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PERCEPTION OF COLOR VISