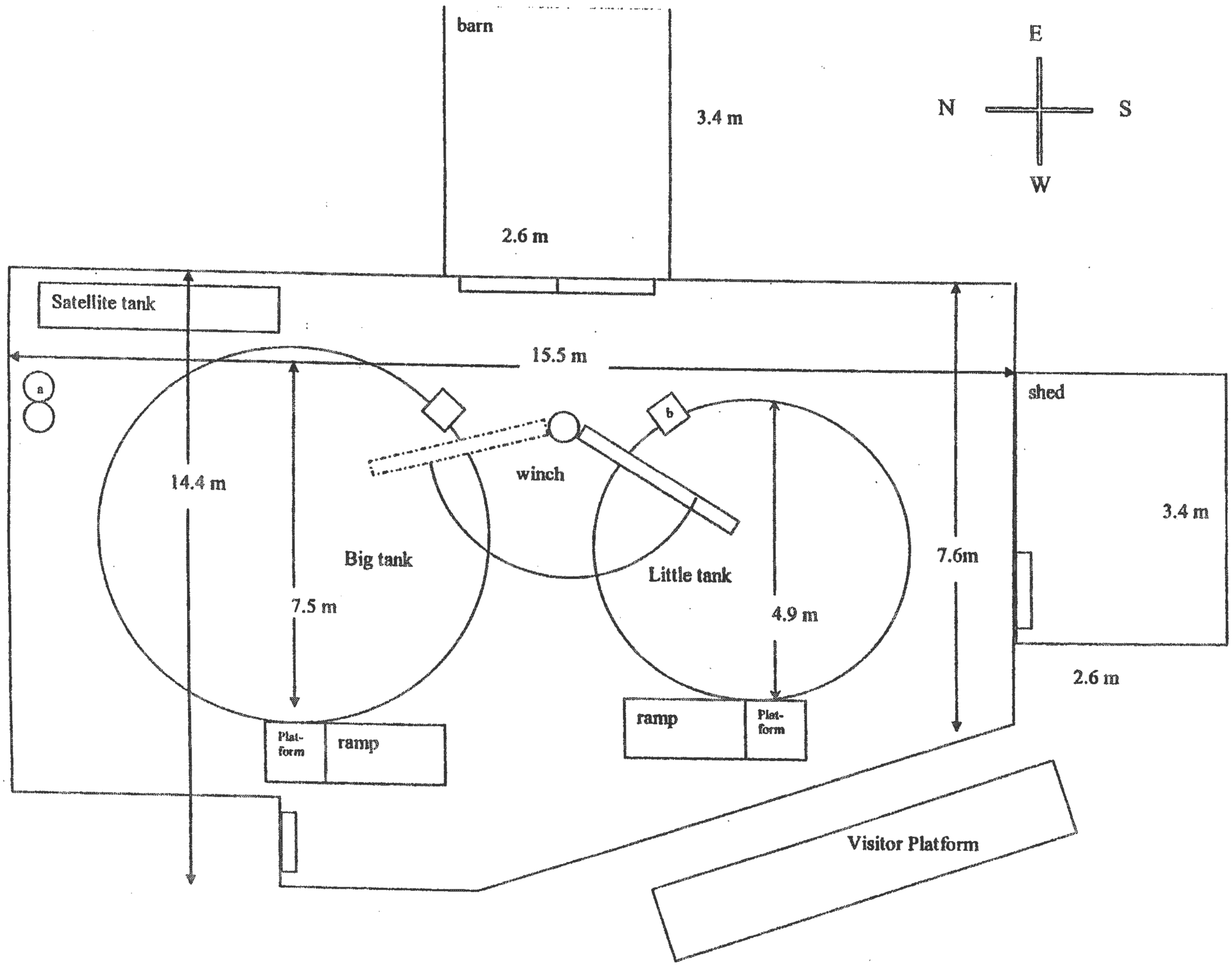
Subjects were 5 harp seals (*Pagophilus groenlandicus*), 2 females and 3 males, ranging in age from 6 months to 20 years at the start of the experiment. Babette, a 20-year-old female (weight: M = 146.8 kg, range = 139.6 – 160.2 kg), was captured as a 10-year old adult from the Magdalen Islands; Tyler, a 12-year-old male (weight: M = 151.3 kg, range = 148.0 – 156.6 kg), was captured from the Magdalen Islands as a 2-week-old whitecoat; Jamie, an 8-year-old male (weight: M = 102.0 kg, range = 99.2 – 102.2 kg), and Lenny, a 2-year-old male (weight: M = 60.8 kg, range = 57.8 – 61.4 kg), were both born in captivity, at the Ocean Sciences Centre. In March 2002, approximately 4.5 months prior to the start of this experiment, Babette gave birth to a female harp seal, Deane. (Babette was not involved in training for several weeks following the birth). As soon as Deane was able to swim safely in the large tanks with the other seals at approximately 2 months old, she was included in the experiments. Deane's mean weight during Experiment 1 was 36.8 kg (range 34.8 – 39.4 kg). Oscar, an adult male harbour seal (*Phoca vitulina*) was also present in the compound for the duration of the study. At the beginning of this study, Babette, Tyler, Jamie and Lenny had been exposed to a series of pilot studies, which are described in Appendix A. Deane had participated in the habituation experiment and also experienced baton training, both described in Appendix A. Also, the seals in this study that were of reproductive age exhibited the same breeding seasonality as wild harp seals. Throughout the study, all animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

2.2.2 Apparatus

2.2.2.1 Training environment

The seals were housed in an outdoor compound at the Ocean Sciences Centre, Memorial University of Newfoundland, Logy Bay, Newfoundland and Labrador (47°38'N, 52°40'W). This location is within the natural range of this species in the Northwest Atlantic; therefore the temperature and weather patterns the seals experienced during the study were similar to that which they would have experienced in their natural environment. The seal compound (approximately 14.4 m x 15.5 m) was roughly rectangular (see Figure 2.1) and contained the front walls of both a barn (2.6 m x 3.4 m) and a shed (3.4 m x 2.6 m). The compound was enclosed in metal wire fencing approximately 2.1 m high that was topped with barbed wire to prevent any unauthorized access by humans or other animals. The seals had access to two large cylindrical tanks (small tank: 4.9 m diameter, 2.1 m deep, 18.8 m^2 surface area, 39.6 m^3 volume; large tank: 7.5 m diameter 2.1 m deep, 44.2 m^2 surface area, 92.7 m^3 volume) and one small rectangular tank ("satellite" tank; 3.8 m x 0.9 m x 0.8 m, 2.7 m^3 volume). Fresh seawater at ambient temperature was continuously pumped from Logy Bay into the three tanks.

The base of the compound was a wooden deck surrounding the two large tanks. Each of these tanks had a wooden platform located on the north side, and, also, a wooden ramp that extended from the platform to the deck so that the seals could enter and leave the tanks. Both platforms and ramps were movable. In the centre of the compound near the east side, a mechanical winch was located so that the horizontal arm could be positioned approximately 2 m above either of the tanks. A rope was used to secure the


barn
3.4 m
2.6 m
E
N
S
W
Satellite tank
15.5 m
shed
a
b
14.4 m
winch
Big tank
7.5 m
Little tank
4.9 m
7.6m
3.4 m
2.6 m
Plat-form
ramp
ramp
Plat-form
Visitor Platform

arm in place, by tying it to the nearest fence. A diagram of the compound is provided in Figure 2.1.

There was a platform where visitors could stand and observe the seals, approximately 1.5m outside of the compound on the west corner (parallel to the west wall). The seals were exposed to visitors (sometimes as many as 30 or 40 at a time) on a daily basis, and often, their pets (e.g., dogs). They appeared to have habituated to stimulation originating from the visitor platform.

2.2.2.2 Feeding

Seals were fed herring (*Clupea harengus*) obtained frozen from (Newfoundland Bait Service, Ltd., Rose Blanche, NL) and thawed prior to feeding. Occasionally, some mackerel (*Scomber scombrus*) were mixed in among the herring, and the seals were fed these as well. Seals received 3 to 6 kg of herring each day. Tyler and Babette were both overweight, and were maintained on a diet of a maximum of 3 kg of herring per day, and limited capelin (*Mallotus villosus*). The seals each got one cystene capsule (0.100 g) per feeding/training day, as well as one vitamin for marine mammals (Sea Tabs®, Pacific Research Laboratories, INC.). Deane, the juvenile seal, received a half-dosage of each of these.

On normal feeding days, Babette, Tyler and Jamie were fed whole herring, while Lenny's herring were cut into 6-8 cm wide chunks, and Deane's, into 3-4 cm chunks. On training days, feeding occurred during training; the seals were required to participate in order to receive their daily allotment of fish. For training, Babette's and Tyler's fish werealso cut into 6-8 cm chunks. This was done to increase the number of available rewards, and, therefore, increase the number of trials possible during one training session. In each experiment, the seals were given as many trials as necessary to use up their daily allotment of fish (or, until they became satiated, as indicated by the seals' unwillingness to eat the fish provided). Because the seals varied greatly in size and weight, their daily allowances of food also varied, such that it was impossible to give all seals the same number of trials in a single training session (See Appendix B, Table B1 for a list of the number of correct choices and trials for each seal on each training day). Also, Lenny, Deane, and Jamie sometimes received a greater number of trials per day than Babette and Tyler simply because their herring were cut into smaller pieces.

Jamie often rejected large chunks of fish or pieces that had any fins attached (i.e., he spat them out), so his fish were cut as small as Deane's (3-4 cm) and often had the fins removed as well. Jamie, Lenny and Deane did not eat fish heads; when the fish were cut, these pieces were removed and used as described below.

Feeding normally took place between 11:30 a.m. and 2:30 p.m., and was often broken into two sessions. The fish was always carried to the compound in large metal buckets; each seal had his or her own bucket. The seals were individually hand-fed. This was done to ensure that each seal received the required amount of fish. The fish was weighed prior to feeding, and whatever was left at the end was weighed to determine the amount each seal had actually eaten. On hot days, the fish was kept on ice in the shed until each seal was fed.

Pieces of capelin, along with the heads that were removed from the fish of the smaller seals, were used to entice the seals that were not being trained at that time, and to reward them for staying away from the training area. The capelin were cut into very small pieces (approximately 1.5 – 3 cm long), so that the seals would not lose their appetite prior to training. Freshwater ice was placed in a central location on the deck within the compound, and was replenished as needed. In addition, seals were offered handfuls of ice formed into balls, once in the morning and once after feeding. This was how the seals obtained their drinking water.

The seals were used to being fed by various different individuals; in addition to the full-time research assistant and his part-time assistant, numerous high school and university students were employed, and these changed frequently. As well, numerous volunteers fed the seals on weekends and holidays.

Seals were not fed on Tuesdays, as this was the day they were weighed and had blood samples taken. The blood samples were taken from the flippers and sent to the local veterinarian for analysis, to assess the health of the seals. This was also "cleaning day", and the seals remained on deck while the tanks were drained and cleaned.

2.2.2.3 Training Equipment

All materials associated with training were stored in the shed or barn until they were needed, so that the seals were never exposed to them in any context other than training.

A baton, made from a 0.8 cm diameter, 90 cm long wooden dowel, with a wooden sphere (5 cm diameter) at the end, was used as a station for the seals at the beginning of each trial. An Acme® stainless steel "silent" dog whistle was used to cue the seals at the moment they performed a correct behaviour.

Two waterproof, transparent Lexan® boxes (30 cm x 30 cm x 30 cm) were designed to hold stimulus objects. Movable stainless steel rods (29.5 cm, 0.5 cm diameter) were used to skewer the objects, and adjustable collars were used to hold them in place inside each box at chosen positions. A removable piece of Lexan® approximately 1mm shorter on each side than the inside of the box, was placed on the bottom inside each box. A row of 8 circular holes (approximately 0.4 cm deep into the bottom of the box) was drilled horizontally across the centre of this piece, and a corresponding row was drilled into the top as well, in order to hold the metal bars in place, and allow for several objects to be positioned inside the box at once. The rim of the box where the cover was attached had a continuous rubber ring around it, embedded in a central groove in the walls approximately 1 mm deep. The cover had 20 holes along the outside edge corresponding to the 20 bolts that were permanently embedded in the Lexan® walls. When the cover was placed down over the bolts, and fastened using 20 acorn nuts, the rubber ring formed an airtight seal, which prevented the objects from getting wet, and kept the seals from obtaining odour cues from the objects. The cover had an additional disk of Lexan® approximately 3.5 cm in diameter (0.45 cm thick) glued to the centre on the outside to which a stainless steel o-ring, approximately 2.5 cm in diameter, was attached, to allow the box to be suspended. An identical ring was also attached to one side of the box., which allowed the box to be suspended horizontally as well as vertically. A piece of white cardboard was cut out and placed in the bottom of each of the boxes (beneath the additional piece of Lexan®) to prevent the seals from viewing the objects inside the box from beneath the surface.

The boxes were attached to opposite ends of a white, plastic-coated hollow metal bar (1.25 m long, 2 cm diameter). Holes were drilled through the bar, approximately 10 cm from the ends, and plastic clothesline was put through each hole and tied around the top o-ring on each box. A loop of clothesline was attached to the centre of the metal bar using duct tape. The centre was determined by lifting the bar with the boxes attached, and placing the loop so that the boxes were balanced. A brass lobster-claw clasp (approximately 8 cm x 4 cm) was attached to a piece of white plastic clothesline that had a loop knot at one end. The clasp was attached to the loop on the metal bar, and the knotted end of the clothesline was attached to the metal clasp that extended down from the chain of the winch above the tank. The electric winch allowed the experimenter to raise and lower the box apparatus according to the water level so that the boxes always rested upright on the surface of the water. A photograph of the experimental apparatus (i.e., the two boxes attached to the metal bar) is provided in Figure 2.2.

Between trials, the boxes were wiped with paper towels. Occasionally, the boxes were cleaned with Windex® glass cleaner, and then rinsed thoroughly with seawater. A white, 19 L beef bucket was used as a stool on which to place the seal's fish bucket during training. A "corner" was constructed out of a wooden frame forming a 90° angle, with two rectangular sides (56 cm wide x 70 cm long). The frame was lined with black netting. This corner was used as a herding device throughout all experiments, but was also used by the experimenter as a "safety shield", when some seals were roaming on the deck during training.

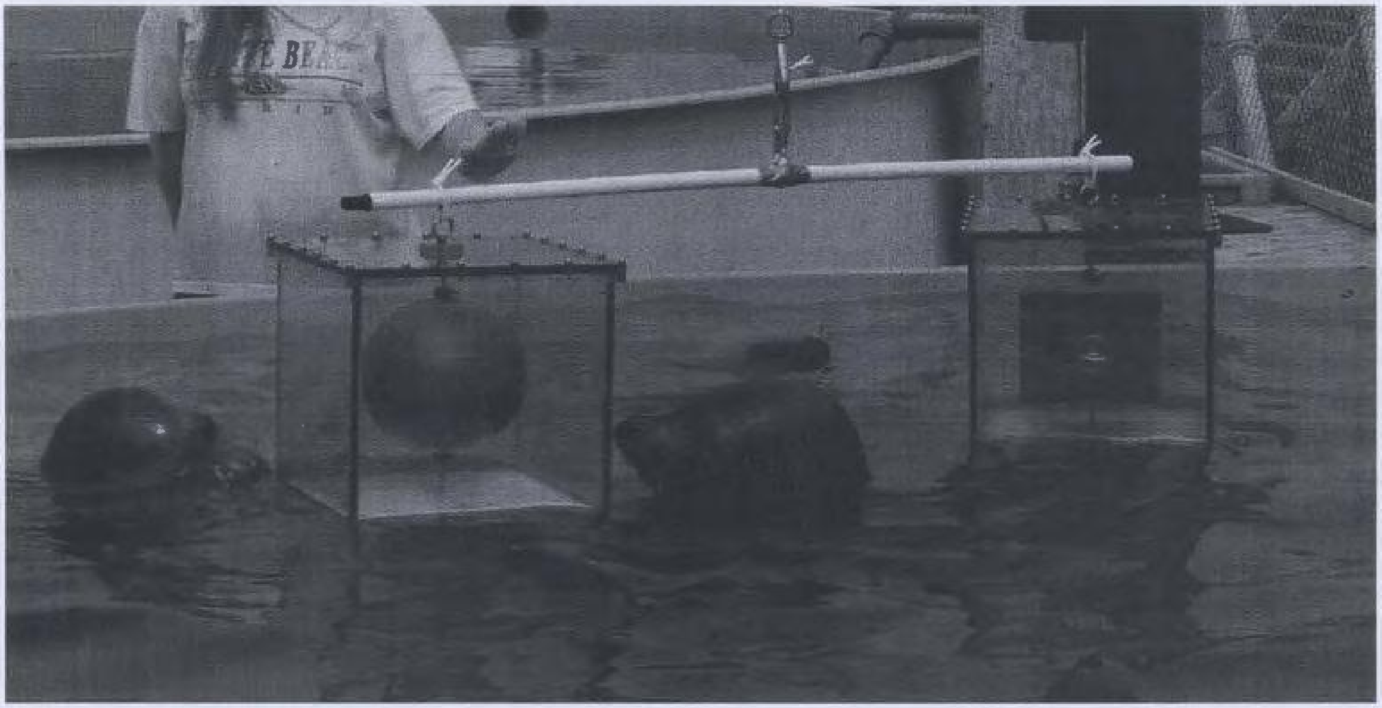


Figure 2.2. Experimental box apparatus used in Experiments 1 and 2. In the above photograph, the red ball and red cube are pictured inside the boxes.

2.2.2.4 Stimuli

The objects chosen differed on several different dimensions. By varying the size, shape, colour, texture, and reflectance of the objects, I attempted to make the discrimination tasks as easy as possible for the seals.

The objects used for the first discrimination task, and in subsequent discriminations, were a large red ball and a large red cube, as shown in Figure 2.1. The ball was a pale red Nerf™ sponge soccer ball (22 cm diameter) that was spray-painted with Colour Place™ Fast Dry Spray Paint for Wood and Metal in bright red. The cube was made from a cardboard box (22 cm x 22 cm x 21 cm) that was covered in white paper and spray-painted with the same paint as the ball. Both were given several coats until they appeared to have the same intensity and reflectance. (Initial use of these particular objects as discriminanda stemmed from inconclusive results of an habituation pilot study, described in Appendix A, that failed to reveal whether the seals were capable of discriminating between these objects).

The second set of objects consisted of 1) a pair of metal coffee cans (12 cm high, 9 cm diameter) with the labels removed, with black plastic lids, stacked so that the lids touched and formed a black line across the centre of the stimulus; 2) a Fisher Price® Rock-n-Stack™ infant toy (Figure 2.3).

Two novel objects introduced in the fourth and fifth discrimination tasks. The first consisted of three red holographic cardboard gift boxes, each with a hexagonal cross-section. These were stacked vertically so that the hexagonal faces were visible. Two of the boxes were 8 cm high, while the one placed in the centre was 7 cm. This object was

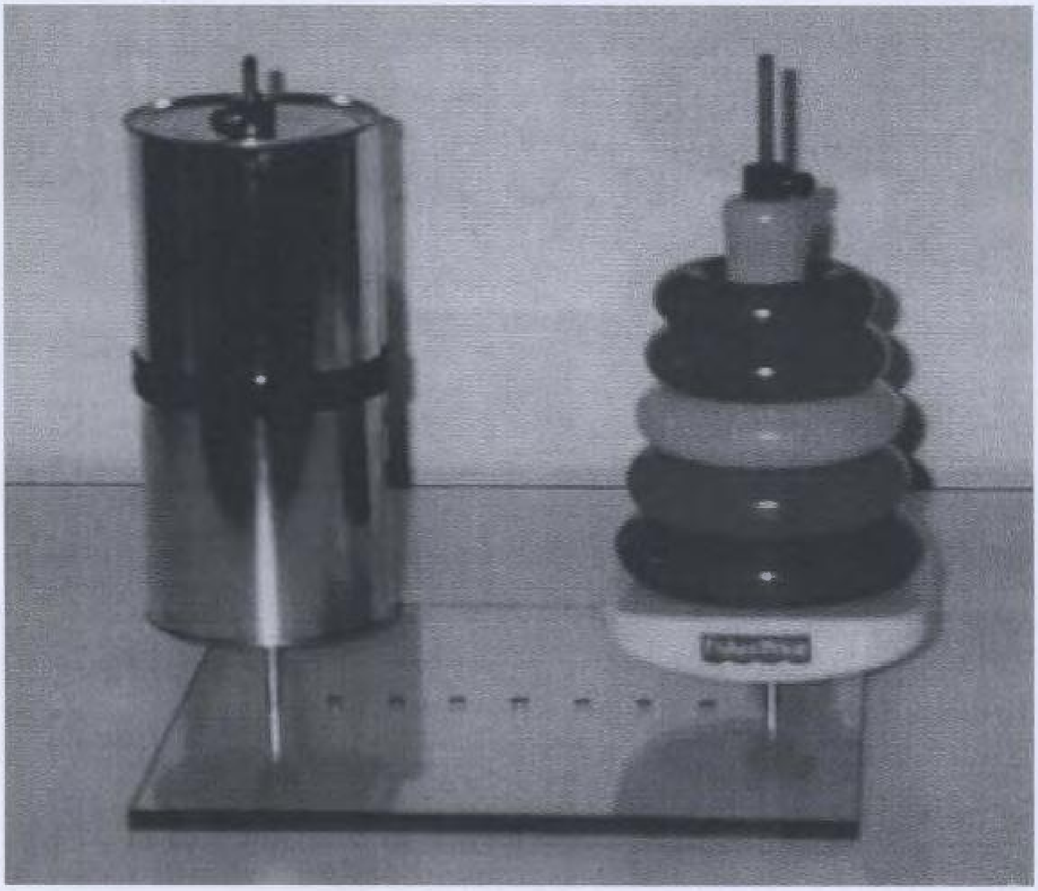


Figure 2.3. The two stimuli used for the second discrimination task in Experiment 1. these two objects were labelled “coffee” and “donuts”. Note: The objects are shown here side-by-side to allow a size comparison. During the experiment, only one of these objects was placed in the centre of each of the boxes.

called "hexagons". The second stimulus consisted of an inverted, frosted magenta (i.e., dark pink) plastic tumbler, atop of which was placed a 6 cm high holographic red hexagonal cardboard gift box. The gift box had strips of Velcro attached to the two top, diagonally-oriented sides. Two plastic Velcro hair rollers were stuffed with a piece of sponge, and Velcro was attached to the sponge at one end. The rollers were then attached to the sides of the hexagonal box. This object was called "bunny" (see Figure 2.4).

The two objects used for the sixth discrimination consisted of 1) a paper, metallic orange holographic gift bag 24 cm x 20 cm x 6 cm, that was taped at the top so that it formed a triangle on two sides; 2) a "tower" consisting of, from the bottom, a white cylindrical container (8.5 cm, 8 cm diameter), a brown rectangular cardboard box positioned horizontally (18 cm x 10 cm x 5.5 cm), and an approximately rectangular piece of blue sponge (7 cm x 7 cm x 8 cm; see Figure 2.5).

2.2.3 Procedure

2.2.3.1 General

Experiment 1 began on the same date for each seal. Prior to this experiment, seals were habituated to the empty boxes for a minimum of 10 hr. The seals were exposed to the boxes for four 30-min sessions per day, four non-consecutive days a week[2], for six days. For each session, the box was suspended into the tank, and the seals were allowed to explore it. They also experienced up to 16 30-min exposures in which a box contained an object, as described in Appendix A. For this part of the experiment, the seals still experiences four sessions per day; the only difference was that, for one of the four trials

---

[2] No data were collected on Tuesdays, Saturdays, or Sundays.

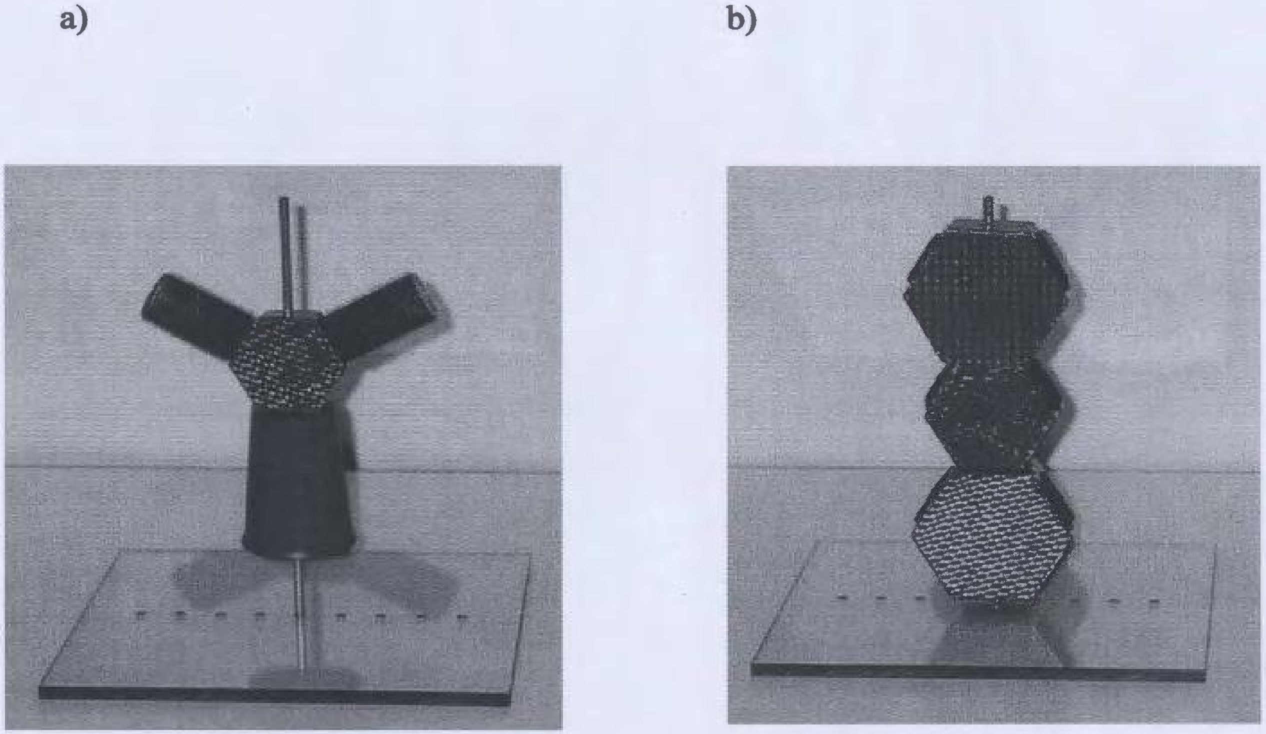


Figure 2.4. The two objects used in the fourth and fifth discrimination tasks in Experiment 1. These objects were labelled a) "bunny" and b) "hexagons".

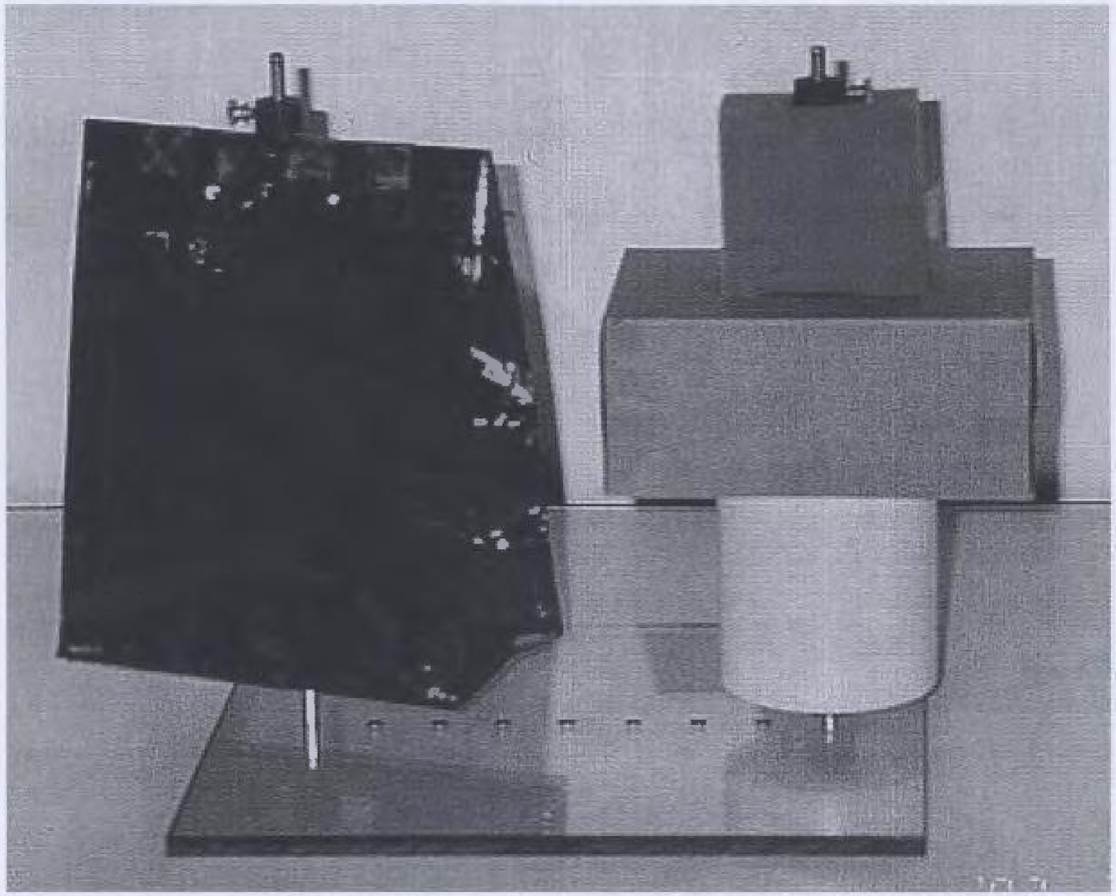


Figure 2.5. The two objects used in the sixth discrimination task in Experiment 1, and in all tasks in Experiment 2. These objects were labelled "bag" and "tower".

on each day, the empty box was replaced with a box containing an object.

2.2.3.1.1 Determination of Training Order

The seals were free to move between the tanks and were trained in whichever tank they were in on each training day. (This meant that seals were trained with zero to four others present). The seals were trained one at a time, and the order in which the seals were trained varied between training days. The order was often determined on the basis of which seals were the hardest to distract from the training situation while not being trained. Sometimes this was Tyler, because, when hungry, he could be very aggressive towards the smaller seals. However, Tyler was usually fairly well behaved and would settle for capelin until it was his turn. However, if Deane and Lenny were very hungry, they were often trained first because they were extremely persistent and would not leave the training area. Trials could not be carried out with other seals in the area, even if they were not aggressive toward the trainee, because they often obstructed the path of the trainee to one or both of the boxes.

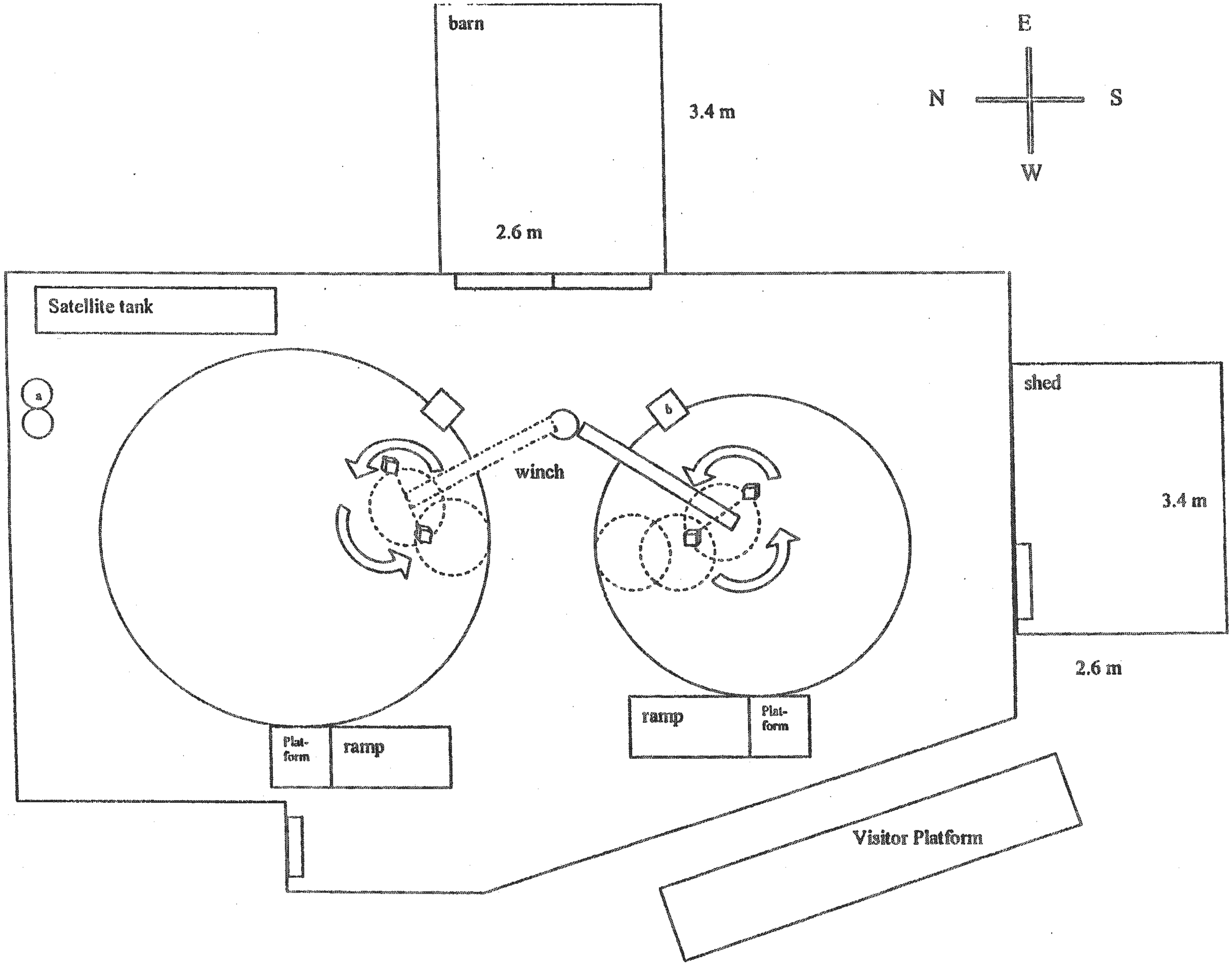
2.2.3.1.2 Set-up

2.2.3.1.2.1 Preparation before training

The experimenter and her assistants always wore non-latex disposable sterile gloves when handling the fish. The experimenter wore the whistle around her neck, and kept it in her mouth for the duration of each seal's training session. The experimenter and two assistants entered the compound, bringing with them the metal buckets belonging to each seal, which contained their daily allotment of fish. The buckets were put inside the barn, and the experimenter and her assistants began the set-up. Inside the shed, the experimenter unscrewed the lids of the boxes and placed the two objects to be used during training inside for whichever seal was to be trained first. The objects were positioned in the centre of the box. The metal rods skewering the objects were each placed in the centre hole, and the objects were centred on the rods and fastened using metal collars. The objects were positioned inside the boxes so that the side having the most surface area was parallel with the metal bar and with the side of the boxes that would be facing the seal.

The chain was lowered from the winch, and the boxes were attached as described above. The boxes were lowered so that they rested upright on the surface of the water, with approximately 0.5 –1 cm of each box beneath the surface, to increase the friction on the boxes caused by the water to help to keep them from swaying or spinning. This also ensured that the box remained in contact with the water despite the continuous rise and fall of the water due to seal movements or wind. The two boxes, with the discriminanda inside, were presented in either tank as needed, and the location of the boxes with respect to the side of the tank was dependent on the range of the winch. In the small tank, the boxes were approximately 1- 1.25 m in from the edge of the tank, and in the big tank, the winch was pulled across as far as was possible (approximately 0.75 m in from the edge). See Figure 2.6 for a diagram of the box positions in each tank relative to the winch.

Each seal was only trained on one pair of objects per training day. However, since the seals progressed through the discrimination tasks at different rates, different seals were often trained on different object pairs on any given training day. This meant that the boxes often had to be taken down between training sessions for different seals, and the


barn
3.4 m
2.6 m
E
N
S
W
Satellite tank
a
shed
winch
b
3.4 m
2.6 m
ramp
Plat-form
Plat-form
ramp
Visitor Platform

objects changed, which took approximately 5-10 min. A white bucket was placed bottom-up on the deck near the edge of the tank, and the seal's metal bucket containing his/her fish was rested on this bucket for easy reach. The seals could not see the fish bucket unless they leaned over the edge, but they could likely smell the fish. The experimenter stood at the edge of the tank in front of the box apparatus, with the training baton in her left hand, and a piece of herring in her right. She kept her right hand behind her back out of sight of the seals, until the seal being trained had chosen correctly. When there were seals on the deck during training, the experimenter would sometimes place the corner behind herself and the bucket so that those seals could not attempt to steal the fish from her hand or the bucket.

2.2.3.1.2.2 Role of Assistants

One assistant stood or sat on the platform approximately 90 ° to the right of the experimenter in the little tank (to the left in the big tank). This assistant was the "distracter"; his/her job was to keep the seals not being trained at that time away from the training area. He/she would call out to the other seals, and reward them with bits of capelin and fish heads for staying away from the experimenter and trainee. It was still very difficult to keep the other seals away, as some of them realized that it was more rewarding to steal a big chunk of herring than it was to stay away for tiny pieces of capelin. The experimenter often had to stop between trials in order to use hand signals to forcefully tell the other seals to "Go!" (this was a palm of the hand extended in front of the seal's face plus a loud, deep voice). Unfortunately, there was not really any better way to set up the training, because the seals were most content, more cooperative and appeared to be less stressed when they were together than when separated for training. A second assistant stood on the opposite side of the experimenter (to the left at the little tank, and to the right at the big tank). This assistant recorded each trial as correct or incorrect, as stated by the experimenter, as well as each time the boxes were switched. In this way, the experimenter did not know when a seal had reached criterion until it was reported by the assistant.

2.2.3.2 Pre-training

Pre-training was required to get the seals to touch the boxes. Since the seals were accustomed to touching the training baton, the baton was used to first station the seals in front of the boxes. The whistle was blown, and the baton was then slowly moved to the correct box. The seal would follow, and while touching the baton, would eventually come into contact with the box. The whistle was then blown again, and the seal got its reward. It did not take long for the seals to learn that the correct response was a two-step process of first stationing on the baton, then touching one of the boxes. All seals but Deane learned within the first pre-training session, within approximately 30 trials. Deane required 10 pre-training sessions. Trials were not counted while the seals were being led to the correct box. Once they began to choose the boxes on their own (i.e., leave the baton and touch one box), choices were recorded.

2.2.3.3 Training

Training usually occurred around the same time each day, twice a day beginning at approximately 11:30 a.m. and 2:30 p.m., four days a week[3]. The seal being trained (the

---

[3] Seals were not trained on Tuesdays, Saturdays, or Sundays.

"trainee") was called over to the edge of the tank in front of the boxes, facing the experimenter. Once everything was in place and all other seals were removed from the training area, the first trial began. The end of the training baton was placed just inside the edge of the tank in front of the trainee, who was facing the experimenter. The seal then placed its chin on the baton, and the experimenter blew the whistle. Upon hearing the whistle, the seal would quickly turn around and swim to one of the boxes, touching it with its face or vibrissae. If the seal swam backward toward the box and touched it with its vibrissae while its eyes were underwater, this was not counted as a choice, because the seal clearly could not see the object. If the seal then emerged and touched the box, it was counted as a choice. Also, a trial was not counted as a choice if the seal touched the baton, but then left the training area without touching one of the boxes. This sometimes happened as the result of one seal harassing or scaring away the trainee. When a non-choice trial occurred, the experimenter said "No choice", and this was recorded by the assistant. The baton was then placed back in the tank and another trial was begun immediately, as with choice trials. The seals were not rewarded for incomplete trials, and these trials were not included in the number of trials to criterion. The number of non-choice trials did not exceed 10% of the total number of successful trials within a training session for any seal.

If the seal chose correctly, the experimenter would blow the whistle a second time, say "Right!" and reward the seal immediately with a piece of fish. If the seal chose incorrectly, the experimenter would say "Wrong!", and place the baton back in the water to allow him to start the next trial. The boxes were switched randomly from left to right so the seals did not merely learn to make a single response of "go left" or "go right". If a seal was performing at chance, and randomly choosing both boxes, the boxes were often not switched until the seal started to consistently choose the same (correct) box.

2.2.3.4 Controls/Considerations

2.2.3.4.1 Criterion

The criterion used to determine whether a seal had learned to discriminate between the objects required the seal to chose correctly on 18/20 consecutive trials. This criterion was used because it fell within the range of criteria used by other experimenters for similar experimental designs; it also allowed for several switches of position of the two boxes, which ensured that the seals were not simply learning a left- or right response. A running count of trials was used, which could carry over between training days. (The number of days for a seal to reach criterion varied from 1 to 19 training days, which may have spanned several weeks). An additional constraint was that, within the 18/20 consecutive trials, the seal must also have at least 3 out of 4 switches correct. There were often more than four switches within a block of 20 trials, but this criterion was added to ensure that, had there been relatively few switches, the seal was not simply learning on the switch trial "this is wrong, pick the other one", and solving the problem that way. (The trials immediately following a switch in object positions were a good indication of whether the seals had learned the correct object.)

2.2.3.4.2 Switches

The occurrence of switches was not planned prior to the training session. Typically, as a seal became better at choosing the correct object, more and more switches were employed. The boxes were switched after one to ten trials. The assistant that recorded the trainee's choices also recorded the occurrence of switches, and was instructed to monitor the number of trials between switches in order to help the experimenter avoid pure alternation or extended bouts without a switch. The apparatus was rotated 180° in order to switch the position of the objects. Thus, the experimenter was also careful to vary which of the boxes she touched when turning the box apparatus, as well as whether the box touched was pulled toward her or pushed away. When the experimenter could not reach the boxes by hand, she used the straight end of the training baton to push one of the boxes away so that the other one would move within her reach. After each rotation, the boxes were steadied before the next trial began.

2.2.3.4.3 Control of Box Positions

All efforts were taken to ensure that on each trial, the seal started off approximately the same distance from each of the boxes, so as not to bias its choice. The actual distance varied between approximately 0.7 m and 2 m. While the boxes were never more than 1.5 m from the edge of the tank when the bar was positioned parallel to the edge, greater distance could be obtained by positioning the boxes perpendicularly to the edge, and leading the seal to one side at the beginning of each trial using the baton.

Initially, the seals had a tendency to choose the closer of the two boxes. Therefore, as the seal became better and better at choosing the correct object, the experimenter was more and more careful of her position with respect to the boxes, and sometimes purposely allowed some trials where the box containing the correct object was a little farther away than the other box. (This was another indication that the seals had learned to choose based on the object, as they were able to overcome the tendency to choose the box that was a little closer.)

Training occurred under all weather conditions. However, on windy days, training was postponed if the experimenter was unable to have adequate control over the position and movement of the boxes. On several occasions, training also had to be aborted due to heavy rain, because it may have interfered with the seals' ability to see the objects inside the boxes.

2.2.3.4.4 Overtraining

In most cases, a seal reached criterion on a certain training day before it had received its full amount of fish for that day. Since the experimenter was not immediately aware that the seal had reached criterion, she continued on and finished training the seal on the correct object for that day. The assistants would usually recognize that a seal had reached criterion shortly thereafter, so if the seal still had many pieces of fish left, training was terminated, and the seal was simply fed the remainder of its fish after the other seals had been trained.

2.2.3.5 Experimental conditions

All five seals were first trained to discriminate between the red ball and red cube, to a criterion of 18/20 consecutive trials correct (plus at least 3 out of 4 correct trials following a left-right switch). For two of the seals, the ball was the correct object, and for three of the seals, the cube was correct. This first discrimination was denoted as "A+ A-", where "A+" refers to the rewarded object, and "A-", to the unrewarded object. All seals were then trained to discriminate between the coffee cans and coloured donut toy. For two of the seals, "coffee" was correct, and for three of the seals, "donuts" was correct. This discrimination was denoted "B+ B-". For the third discrimination task, all seals were exposed to a pairing of two familiar objects; that is, the object that had been correct from the first task (A+), and the object that had been incorrect from the second task (B-). For the fourth and fifth discriminations, the seals received two separate pairings of a novel object (i.e., the "bunny" or the "hexagons") with 1) the object that was incorrect from the first set (A-), and 2) the object that was correct from the second set (B+). The order of these two tasks was counterbalanced, so that three of the seals (Babette, Jamie and Deane) experienced B+/C- first, followed by C+/A-, and two of the seals (Tyler and Lenny) experienced C+/A- first, followed by B+/C-. This was done to help control for practice effects. See Table 2.1 for a list of the order of the tasks experienced by each seal.

The sixth discrimination involved two novel objects. The objects used for this task ("D+ D-") were the orange gift bag and the "tower". Babette did not complete this task. For two of the seals, "bag" was correct, and for the other two, "tower" was correct.

2.2.3.6 Overlap with Experiment 2

The experiment was designed so that the data from the sixth discrimination of Experiment 1 could also be used for the first discrimination of Experiment 2. All aspects of training remained the same except that the seals were no longer trained in either of the tanks on each training day; the tank they were trained in was pre-determined and was kept constant for that task. The seals were trained in either the small tank (Lenny and Jamie) or the large tank (Tyler and Deane). When the experimenter was unable to get one of the seals into the correct tank on a particular training day, that seal was not trained on

Table 2.1

Order of Discrimination Tasks for each Seal in Experiment 1.

	Discrimination Task					
	1		2		3	
Seal	A+	A-	B+	B-	A+	B-
Babette	cube	ball	donuts	coffee	cube	coffee
Tyler	ball	cube	coffee	donuts	ball	donuts
Jamie	cube	ball	donuts	coffee	cube	coffee
Lenny	cube	ball	donuts	coffee	cube	coffee
Deane	ball	cube	coffee	donuts	ball	donuts

Table continues.

Table 2.1 (continued).

	Discrimination Task							
	4			5			6	
	Order of tasks							
Seal	order	B+	C-	order	C+	A-	D+	D-
Babette	1st	donuts	hexagons	2nd	bunny	ball	-	-
Tyler	2nd	coffee	bunny	1st	hexagons	cube	tower	bag
Jamie	1st	donuts	hexagons	2nd	bunny	ball	bag	tower
Lenny	2nd	donuts	hexagons	1st	bunny	ball	bag	tower
Deane	1st	coffee	bunny	2nd	hexagons	cube	tower	bag

Note. The first three discrimination tasks occurred in the same order for each seal; only the fourth and fifth tasks were reversed, for two of the seals.

that day. This happened on only a few occasions. It was sometimes necessary to drain one or both of the tanks and winch the seals out prior to training in order to have them in the correct tanks. Sometimes, the ramps were taken away so that the seals were either forced to remain on deck until we gave them access to the correct tank, or, so that certain seals could not leave a tank and go to the incorrect tank. However, this was not always the best option, as it sometimes required certain seals to be isolated. They appeared not to like this, and on several occasions, a seal even "jumped" out of the tank to be with the others. Also, when any amount of snow or ice built up in the compound, the seals were able to use the resulting snow bank to climb in and out of the tanks, which made it difficult to isolate them.

2.3 Results

2.3.1 Discriminations

The results support the hypothesis that harp seals are able to discriminate between two objects presented visually. All seals reached a criterion of 18/20 consecutive trials correct, plus at least 3 out of 4 correct switches within those 18/20 trials. (However, one subject, Babette, did not complete the sixth discrimination task). Raw scores for each seal, as well as the mean number of trials to criterion (+SE) for the six discrimination tasks, can be found in Table 2.2. These data are organized in two ways. First, in Table 2.2a, they are organized according to the specific task category. Second, in Table 2.2b, the data are organized sequentially in the order the tasks were experienced. These data are presented graphically in Figure 2.7, which shows the mean trials to criterion (± SE) across the six discrimination tasks in Experiment 1, for all five seals, and when Babette's

Table 2.2

Trials to Criterion for all Five Harp Seals for Each of the Six Discrimination Tasks in Experiment 1, Organized a) According to Specific Task Category, and b) According to the Order in Which the Tasks Were Experienced.

Seal		a) Task Category						b) Task Order					
		A+A-	B+B-	A+B-	B+C-	C+A-	D+D-	1	2	3	4	5	6
Babette		1042	941	82	59	104	-	1042	941	82	59	104	-
Tyler		398	248	27	67[a]	119[a]	134	398	248	27	119[a]	67[a]	134
Jamie		902	518	46	241	85	113	902	518	46	241	85	113
Lenny		252	275	31	28[a]	107[a]	149	252	275	31	107[a]	28[a]	149
Deane		226	182	46	50	40	275	226	182	46	50	40	275
	M	564	433	46.4	89.0	91.0	167.8	564	433	46.4	115.2	64.8	167.8
	SE	171	139	9.7	38.6	13.9	36.5	171	139	9.7	34.1	14.0	36.5
	M[b]	445	305.8	37.5	96.5	87.8	167.8	445	305.8	37.5	129.3	55.0	167.8
	SE	157	73.4	5.0	48.8	17.4	36.5	157	73.4	5.0	40.2	12.9	36.5

Note. [a] Tasks were counterbalanced so that Babette, Jamie and Deane experienced task B+C- fourth and task C+A- fifth, whereas the reverse is true for Tyler and Lenny. These are the only scores affected by the change in organization. [b] Because Babette did not complete the sixth discrimination, her data could not be included in a oneway within-groups analysis of variance; thus, means excluding Babette's data were also calculated.

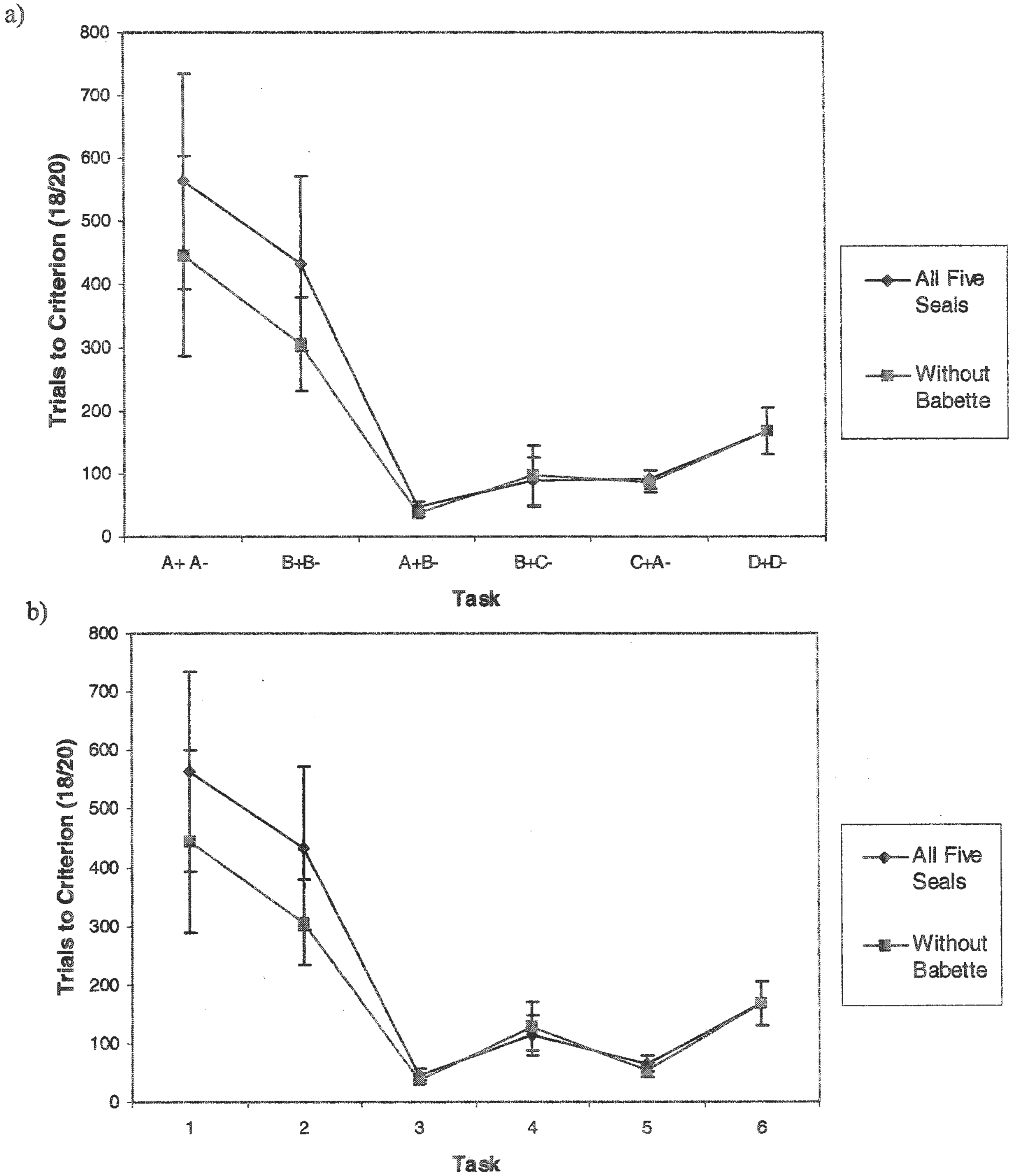


Figure 2.7. Mean trials to criterion (± SE) across the six discrimination tasks in Experiment 1, for all five seals, and when Babette's data are excluded, organized a) by category, and b) in the order they were experienced. Note that Babette did not complete the sixth task.

data are excluded, organized a) by category, and b) in the order they were experienced. This organization was necessary to properly analyse the data in light of the counterbalancing that occurred between tasks 4 and 5, for the B+/C- and C+/A- tasks. Figure 2.8 shows a breakdown of individual performance of the five subjects, organized categorically, across the six discriminations. Figure 2.9 presents individual scores for each seal across the six discriminations, organized according to the order in which the tasks were experienced.

2.3.2 Transfer of learned object valence

The results also support the hypothesis that what the seals learned about whether an object was associated with a reward (S+) or no reward (S-) would improve their performance on later tasks involving these familiar objects, in comparison to tasks in which both objects were novel.

A one-way within-subjects analysis of variance was performed on the data for the six discrimination tasks. For this analysis, the data were organized as shown in Table 2.2a. Because Babette did not complete the final discrimination, her data were not included in this analysis. (Note that Figure 2.7 shows that the means do not differ when Babette is excluded, i.e., the error bars overlap).

There was a significant effect of task ($F (5, 15) = 5.60, p < .01$). In order to determine the origin of the differences between tasks, several planned comparisons were carried out. A question of key interest was whether the three tasks in which both objects were novel to the seals (i.e., A+/A-, B+/B-, and D+/D-) required more trials to solve than the three tasks in which either one or both of the objects were familiar (i.e., A+/B-,

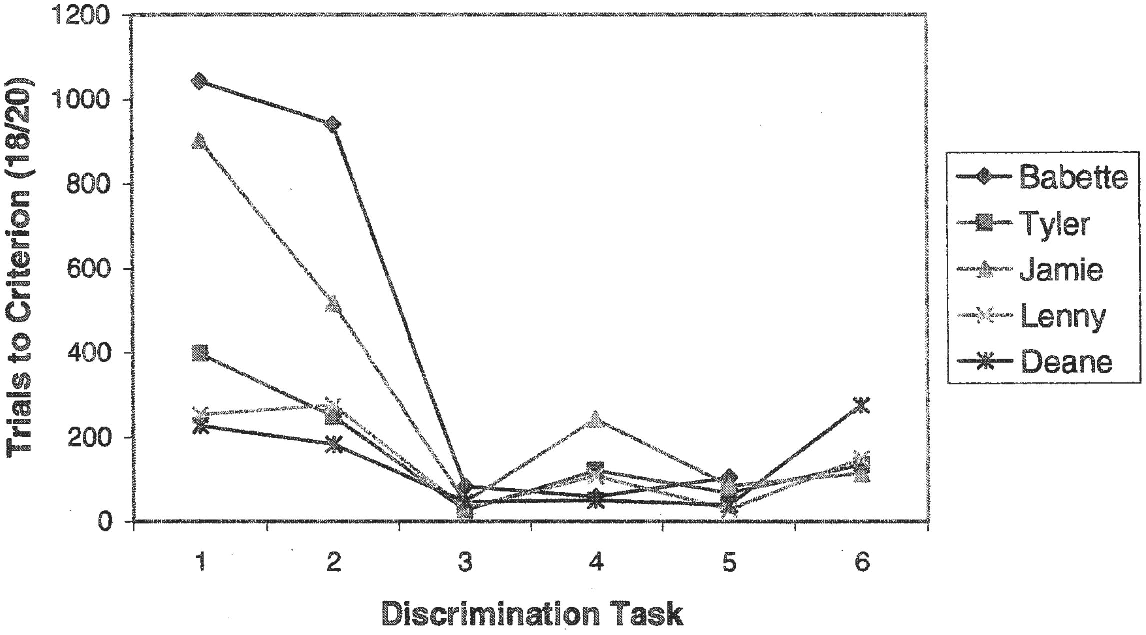


Figure 2.8. Trials to criterion for each of the five seals across the six discrimination tasks in Experiment 1, organized by category. Note that Babette did not complete the sixth task.

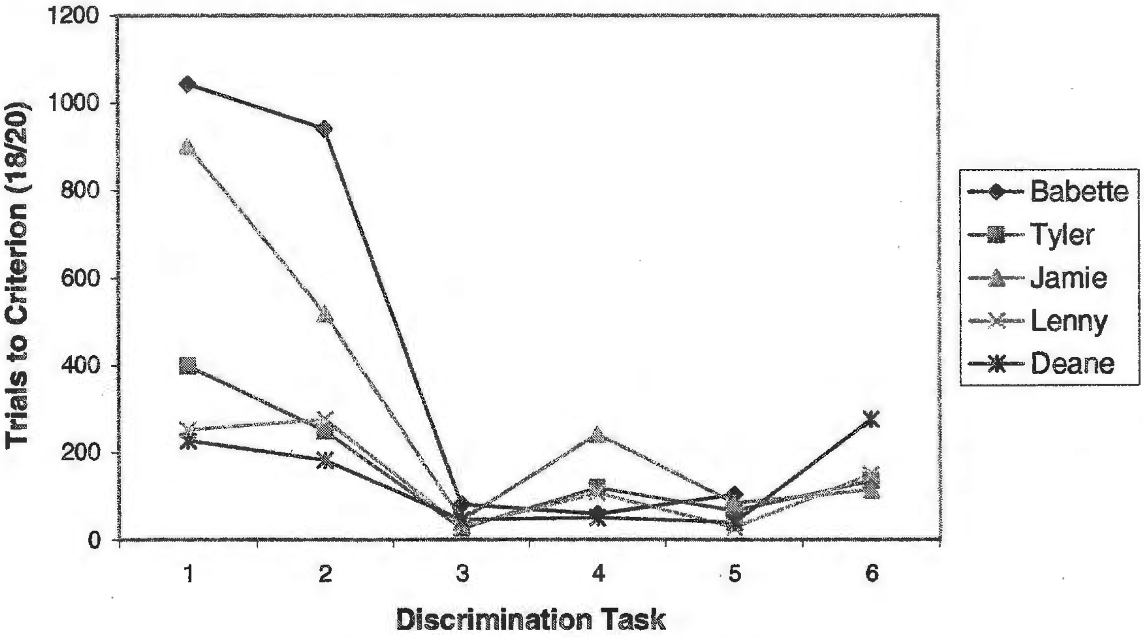


Figure 2.9. Trials to criterion for each of the five seals across the six discrimination tasks in Experiment 1, in the order they were experienced. Note that Babette did not complete the sixth task.

B+/C-, and C+/A-). A complex comparison revealed that this was the case (F (1, 3) = 20.08, p = .021). All four seals showed this effect[4]. Simple comparisons between the task with two familiar objects and the tasks with either one positive (i.e., previously rewarded) object (B+/C-; F (1, 3) = 1.62, p = .293) or one negative (i.e., previously unrewarded) object (C+/A-; F (1, 3) = 5.32, p = .104) yielded non-significant results. A complex comparison revealed that the two novel tasks experienced at the beginning (A+/A- and B+/B-) did not differ significantly from the final novel task (D+/D-; F (1, 3) = 2.17, p = .237) in the number of trials the seals required to reach criterion. Finally, a complex comparison revealed that the three novel tasks (Tasks 1, 2, and 6) did not differ significantly from each other (F (1, 3) = 2.22, p = .19) in the number of trials the seals required to reach criterion. However, three of the four seals did show an effect of learning set formation in that the number of trials to criterion was reduced by half from Task 2 to Task 6. Deane did not show this effect. See Figure 2.8 for the seals' individual performance across tasks.

The strongest test of whether the seals transferred learned information about object valence in order to solve the familiar-object problems in fewer trials than the novel-object problems was to give them a completely novel discrimination task, and see if the number of trials increased. A simple comparison of A+/B- (i.e., two familiar objects) with D+/D- (i.e., two novel objects) revealed a significant difference (F(1,3) = 14.1, p = .03) between these two tasks. Again, all four seals showed this effect. Thus, the seals required significantly fewer trials to solve the task involving two familiar objects, despite the fact

---

[4] Babette's data were not included in the analysis.

that they had had more practice at solving two-choice discriminations by the time they experienced the D+/D- task.

A Bonferroni correction for family-wise error increases the required significance level of each of these five comparisons from $\alpha = 0.05$ to $\alpha = 0.01$, in which case, none of the above comparisons are significant. However, Keppel (1991) and O'Brien (1983) both suggest that no correction is necessary for a reasonable number of planned comparisons, for example, equal or fewer in number than the degrees of freedom associated with the treatment variance (in the present case, $df_A = a - 1 = 6 - 1 = 5$). Given the limited number of planned comparisons carried out, the author believes it is reasonable to accept the difference found between the three novel-object tasks versus the three familiar-object tasks, as well as between A+/B- and D+/D-, as significant.

2.4 Discussion

2.4.1 Discriminations

The results of Experiment 1 demonstrate that harp seals are capable of learning to solve two-choice visual discriminations. With the exception of Babette (who was only trained on the first five tasks), all of the seals reached the specified criterion for each of the six discriminations. This result coincides with those of many other researchers who have reported that other pinnipeds solve two-choice discriminations using various modalities (e.g., Dehnhardt, 1990; Dehnhardt et al., 1998; Dehnhardt & Kaminski, 1995; Kastelein & van Gaalen, 1988; Renouf, 1985; Renouf & Gaborko, 1989; Schusterman, 1967a, 1968, 1981; Sticken & Denhardt; 2000).

2.4.2 Transfer of learned object valence

The results show that harp seals transfer learned information about whether an object is associated with a reward (S+) or no reward (S-) to new discriminations involving one or two familiar objects. The three tasks in which both objects were novel to the seals required significantly more trials to solve than the three tasks in which either one or both of the objects were familiar. Further evidence to suggest that the seals transferred learned object valences to new tasks comes from the result that the seals required significantly more trials to solve the final novel discrimination (D+/D-) than they did to solve the third discrimination, which involved two objects for which the valences had previously been learned (A+/B-). Had the seals' improved performance been due solely to practice effects, they should have performed better on the final task than on earlier tasks, which was not the case.

This result is similar to the findings of Klüver (1933) and Lashley (1916), who both demonstrated that what animals learn about the value of a specific familiar stimulus (in terms of its association with reward or no reward) can later improve their performance in subsequent choice tasks involving this stimulus and other novel stimuli. Similarly, both Klüver and Lashley demonstrated that animals learn and remember associations equally well regardless of whether the object valence is positive or negative. That is, the animals learned not only to continue to respond to a previously rewarded stimulus, they also learned to continue to avoid, or not respond to, a previously unrewarded stimulus. In the present experiment, there were no significant differences between the number of trials required to solve the tasks when the seals had two familiar objects in comparison to when they had either one previously rewarded object, or one previously unrewarded object. As long as the seals knew the value of one of the objects of a pair, this information helped them to learn the value of the second object more quickly than if both objects were novel. It also appears that S- is just as useful as S+ in providing information about the correct choice. I do not directly compare B+/C- to C+/A- because I have already used up the five uncorrected comparisons allowed, as suggested by Keppel (1991) and O'Brien (1983). However, given that a Bonferroni correction is put in place to control for Type I error, it seems reasonable to conclude that B+/C- and C+/A- do not differ from each other, given that each of these does not differ from A+/B-.

2.4.3 Methodological Considerations

2.4.3.1 Practice effects

When analysing the data, I considered the fact that the seals may have become better at solving the series of two-choice discriminations with practice. That is, the observed improvement could have been due to the seals "learning to learn" how to solve a two-choice discrimination, rather than due to their ability to remember the value of previously rewarded or unrewarded objects. Unfortunately, there was no way to counterbalance the presentation of the stimuli; an object will always be novel to a seal before it is familiar. Because it was impossible to counterbalance the presentation of stimuli across tasks, the ability to discriminate between stimulus pairs may be confounded with tasks.

The seals' performance on the sixth task did not differ significantly from that on the first and second tasks, which suggests that the seals did not improve across the three novel discriminations. However, three of the four seals did show improvement from the second task to the sixth; that is, the number of trials to criterion was reduced by half. Also, the three tasks involving either one or two familiar objects did not differ significantly from each other, but differed significantly from the three tasks in which both objects were novel. Again, it is important to note here that despite the non-significant comparison between the three novel tasks, Figure 2.7 shows that the means do appear to differ; that is, there appears to be a trend towards improvement, even if it is not significant. Because of the small *n* within each group, the power of the analysis is considerably lowered. Thus, no conclusions can be drawn about whether learning set formation was a factor that contributed to the observed results.

Also, the task involving two familiar objects was solved in significantly fewer trials than the final novel discrimination. Thus, it appears that discriminating between two novel objects is more difficult than discriminating between a pair of objects in which one or both is familiar and has a previously learned value associated with it (i.e., S+ or S-). This provides further evidence to suggest that improvement was not simply due to practice effects or formation of a learning set for two-choice discriminations.

Other experimenters have shown that animals, including some pinnipeds, do improve with practice on a series of novel discriminations. For example, Slotnick et al. (2000) showed that rats improved across a series of two-choice odour discriminations when given plenty of experience. Similarly, Schusterman (1968) demonstrated learning set formation for two-choice visual discriminations in both a California sea lion and a harbour seal. It is important to note that in these studies the number of discrimination tasks was far greater than in the present experiment. Had the seals experienced more than six tasks, it would have likely been clearer as to whether any learning set formation occurred.

2.4.3.2 Conspecific interference

In the current experiment, conditions were not ideal in that the seals could not be trained individually. Thus, the distraction of having conspecifics present, especially when they were aggressive and attempted to steal the trainee's fish, may have interfered with the seals' performance, and resulted in the high number of trials required to reach criterion. This may have been especially true for Deane, since she was very young at the beginning of the study, and may have been more susceptible to distraction due to her lack of experience in the training situation.

When attempts were made to isolate the seals for training, they showed visible signs of stress, and sometimes even jumped out of the tank onto the deck rather than be alone. On days when a seal was alone by choice, he/she still did not show any noticeable improvement in performance (personal observation). Some of the seals had a habit of playing with each piece of fish before eating it when alone. In fact, a single training session with one seal sometimes took up to an hour, with no noticeable improvement in performance.

2.4.3.3 Nature of the stimuli

An additional consideration is that the nature of the objects may have had an effect on the level of difficulty of the tasks. For example, the red ball and red cube were the same colour and approximately the same size, which may have made them more difficult to discriminate between than subsequent pairs of objects. On the other hand, the objects used in the second discrimination (i.e., the "coffee" and "donuts") as well as the third novel discrimination (i.e., "bag" and "tower") were chosen specifically to be highly discriminable. However, the seals' performance did not improve significantly from the first discrimination task to the second. The number of trials to criterion was not reduced significantly from the first to the sixth tasks, but three of the four seals did show a large improvement. While it is unknown what a harp seal would perceive as "highly discriminable", this result would suggest that visual discriminations are very difficult for harp seals. Similar performance on a visual task (in terms of numbers of trials to criterion) was reported for harbour seals by Renouf and Gaborko (1988, 1989).

In the habituation pilot study conducted just prior to the start of Experiment 1, the seals experienced both the red ball and red cube, and habituated to them within four 30 min sessions. Experiencing both stimuli in the absence of reward may have set up a situation of latent inhibition, where this pre-exposure to the neutral stimuli may have made it more difficult for the seals to learn S+ and S- associations involving these objects. However, had this been the case, the seals should have shown significant improvement on the second discrimination, which involved two completely novel (and, presumably, highly discriminable) objects. While this was not directly assessed, three of the four seals did show improvement on Task 2.

2.4.4 Conclusions

The results of the present experiment suggest that harp seals do appear to use object valence to solve two-choice visual discriminations. However, no clear conclusions can be drawn about whether the seals formed a learning set for two-choice discriminations. While not statistically significant, three of the four seals included in the analysis did show substantial improvement across tasks. The seal that failed to show improvement was very young, which leads to the consideration of developmental issues, which may have led to differences in her performance compared to the other seals. Because substantially fewer discrimination tasks were used in this experiment than in other studies (e.g., 12 and 16 tasks for a sea lion and harbour seal, respectively, Schusterman, 1968), it is possible that not all seals had sufficient experience to reveal learning set formation. Some of the variation could be due to varying degrees of overtraining and/or conspecific interference during different tasks. Finally, because it was impossible to counterbalance the stimuli across trials, the ability to discriminate between stimulus pairs may be confounded with tasks.

Chapter 3: Experiment 2

3.1 Introduction

Experiment 1 showed that harp seals appear to transfer learned object valence (S+ and S-) to new tasks involving previously reinforced or unreinforced stimuli, which is consistent with the findings for other species (e.g., monkeys, Klüver, 1933; chickens, Lashley, 1916). Experiment 1 also confirmed that harp seals are capable of solving two-choice visual discriminations. This is consistent with previous studies on discrimination learning in other pinnipeds (e.g., Renouf & Gaborko, 1989; Schusterman, 1967a, 1968), as well as the perceptually-based harp seal studies, which involved choice training (Lavigne, 1973; Lavigne & Ronald, 1972a, 1972b; Terhune and Ronald, 1971, 1972; Møhl & Ronald, 1975).

Having demonstrated harp seals' ability to solve two-choice visual discriminations, this discrimination method could now be used to test hierarchical learning. I took advantage of the possibility that harp seals may be highly sensitive to spatial cues, as suggested by field observations of their navigation and orientation behaviour (Bowen, 1991; Kovacs, 1987, 1995; Lydersen & Kovacs, 1993). As well, in a captive study, Renouf and Gaborko (1989) found that harbour seals learned tasks based on a spatial component much more easily than tasks based on a visual component. This result suggests that phocids, such as harp seals and harbour seals, may be better able to attend to, remember, or make use of spatial information than visual information. In the present experiment, I explored whether the seals could make use of a change in context (i.e., a switch to a different tank) as a conditional cue to solve a discrimination reversal task. In addition, the seals' ability to formulate a learning set was investigated further. In this case, learning set formation entailed examining the capacity of the harp seals to master a discrimination reversal task.

3.1.1 Learning-set formation

The second type of learning set formation identified by Schusterman (1968) is characterized by improvement across successive discrimination reversals. One such strategy is known as a "win-stay, lose-shift" strategy (Restle, 1958; cited in Mackintosh, 1969). When an animal is presented with a choice between two stimuli, a correct choice followed by reinforcement causes the animal to persist in choosing a particular object, while an incorrect choice causes the animal to convert its responding to the opposite object. Komischke et al (2002) noted that perfect reversal performance using such a strategy would be reflected by only a single error on each reversal.

There is evidence to suggest that certain species do acquire this type of strategy (e.g., chimpanzees, Schusterman, 1962; rhesus monkeys, Warren, 1966; fat-tailed dunnarts, Bonney & Wynne, 2002; mice, Larson & Sieprawska, 2002), while others may not (e.g., cats, Warren, 1966; horses, Sappington, McCall, Coleman, Kuhlers & Lishak, 1997; honeybees, Komischke et al., 2002). However, it is important to note that whether or not any member of a species shows an ability to perform a particular behaviour depends crucially upon how well the details of the task and procedure map onto the sensitivities of the species.

3.1.2 Reversal learning

The reversal task is a commonly used method of assessing animals' ability to form a learning set. The original discrimination phase is the same as a two-choice discrimination task. That is, the animal is presented with two choices (e.g., objects, odours, textures, positions); one is correct and the other is incorrect. The animal is rewarded each time it makes a correct choice, and receives no reward (or, is punished) each time an error is made. The individual learns this discrimination to a set criterion, at which point the reinforcement contingency is reversed. In other words, the animal has to learn to reverse its response to the stimuli, such that S+ becomes S-, and vice versa. This reversal is usually repeated several times. Komischke et al. (2002) suggested that the difficulty with such tasks lies in the fact that animals will often persist in responding to the previously rewarded stimulus (i.e., the original S+). Such negative transfer effects eventually become weaker until responding to the new S+ is consistent (Komischke et al., 2002).

Many early experiments on reversal learning (e.g., Buytendijk, 1930; Dufort, Guttman, & Kimble, 1954; Krechevsky, 1932; Mackintosh, McGonigle, Holgate, & Vanderver, 1968; Theios, 1965) showed that rats are very good at spatial discrimination tasks, and also perform well on visual tasks when the stimuli are simple. It may be useful here to clarify the meaning of a "spatial discrimination". In a two-choice spatial discrimination, the task is characterized by the nature of the required response; that is, the choices differ on a spatial dimension. For example, making a choice based on the relative position of two stimuli, e.g., left versus right, is a spatial discrimination, whereas a visual discrimination may require an animal to correctly choose a black or white panel, regardless of whether it appears to the left or right of the other panel. As noted above, seals have been shown to learn spatial discriminations more easily than other types of discriminations (Renouf & Gaborko, 1988, 1989). Gossette and Brown (1967) trained capuchin monkeys on three types of successive discrimination reversal tasks. The monkeys were assigned to either spatial, form, or brightness problems. Gossette and Brown found that the spatial tasks were the easiest for the monkeys to solve, while the form discriminations were the hardest. Bitterman (1965) reported that both pigeons and rats improve across a series of reversals, whether the discrimination tasks were spatially (e.g., left versus right) or visually (e.g., black versus white) defined. Bitterman (1965) also trained various species of fish to solve both visual and spatial discriminations, and found that fish did not improve across a series of reversals for either type of task. However, Setterington and Bishop (1967) trained African mouthbreeders (*Tilapia* *macrocephala*) for 20 trials a day on a spatial reversal task. After reversing them every day for 80 days, the fish made significantly fewer errors over the course of the experiment. This result suggests that even some fish can form a simple learning set if given enough experience. Ishida and Papini (1997) demonstrated that turtles learned a spatial discrimination task to a criterion of 19/20 consecutive trials correct within an average of 100 trials. Upon reversal of reward contingencies, the turtles learned to switch their response after approximately 200 trials. Gossette and Hombach (1969) demonstrated improvement across successive discrimination reversals on a spatial task in two other reptiles, although the performance of crocodiles was significantly better than that of alligators. Mackintosh and Mackintosh (1963) demonstrated discrimination reversal learning in an octopus.

Mackintosh (1969) pointed out that rats are so proficient at learning discrimination reversal tasks that they can often learn to complete each new reversal with only a single error. Schusterman (1967a) reported a similar result with a sea lion; similarly, Gossette and Cohen (1966) reported that, after 29 reversals, pigeons trained on a spatial reversal task reached near errorless performance. Schusterman (1968) trained two California sea lions on a series of 60 discrimination reversal tasks using visual stimuli (i.e., a black circle and a black triangle with equal surface area). Both subjects committed a large number of errors on the first reversal, but by the second and third reversals, the number of errors decreased considerably. By the fifth reversal, both animals made less than 20 errors before reaching criterion. After 60 reversals, both animals had an average performance of only nine errors to criterion. All of these examples provide evidence for the formation of a learning set for successive discrimination reversals.

3.1.2.1 Reversal Learning as an Interference Paradigm

As Komischke et al. (2002) suggested, transfer effects are thought to interfere with animals' ability to learn discrimination reversal tasks, in that animals will often persist in responding to the previously rewarded stimulus. McDonald, King and Hong (2001) suggested that reversal learning should be considered an interference paradigm, due to the fact that the contextual cues of the training environment during acquisition and reversal stay the same, while the correct stimulus-response association changes. If the context acts a retrieval cue for the correct response in the original training situation, it also re-activates the previously learned response even after the reward contingencies have been reversed (McDonald et al., 2001). Thus, cued memory of the original S+ may interfere with learning the new reversal discrimination. The presence of a conditional cue, in terms of a change in context between learning situations, may help animals to overcome such interference from previously learned associations, and, thus, increase the rate of reversal learning (Chiszar & Spear, 1969; McDonald et al., 2001; Thomas, McKelvie, and Mah, 1985).

3.1.3 Use of Conditional Cues

Conditional control has been demonstrated in various operant situations. In particular, many investigators have shown that animals are capable of using information about the physical context of the test situation in order to solve discrimination reversal problems (e.g., Chiszar & Spear, 1969; McDonald et al, 2001; Thomas et al., 1985). That is, when the solution is contingent on the context, animals can use differences in context as a conditional cue to solve the problem. Differences in context may be spatial, as when acquisition and reversal training take place in different rooms or different locations (e.g., Chiszar & Spear, 1969); they may be visual, as when colour, pattern or brightness cues differ between contexts (e.g., Avery, 1993; McDonald et al., 2001; McDonald & Sutherland, 1992, cited in Avery, 1993). Changes in context may be multimodal, and include visual, auditory, tactual, and/or olfactory elements (e.g., McDonald et al., 2001; Thomas et al., 1985). In addition, some authors have argued that context can even include the time of day that training occurs (e.g., Moron et al., 2002; Pearce & Bouton, 2001).

3.1.3.1 Spatial cues

A spatial cue, by definition, provides information relevant to the determination of one's physical location (Thinus-Blanc, 1996). Cheng and Spetch (1998) suggested that animals use landmarks in order to locate and identify a particular place within their environment. Bingman (1998) noted that landmarks may include visual, auditory, olfactory, and other cues (e.g., changes in magnetism). Thus, a visual cue can also be a spatial cue if it provides useful information about place. A cue is not considered "spatial" if it does not provide information about place.

Many investigators have reported that animals appear to be able to make use of spatial cues more easily than other types of cues (e.g., Chiszar & Spear, 1969; Thomas, McKelvie, & Mah, 1985; Perkins, Lydersen, & Chairez, 1976, Komischke et al. 2001). That is, when, acquisition and reversal occur in two different places, animals appear to solve conditional discriminations more easily than when place does not change, but other contextual cues are provided. Chiszar and Spear (1969) showed that rats could easily learn to turn left in a T-maze in one room, and to turn right in the same maze when tested in a different room, to a criterion of two errorless training days (i.e., 8 consecutive trials correct). In this case, the rats were able to use the room they were in as a conditional cue. In a second experiment, Chiszar and Spear (1969) also showed that rats trained in one T-maze could quickly learn to reverse their response when trained in a slightly different (i.e., larger, with small differences in brightness) T-maze. When placed in the original maze, the rats again reversed their response with an average of less than one error to criterion. In Chiszar and Spear's (1969) experiments, the rats likely used spatial cues such as the contrasting visual (e.g., brightness) and geometric (i.e., size) cues between the two mazes and training locations in order to recognise that they were in two different places.

McDonald et al. (2001) trained rats to obtain a food reward from four randomly lit arms of an eight-arm radial maze. Unlit arms were not baited, and entrance into one of these arms was counted as an error. All rats reached a criterion of 85% choice accuracy. Half of the rats were then exposed to a reward contingency reversal in the same maze in the same training room. That is, the rats were only rewarded for choosing unlit arms. The other half were reversed in an identical maze, but trials took place in a different room (i.e., the original training room had black walls, a yellow plastic pail, and various other visual cues; the second room had white walls, a blue pail, and was a different overall shape than the first room. Music was also played in the second room as an auditory cue). Upon reversal, both groups initially showed below chance performance, suggesting interference from the previously learned reward contingencies. However, after 23 training sessions, the different-context group again reached criterion, while the same-context group failed to reach criterion after 49 training sessions. McDonald et al (2001) concluded that reversal learning was severely inhibited by the original training context for those rats reversed in the same context as acquisition. McDonald et al.'s results further demonstrate the importance of a spatial cue in solving a discrimination reversal task.

McDonald et al. (2001) suggested that the novelty of the reversal context for the different-context rats likely increased exploratory behaviour, which may have acted to distract the animals from the learning task. In a second experiment, McDonald et al (2001) controlled for the effects of the novelty of the situation by giving all rats pre-exposure to both training contexts. When the novel component of the different context was removed, the rats that experienced a switch in context in coincidence with a reversal in reward contingency again required fewer trials to reach criterion than those that did not experience such a switch. This result suggests that, in order to improve reversal learning, the reversal context does not need to be novel, it only needs to be different.

The preceding studies demonstrated that, when a spatial conditional cue is provided, animals consistently learn to solve the problem. In these experiments, the animals always appeared to have either visual or auditory cues, or both, that differed between the two training locations, to help the animals differentiate between them. However, all of these authors have argued that it is the change in location alone that is the essential cue, and that providing a visual or other cue in the absence of a change in place is not as effective as a spatial cue in improving performance on a discrimination reversal task.

3.1.3.2 Non-Spatial Cues

Other authors have demonstrated that a non-spatial conditional cue is not used as readily as a change in location. Both Avery (1993) and McDonald and Sutherland (1992; cited in Avery, 1993) found that rats do not easily learn to reverse a discrimination when non-spatial cues are changed, such as when they are trained in a light versus dark room. For example, Avery (1993) found that, after nine reversals, rats were unable to use time-of-day as a conditional cue to solve a two-choice discrimination involving a left or right response. Since the illumination of the room was altered in accordance with the time of day (on a 12 hr light/dark cycle), this result suggests that the rats in Avery's experiment also failed to use brightness as a conditional cue. Since only nine reversals were carried out in Avery's experiment, it is possible that the rats may have learned to use brightness as a cue to solve the reversal task had more reversals been employed. This result merely demonstrated the difficulty that rats have with using brightness as a conditional cue.

Iversen (1998) demonstrated the ability of rats to perform a conditional discrimination based on a different type of visual cue. Rats were trained to press one of two keys with their nose in order to gain access to a running wheel. When both of the keys were lit with a steady light, the left key was correct; when both keys were blinking, the right key was correct. In either case, pressing the incorrect key extinguished the lights for a 10 s delay, during which the rat was unable to initiate another trial. After approximately 14 sessions (i.e., approximately 280 trials), the rats' performance was above 80% correct. Iversen (1998) then reversed the reward contingencies, such that the left key was correct when the keys were blinking, and the right key was correct when both keys showed a steady light. Performance dropped considerably for all rats, but after approximately 10 sessions with the reversed contingencies, two of the three rats were again performing with 80% accuracy. Iversen demonstrated that rats are capable of learning and adapting to fairly complex operant tasks involving visual cues. However, it is possible that the visual cues were more salient to the rats in Iversen's experiment than in Avery's (1993) experiment, where only the ambient lighting conditions differed. In Iversen's experiment, the required response was directly associated with the visual stimulus; that is, the lit keys were also the choice stimuli, which may have resulted in the rats better attending to them. This finding fits with the notion that rats can learn to use a visual conditional cue, but that they require much training.

There is some evidence to suggest that certain species are also capable of using time-of-day as a conditional cue in order to solve a two-choice discrimination. While Avery (1993) reported a failure of rats to use time-of-day (along with ambient light level) as a conditional cue, (later confirmed by McDonald, Hong, Ray, & Ralph, 2002), Wahl (1932; cited in Gallistel, 1990) demonstrated such an ability in honeybees. The bees were trained to fly to, land on, and enter a feeding beaker on two different tables. In the morning (i.e., between 09:00 and 10:30) the bees were only rewarded at Table A, while in the afternoon (i.e., between 15:30 and 17:00) food was only available at Table B. Wahl found that the bees were much more likely to land on Table A in the morning, while avoiding Table B, and vice versa in the afternoon. In this study, there were likely many other cues available to the bees that covary with time of day. Carr and Wilkie (1997) recently demonstrated that, after approximately 8 weeks of training, rats are capable of learning a conditional discrimination in which the time of day determined which of four levers, if pressed, would result in a food reward. Carr and Wilkie suggested that the rats had learned to use an ordinal timer, in that they learned to make one response on the first trial of the day, and another response on the second trial of the day. Other authors (e.g., Saksida and Wilkie, 1994; Saksida, Wilkie, Samson, & Lee, 1994) have reported that pigeons are capable of using time-of-day as a contextual cue to solve discriminations. Coincidentally, the pigeons also required approximately 8 weeks of training to reach 80% accuracy. This is again consistent with the idea that other cues may be used as conditional cues, but not as easily as spatial cues.

Thomas et al. (1985) trained pigeons inside a Skinner box on a two-choice discrimination reversal task involving several contextual changes, including a visual and an auditory cue. Thomas et al showed that pigeons were capable of learning to respond to one wavelength (555 nm) in the context of a house-light off and white noise, and to respond to a different wavelength (576 nm) when the house-light was on and a tone was present. They also demonstrated, through a series of graded generalization trials, that the pigeons responded most to the lower spectral value (555 nm) when the house light was off and the white noise was present, and also, responded most to the higher spectral value (576 nm) in the presence of the house light and tone. This suggests that the pigeons were attending to the combination of visual and auditory cues, and not simply one or the other. Although the spatial location of training did not change, Thomas et al. (1985) speculated that the pigeons were treating the Skinner box as two different places when the context was altered. Subsequent experiments (e.g., Thomas, Cook, & Terrones, 1990; Thomas, Curran & Russell, 1988; Thomas & Schmidt, 1989; Thomas, Stengel, Sherman, & Woodford, 1987) showed that other stimuli were not as easily used as conditional cues (e.g., changes in the tilt of the floor of the Skinner box), even though they were prominent. It is not clear from these experiments whether the perception of a spatial change (if this interpretation is accurate) constitutes a spatial cue. Nonetheless, a change in contextual cues, whatever the nature of the cues, appears to be of use to animals in solving certain types of discrimination reversal problems.

3.1.4 Cognitive Mapping

It is now widely accepted that animals use information from multiple sensory modalities to create internal representations of their environments (see Gallistel, 1990). This phenomenon was first labelled "cognitive mapping" by Tolman, Ritchie, and Kalish, (1946) and has been documented in countless different species (see Thinus-Blanc, 1996). Gallistel (1990) argued that animals learn associations in the contexts of both time and space, and that these contribute equally to the formation of a cognitive representation of one's environment. In the present experiment, we chose to investigate an aspect of the spatial dimension in terms of its importance to learning specific S-R associations. Previous studies with pinnipeds have suggested that they may be especially well adapted to make use of spatial information (e.g., Kovacs, 1995; Renouf & Gaborko, 1989).

Renouf (1991) suggested that, in the absence of visual and auditory cues, pinnipeds may use speed and other kinaesthetic information to form a cognitive map to which they refer for navigation and orientation. In a captive setting, Renouf and Gaborko

(1989) demonstrated that harbour seals more readily learn discriminations based on a spatial component than those based on a visual component, which suggests that these animals more readily attend to spatial cues than to visual ones. Renouf and Gaborko (1989) suggested that the apparent ease with which the seals learned the spatial tasks compared to the visual tasks might suggest something about the relative importance of such cues to these animals.

3.1.5 The Present Experiment

The ability to use spatial information for navigation is thought to be especially important for harp seals, due to the instability of the pack-ice environment (Kovacs, 1995). Given the instability of cues, harp seals may actually be predisposed to reversal learning. The goal of the present experiment was to demonstrate the usefulness of a spatial contextual cue to the solution of a discrimination reversal problem in harp seals. In the present study, it was hypothesized that harp seals would be able to solve a visual, two-choice discrimination reversal task when the tank they were in was used as a conditional cue. Specifically, I hypothesized that, of the two treatment groups, the group that experienced a switch in tank that coincided with a switch in the reward value of the two stimuli (i.e., a reversal of S+ and S-) would require fewer trials to reach criterion than the group that did not switch between tanks upon S+/S- reversal. The rationale for this hypothesis was that the two tanks provide two different spatial contexts. The seals trained in only a single context are expected to suffer from more interference due to transfer effects, while the presence of a conditional cue is predicted to reduce the effects of interference on the seals that switch between tanks (Komischke et al., 2002; McDonald et al, 2001).

I also hypothesized that an interaction between group and tasks would occur, such that switchers would show more improvement across tasks than controls in terms of a reduction of the number of trials to criterion. This hypothesis was based both on previous research demonstrating the ability of rats (Bitterman, 1965; Buytendijk, 1930; Dufort, Guttman, & Kimble, 1954; Krechevsky, 1932; Mactintosh, 1969; Mackintosh, McGonigle, Holgate, & Vanderver, 1968; Theios, 1965), pigeons (Bitterman, 1965), fish (Setterington & Bishop, 1967), sea lions (Schusterman, 1967, 1968) and harbour seals (Renouf & Gaborko, 1989) to show improvement across a series a similar discrimination tasks, as well as on research demonstrating that a conditiona cue improves performance on learning tasks (Chiszar & Spear, 1969; Iversen, 1998, McDonald et al., 2001; Thomas et al., 1985).

3.2 Method

3.2.1 Subjects

Four of the subjects from Experiment 1 were used: Tyler (158.8 – 176.0 kg, M = 166.9 kg), Jamie (98.2 – 105.3 kg, M = 98.6 kg), Lenny (60.0 – 64.0 kg, M = 62.3 kg), and Deane (37.4 – 38.6 kg, M = 37.9 kg). (Babette was omitted from further testing because she frequently refused to participate, despite not being fed).

3.2.2 Apparatus

3.2.2.1 Training Environment

The training environment remained the same as in Experiment 1.

3.2.2.2 Feeding

All aspects of feeding remained the same as in Experiment 1.

3.2.2.3 Training equipment

The box apparatus, baton, and whistle were used, as in the previous experiment. When the temperature dropped below 0°C, a plastic whistle was used instead of the stainless steel whistle, to prevent the whistle from freezing onto the experimenter's lips.

3.2.2.4 Stimuli

The orange gift bag and the tower used in the sixth discrimination of Experiment 1 were used.

3.2.3 Procedure

3.2.3.1 Training groups

Seals were assigned randomly to groups. The groups were set up as follows: Lenny and Deane were the "switchers" (i.e., the experimental group). For the first discrimination task, Lenny was trained in the little tank, while Deane was trained in the big tank. Both were trained to choose the orange gift bag. Tyler and Jamie were controls. Tyler was trained in the big tank for the entirety of the experiment, while Jamie was trained only in the little tank. Jamie was first trained that "bag" was correct, while Tyler was first trained that "tower" was correct. When Lenny and Deane reached the criterion for the first discrimination task, they were switched to the opposite tank, and trained that "tower" was correct. When the control group reached the criterion, the reward contingencies were switched (i.e., S+ became S-, and vice versa); however, these seals did not switch between tanks.

3.2.3.2 General

The general training procedure remained the same as in Experiment 1, except that seals were only trained when they were in the correct tank for that particular discrimination task. On days when the seals could not be moved to the correct tank for training, they were simply fed their daily ration.

The same criterion was used as in Experiment 1. That is, all seals were trained to a criterion of 18/20 consecutive trials correct, using a running count, which could carry over between training days. Seals also had to reach a minimum criterion of 3 out of 4 correct switches within the 18/20 correct trials.

This experiment began as a continuation of the previous experiment, where the seals learned to discriminate between pairs of objects. As each seal progressed through the series of discrimination tasks, he/she was eventually exposed to the present set of objects. Therefore, this experiment began at different times for different seals, but at the same level of progression, in that all seals had completed the same previous discrimination tasks (i.e., Experiment 1) prior to the start of this experiment. Lenny and Tyler were the first two seals to begin the reversal learning task. Being the first two seals to complete all of the previous tasks, one (Lenny) was chosen to be the first seal in the experimental treatment group (the "switchers") and the other (Tyler) was chosen to be the first seal in the control treatment group. Deane and Jamie were subsequently assigned to the experimental and control conditions, respectively.

3.2.3.3 Reversal Training

A total of six discrimination tasks were carried out. The experimental treatment group, the "switchers", were trained three times in each tank. The control seals were trained six times in the same tank. This meant that all four seals experienced five switches in object value; that is, they learned which object was rewarded, and which was not rewarded, in the first discrimination task (i.e., acquisition), and this value was reversed after each subsequent task. In this way, each object was correct three times, and incorrect three times, for each seal.

3.3 Results

The results support the hypothesis that, of the two treatment groups, the group that experienced a switch in tank that coincided with a switch in the reward value of the two stimuli (i.e., a reversal of S+ and S-) would require fewer trials to reach criterion than the group that did not switch between tanks upon S+/S- reversal.

Table 3.1 shows the means and standard deviations for each of the groups across the six discrimination tasks. (Note that one of the subjects in the control group, Jamie, did not complete the sixth discrimination task). These data are presented graphically in Figure 3.1. Raw scores are provided for each subject in Appendix C, Table C1. Figure 3.2 provides a breakdown of individual performance of the five subjects across discriminations.

A two-tailed t-test carried out on the scores for the first discrimination task determined that the control group (M = 123.50, SE = 10.47) and the experimental group (M = 212.00, SE = 63.00) were performing equally at the onset of the experiment, (t (2) = -1.39, p = .30).

An analysis of variance was performed on the data using the general linear model in order to analyze the effects of treatment group, discrimination task, and their

Table 3.1

Mean Trials to Criterion (+SE) for the Control Versus Experimental Groups for each of the Six Discrimination Tasks in Experiment 2.

	Group			
	Control		Experimental	
Discrimination Task	M	SE	M	SE
1	123.5	10.5	212.0	63.0
2	289.5	72.5	347.0	24.0
3	415.0	26.0	139.0	100.0
4	241.0	9.0	60.5	1.5
5	338.0	219.2	40.5	22.5
6	391.0[a]	-	66.0	46.0

Note: [a] One of the two subjects in this group did not complete the sixth discrimination. Hence, this value is for a single subject. The dash in the table represents an item that could not be calculated because data was available for a single subject only.

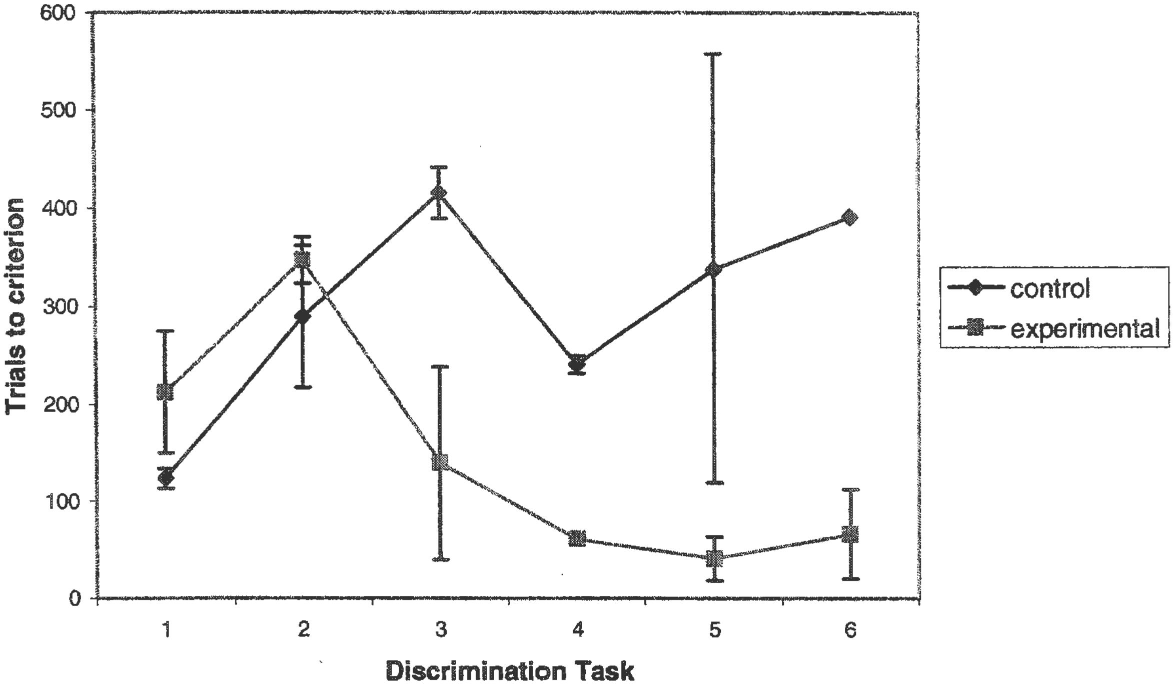


Figure 3.1. Mean trials to criterion (+SE) for the control versus experimental groups for each of the six discrimination tasks in Experiment 2. Note that no error bar can be drawn for the control group on the sixth discrimination because this data is for a single subject.

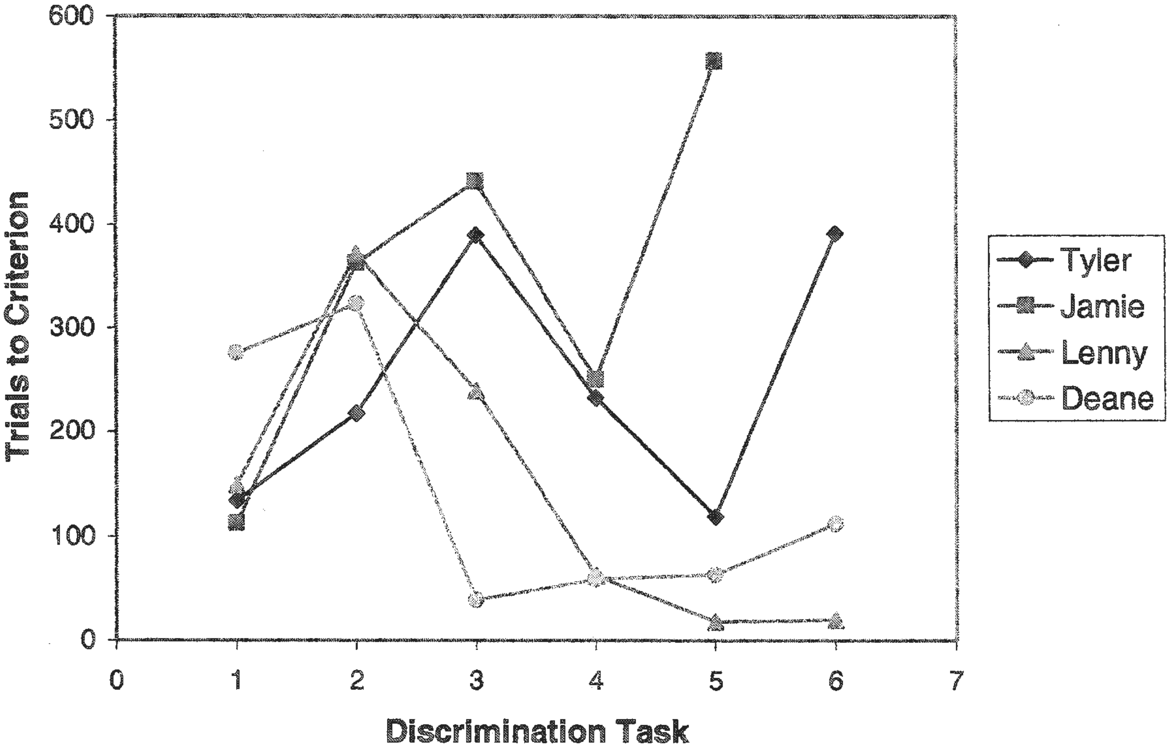


Figure 3.2. Number of trials to criterion for each seal across the six discrimination tasks in Experiment 2. Note that Jamie did not complete the sixth discrimination task.

interaction. (Sums of squares were adjusted to account for the missing data cell in the control group for the sixth discrimination). A significant main effect of treatment group was found (F (1, 11) = 10.34, p = .01). That is, the experimental group required significantly fewer trials (M = 144.20, SE = 36.30) to reach criterion than the control group (M = 291.40, SE = 44.20) across discriminations. There was no effect of discrimination task (F (5, 11) = 1.32, p = .33). This suggests that, when the discriminations are treated as discrete learning experiences (i.e., a categorical variable), the number of trials to criterion did not improve from the first discrimination (M = 167.80, SE = 36.50) to the sixth (M = 174.00, SE = 112.00). The interaction between treatment group and discrimination task did not reach significance (F (5, 11) = 2.45, p = .10).

3.4 Discussion

The results show that the control group required significantly more trials to solve the six discriminations tasks than the experimental group. As predicted, the seals that experienced a switch in the reward value of the two stimuli (i.e., a reversal of S+ and S-) that coincided with a switch in tank required significantly fewer trials to reach criterion than the group that did not switch between tanks upon S+/S- reversal.

The results of Experiment 2 show that performance on a discrimination reversal task will improve when animals are provided with a conditional cue, i.e., a change in context. These results support the findings of McDonald et al. (2001), in that a change in context allowed the subjects to solve the problem in fewer trials than when reversal took place in the same context. McDonald et al. (2001) suggested that reversal learning is severely inhibited by the original training context for animals reversed in the same context as acquisition.

A significant main effect of treatment group was observed. This means that, overall, the performance of the two groups differed. In the first discrimination task, neither group had experienced a reversal; performance was equivalent between the two groups. Upon reversal, i.e., the second discrimination, both groups showed an increase in the number of trials to criterion (see Figure 3.1) due to an increase in the number of errors. Other investigators have reported that animals typically make many errors during the first few reversals (e.g., Iversen, 1998; McDonald et al., 2001; Schusterman, 1968). By the third and fourth discriminations, a difference began to emerge between the two treatment groups. It appears that, as trials progressed, the experimental group learned to use the tank they were in as a conditional cue to solve the problem, and, thus, began to make fewer errors, while the control group continued to perform at or below chance when presented with each new reversal. While the interaction failed to reach statistical significance, it is important to keep in mind that the two treatment groups each had $n = 2$ subjects. In Figure 3.1, it appears that a trend toward an interaction is present, in that both groups performed equally at the outset, but begin to diverge across tasks. This pattern was expected, given that it was predicted that the experimental group would improve more over tasks than the control group. Note that, within the switchers group, Lenny showed a clear pattern of improvement across tasks, whereas Deane's data show a lot of variation. (See Figure 3.2).

Of secondary importance was the finding that, overall, the four harp seals' performance did not show improvement across tasks (as evidenced by the non-significant main effect of task). This study has low power due to the small number of subjects. This may be one reason why the results of the present experiment do not correspond with the findings of many other investigators, who have shown that rats (Bitterman, 1965; Buytendijk, 1930; Dufort, Guttman, & Kimble, 1954; Krechevsky, 1932; Mactintosh, 1969; Mackintosh, McGonigle, Holgate, & Vanderver, 1968; Theios, 1965;), pigeons (Bitterman, 1965), fish (Setterington & Bishop, 1967), sea lions (Schusterman, 1967a, 1968) and harbour seals (Renouf & Gaborko, 1989) show improvement across a series a reversals. However, this result was not surprising, given that the harp seals in the present experiment experienced only five reversals. The studies listed above demonstrated that, with many reversals, these animals show improvement.

One possible explanation for the lack of improvement is that there were not enough reversals carried out in order for the seals to learn a "win-stay, lose-shift" strategy. In earlier studies, animals experienced many reversals of reward contingencies. In one experiment, Setterington and Bishop (1967) reported that mouthbreeders find reversal tasks very difficult; but, after experiencing 80 reversals, they showed significant improvement. Similarly, Slotnick et al. (2000) showed that when rats were given enough prior experience at solving discrimination tasks, they showed improvement in terms of above-chance performance on novel discriminations. In the present experiment, five reversals may not have been enough for the seals to form a learning set in order to solve the problem. While the experimental group (the "switched" seals) did show improvement, this was arguably attributable to the change in context. The control seals clearly did not adopt a win-stay, lose-shift strategy, as has been demonstrated in other species (Bonney & Wynne, 2002; Larson & Sieprawska, 2002; Schusterman, 1962; Warren, 1966). Again, if more reversals had been employed, some improvement may have occurred in the controls as well as the switchers. In the six tasks (i.e., acquisition, plus five reversals) only one animal (Lenny) reached near errorless performance. Lenny performed errorlessly on the fourth reversal (18/18 trials correct), and made only two errors on the fifth reversal. While Deane's performance also improved across the successive reversals, she had not achieved a level of errorless performance by the fifth reversal. This would suggest that individual differences likely play a role in the speed of acquisition of learning strategies. Had more reversals been employed, Deane's performance would have likely continued to improve. In the future, studies of reversal learning in harp seals will require a greater number of reversals in order to determine whether they are capable of learning a win-stay, lose-shift strategy.

The fact that the experimental group continued to make errors despite a change in context suggests that these seals still suffered from interference from previously learned associations (McDonald et al., 2001). This phenomenon was even more evident in the control group than the experimental group.

The results of the present experiment offer further support for the notion that spatial information is of special importance to harp seals. Had the seals been unable to use "place" as a conditional cue, those that switched between tanks in concordance with reversals in reward contingency would not have shown improvement across tasks compared to those that did not have the benefit of a contextual change. This result is consistent with the findings of other investigators, who have shown that location is an important conditional cue (e.g., Chiszar & Spear, 1969; Komischke et al., 2002; McDonald et al., 2001; Thomas et al., 1985). These results provide a starting point from which more specific questions about the harp seal's spatial abilities can be investigated.

Chapter 4: Summary

Experiment 1 demonstrated that harp seals can solve two-choice visual discriminations, and that they can use previously learned object valence to solve new tasks involving previously reinforced or unreinforced stimuli more quickly than completely novel stimuli. This result is consistent with those of other investigators who have shown similar learning transfer in other species (e.g., squirrel monkeys, Klüver, 1933; chickens, Lashley, 1916). Alternative explanations for the superior performance on the known valence tasks in Experiment 1 (e.g., practice effects), do not seem to account for the data. In Experiment 2, harp seals used the tank they were in as a conditional cue to solve a discrimination reversal task. The results of Experiment 2 provide support for the notion that spatial information may be of special importance to harp seals. Had the seals been unable to use "place" as a conditional cue, those that switched between tanks in concordance with reversals in reward contingency would not have reached criterion on the discrimination reversals faster than those that did not have the benefit of a tank change on successive discrimination reversals. Thus, the spatial component of the task appears to be important, which is consistent both with the observation that spatial cues are more easily used relative to other cues (e.g., Chiszar & Spear, 1969; Perkins, Lydersen, & Chairez, 1976; Renouf & Gaborko, 1988, 1989; Thomas et al., 1985), as well as the data that show that seals are sensitive to spatial information (Renouf & Gaborko, 1988, 1989).

4.1 Learning Set Formation

As identified by Schusterman (1968), the potential existed for two types of "learning to learn" in these experiments. That is, in Experiment 1, the potential existed for the seals to show improvement across a series of two-choice discriminations. In Experiment 2, the potential existed for the seals to improve across successive discrimination reversals. In Experiment 1, while no significant difference was found between D+/D- and the first two novel discriminations, there appeared to be a trend toward improvement across tasks, as can be seen in Figure 2.7. Schusterman (1968) previously demonstrated that at least two other pinniped species, California sea lions and harbour seals, are capable of forming a learning set for two-choice discriminations. (However, see Renouf & Gaborko, 1988 and 1989, for examples of the difficulty harbour seals have solving successive visual discrimination tasks). The development of a learning set has also been demonstrated in other species, such as rats (Slotnick et al, 2002), sea lions (Schusterman, 1967a), monkeys (Schusterman, 1962), and chickens (Révész, 1924). In Experiment 2, the harp seals showed more improvement across a series of reversal tasks when a conditional cue was provided than when no cue was provided. This result suggests that the harp seals in the present experiment did not "learn to learn" how to solve a series of reversal tasks by adopting a strategy such as "win-stay, lose-shift". Had the seals learned such a strategy, the control group in Experiment 2 should have switched their response each time the reward contingencies were reversed at approximately the same rate as the experimental group. However, one could argue that Lenny did appear to have acquired such a strategy in that, by the fifth task, he reversed his response with no errors, and only one error at the beginning of the sixth task. As was predicted, the seals were able to use tank as a conditional cue to solve the reversal task.

The data from both Experiments 1 and 2 indicate that the valence of stimuli is important. Experiment 1 demonstrated that consistency in object valence improved performance on successive discriminations. Experiment 2 demonstrated that reversing the valence impeded performance when not cued by a switch to a different tank. Had the seals been employing a learning strategy that did not involve the use of object valences in Experiment 1, their performance should not have been affected by the reversals in Experiment 2. That is, if they were treating each task as completely novel, they should not have suffered from interference from previously learned associations. Also, had the harp seals simply formed a learning set for two-choice visual discriminations, the number of trials to criterion should have decreased across tasks all the way through from the first task of Experiment 1 to the final task of Experiment 2 (i.e., a total of 11 discriminations), and this did not happen.

4.2 Multiple Interpretations of Trends

In Experiment 1, the statistical analysis revealed that the final novel task, D+/D-, did not differ significantly from the initial two novel tasks, A+/A- and B+/B-, but did differ significantly from A+/B-. However Figure 3.1 does appear to show considerable differences in the means of the three novel tasks, despite the non-significant result. In addition, the final task does not appear to be as different from the three preceding tasks as the statistics would suggest. My aim is not to contradict the results of the statistical analyses, but merely to point out that caution is necessary in their interpretation, given that $n = 4$.

There are several explanations for the trends observed in the means in Figure 3.1. For example, the increase in trials required on the sixth task may have been due to the fact that it involved two novel objects, and was, therefore, more difficult than the three previous tasks involving either one or two familiar objects (i.e., objects with which the seals were thought to have previously come to associate a valence, S+ or S-). The results confirmed that it was more difficult than the third task, which involved two familiar objects. Such an interpretation would support the notion that harp seals are able to use object valence in order to solve tasks involving familiar objects. However, at this point, the true cause of this trend remains unknown. It may have been that the seals performed better during the particular weather conditions or season experienced during training of the third, fourth, and fifth tasks. This is unlikely, because the dates on which each seal was trained on each task varied considerably between seals. For example, while Lenny completed Experiment 2 between September 11 and October 21, 2002, Jamie did not begin Experiment 2 until October 23, and did not finish until January 17, 2003. It may have been that the seals were treating each of the tasks as completely novel, but that some pairs of objects were more dissimilar, and easier to differentiate, than others. I noted earlier that the first discrimination was likely a difficult one; however, I do not know whether the seals perceived the sixth discrimination task as more difficult than the three preceding tasks, which would also account for the increased number of trials required to solve this task.

Deane appears to have a story all her own. Her data do not appear to fit with those of the other seals, which likely contributed to the high variance and non-significant results. Deane was a young pup when the study started. She had less pretraining experience than the other seals, and it was possible that her limited experience made her more susceptible to distraction by the other seals. It is also possible that, as a juvenile, her motivations differed from that of the adults in that she may have been more inclined to engage in play behaviour, rather than purely hunger-motivated behaviour.

Although, statistically, the three novel tasks do not differ, it is apparent from Figure 3.1 that there is at least a trend toward improvement. The cause of this trend is difficult to determine. It is possible that this trend towards improvement was real, and may be the result of the seals beginning to form a learning set for two-choice discriminations. It may have also been an artefact of the stimulus pairs, in that they may have simply become increasingly differentiable. In the future, counterbalancing the stimulus order, and increasing the numbers of subjects and of reversals, may provide clearer evidence that seals do learn to learn.

The findings from Experiment 1 indicate that harp seals are able to use learned object valence to solve subsequent problems in fewer trials. When this information is in conflict with the correct solution to the problem, as with the reversal tasks in Experiment 2, having this information appeared to make the problem more difficult. This is true across discriminations for the control group in Experiment 2, because learned object valence was the only information they had. This result is consistent with the observations of McDonald et al. (2001), who also reported that interference occurs on reversal tasks when the context does not change. Other researchers have also reported that animals solve reversal problems more easily when the context changes between reversals (e.g., Chiszar & Spear, 1969; Komischke et al. 2002; Thomas et al, 1985). It appears that context may have acted as a retrieval cue for the previously learned choice behaviour. On the other hand, the seals in the experimental group were able to learn to use contextual information about the tank they were in to solve the problem, despite conflicting information about the previously learned object valences.

4.3 Evidence for the Importance of Spatial Cues

Experiment 2 showed that changing tanks supported discriminative reversals. A number of factors could produce this result, e.g., spatial, visual, mechanosensory, or other properties of the experimental environment. The paradigm employed throughout this study allows further examination of these other cues.

While the contexts of the two tasks were different spatially, the visual cues associated with each tank may not have been highly discriminable or salient to the seals, which likely made the task of differentiating between the two physical locations more difficult. The fact that the seals were able to differentiate between the two tanks provides further evidence for the salience of a spatial cue, as the seals were able to use tank location as a cue, despite similarities in visual, auditory, and olfactory cues between tanks. It is also likely that the seals were aware of the size differences between the two tanks, and used this cue to help them differentiate between them. In future studies, it may be useful to alter the contexts for the experimental group in other ways. For example, the experimenter could train the seals to perform one discrimination in the tank, and reverse the discrimination on land. It may also be possible to design an apparatus that could be sunk to the bottom of the tank, such that the seals could be trained both at the bottom of the tank and at the surface. To test for tank size as a cue, it may be possible to keep the location of training constant, while altering the size of the tank, e.g., by inserting a hollow cylinder vertically into the tank to decrease the volume. These types of discriminations based on physical context may help us to better understand what constitutes a "place" for a harp seal, by determining what types of changes in context are more salient, and thus, result in faster reversal learning.

The importance of modality needs to be considered further, not only in determining the type of cue, but also, the nature of the discrimination task. There is ample evidence to suggest that animals generally find spatial tasks easier to solve than visual ones. The harp seals in the present experiment clearly experienced difficulty in solving a visual task; recall that they each required between approximately 200 and 1000 trials to solve the first discrimination task alone. This finding is consistent with that of Lavigne and Ronald (1972a), who reported that it took a harp seal three months to learn a two-choice visual discrimination. Thus, perhaps the harp seals would have shown more improvement had the discrimination task itself been spatial instead of visual. Herman, Hovancik, Gory, and Bradshaw (1989) noted that certain cognitive skills might be restricted to the dominant sensory modality of the species being tested. This means that performance on comparable tasks experienced through different modalities would likely produce non-equivalent results. Thus, given their apparent difficulty with solving visual discrimination tasks, it is likely that the visual modality is not the dominant one for harp seals. That being said, the question of the dominant modality of harp seals is left open to be examined further in the future.

Another factor that may have affected the seals' absolute performance across experiments was that they were already familiar with the contexts, i.e., the two tanks. All of the seals in the present experiment were abundantly familiar with all aspects of the training environment, especially the two tanks. Even the youngest, Deane, had lived in the compound for approximately four months prior to the start of Experiment 1. While the present study did not evaluate context familiarity, it may be an important factor in determining the absolute performance of the seals in Experiments 1 and 2. Mackintosh (1983) suggested that animals will learn a difficult discrimination task more quickly in a familiar context than a novel one simply because they are not as distracted. However, that does not mean that they ignore the contextual cues or are not aware of them. Similarly, McDonald et al. (2001) argued that, in addition to learning a simple stimulus-response sequence, animals also use the context of that learning as a retrieval cue. In Experiment 1, the solution was the same regardless of the tank a subject was in. Since the seals frequently moved between tanks, they all experienced training on each pair of stimuli in both tanks. Therefore, the most likely scenario is that, as McDonald et al. (2001) suggested, both training contexts, i.e., the two tanks, acted as retrieval cues for the correct response. That is, when being trained on the various S+/S- pairs, the seals learned the association between each tank and the correct choice (S+) for each pair. In Experiment 1, the correct response for each pair just happened to be the same in each tank. In

Experiment 2, the seals had experienced a training situation similar to that of Experiment 1 (i.e., a two-choice visual discrimination using the same two boxes within the same training environment), except that, in this situation, the two tanks may have acted as retrieval cues for the responses to two different stimuli (i.e., the S+ was not the same in each tank). It is plausible that the seals had simply learned that location was irrelevant to the task in Experiment 1. However, based on McDonald et al's findings, it is likely that the seals had not learned to ignore tank as a conditional cue in Experiment 1; they would have simply learned two new associations when presented with the two novel stimuli in Experiment 2. Again, the fact that the harp seals were able to attend to tank location as a cue despite any effects of previous experience in each context further demonstrates that harp seals may be sensitive to spatial cues.

4.4 Spatial Sensitivity as an Adaptation

Given that feral harp seals spend the majority of their lives in arctic and subarctic ecosystems (Vikingsson & Kapel, 2000), which includes the North Atlantic and Arctic ice floes, their visual environment is, for the most part, constantly changing in an unpredictable way. Harp seals are associated with an environment that consists of ice pans, icebergs, open water, and little else. For this reason, Kovacs (1995) suggested that harp seals may have an enhanced sensitivity to small changes in spatial cues (e.g., configurations of solid ice forms and open water), and may frequently adjust their spatial map to account for such changes. Because visual cues may not be reliable in that they are not constant, it may be of critical importance for harp seals to have a keen spatial sense, which would allow them to navigate despite conflicting or changing visual cues. For example, it would be crucial for an individual to remember and be able to locate the breathing hole from which it entered the water (Lydersen & Kovacs, 1993). In addition, pup survival most certainly depends on the ability of harp seal mothers to relocate their pre-weanling pups in order to nurse them and protect them from predators (Kovacs, 1995).

Similarly, an effective forager would likely alter its diving depth in accordance with the location where the most prey can be found (Schreer, Kovacs, & Hines, 2001). This location or depth would most certainly differ between Arctic regions and the Grand Banks, for example. On this larger scale, it is not only important for harp seals to know where they are at the surface relative to the ocean floor, but also, to have a sense of where they are in terms of longitude and latitude. This knowledge would likely correspond to making different choices about the direction and distance an individual would travel in order to find prey. Harp seals likely encounter these types of conditional problems frequently in their natural habitat, which may provide them with many opportunities to make use of spatial cues. Thus, further study may help us to better understand the adaptiveness of a keen spatial sense to harp seals.

4.5 Generalization from A Captive Population

An assumption that has to be made before these results can be generalized is that the performance of the harp seals in the present study is representative of the entire harp seal population, and that the observed variation is not a product of the captive environment. Unfortunately, this is impossible to determine. Because of the limited number of subjects per group, it is impossible to calculate the amount of error variance due to individual variation. That is, there are simply not enough degrees of freedom to consider "seal" as an additional factor in the equation. Thus, while the results of Experiment 2 do show significant improvement in the seals' performance when a conditional cue was provided, the actual applicability of this study in terms of generalization to a larger population is extremely limited. Because of this, the current study must be viewed more in terms of being a guide for future research.

Captive harp seals, especially those born and raised in captivity (as were three of the subjects in the current study; a fourth was captured at approximately 2 weeks of age), likely have access to very different visual and spatial environments than feral seals. In addition, their physical environment is stable, and, therefore, provides reliable visual and spatial cues. It is difficult to say whether the visual environment available to the captive harp seals in the present study is more or less enriched than that experienced by feral harp seals in their natural environment. Captive harp seals are limited to the consistent stimuli present in their compound. However, they do frequently experience interactions with humans, other animals (such as sea gulls), and, throughout the course of the present study, various contrived materials. Wild seals, on the other hand, face a visual landscape that changes on a daily basis. They encounter both familiar and novel conspecifics, other marine mammals, birds, and fish, as well as humans and various marine craft. During their yearly migration, they cover thousands of kilometres, and are, at least infrequently, close enough to land to gain some visual stimulation other than that provided by the vast seas of ice and open water. Because the captive harp seals are confined to a very small area, the spatial environment of these seals is arguably very limited compared to that of feral harp seals. One may argue that in such a physically small environment, visual cues may suffice for navigation.

In the present study, a comparison between the performances of the captive-raised seals with that of Babette (who had lived as a feral seal for approximately ten years prior to capture) was not possible. While Babette consistently required slightly more trials to solve each of the tasks in Experiment 1 than the other seals, Figure 2.7 shows that her scores did not differ from the others' in that they did not significantly alter the means. Also, Babette did not complete Experiment 2, which precludes any comparison of her use of contextual cues. Babette's difficulty with Experiment 1, and her refusal to participate in Experiment 2, may have stemmed from diminished capacities as a result of her age. Also, Babette tended to show more aggressive behaviours, as well as less tolerance for human interaction (which likely resulted from her maturation as a feral seal prior to capture), which made her less amenable to training.

It is possible to conclude that the captive harp seals in the present study are considerably impoverished in their level of visual and spatial stimulation in comparison to the vast potential for such stimulation in their natural habitat. However, despite these limitations, the findings suggest that captive harp seals can use tanks as conditional cues, and that this may indicate their sensitivity to spatial cues.

4.6 Recommendations for Future Research

The most obvious problem with the current study is the small sample size. If I were to repeat this experiment, I would require at least three subjects in each group so that within-subjects error variance could be calculated. An alternative solution would be to replicate Experiment 2, but expose each harp seal to both conditions. However, the number of subjects used in the present study meets or exceeds that of the experiments of various other investigators in the field of pinniped research (e.g., Schusterman and colleagues, Dehnhardt and colleagues, Lavigne and Ronald, Renouf and Gaborko, etc.). Typically, only one or two subjects have been employed in studies involving captive pinnipeds, which highlights the contribution of the present study to pinniped research. In line with other pinniped learning studies, I would also like to increase the number of discrimination tasks and reversal tasks to which the seals are exposed. This would give a clearer indication of whether seals are capable of learning set formation.

In a study similar to the present one, Renouf and Gaborko (1988) reported that harbour seals were difficult to motivate and failed to reach criterion on several successive days simply because they lost interest or appetite prior to completing a training session. These authors suggested that it would be advisable to use a less strict criterion in this species, and also, that rate of learning (i.e., number of trials to criterion) may not be the best way to measure their ability to transfer learning strategies or concepts to new tasks. This advice may well be applicable to harp seals. In the present study, the seals sometimes suffered from loss of interest or appetite, which may have lowered their performance on later trials within a session prior to the session being aborted. This lack of motivation may also explain some of the individual differences in performance that were observed. While Babette often became frustrated, her performance was reliable in that she would immediately refuse to participate. On the other hand, Deane or Jamie would often attempt to continue to participate in the training by touching the baton and then the boxes, while not accepting the fish reward. In this situation, it may have been that the seals were motivated by the desire to play rather than by the desire to choose correctly in order to receive a food reinforcement. This behaviour was more common to the two youngest seals (Deane and Lenny), but even Tyler sometimes reacted playfully during training, suggesting that the differences may not have been specifically age-related. Even when the seals were hungry, they still had "good days" and "bad days" in terms of their level of attention and cooperation.

While the exact number of pre-training trials was not recorded, it may be of interest to note that Deane required 10 days of pre-training before learning to choose on her own, while the other seals each began to choose on his or her own within one pre-training session, and often, within only a few trials of being led to the correct box. It was clear that Deane did not learn to choose at the same rate as the others. When she touched the baton and the whistle was blown, instead of swimming to touch a box like the others, she would remain at the baton, become frustrated, and bite it. Since Deane was born during the later pilot studies, she was the only seal who did not experience previous training on a two-choice visual discrimination (as described in Appendix A, 2D Discriminations). Thus, having this previous experience on a two-choice discrimination, even though the apparatus and stimuli used were very different, may have helped the other four seals to learn the present training protocol more easily. Another interesting fact is that Deane solved the first discrimination in the fewest number of trials. By the time she had learned to choose on her own, she had already been rewarded many times for touching the box containing the red ball, which may have made this discrimination easier once she learned to choose. In the future, it may be worthwhile to examine the effect of number of pre-training trials received on later choice performance more closely. While impossible in the present study, it is also recommended that, in the future, each subject be exposed to exactly the same training techniques and/or pilot studies, to control for any effects of prior experience.

In future studies, I would recommend that the number of overtraining trials be examined, or eliminated altogether, as this additional experience on any particular discrimination may have later affected the ease with which the harp seals learned subsequent discriminations. In the present experiments, no systematic study of overtraining was carried out, and its effects are impossible to evaluate. The seals received a random number of unrecorded overtraining trials based on the number of pieces of fish they had left after they had reached criterion. There was no apparent improvement in performance on subsequent discriminations following overtraining on previous discriminations (personal observation). Ischida and Papini (1997) reported that turtles that experienced 100 trials of overtraining after reaching a criterion of 19/20 on a spatial discrimination task performed significantly better on a subsequent reversal than turtles that were not given any additional trials after reaching criterion. Mackintosh (1983) explained that overtraining likely enhances the associability of the relevant stimuli, which makes the reversal more apparent when the contingencies change. Thus, in future investigations, it would be wise to either eliminate, equalize, or experimentally manipulate, the number of overtraining trials each subject receives.

Another consideration that lends itself to further investigation is that, in the present experiment, the seals were not permitted to view the objects from below. Since Hobson (1966) suggested that feral pinnipeds view objects in the water from below in order to identify the silhouette while remaining undetected, this may be a preferred method for the seals to view and discriminate between objects. Investigators have previously demonstrated the ability of other pinnipeds, such as sea lions and harbour seals, to perform underwater visual discriminations (e.g., Schusterman, 1968). The reason the seals were not permitted to view the objects from below in the present experiment was a purely methodological one. The seals often swam underneath the boxes and touched them which their backs or stomachs, etc. It would have been much more difficult to define a "choice" if the seals were permitted to choose while underwater, because it was very difficult to determine whether the seals were actually looking at the objects. Also, it was not known whether the seals could easily hear the whistle from beneath the surface, which signalled the correct behaviour. However, given their ability to detect tones underwater (e.g., Terhune & Ronald, 1972b), hearing the whistle likely would not have been a problem.

4.7 Conclusion

In conclusion, the results of the present study highlight the potential for further exploration of the importance of spatial cues to harp seals. In addition to speculation based on field observations (e.g., Bowen's, 1991, and Kovacs', 1987, 1995, observations that harp seal females are very good at finding and recognizing their pups despite a lack of visual or auditory cues), these findings add to the current knowledge base in that there is now some experimental evidence that harp seals are sensitive to spatial cues. This finding is consistent with reports that many other species (e.g., harbour seals, Renouf & Gaborko, 1988, 1989; rats, Chiszar & Spear, 1969; and pigeons, Thomas et al., 1985) more easily use spatial cues to solve learning problems than they do other types of cues. The harp seal's ability to navigate in the pack ice environment further suggests that they are highly sensitive to small changes in spatial cues (Kovacs, 1995). Clearly, the sensitivity to spatial cues that harp seals appear to possess warrants further investigation.

References

Avery, S. (1993). *Rat's failure to use time-of-day in a conditional discrimination task.* Unpublished honours thesis, Memorial University of Newfoundland, St. John's.

Bardach, J. E., Todd, J. H., & Crickmer, R. (1967). Orientation by taste in fish by the genus *Ictalurus*. *Science, 155*, 1276-1278.

Bartholomew, G. A. (1952). Reproductive and social behavior of the northern elephant seal. *University of California Berkeley Publication of Zoology, 47*, 369-471.

Bitterman, M. E. (1965). Phyletic differences in learning. *American Psychology, 20,* 396-410.

Bingman, V. P. (1998). Spatial representations and homing pigeon navigation. In S. Healy (Ed.) *Spatial representation in animals* (pp. 69-85). New York: Oxford University Press.

Bonner, W. N. (1968). The fur seal of South Georgia. *British Antarctic Survey Science Report, 56*, 81.

Bonney, K. R., & Wynne, C. D. L. (2002). Visual discrimination learning and strategy behavior in the fat-tailed dunnarts (*Sminthopsis crassicaudata*). *Journal of Comparative Psychology, 116*, 55-62.

Bowen, W. D. (1991). Behavioural ecology of pinniped neonates. In D. Renouf (Ed.), *Behaviour of pinnipeds* (pp. 66-127). New York: Chapman and Hall.

Buytendijk, F. J. J. (1930). Uber das Umlernen. *Archiv Neerl Physiologie 15*, 283-310.

Carlstead, K., Seidensticker, J., & Baldwin, R. (1991). Environmental enrichment for zoo bears. *Zoo Biology, 10*, 3-16.

Carr, J. A. R., & Wilkie, D. M. (1997). Rats use an ordinal timer in a daily time-place learning task, Journal of Experimental Psychology: *Animal Behavior Processes, 23*, 232-247.

Carr, S. M., & Perry, E.A. (1997). Intra- and interfamilial systematic relationships of phocid seals as indicated by mitochondrial DNA sequences. In A. E. Dizon, S. J. Chivers, and W. F. Perrin (Eds.). *Molecular Genetics of Marine Mammal*, Special Publication No.3 (pp. 277-290). Lawrence, KS: Society for Marine Mammalogy.

Cheng, K. & Spetch, M. L. (1998). Mechanisms of landmark use in mammals and birds. In S. Healy (Ed.) *Spatial representation in animals* (pp. 1-17). New York: Oxford University Press.

Chiszar, D. A. & Spear, N. E. (1969). Stimulus change, reversal learning, and retention in the rat. *Journal of Comparative and Physiological Psychology, 69*, 190-195.

Colombo, M. & D'Amato, M. R. (1986). A comparison of visual and auditory short-term memory in monkeys (*Cebus apella*). *Quarterly Journal of Experimental Psychology, 38B*, 425-448.

Davis, R.W., Fuiman, L.A., Williams, T.M., Collier, S.O., Hagey, W.P., Kanatous, S.B., Kohin, S., & Horning, M. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast ice, *Science, 283*, 993-996.

Dehnhardt, G. (1990). Preliminary results from psychophysical studies on the tactile sensitivity in marine mammals. *Acta Physiol. Scand., 135*, 405-410.

Dehnhardt, G. (1994). Tactile size discrimination by a California sea lion (*Zalophus californianus*) using its mystacial vibrissae. *Journal of Comparative Physiology A, 175*, 791-800.

Dehnhardt, G. & Kaminski, A. (1995). Sensitivity of the mystacial vibrissae of harbour seals (Phoca vitulina) for size differences of actively touched objects, *The Journal of Experimental Biology, 198,* 2317-2323.

Dehnhardt, G., Mauck, B., & Bleckmann, H. (1998). Seal whiskers detect water movements, *Nature, 394*, 235-236.

Dehnhardt, G., Mauck, B., & Hyvarinen, H. (1998). Ambient temperature does not affect the tactile sensitivity of mystacial vibrissae in harbour seals, *The Journal of Experimental Biology, 201,* 3023-3029.

DiGello, E., Brown, M. F. & Affuso, J. (2002). Negative information: Both presence and absence of spatial pattern elements guide rats' spatial choices, *Psychonomic Bulletin & Review, 9*, 706-713.

Drickamer, L. C., & Vessey, S. H. (1992). *Animal Behavior: Mechanisms, ecology, and evolution.* Dubuque, Iowa : Wm. C. Brown Publishers.

Dufort, R. H., Guttman, N. & Kimble, G. A. (1954). One-trial discrimination reversal in the white rat. *Journal of Comparative and Physiological Psychology, 47*, 248-249.

Gallistel, C. R. (1990). *The Organization of Learning*. Palatino: Massachusetts Institute of Technology.

Gentry, R. L. (1970). *Social behavior of the Steller sea lion*. PhD. Thesis, University of California, Santa Cruz.

Gentry, R. L. (1975). Social behavior of eared seals. *Rapports et Proces-Verbaux des Reunions. Conseil International pour l'Exploration de la Mer*, *169*, 189-194.

Gilbert, R. M., & Sutherland, N. S. (1969). *Animal discrimination learning*. London: Academic Press.

Gisiner, R. & Schusterman, R. J. (1991). California sea lion pups play an active role in reunions with their mothers. *Animal Behaviour, 41*, 364-366.

Goldblatt, A. (1993). Behavioural needs of captive marine mammals. *Aquatic Mammals, 19*, 149-157.

Gossette, R. L., & Brown, H. R. (1967) The scaling of relative task difficulty across spatial, brightness, and form successive discrimination reversal (SDR) problems with capuchin monkeys. *Psychonomic Science*, *9*, 1-2.

Gossette, R. L., & Cohen, H. (1966). Error reduction by pigeons on a spatial successive reversal task under conditions of non-correction *Psychological Reports. 18,* 367-370.

Gossette, R. L., & Hombach, A. (1969). Successive discrimination reversal (SDR) performances of American alligators and American crocodiles on a spatial task *Perceptual & Motor Skills. 28,* 63-67.

Grindrod, J.A.E., & Cleaver, J.A. (2001). Environmental enrichment reduces the performance of stereotypic circling behaviour in captive common seals (*Phoca vitulina*), *Animal Welfare, 10,* 53-63.

Hanggi, E. B., & Schusterman, R. J. (1990). Kin recognition in captive California sea lions (*Zalophus californianus*). *Journal of Comparative Psychology, 104*, 368-372.

Hanlan, S. K. (1998). Nosing Behaviour in Captive Harbour Seals (*Phoca vitulina concolor*): Implications for Olfaction and Affiliation. Unpublished M. Sc. thesis, Biopsychology Programme, Memorial University.

Harlow, H. F. (1949). The formation of learning sets. *Psychological Review, 56*, 51-65.

Herman, L.M., Hovancik, J. R., Gory, J. D., & Bradshaw, G. L. (1989). Genrealization of visual matching by a bottlenosed dolphin (*Tursiops truncatus*): Evidence for invariance of cognitive performance with visual and auditory materials, *Journal of Experimental Psychology: Animal Behavior Processes, 15*, 124-136.

Higgins, L.V., and Gass, L. (1993). Birth to weanling: parturition, duration of lactation, and attendance cycles of Australian sea lions (*Neophoca cinerea*), *Canadian Journal of Zoology, 71*, 2047-2055.

Hobson, E. S. (1966). Visual orientation and feeding in seals and sea lions, *Nature, 210*, 326-327.

Honig, W.K. (1969). Attentional factors governing the slope of the generalization Gradient, In R. M. Gilbert and N.S. Sutherland (Eds.) *Animal Discrimination Learning* (pp. 35-62). London: Academic Press.

Ishida, M. and Papini, M. R. (1997). Massed-trial overtraining effects on extinction and reversal performance in turtles (*Geoclemys reevesii*). *The Quarterly Journal of Experimental Psychology, 50B*, 1-16.

Iversen, I. H. (1998). Simple and conditional visual discrimination with wheel running as reinforcement in rats. *Journal of the Experimental Analysis of Behaviour, 70,* 103-121.

Kapel, F.O. (1995). Feeding ecology of harp and hooded seals in the Davis Strait – Baffin Bay region. In A.S. Blix, O. Ultang, and L. Walloe (Eds.) *Seals, whales, fish and man* (pp. 287-304). London: Elsevier Science.

Kastak, D., & Schusterman, R. J. (1994). Transfer of visual identity matching-to-sample in two California sea lions (*Zalophus californianus*). *Animal Learning & Behavior, 22,* 427-435.

Kastelein, R.A., & van Gaalen, M. A. (1988). The sensitivity of the vibrissae of a Pacific walrus (*Odobenus rosmarus divergens*). *Aquatic Mammals, 14,* 123-133.

Kastelein, R.A., & Wiepkema, P.R. (1989). A digging trough as occupational therapy for Pacific Walruses (*Eumetopias jubatus*) in human care. *Aquatic Mammals, 14,* 39-41.

Keppel, G. (1992). *Design and analysis: a researcher's handbook.* (3rd ed.). New Jersey: Prentice Hall.

Klüver, H. (1933). *Behavior mechanisms in monkeys.* Chicago: University Chicago Press.

Komischke, B., Giurfa, M., Lachnit, H., & Malun, D. (2002). Successive Olfactory Reversal Learning in Honeybees, *Learning and Memory, 9,* 122-129.

Kovacs, K. M. (1995). Mother-pup reunions in harp seals, *Phoca groenlandica*: cues for the relocation of pups. *Canadian Journal of Zoology, 73,* 843-849.

Kovacs, K. M. (1987). Maternal behaviour and early behavioural ontogeny of harp seals, *Phoca groenlandica. Animal Behaviour, 35*, 644-855.

Kovacs, K. M. (1986). Maternal investment and early behavioural development in the harp (Phoca groenlandica) and grey seals (*Halichoerus grypus*). Ph. D. thesis, Univ. Guelph, Guelph, Ontario.

Kovacs, K. M., & Lavigne, D.J. (1985). Neonatal growth and organ allometry of northwest Atlantic harp seals (*Phoca groenlandica*). *Canadian Journal of Zoology, 63,* 2793-2799.

Krechevsky, I. (1932). Antagonistic visual discrimination habits in the white rat. *Journal of Comparative Psychology, 14*, 263-277.

Lashley, K.S. (1916). The color vision of birds. I. The spectrum of the domestic fowl. *Journal of Animal Behavior,*, 1-26.

Larson, J., & Sieprawska, D. (2002). Automated study of simultaneous-cue olfactory discrimination learning in adult mice, *Behavioral Neuroscience, 116,* 588-599.

Lavigne, D. M. (1973). Visual sensitivity in seals. Doctoral dissertation, University of Guelph, Ontario, Canada.

Lavigne, D. M. & Ronald K. (1972a). The harp seal, Pagophilus groenlandicus (Erxleben 1777). XXIII. Spectral Sensitivity. Canadian Journal of Zoology, 50, 1197-1206.

Lavigne, D. M. & Ronald K. (1972b). The harp seal, Pagophilus groenlandicus (Erxleben 1777). XXIII. The underwater audiogram. Canadian Journal of Zoology, 50, 565-569.

Lavigne, D. M. & Ronald K. (1975). Pinniped visual pigments. *Comparative Biochemistry and Physiology, 52B*, 325-329.

Lawson, J. W., & Stenson, G. B. (1995). Historic variation in the diet of harp seals (*Phoca groenlandica*) in the Northwest Atlantic. In A. S. Blix, Ø. Ultang, and L. Walløe (Eds.) *Seals, whales, fish and man* (pp. 261-269). London: Elsevier Science.

Levenson, D. H., & Schusterman, R.J. (1999). Dark adaptation and visual sensitivity in shallow and deep-diving pinnipeds, *Marine Mammal Science, 15,* 1303-1313.

Lydersen, C., & Kovacs, K.M. (1993). Diving behaviour of lactating harp seal, *Phoca groenlandica*, females from the Gulf of St. Lawrence, Canada, *Animal Behaviour, 46*, 1213-1221.

Mackintosh, N. J. (1969). Comparative studies of reversal and probability learning: Rats, birds and fish. In: Gilbert R. M. and Sutherland, N.S. (Eds.) *Animal Discrimination Learning* (pp. 137-162). London: Academic Press.

Mackintosh, N. J. (1974). *The psychology of animal learning*. London: Academic Press.

Mackintosh, N. J. (1983). *Conditioning and association learning*. London: Oxford University Press.

Mackintosh, N. J., & Macintosh, J. (1963). Reversal learning in Octopus vulgaris Lamarck with and without irrelevant cues. *Quarterly Journal of Experimental Psychology, 15,* 236-242.

Mackintosh, N. J., McGonigle, B., Holgate, V., & Vanderver, V. (1968). Factors underlying improvements in serial reversal learning. *Canadian Journal of Psychology, 22*, 85-95.

Maier, N. R. F., & Schneirla, T. C. (1935). *Principles of animal psychology*. New York: Dover Publications, Inc.

Markowitz, H. (1977). Environmental opportunities and healthcare for marine mammals. In H. Markowitz and V. J. Stevens (Eds.) *The behavior of captive wild animals* (pp. 483-487). Chicago: Nelson-Hall.

Mass, A.M. (1997). Adaptive features of vision in aquatic mammals. *Sensory Systems, 11(3)*, 181-209.

Mauck, B., & Dehnhardt, G. (1997). Mental rotation in a California sea lion (*Zalophus californianus*), *The Journal of Experimental Biology, 200*, 1309-1316.

McDonald, R. J., Hong, N. S., Ray, C., & Ralph, M. R. (2002). No time of day modulation or time stamp on multiple memory tasks in rats. *Learning and Motivation*, *33*, 230-252. [on-line electronic version, http://www.idealibrary.com].

McDonald, R. J., King, A. L., & Hong, N. S. (2001). Context-specific interference on reversal learning of a stimulus-response habit. *Behavioural Brain Research, 121*, 149-165.

McDonald, R. J., & Sutherland, R .J. (1992). *Navigation through time depends upon the hippocampal formation*. Unpublished manuscript.

McFarland, D. (1989). *Problems of Animal Behaviour*. Harlow: Longman Scientific and Technical.

McNab, A.G., & Crawley, M. C. (1975). Mother and pup behaviour of the New Zealand fur seal, Arctocephalus forsteri (Lesson). Mauri Ora. 3, 77-88.

Miller, E. H., & Murray, A. V. (1995). Structure, complexity, and organization of vocalizations in harp seal (Phoca groenlandica) pups. In R. A. Kastelien, T. Nachtigall, and P. E. Nachtigall (Eds.) *Sensory systems of aquatic mammals* (pp. 237-264). The Netherlands: De Spil Publishers.

Møhl, B. & Ronald, K. (1970). The harp seal, Pagophilus groenlandicus (Erxleben, 1777). IV. Underwater phonations with special references to the click. *International Council for the Exploration of the Sea, Copenhagen, 5*, 1-6.

Møron, I., Manrique, T., Molero, A., Ballesteros, A., Gallo, M., & Fenton, A. (2002). The contextual modulation of conditioned taste aversions by the physical environment and time of day is similar. *Learning & Memory, 9*, 218-223.

Moulton, V. D., Miller, E.H., & Ochoa-Acuna, H. (2000). Haulout behaviour of captive harp seals (*Pagophilus groenlandicus*): Incidence, seasonality, and relationships to weather. *Applied Animal Behaviour Science, 65*, 367-378.

Nagy, A.R., & Ronald, K. (1975). A light and electronmicroscopic study of the structure of the retina of the harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). *Rapports et Proces-Verbaux des Reunions. Conseil International pour l'Exploration de la Mer, 169*, 92-96.

O'Brien, P. C. (1983). The appropriateness of analysis of variance and multiple-comparison procedures. *Biometrics, 39*, 787-794.

Oliver, G.W. (1978). Navigation in mazes by a grey seal, *Halichoerus grypus (Fabricius)*, *Behaviour, 67*, 97-114.

Pavlov, I. (1927). *Lectures on conditioned reflexes.* New York: International Publishers.

Pearce, J. M., & Bouton, M. E. (2001). Theories of associative learning in animals. *Annual Review of Psychology, 52(1)*, 111-139.

Peichl, L., Behrmann, G., & Kroger, H.H. (2001). For whales and seals the ocean is not blue: A visual pigment loss in marine mammals, *European Journal of Neuroscience, 13,* 1520-1528.

Perkins, D., Lydersen, T., & Chairez, H. (1976). Fixed-ratio discrimination: Comparison of spatial and nonspatial choice procedures, *Perceptual & Motor Skills*, *43,* 587-593.

Pepperberg, I. M. (1987). Acquisition of the same/different concept by an African grey parrot (*Psittacus erithacus*): Learning with respect to categories of color, shape, and material. *Animal Learning and Behavior, 15*, 423-432.

Perry, E.A., Carr, S. M., Bartlett, S. E., & Davidson, W. S. (1995). A phylogenetic perspective on the evolution of reproductive behavior in pagophilic seals of the northwest Atlantic as indicated by mitochondrial DNA sequences. *Journal of Mammalogy, 76*, 22-31.

Reidman, M. (1990). The pinnipeds. Seals, sea lions and walruses. Berkeley: University of California Press.

Renouf, D. (1979). Preliminary measurements of the sensitivity of the vibrissae of harbour seals (Phoca vitulina) to low frequency vibrations, *Journal of Zoology London, 188*, 443-450.

Renouf, D. (1980). Masked hearing thresholds of harbour seals (*Phoca vitulina*) in air. *The Journal of Auditory Research, 20*, 263-269.

Renouf, D. (1985). Demonstration of the ability of the harbour seal *Phoca vitulina* (*L.*) to discriminate among pup vocalizations. *Journal of Experimental Marine Biology and Ecology, 87*, 41-46.

Renouf, D. (1991). Sensory reception and processing in Phocidae and Otariidae. In D. Renouf (Ed.) *Behaviour of pinnipeds* (pp.345-394), London: Chapman and Hall.

Renouf, D. and Gaborko, L. (1988). Spatial matching to sample in harbour seals (*Phoca vitulina*). *Biology of Behaviour, 13*, 73-81.

Renouf, D., & Gaborko, L. (1989). Spatial and visual rule use by harbour seals (*Phoca vitulina*). *Biology of Behaviour, 14,* 169-181.

Restle, F. (1958). Towards a quantitative description of learning set data. *Psychological Review, 65*, 77-91.

Révész, G. (1924). Experiments on animal space perception. *British Journal of Psychology, 14,* 387-414.

Ronald, K., & Dougan, J.L. (1982). The ice lover: Biology of the harp seal (*Phoca groenlandica*). *Science, 215*, 928-933.

Roux, J. P., & Jouventin, P. (1987). Behavioural cues to individual recognition in the subarctic fur seal, *Arctocephalus tropicalis*. In J. Croxall and R.L. Gentry (Eds.)

Status, biology and ecology of fur seals (pp. 95-102). Washington, D.C.: U.S. Department of Commerce .

Saksida, L. M., & Wilkie, D. M. (1994). Time-of-day discrimination by pigeons, *Columba livia. Animal Learning and Behavior, 22(2)*, 143-154.

Saksida, L. M., Wilkie, D. M., Samson, P. & Lee, A. (1994). Properties of time-place learning by pigeons, Columba livia. *Behavioural Processes, 31,* 39-56.

Sappington, B. K. F., McCall, C. A., Coleman, D. A., Kulhers, D. L., & Lishak, R. S. (1997). A preliminary study of the relationship between discrimination reversal learning and performance tasks in yearling and 2-year-old horses, *Applied Animal Behaviour Science*, *53*, 157-166.

Schusterman, R.J. (1962). Transfer effects of successive discrimination-reversal training in chimpanzees. *Science, 137*, 422-433.

Schusterman, R.J. (1967a). Attention shift and errorless reversal learning by the California sea lion. *Science, 156,* 833-835.

Schusterman, R.J. (1967b). Perception and determinants of underwater vocalization in the California sea lion. In Busnel, R. G. (Ed.) *Les Systemes Sonars Animaux, Biologie et Bionique, Laboratoire de Physiologie Acoustique* (pp. 535-617). France: Jouy-en-Josas.

Schusterman, R.J. (1968). Experimental laboratory studies of pinniped behavior. In R.J. Harrison, R.C. Hubbard, R. S. Peterson, C.E. Rice, & R. J. Schusterman (eds.) *The Behavior and Physiology of Pinnipeds*, New York: Appleton-Century-Crofts.

Schusterman, R.J. (1969). *Concurrent visual discrimination learning by a California sea lion, a Stellar sea lion and a harbour seal.* Unpublished manuscript, SRI, Menlo Park, California.

Schusterman, R.J. (1981). Behavioral capabilities of seals and sea lions: A review of their hearing, visual, learning and diving skills, *The Psychological Record, 31*, 125-143.

Schusterman, R.J., & Balliet, R.F. (1970a). Conditioned vocalization technique for determining visual acuity thresholds in the sea lion, *Science, 169,* 498-501.

Schusterman, R.J., & Balliet, R.F. (1970b). Visual acuity of the Harbour seal and Stellar sea lion under water, *Nature, 226*, 563-564.

Schusterman, R.J., & Balliet, R.F. (1971). Aerial and underwater visual acuity in the California sea lion (*Zalophus californianus*) as a function of luminance, *Annual New York Academy of Science, 188,* 37-46.

Schusterman, R. J., Kastak, D., Levenson, D. H., Reichmuth, C. J., & Southall, B. L. (2000). Why pinnipeds don't echolocate. *Journal of the Acoustical Society of America, 107*, 2256-2264.

Schusterman, R. J., & Thomas, T. (1966). Shape discrimination and transfer in the California sea lion. *Psychonomic Science, 5(1)*, 21-22.

Schreer, J. F., Kovacs, K. M., & Hines O'Hara, R. J. (2001). Comparative diving patterns of pinnipeds and seabirds. *Publication Ecological Monographs. 71*, 137.

Scronce, B.L., & Ridgway, S.H. (1980). Grey seal, Halichoerus: Echolocation not demonstrated. In: R.G. Busnel and J.F. Fish (Eds.) *Animal Sonar Systems* (pp.991-993), New York: Plenum.

Sergeant, D.E. (1973). Feeding, growth, and productivity of northwest Atlantic harp seals (*Pagophilus groenlandicus*). *Journal Fish. Res. Bd. Can. 30*, 17-29.

Sergeant, D.E. (1976). History and present status of populations of harp and hooded seals, *Biological Conservation, 10,* 95-118.

Sergeant, D.E. (1991). Harp seals, man, and ice. *Can. Spec. Pub. Fish. Aquat. Sci. 114*, 153.

Serrano, A. (2001). New underwater and aerial vocalizations of captive harp seals (*Pagophilus groenlandicus*). *Canadian Journal of Zoology, 79*, 75-81.

Serrano, A., & Terhune, J. M. (2002). Stability of the underwater vocal repertoire of harp seal (Pagophilus groenlandicus), *Aquatic Mammals, 28*, 93-101.

Setterington, R. G., & Bishop, H. E. (1967). Habit reversal improvement in the fish. *Psychonomic Science, 7*, 41-42.

Shelton, P.A., Stenson, G.B., Sjare, B.L., & Warren, W.G., (1996). Model estimates of harp seal numbers-at-age for the Northwest Atlantic. *NAFO Sci. Coun. Studies, 26*, 1-14.

Shyan, M. R., Wright, A. A., Cook, R. J., & Jitsumori, M. (1987). Acquisition of the auditory same-different task in a rhesus monkey. *Bulletin of the Psychonomic Society, 25*, 1-4.

Skinner, B.F. (1938). *Behavior of Organisms: An experimental analysis*. New York: Appleton-Century-Crofts.

Slotnick, B., Hanford, L., & Hodos, W. (2000). Can rats acquire an olfactory learning set? *Journal of Experimental Psychology: Animal Behavior Processes, 26*, 399-415.

Stenson, G. B., Hammill, M. O., & Lawson, J. W. (1997). Predation by harp seals in Atlantic Canada: Preliminary consumption estimates for Arctic cod, capelin and Atlantic cod, *Journal of Northwest Atlantic Fisheries Science, 22,* 137-154.

Stewart, R.E.A. (1987). Behavioral reproductive effort of nursing harp seals Phoca groenlandica, *Journal of Mammalogy, 68*, 348-358.

Sticken, J., & Dehnhardt, G. (2000). Slainity discrimination in harbour seals: a sensory basis for spatial orientation in the marine environment? *Naturwissenschaften, 87*, 499-502.

Stirling, I. (1971). Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). *Australian Journal of Zoology, 19*, 267-273.

Sutterlin, A. M., & Sutterlin, N. (1970). Taste response in Atlantic Salmon (*Salmo salar*). *Parr. J. Fish. Res. Bd. Can., 27,* 1927-1942.

Task, L. (1992). *Visual problems in night operations* (pp. 8.1-8.6). Neuilly Sur Seine, France: NATO Advisory Group for Aerospace Research & Development (NTIS No. AGARD-LS-187).

Terhune, J. M., & Ronald, K. (1971). The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). X. The air audiogram. *Canadian Journal of Zoology, 49,* 385-390.

Terhune, J. M., & Ronald, K. (1972). The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). III. The underwater audiogram. *Canadian Journal of Zoology, 50*, 565-569.

Terhune, J. M., Terhune, M. E., & Ronald, K. (1979). Location and recognition of pups by female harp seals. *Applied Animal Ethology, 5,* 375-380.

Theois, J. (1965). The mathematical structure of reversal learning in a shock escape T-maze; over-training and successive reversals. *Journal of Mathematical Psychology, 2,* 26-52.

Thinus-Blanc, C. (1996). *Animal Spatial Cognition*. Singapore: World Scientific Publishing Co.

Thomas, D. R. (1969). The use of operant conditioning techniques to investigate perceptual processes in animals. In: Gilbert R. M. and Sutherland, N.S. (Eds.) *Animal Discrimination Learning* (pp. 1-33). London: Academic Press.

Thomas, D. R., Cook, S. C., & Terrones, J. P. (1990) Conditional discrimination learning by pigeons: The role of simultaneous versus successive stimulus presentations. *Journal of Experimental Psychology: Animal Behavior Processes, 16*, 390-401.

Thomas, D. R., Curran, P., J. & Russell, R. J. (1988). Factors affecting conditional discrimination learning by pigeons: II. Physical and temporal characteristics of stimuli. *Animal Learning & Behavior. 16*, 468-476.

Thomas, D. R., McKelvie, A. R., & Mah, W. (1985). Context as a conditional cue in operant discrimination reversal learning. *Journal of Experimental Psychology: Animal Behaviour Processes, 11*, 317-330.

Thomas, D. R., & Schmidt, E.K. (1989). Does conditional discrimination learning by pigeons necessarily involve hierarchical relationships? *Journal of the Experimental Analysis of Behavior. 52,* 249-260.

Thomas, D. R., Stengel, T., Sherman, L., & Woodford, M. (1987) Factors affecting conditional discrimination learning by pigeons, *Journal of the Experimental Analysis of Behavior. 48*, 277-287.

Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946). Studies in spatial learning: II. Place learning versus response learning. *Journal of Experimental Psychology, 3,* 221-229.

Trillmich, F. (1981). Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. *Behaviour, 78*, 21-42.

Vikingsson, G. A., & Kapel, F. O. (2000). Minke whales, harp and hooded seals: major predators in the North Atlantic ecosystem. Tromso: NAMMCO Scientific Publications.

Warren, J. M. (1966). Reversal learning and the formation of learning sets by cats and rhesus monkeys. *Journal of Comparative and Physiological Psychology, 61*, 421-428.

Wartzok, D. (1991). Physiology of behaviour in pinnipeds. In Gilbert R. M. and Sutherland, N.S. (Eds.) *Animal Discrimination Learning* (pp. 236-286). London: Academic Press.

Wartzok, D., Elsner, R., Stone, H., Kelly, B.P., & Davis, R.W. (1992). Under-ice movements and the sensory basis of hole finding by ringed and Weddell seals. *Canadian Journal of Zoology, 70(9),* 1712-1722.

Watkins, W.A., & Schevill, W.E. (1979). Distinctive characteristics of underwater calls of the harp seal, Phoca groenlandica during the breeding season, *Journal of the Acoustical Society of America, 66*, 983-988.

Watkins, W.A. & Wartzok, D. (1985), Sensory biophysics of marine mammals. *Marine Mammal Science, 1,* 219-260.

Wilkie, D. M., Saksida, L. M., Samson, P., & Lee, A. (1994). Properties of time-place learning by pigeons, *Columba livia. Behavioural Processes, 31*, 39-56.

Appendix A – Pilot Studies

Training to Station

When I began working with the seals in May of 2001, they had very little training experience. In fact, the four harp seals had not experienced any training other than baton training, in which they were required to place their chins on the end of a wooden baton in order to receive a piece of herring. Shortly after I started, the seals were introduced to a whistle in addition to the baton. The seals were individually trained to place their chins on the baton, and stay there until the whistle was blown. They would then leave the baton and approach the experimenter, and were rewarded with a piece of herring.

My goal was to teach the seals to perform a choice discrimination, so that I would be able to use this discrimination method as way of testing more specific abilities. However, the seals required very basic preliminary training before they would be in a position to learn a choice discrimination. Also, many aspects of the training environment were difficult to control, which made the determination of training methods even more difficult.

Within the compound (as described in Experiment 1, Training environment), the seals had free access to both tanks. Even though the ramps could be moved away from the tanks so that the seals could not easily leave, for safety reasons, they were always replaced at the end of the day. This made it impossible to keep the seals separated for training if they were already in a tank when we arrived in the morning. It was desirable to be able to train each seal separately. Because we could not control the whereabouts of each seal during training, we decided to attempt to train the seals to station at a particular place in the tank, so that we could select one seal for training, and have the others remain at their stations until it was their turn to be trained.

Based on the suggestion of Kirsten Bilgmann, a visiting student of Dr. Guido Dehnhardt, who had had experience with similar training in harp seals, we decided to assign each seal a geometric shape that would act as its station. These shapes were suspended from a rope fastened across the tank, and the seals were trained to station at their respective shapes for a fish reward.

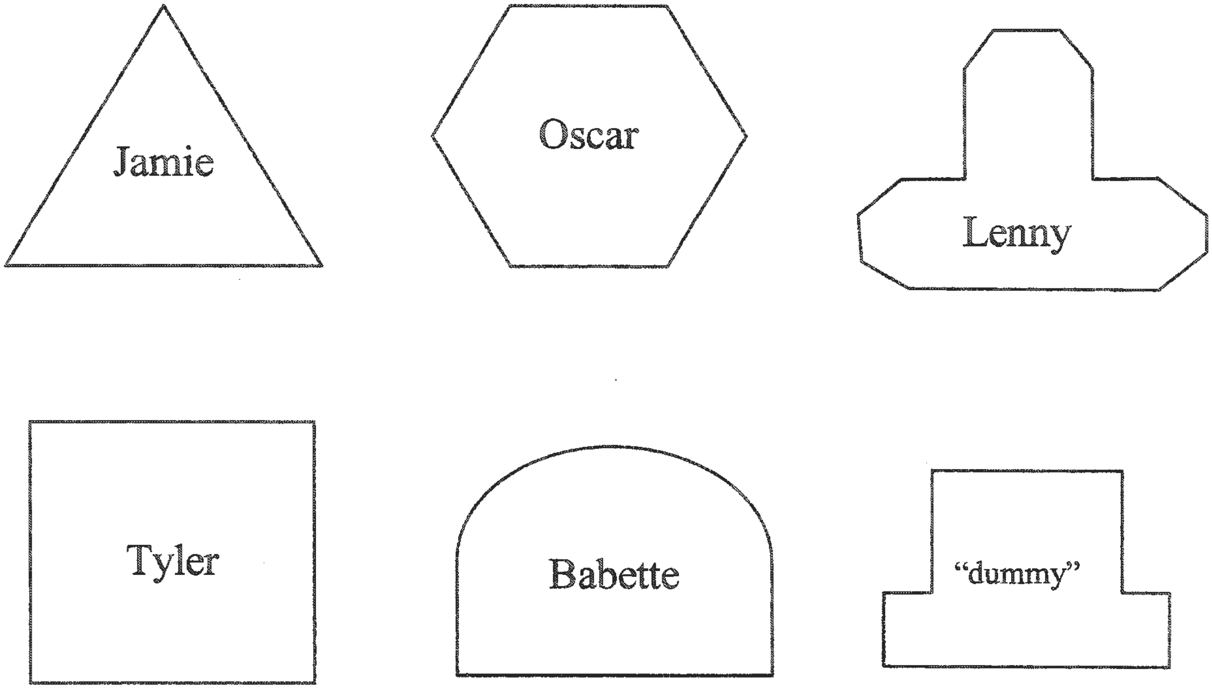
Method

Subjects

Subjects were four harp seals (Babette, Tyler, Jamie, and Lenny), as described in Experiment 1, and Oscar, a 28-year-old male harbour seal. At the beginning of this experiment, the harp seals ranged in age from 1-19 years old.

Apparatus

Six geometric shapes were cut from a piece of white polyethylene (0.5 cm thick). There was one shape for each seal, plus one "dummy" shape. The outlines of the shapes were traced onto the plastic, and professionally cut using a table-saw. All edges of the plastic shapes were filed down and rounded so that the seals would not injure themselves. The shapes were made hollow by drawing a smaller replica of each shape inside the tracing, with approximately 2 cm between the tracing and the inner drawing. This was cut out as well. Figure A1 provides a diagram of the six shapes. Each shape had two holes drilled near the top through which pieces of black nylon ribbon were pulled through and tied. Each piece had a plastic clasp attached, to allow the shape to be suspended from a rope



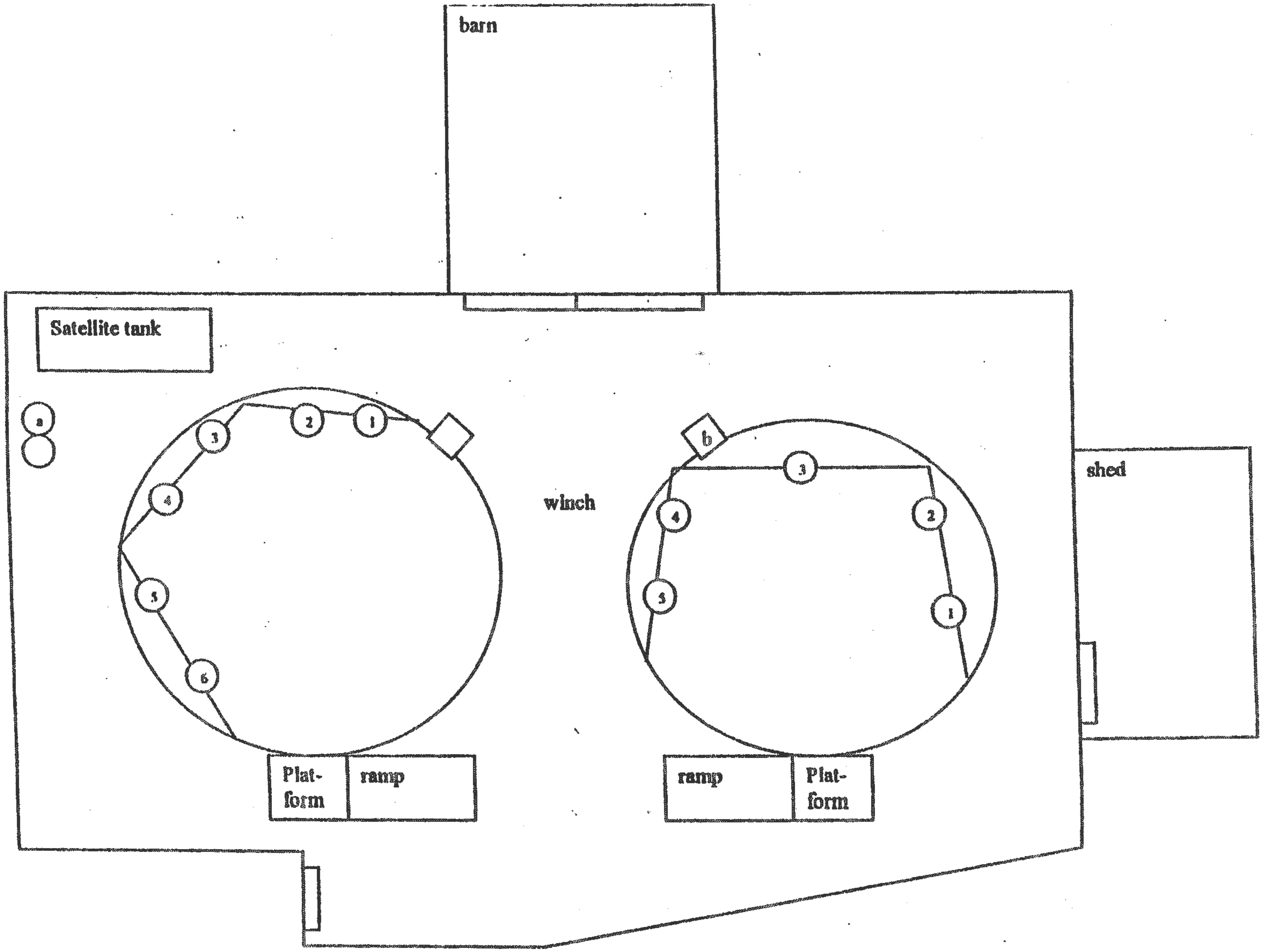
<u>Figure A1</u>. The six shapes used as stations for the seals. Note that the shapes were approximately 2 cm thick and hollow so that the seals could place their heads through. Jamie, Tyler, Babette and Lenny were the harp seals; Oscar was the harbour seal. The “dummy” shape was an extra shape that was used to give the seals an additional choice.

extending across each of the tanks. Two lengths of white, nylon rope were measured to extend roughly 2/3 of the way around each of the tanks. The rope was clamped onto the edge of the tank at one point, and then pulled loosely across to the opposite side. Two short bungee cords (45 cm) with hooks attached on both ends were hooked onto the edge of the tank, and onto the rope, to divide the rope into three approximately equal sections. The rope was then pulled tight, and clamped as far on the other side as possible. The rope extended approximately 60 cm in from the edge of the tank. Pairs of knots were tied along the rope (approximately 45 cm apart), to mark the positions of the shapes. The two clasps attached to each shape were clipped onto the outside of each knot. This allowed us to keep all the shapes at the same height above the water. Figure A2 shows a schematic diagram of the rope set-up.

Procedure

Training was broken into two identical sessions, one in the late morning, and one in the afternoon. The rope was clamped onto the tank, and the shapes were suspended in the tank by clipping them onto the rope using the clasps, so that the bottom of each shape just touched the surface of the water. The experimenter held the baton in one hand, and a piece of fish behind her back in the other. Initially, the seals were trained to rest their chins on the shape by luring them through using the baton, which they would readily follow. By using the whistle to signal the correct action of placing their heads inside their respective shapes, the baton was no longer necessary.

The position of each seal's shape was alternated randomly between five (or six, depending on the tank) stations, or places marked along the rope, so that the seals would


barn
Satellite tank
a
1
2
3
4
5
6
Plat-
form
ramp
winch
b
3
2
1
4
5
ramp
Plat-
form
shed

not simply learn to go to a certain place in the tank. Initially, the seals were trained several at a time. In order to do this, hand signals were used instead of the whistle. Each seal would swim around the tank, find its shape, and put its head though. It would then wait there until it was rewarded with a piece of fish. The experimenter or assistant would then point past the seal into the tank and say, "Go!". The seal would then withdraw its head from the shape, and quickly return.

Soon after, we decided to reintroduce the whistle and train the seals individually. Each seal was always given a choice between at least two shapes, its own plus the dummy shape. If other seals were not in the same tank at the time of training, their shapes could be used as well to provide more choices. The experimenter would stand equidistant from the two shapes, and call the seal that was to be trained by name. The "trainee" would approach and choose a shape. It he/she chose correctly, the experimenter blew the whistle and rewarded him/her with a piece of fish. If the seal chose incorrectly, he/she was told to "Go!" from the incorrect shape. After being rewarded, the seal would remove its head, and then quickly return to the same shape again and again until all of its fish was gone. The position of the correct shape was not altered within a training period, but was switched between training sessions, so that the seals had to go to two different positions per day, and to different positions on different days.

Results/Discussion

Because the positions of the shapes were not changed within a training session, it was difficult to determine whether the seals actually learned to recognize their respective shapes. They may have merely learned which position was correct for each training session through trial-and-error, or, (prior to being trained individually) by simply taking what was "left over" after other seals had chosen their shapes.

However, there was some evidence to suggest that the seals had learned to recognize their individual shapes. On several occasions, Lenny and Tyler were each alone in a tank. This meant that all shapes could be provided as choices while not leading other seals to believe that it was their turn to be trained. Lenny was given the choice between his own shape and five others simultaneously. After a quick visual inspection of the shapes, he immediately chose his own. At the time, there were five individuals present (four assistants, plus the experimenter), so each of them took down one shape (the experimenter took two), switched them around below the edge of tank, out of view, then clipped them back onto the rope at different stations. Again, Lenny was observed to look at all of the shapes until he found his own. This was done four times on that day, and each time, Lenny chose correctly. The assistants and experimenter also made sure to switch themselves around, so that Lenny was not able to associate the correct shape with a certain person. This happened on two separate days. On one occasion, Tyler passed the same test. These were the only instances during this training that any of the seals were alone to permit this type of probe testing. Interestingly, while most of the time the seals appeared to recognize their own shapes, the only two that sometimes had trouble were Babette and Oscar; they often confused each others' semicircle and hexagon

This training had been designed only to familiarize the seals with an individual shape, with the possibility of later having them learn to station at their respective shapes while waiting their turn to be trained on another task. It was very difficult to assess the seals' ability to recognize their individual shapes given the present procedure. More importantly, the seals were reluctant to remain stationed at the shape despite being rewarded almost continuously. We decided that this training would not be a successful method of keeping the seals separate during later training. At this point, we decided to design a basic discrimination experiment to better understand the types of problems to be encountered.

2D Discriminations

In this experiment, the seals were individually trained to discriminate between a pair of black and white two-dimensional panels that were attached to the side of the tank.

Method

Subjects.

The subjects were the same as those used in the previous experiment.

Apparatus

The apparatus used for the two-dimensional panel discriminations consisted of a backing of grey plastic hole-board (46 cm x 36 cm x 0.6 cm) with a wooden knob attached and centred 10 cm from the bottom. Two such backings were clamped onto the inside edge of the tank approximately 46 cm apart, and the water level was dropped so that the knobs were halfway above the surface. Two 22 cm x 28 cm reversible laminated pieces of cardboard were used as stimuli. Each was white on one side and black on the other. Each had a piece of string taped to it with a strip of grey duct tape that went around both sides of the panel. Two large metal washers were also taped to the bottom of each panel beneath a similar strip of duct tape (this was done to weight the stimuli and prevent them from blowing around and flipping), so that each side of both stimuli appeared as a solid black or white rectangle between two grey bars. This apparatus is shown in Figure A3. Two other stimuli were created in a similar fashion, using a solid black line, oriented either horizontally or vertically, on a solid white background. The seals' individual geometric shapes from the previous experiment were used as well.

Procedure

Seals were required to choose between two stimulus panels that hung on the side of the tank. The correct choice was counterbalanced across seals so that, for two of the seals, black was correct, and for the other two, white was correct. Each of the seals' individual geometric shapes was used as a 'name tag' to facilitate them recognizing when it was and was not "their turn" to be trained. When it was a seal's turn to be trained, the trainer clamped his/her shape onto the inside edge of the tank between the two backings. The trainer stood directly behind the "name tag" shape, midway between the stimulus panels, and lowered the baton into the tank until it touched the surface of the water, approximately 1 m from the edge of the tank. A trial began when the seal approached and placed his/her chin on the baton, at which point the trainer blew the whistle for approximately 2 sec. This indicated to the seal that it was time to choose, and the baton was drawn toward the trainer and brought up against the edge of the tank between the two backings. For the first few trials, each seal was led with the baton to the correct knob, and rewarded for touching it. Eventually, the seals had to learn that only choosing black, or, only choosing white, would result in a fish reward. A correct choice was judged as one

Figure A3. Two-dimensional panel discrimination apparatus. Note that this picture was taken before the metal washers and duct tape were added at the bottom of the panels in order to weight them. The active seal in the picture is Oscar, the harbour seal.

where the seal left the baton and rested his/her chin on the knob below the correct stimulus[5]. The trainer would then give a short whistle (approximately ½ sec) and reward the seal with a piece of fish. The seal would then have to place his/her chin back on the baton and wait for the starting whistle before he/she could make his/her next choice. Because the panels were reversible, the trainer could flip them over so that sometimes black was on the left and white was on the right, and vice versa. This prevented the seals from learning to go to a consistent position. Once the seals began to perform with higher accuracy, the trainer included a trial or two in which the panels were flipped over, but then immediately switched back again, to control for any cues form the actual manipulation of the stimuli.

As each seal learned the black-white task, they were moved on to a horizontal-versus vertical line discrimination, to test for the ability to focus on only a small aspect of the rectangular stimuli. Although all harp seals reached criterion on the first discrimination, we were unable to complete this experiment, as described below.

Results/Discussion

All harp seals learned to choose correctly based on a criterion of 18/20 consecutive trials correct. (Babette required 849 trials, Tyler, 654 trials, Jamie, 323 trials, and Lenny, 393 trials.) Oscar did not complete the task. There were problems with this task as well, which is why the horizontal/vertical line discrimination could not be completed.

The seals were being trained and rewarded using their daily allotment of fish. This

---

[5] No time limit was placed on the trials because the seals were either hungry and would choose immediately, or were not hungry and would refuse to participate altogether.

meant that they had not been fed prior to training, and would not be fed until they performed correctly. The seals appeared to find this frustrating to begin with and were often uncooperative. The greatest problem was the fact that the seals received unequal portions. Due to dietary requirements in the interest of the seals' health, Babette and Tyler were on a limited 'diet' of 3 kg of fish per day, while the other seals were not limited and could have more than this if they wanted it. The problem was that after Babette and Tyler had their turn at training and had quickly consumed their food, they were still hungry, and harassed the two smaller seals during their training trials. This was an especially great problem for Jamie because he was more timid than Lenny; he was often observed surrendering his fish over to Tyler. Thus, we could not continue to train Jamie in this manner, 1) because he was not getting his rewards or his daily allotment of fish, and 2) Tyler was getting more than his share, which was counteracting our attempts to help control his weight. It got to the point where Jamie routinely refused to participate in training.

Because of these problems, we decided to make another attempt at solving the problem of not being able to train the seals separately. This led to the idea of training the seals to come out of the tank on command so that they could be separated prior to training.

Out-of-Tank Training

We attempted to train the seals to come out of the tanks on command so that we would be able to separate them prior to training.

Method

The platform was completely removed from alongside the tank. The ramp was pulled about 2 m toward the centre of the compound, and turned so that the upper part of the ramp was against the edge of the tank. (This was done to change the context somewhat from that experienced during normal feeding, where the seals were expected to return to the water after each piece of fish.) One trainer stood or bent down on her knees at the bottom of the ramp with the training baton and a herring or piece of herring, and called each seal individually, using the command, "Come!" (e.g., "Lenny, come!") Initially, the seals were rewarded for coming partway down the ramp, but this was unsuccessful because they would quickly turn around and go back in the tank. Once the seals were on deck, we could herd them into the desired tanks, and tip one or both of the ramps on their side so that certain seals could not enter/leave a tank. This training continued throughout the month of January 2002.

Results/Discussion

While a great idea in theory, training the seals to come out of the tank on command proved to be very difficult. The harp seals were especially unwilling to leave the water, even for a full herring. After four weeks of out-of-tank training, Lenny, Jamie, and Babette came out of the tank onto the deck at least once. However, the whole process was very labour intensive and did not amount to the simple command-response sequence that was desired. It took approximately 1 hr of coaxing to get a single seal completely out of the tank, which was unacceptable. The only other way to get the seals out of the tank was to drain the tank and winch the seals out, which required approximately four hours.

Despite the slight change in context, moving the ramp may not have been sufficient for the seals to perceive the situation as different from feeding. The out-of-tank training was in direct opposition to the previously learned feeding situation, where each seal was expected to lean over the edge of the tank, take a piece of fish, then return to the water before it was given its next piece. (This was done to prolong the feeding activity, such that the seals experienced more interaction with the trainers. Also, the slower the seals ate, the better it was for them; if fed too quickly, the seals would often vomit or regurgitate undigested fish).

In addition, there may be a biological explanation for the difficulty in training the harp seals to come out of the tanks on command. Haulout behaviour of both wild and captive harp seals has been studied fairly extensively. In both cases, harp seals have been observed to spend a significant part of their lives in the water. Some studies report that harp seals haul out strictly for the purpose of breeding and moulting (e.g., Sergeant, 1973; Ronald & Dougan, 1982), while more recent studies suggest that haulout patterns are much more complex and vary throughout the year, depending on such factors as time of day, solar radiation, air temperature, wind velocity and relative humidity (see Moulton, Miller, & Ochoa-Acuna, 2000). Out-of-tank training took place in the early afternoons during the month of January in the winter of 2002. Captive harp seals have been reported to show more haulout behaviour at night than during the day (Moulton, Miller, & Ochoa-Acuna, 2000). As well, while the exact seasonal pattern of haulout behaviour is unknown, it is suggested that harp seals haulout much less frequently during colder winter months than during the spring moulting period (Moulton, Miller, & Ochoa-Acuna, 2000). Given these biological constraints, harp seals may be considered contra-prepared to learn to perform haulout behaviour at specific random times, as suggested by related studies on contra-preparedness in other species (e.g., Bolles, 1970; see Drickamer & Vessey, 1992).

Given the lack of success with finding ways of separating the seals, and the associated problems this caused for discrimination training, a different experimental design was employed.

Habituation

A new protocol was designed in an attempt to resolve the problem of harassment and stealing of fish. The proposed strategy was to remove the reward aspect of training altogether and switch to a habituation paradigm. This would test the seals' ability to recognize and discriminate between objects, while removing the reward component so that the seals would not have to "fight over" their fish as they did during training. The seals were exposed to an object that was suspended inside the tank for a period of 30 min. From inside the shed, I observed the seals and recorded the amount of time each spent investigating the object. My design was based on the assumption that the seals would show a preference for novel over familiar objects, and would, therefore, show more interest in an object that they perceived as novel than one that they perceived as familiar. Such a pattern preference has been documented in countless other species, including humans (Fantz, 1964).

In the initial phase of this experiment, objects were suspended directly into the tank; however, these were treated as playthings, and were pushed, chewed, etc., but not necessarily attended to visually. To test for recognition, and not simply for play-preference, the objects had to be presented to the seals visually while not allowing them to have physical contact with them. To maintain the integrity of the stimulus objects, as well as remove any confound of physical manipulation, a clear plastic container was then designed to hold the stimulus objects.

Uncontained Objects

Method

Subjects. The subjects used were the same as those above.

Apparatus. For the early habituation pilot studies, a 2L pop bottle, a plastic coat hanger, and a rectangular, frosted, transparent plastic container (35 cm x 30 cm x 18 cm) with a solid blue lid, and a grey plastic handle and snaps, were used as stimuli. A medium-sized (14 cm diameter) blue-green plastic ball was used as a test object inside the container. The bottle and coat hanger each had a piece of string tied around the neck that formed a loop from which the objects could be suspended. A brass lobster-claw clasp (approximately 8 cm x 4 cm) was attached to a piece of white plastic clothesline that had a loop knot at the other end. The knotted end of the clothesline was attached to a metal clasp that extended down from the chain of the winch above the tank (as described in Experiment 1). The object was attached to the brass clasp attached to the clothesline. The electric winch allowed the experimenter to raise and lower the object according to the water level so that it rested on the surface of the water. A stopwatch was used to record times and durations of behaviours in seconds.

Procedure. The objects were tested separately. The pop bottle was suspended into the tank from the chain connected to the winch; it floated on the surface of the water at an angle of approximately 45°, for a period of 30 min on four observation days. From inside the shed, the experimenter observed and recorded the amount of time each seal spent investigating the object, using a stopwatch. Investigation was defined as any time a seal was within 60 cm of the object and facing it. Five minutes after the fourth trial with the pop bottle, the coat hanger was suspended from the winch for 30 min. Investigation of the coat hanger was also recorded over four 30-min trials on one day. On the following day, the empty container was suspended. The empty container was observed for four trials over two days. To test whether the seals would show increased interest when an object was placed inside this container, a green-blue ball was fastened inside the container using strips of Velcro, and also observed for four trials.

Results/Discussion

At the end of the four trials, the seals had not habituated to the pop bottle. In fact, their interest remained fairly constant. When presented with the first novel object, the coat hanger, their interest was much lower than it had been on the first presentation of the pop bottle. In this case, the interest was clearly due to the nature of the objects, and not to their novelty or familiarity. The seals appeared to enjoy playing with the pop bottle; both Jamie and Lenny were observed to lie on their backs at the surface with the bottle on their stomach, and pat it with their flippers. The coat hanger did not appear to have much "play value", and was basically ignored.

This led to the presentation of the plastic container, to which the seals showed little more interest than to the coat hanger. When the ball was placed inside the container, the level of investigation did not appear to increase. This was likely because the box was frosted and not completely transparent, making the object somewhat difficult to see. Thus, a more suitable container was required in order to display the objects to the seals.

Habituation to the Empty Box/Novel Objects

The early habituation pilot studies demonstrated that, in order to use visual attention time as a dependent variable, the seals must not be able to physically manipulate the stimuli, otherwise, they become “toys”, and their usefulness as habituation stimuli greatly decreases. In this experiment, two completely transparent boxes were designed to hold stimulus objects. To remove any effects of novelty, and to rule out the “play value” of the boxes themselves as stimuli, the seals were initially habituated to the empty boxes over a series of 22 1-hr trials. After habituation, the seals were exposed to four novel objects for 1 30-min session per day over four days, and the levels of investigation of each object by each seal were recorded.

Method

Subjects. The subjects were the same as those used in the previous experiments. Around the time this experiment began, a fifth seal, Deane, was born. Deane was trained using the baton and whistle in the satellite tank until she was approximately 2 months old. Once she was safely swimming in the larger tanks with the other seals, she was included in the observations.

Apparatus. The boxes used were those described in Experiment 1, Apparatus, Training equipment. A brass lobster-claw clasp was attached to a piece of white plastic clothesline that had a loop knot at one end. The clasp was attached to the top o-ring on the box, and the knotted end of the clothesline was attached to a metal clasp that extended down from the chain of the winch above the tank. The electric winch allowed the experimenter to raise and lower the box according to the water level so that the box always rested upright on the surface of the water. Figure A4 shows the empty box suspended from the winch.

Four objects were used in this experiment. The first two objects were the red ball and red cube described in Experiment 1, Apparatus, Stimuli. The third object was the end of a training baton that had broken off. Two metal rods were placed inside the box, and the baton was attached to the rods using transparent tape so that the wooden sphere at the end pointed upward at an angle of approximately 45°. The final object used was a 25 cm long frozen herring that was skewered with a metal rod and positioned horizontally across the centre of the box. The fish remained frozen for the full 30-min session, and was then immediately returned to the freezer. The same fish was used on all four days. The four stimuli for the habituation experiment are presented in Figure A5.

Procedure.

Habituation to empty box. Efforts were made to get as many seals into the same tank as possible prior to the observation period. The experimenter nearly always chose to observe the tank with the most seals in it, unless one seal had not been observed for several sessions. The platform and ramp were often moved so that the seals could not leave during the observation period. However, once Deane started, the platform was left in place for several trials, until she learned to check for it first before jumping out. There were two trials per day, over 11 days, for a total of 22 trials. Ten trials had been carried

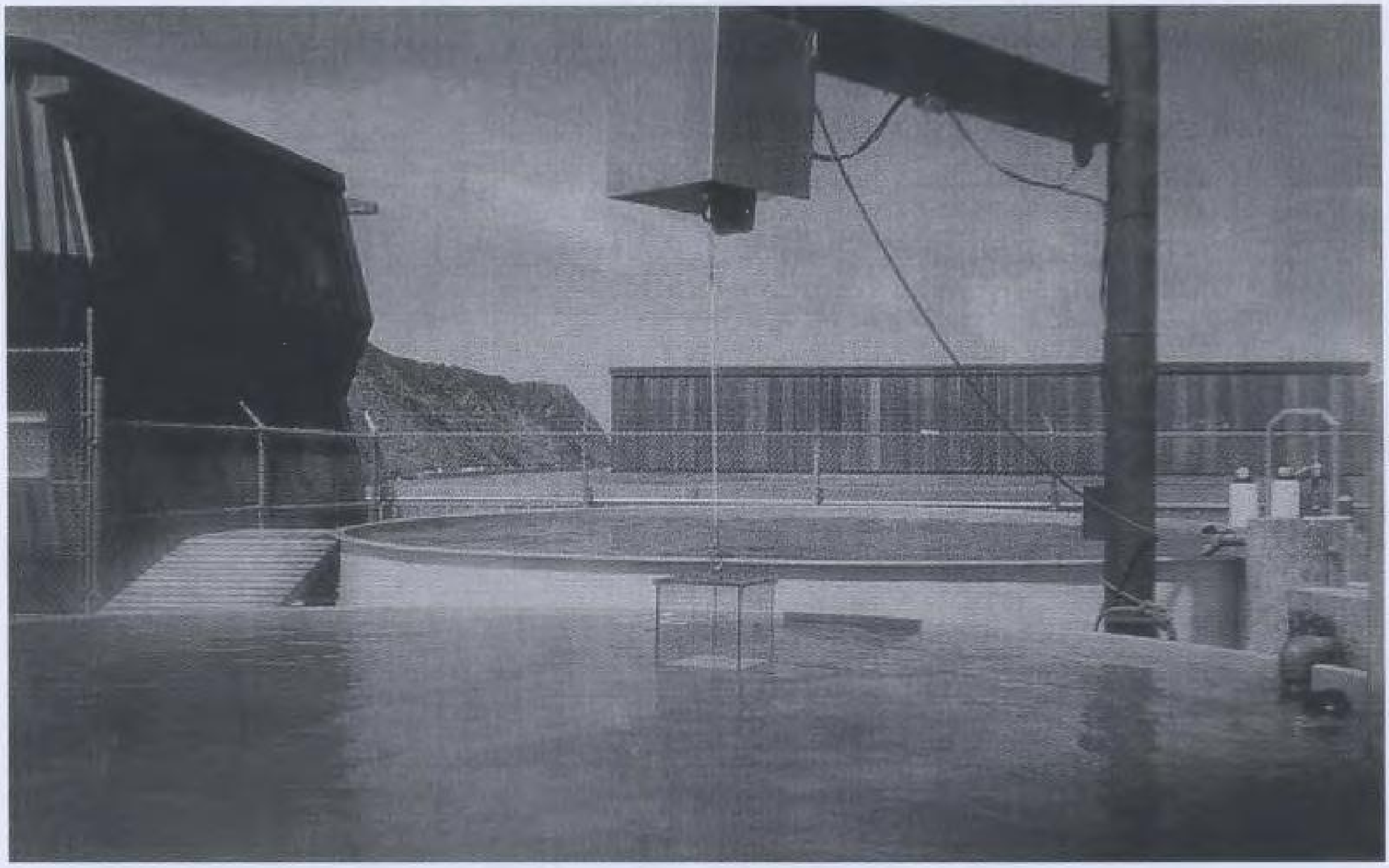


Figure A4. The empty box suspended from the winch in the little tank.

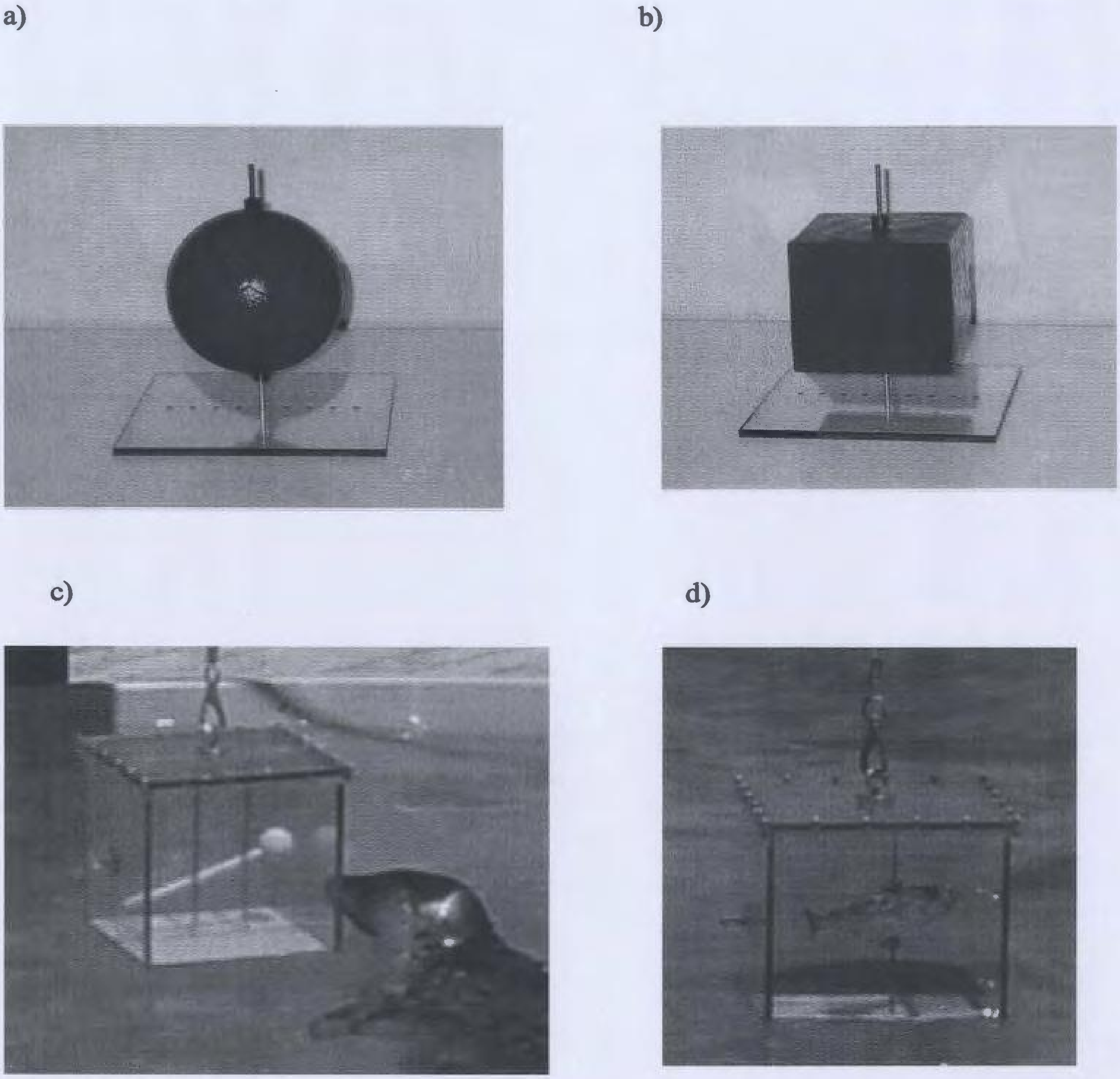


Figure A5. The four objects used in the habituation to novel stimuli experiment during pre-training. The first, in the top-left (a), is a large red ball; the second, in the top-right (b), is a large red cube; the third, in the bottom left (c), is the end of a training baton; the fourth (d) is a frozen herring. This is the order in which the stimuli were presented to the seals.

out before Deane was included in the observations. Twelve additional trials were carried out. Deane was present for 10 of these. For two of them, she had been in the tank at the beginning of a trial, but had gotten up onto the platform, and then fallen off the platform onto the deck. She was not put back in for the second half of the trials because her behaviour may have been influenced by such a potentially stressful event.

Trials were set up as follows: One trial consisted of two 30-min exposures to the box with a short break in between (approximately 3-5 min) to allow for the box to be removed and replaced. There were two identical boxes to which the seals were exposed randomly during each 30-min session. One box was suspended from the winch above the tank and lowered, then pulled across the tank until it rested on the surface of the water as far into the tank as the winch would allow (approximately 1.5 m from the edge). This was done by an assistant, who then left the compound for 30 min. Meanwhile, the experimenter sat in the window of the shed, facing the tanks, and started a stopwatch as soon as the box was in position. The experimenter recorded the time beginning when a seal got within approximately 60 cm of the box and was facing it (with its eyes above water). When that seal left the area or was no longer facing the box, this time was recorded as well. If two or more seals were investigating the box simultaneously, beginning and end times for the durations were recorded independently for each seal. At any point during the trial, if a seal left the tank and got up onto the adjacent platform, the time it spent on the platform was recorded. At the end of the first 30-min exposure, the experimenter left the shed, removed the box from the tank, brought it in the shed and wiped it with paper towels. The assistant returned, entered the shed, took either the same box or the second one, put that box into position, and then left again. (While the boxes were virtually identical, one had a small scratch on top, which allowed them to be distinguished.) The box used for each 30-min exposure was noted. The experimenter again recorded the seals' investigation times as before. At the end of this trial, the experimenter removed the box, returned it to the shed, and left the compound for approximately 3 hr before returning to do the afternoon trial. During this 3-hr period, the seals were fed, given ice, and took part in various forms of training including out-of-tank training and baton training.

Habituation to novel objects. Once the seals had been habituated to the empty box (that is, each seal spent less than 5 s investigating the box in the last trial) novel objects were introduced. The same protocol was used as with the empty box habituation. On each training day, the seals were exposed to the box for four 30-min sessions. The first two exposures in the morning session comprised the first trial, and the third and fourth exposures in the afternoon session comprised the second trial. Each novel object was presented in only one of the four 30-min exposures per day over four days, so that the seals saw each object a total of four times. The object was presented in a different 30-min session each day. The order of this presentation over the four days varied between objects. Investigation times were recorded for each 30-min session, so that, for each day, there were three sets of scores for empty box presentations, and one set of scores for the object presentation. The first object presented was the large red ball. The next object presented was the large red cube. The third was a training baton with part of the handle broken off. Finally, the fourth novel object presented to the seals was a frozen herring.

Results/Discussion

This experiment was designed to control extraneous variables that may have been contributing to the seals' interest in the box. Because each trial had two exposures (first and second), this controlled for a possible effect of order. Because the trials were carried out in the morning prior to feeding, and again after feeding, this controlled for a possible effect of state (i.e., hungry versus sated). The two boxes were switched randomly, but the box used was noted for each session within each trial.

The data were analysed for the first ten trials in which each seal participated, for which there was an alternation of hungry versus sated trials. In cases where a seal was absent for one 30-min session of a trial, his/her score for the other half of the trial was used as an estimate. Overall, statistical analysis revealed that the seals did not show any interest in the empty box, and the level of interest was not affected by the order of trials, the box used, or the state of the seals (all p's > .05). There were within-subjects differences in the level of investigation. Deane was the only seal to initially show interest in the box, which decreased over time. All others investigated the box for seconds, at most. The empty box was not interesting to the seals. In the one case where interest was shown initially, it quickly dropped to zero through rapid habituation. This allowed us to proceed with presenting objects inside the box, in that we could safely presume that any interest shown could be attributed to the objects, and not to the box.

Seals showed significantly more interest (i.e., higher investigation times) in the red ball ($\underline{M} = 3.26$, $\underline{SD} = 3.35$) over the four days than the empty box ($\underline{M} = 1.79$, $\underline{SD} = 2.63$; $\underline{t}(18) = 1.75$, $p = .049$). For this analysis, the mean of the three empty box trials was calculated for each day, for each seal. These scores were compared to those on the object trials for each seal.[6] Seals did not show an increase in interest in the red cube (*M* = 1.05, *SD* = 1.73) compared to the empty box (*M* = 2.17, *SD* = 3.70; *t* (19) = -1.31, p = .11). Seals showed significantly more interest in the baton (*M* = 7.73, *SD* = 12.33) than the empty box (*M* = 3.38, *SD* = 6.10; *t* (14) = 2.56, p = .011). Seals did show a slight increase in interest to the frozen herring (*M* = 19.12, *SD* = 41.52) when compared to the empty box (*M* = 7.08, *SD* = 13.80; *t* (16) = 1.74, p = .051), but this did not meet the required significance level of $\alpha = .05$.

The results of this pilot study showed that the seals did not discriminate between the red ball and red cube. It was not known whether the seals were unable to discriminate perceptually between these objects, or whether the seals had simply generalized their habituation of the ball to the cube, as the two stimuli were very similar.

At this point, I decided to try a discrimination task, using the new apparatus, to determine whether the seals could be trained to discriminate between the ball and cube. The difference was that, in addition to having three-dimensional stimuli as opposed to two-dimensional, the new apparatus could be suspended rather than clamped onto the side of the tank, which gave both the seals and the trainer more room to work with. Thus, this is where Experiment 1 began.

Enrichment

In addition to training, on Saturdays and Sundays, the seals were also fed capelin as part of an enrichment activity. The capelin (approximately 75) were placed inside a

---

[6] The *df* vary between objects because missing scores occurred when seals were not in the tank when the object or empty box was presented.

plastic ball that had shapes cut out of it (Shape Sorting Ball, Blue-Box®), packed with ice and frozen in seawater. This "fish ball" was then placed into the tank with the seals and allowed to melt. The seals were able to manipulate the ball to remove a few capelin at a time as the ice melted. This activity kept the seals mildly occupied for about an hour; such stimulating activity is thought to be beneficial to captive animals (Goldblatt, 1993).

Goldblatt (1993) notes that the two major needs of captive marine mammals are the need to receive sensory stimulation, and the need to have control over their environment. The second point may explain why the seals quickly became stressed when they were not allowed to enter or leave the tanks. The freedom to roam, or control their location within the compound, had been taken away. Goldblatt (1993) notes that one common sign of stress is stereotyped swimming behaviour. Babette often exhibited this type of behaviour immediately upon refusing to participate in, or continue, a training session. She would vocalize her discontent (i.e., a high-pitched growl/whine), and then proceed to enter into a stereotypical swimming pattern consisting of a dorsal surface (i.e., on her back, with her head tilted backward), a dorsal swim across the tank, followed by submersion from the dorsal position. This stereotypical circling is typical of captive marine mammals (Kastelein & Wiepkema, 1989). Kastelein and Wiepkema (1989) suggest that such stereotypies are the result of boredom due to lack of engagement in feeding and foraging behaviours. Given that Babette has spent approximately 10 years in the wild prior to being captured, and has also been in captivity for the longest (next to Oscar), she was likely the most susceptible to such behaviours. While the seals apparently did become frustrated with training, many authors have shown that training can be beneficial to captive animals. It may give the animals some control over feeding, such as performing certain behaviours to receive a food reward (Grindrod & Cleaver, 2001; Carlstead, Seidensticker, & Baldwin, 1991; McFarland, 1989). It engages them mentally, and may also be used to facilitate veterinary procedures (Markowitz, 1977). Thus, the present study served a secondary purpose: to stimulate and enrich the lives of its participants.

Appendix B - Number of correct choices out of total number of trials for each seal on each training day of Experiments 1 and 2

Seal	Date	Task^{a}	Correct Choices/Trials
Babette	31-Jul	CUBE/ball	35/80
Babette	1-Aug	CUBE/ball	37/71
Babette	5-Aug	CUBE/ball	35/55
Babette	8-Aug	CUBE/ball	27/36
Babette	9-Aug	CUBE/ball	19/36
Babette	12-Aug	CUBE/ball	36/52
Babette	14-Aug	CUBE/ball	32/45
Babette	15-Aug	CUBE/ball	16/33
Babette	16-Aug	CUBE/ball	34/52
Babette	19-Aug	CUBE/ball	31/70
Babette	21-Aug	CUBE/ball	32/53
Babette	23-Aug	CUBE/ball	32/62
Babette	28-Aug	CUBE/ball	35/62
Babette	29-Aug	CUBE/ball	35/50
Babette	30-Aug	CUBE/ball	45/86
Babette	4-Sep	CUBE/ball	34/51
Babette	5-Sep	CUBE/ball	32/60
Babette	6-Sep	CUBE/ball	36/63
Babette	9-Sep	CUBE/ball	21/25

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Babette	11-Sep	DONUTS/coffee	33/52
Babette	16-Sep	DONUTS/coffee	48/83
Babette	18-Sep	DONUTS/coffee	31/56
Babette	19-Sep	DONUTS/coffee	34/62
Babette	23-Sep	DONUTS/coffee	35/75
Babette	25-Sep	DONUTS/coffee	36/64
Babette	26-Sep	DONUTS/coffee	32/48
Babette	27-Sep	DONUTS/coffee	34/56
Babette	30-Sep	DONUTS/coffee	33/49
Babette	2-Oct	DONUTS/coffee	38/64
Babette	3-Oct	DONUTS/coffee	21/36
Babette	4-Oct	DONUTS/coffee	27/45
Babette	7-Oct	DONUTS/coffee	32/50
Babette	9-Oct	DONUTS/coffee	29/59
Babette	10-Oct	DONUTS/coffee	33/48
Babette	11-Oct	DONUTS/coffee	32/50
Babette	16-Oct	DONUTS/coffee	32/44
Babette	17-Oct	CUBE/coffee	33/40
Babette	18-Oct	CUBE/coffee	29/37

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Babette	21-Oct	CUBE/coffee	5/5
Babette	23-Oct	DONUTS/hexagons	29/48
Babette	24-Oct	DONUTS/hexagons	10/11
Babette	25-Oct	BUNNY/ball	21/28
Babette	28-Oct	BUNNY/ball	32/49
Babette	30-Oct	BUNNY/ball	24/27
Tyler	31-Jul	BALL/cube	36/74
Tyler	1-Aug	BALL/cube	29/56
Tyler	8-Aug	BALL/cube	35/54
Tyler	9-Aug	BALL/cube	36/58
Tyler	12-Aug	BALL/cube	32/73
Tyler	14-Aug	BALL/cube	22/28
Tyler	16-Aug	COFFEE/donuts	33/60
Tyler	19-Aug	COFFEE/donuts	32/51
Tyler	21-Aug	COFFEE/donuts	27/35
Tyler	23-Aug	COFFEE/donuts	35/52
Tyler	28-Aug	COFFEE/donuts	31/41
Tyler	29-Aug	COFFEE/donuts	8/9
Tyler	30-Aug	BALL/donuts	24/27
Tyler	4-Sep	HEXAGONS/cube	31/60

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Tyler	5-Sep	HEXAGONS/cube	33/49
Tyler	6-Sep	HEXAGONS/cube	9/10
Tyler	9-Sep	COFFEE/bunny	33/49
Tyler	11-Sep	COFFEE/bunny	17/18
Tyler	16-Sep	TOWER/bag	32/56
Tyler	18-Sep	TOWER/bag	39/65
Tyler	19-Sep	TOWER/bag	12/13
Tyler	23-Sep	BAG/tower	33/98
Tyler	25-Sep	BAG/tower	27/45
Tyler	26-Sep	BAG/tower	34/52
Tyler	27-Sep	BAG/tower	18/22
Tyler	30-Sep	TOWER/bag	33/63
Tyler	2-Oct	TOWER/bag	34/53
Tyler	3-Oct	TOWER/bag	27/46
Tyler	4-Oct	TOWER/bag	30/50
Tyler	7-Oct	TOWER/bag	33/51
Tyler	9-Oct	TOWER/bag	32/50
Tyler	10-Oct	TOWER/bag	2/53
Tyler	11-Oct	TOWER/bag	20/23
Tyler	16-Oct	BAG/tower	33/92

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Tyler	17-Oct	BAG/tower	32/65
Tyler	23-Oct	BAG/tower	29/46
Tyler	24-Oct	BAG/tower	23/29
Tyler	25-Oct	TOWER/bag	32/45
Tyler	30-Oct	TOWER/bag	26/35
Tyler	31-Oct	TOWER/bag	29/39
Tyler	1-Nov	BAG/tower	30/54
Tyler	4-Nov	BAG/tower	27/44
Tyler	7-Nov	BAG/tower	26/43
Tyler	13-Nov	BAG/tower	32/47
Tyler	14-Nov	BAG/tower	27/36
Tyler	15-Nov	BAG/tower	31/53
Tyler	20-Nov	BAG/tower	26/45
Tyler	21-Nov	BAG/tower	29/42
Tyler	22-Nov	BAG/tower	24/27
Jamie	31-Jul	CUBE/ball	27/49
Jamie	1-Aug	CUBE/ball	32/75
Jamie	5-Aug	CUBE/ball	17/33
Jamie	8-Aug	CUBE/ball	33/53
Jamie	9-Aug	CUBE/ball	12/19

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Jamie	12-Aug	CUBE/ball	27/50
Jamie	14-Aug	CUBE/ball	27/44
Jamie	15-Aug	CUBE/ball	15/28
Jamie	16-Aug	CUBE/ball	46/78
Jamie	19-Aug	CUBE/ball	22/36
Jamie	21-Aug	CUBE/ball	24/44
Jamie	23-Aug	CUBE/ball	30/43
Jamie	28-Aug	CUBE/ball	44/80
Jamie	29-Aug	CUBE/ball	43/70
Jamie	30-Aug	CUBE/ball	45/70
Jamie	4-Sep	CUBE/ball	22/32
Jamie	5-Sep	CUBE/ball	40/60
Jamie	9-Sep	CUBE/ball	30/38
Jamie	11-Sep	DONUTS/coffee	28/49
Jamie	16-Sep	DONUTS/coffee	33/60
Jamie	18-Sep	DONUTS/coffee	34/46
Jamie	19-Sep	DONUTS/coffee	24/36
Jamie	23-Sep	DONUTS/coffee	39/74
Jamie	25-Sep	DONUTS/coffee	26/33
Jamie	26-Sep	DONUTS/coffee	16/23

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Jamie	27-Sep	DONUTS/coffee	28/40
Jamie	30-Sep	DONUTS/coffee	25/47
Jamie	2-Oct	DONUTS/coffee	41/66
Jamie	3-Oct	DONUTS/coffee	36/44
Jamie	4-Oct	CUBE/coffee	34/46
Jamie	7-Oct	DONUTS/Hexagons	49/73
Jamie	9-Oct	DONUTS/Hexagons	37/55
Jamie	10-Oct	DONUTS/Hexagons	38/59
Jamie	11-Oct	DONUTS/Hexagons	42/54
Jamie	16-Oct	BUNNY/ball	44/65
Jamie	17-Oct	BUNNY/ball	18/20
Jamie	23-Oct	BAG/Tower	41/56
Jamie	24-Oct	BAG/Tower	3/50
Jamie	25-Oct	BAG/Tower	7/7
Jamie	30-Oct	TOWER/bag	24/35
Jamie	7-Nov	TOWER/bag	19/35
Jamie	13-Nov	TOWER/bag	55/87
Jamie	14-Nov	TOWER/bag	10/16
Jamie	15-Nov	TOWER/bag	11/15
Jamie	20-Nov	TOWER/bag	20/36

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Jamie	21-Nov	TOWER/bag	15/21
Jamie	22-Nov	TOWER/bag	30/48
Jamie	25-Nov	TOWER/bag	46/59
Jamie	27-Nov	TOWER/bag	10/10
Jamie	28-Nov	BAG/Tower	45/76
Jamie	29-Nov	BAG/Tower	44/74
Jamie	2-Dec	BAG/Tower	49/88
Jamie	5-Dec	BAG/Tower	57/89
Jamie	9-Dec	BAG/Tower	45/63
Jamie	11-Dec	BAG/Tower	39/51
Jamie	12-Dec	TOWER/bag	53/85
Jamie	13-Dec	TOWER/bag	48/71
Jamie	16-Dec	TOWER/bag	45/66
Jamie	20-Dec	TOWER/bag	22/28
Jamie	6-Jan	BAG/Tower	54/86
Jamie	9-Jan	BAG/Tower	57/89
Jamie	10-Jan	BAG/Tower	61/94
Jamie	13-Jan	BAG/Tower	53/88
Jamie	15-Jan	BAG/Tower	55/87
Jamie	16-Jan	BAG/Tower	60/83

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Jamie	17-Jan	BAG/Tower	24/30
Lenny	31-Jul	CUBE/ball	38/52
Lenny	1-Aug	CUBE/ball	24/35
Lenny	5-Aug	CUBE/ball	37/61
Lenny	8-Aug	CUBE/ball	50/69
Lenny	9-Aug	CUBE/ball	27/35
Lenny	14-Aug	DONUTS/coffee	18/43
Lenny	15-Aug	DONUTS/coffee	21/30
Lenny	16-Aug	DONUTS/coffee	31/50
Lenny	19-Aug	DONUTS/coffee	36/57
Lenny	21-Aug	DONUTS/coffee	37/57
Lenny	23-Aug	DONUTS/coffee	28/37
Lenny	28-Aug	DONUTS/coffee	1/1
Lenny	30-Aug	CUBE/coffee	25/31
Lenny	4-Sep	BUNNY/ball	32/59
Lenny	5-Sep	BUNNY/ball	18/27
Lenny	6-Sep	BUNNY/ball	18/21
Lenny	9-Sep	DONUTS/Hexagons	23/28
Lenny	11-Sep	BAG/Tower	44/63

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Lenny	16-Sep	BAG/Tower	33/41
Lenny	19-Sep	BAG/Tower	23/45
Lenny	25-Sep	TOWER/bag	36/75
Lenny	26-Sep	TOWER/bag	11/42
Lenny	27-Sep	TOWER/bag	39/75
Lenny	30-Sep	TOWER/bag	35/65
Lenny	2-Oct	TOWER/bag	34/59
Lenny	3-Oct	TOWER/bag	38/55
Lenny	4-Oct	BAG/Tower	50/86
Lenny	7-Oct	BAG/Tower	42/70
Lenny	9-Oct	BAG/Tower	43/63
Lenny	10-Oct	BAG/Tower	18/20
Lenny	16-Oct	TOWER/bag	43/61
Lenny	17-Oct	TOWER/bag	1/1
Lenny	18-Oct	BAG/Tower	18/18
Lenny	21-Oct	TOWER/bag	18/20
Deane	29-Aug	BALL/cube	31/58
Deane	30-Aug	BALL/cube	35/44
Deane	4-Sep	BALL/cube	36/51
Deane	5-Sep	BALL/cube	43/68

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Deane	6-Sep	BALL/cube	5/5
Deane	9-Sep	COFFEE/donuts	45/82
Deane	11-Sep	COFFEE/donuts	38/64
Deane	16-Sep	COFFEE/donuts	29/36
Deane	18-Sep	BALL/donuts	35/46
Deane	19-Sep	COFFEE/bunny	39/50
Deane	23-Sep	HEXAGONS/cube	28/40
Deane	25-Sep	BAG/tower	59/85
Deane	26-Sep	BAG/tower	32/47
Deane	27-Sep	BAG/tower	37/56
Deane	30-Sep	BAG/tower	32/41
Deane	2-Oct	BAG/tower	33/43
Deane	3-Oct	BAG/tower	3/3
Deane	4-Oct	TOWER/bag	45/78
Deane	7-Oct	TOWER/bag	50/82
Deane	9-Oct	TOWER/bag	45/65
Deane	10-Oct	TOWER/bag	39/52
Deane	11-Oct	TOWER/bag	33/40
Deane	21-Oct	TOWER/bag	6/6
Deane	23-Oct	BAG/tower	23/28

Appendix B continued.

Seal	Date	Task	Correct Choices/Trials
Deane	24-Oct	BAG/tower	10/11
Deane	25-Oct	TOWER/bag	29/38
Deane	28-Oct	TOWER/bag	18/21
Deane	30-Oct	BAG/tower	36/47
Deane	31-Oct	BAG/tower	15/16
Deane	1-Nov	TOWER/bag	58/87
Deane	4-Nov	TOWER/bag	22/25

<u>Note</u>. [a]For each task, the object in all capitals was the correct choice.

Appendix C – Experiment 2 Raw Data

Table C1

Trials to Criterion for Control and Experimental Subjects Across Discrimination Tasks for Experiment 2.

	Group			
	Control		Experimental	
	Subject			
Discrimination task	Tyler	Jamie	Lenny	Deane
1	134	113	149	275
2	217	362	371	323
3	389	441	239	39
4	232	250	62	59
5	119	557	18	63
6	391	-	20	112

Note. The dash indicates that this subject did not complete this discrimination (due to lack of time and poor weather conditions).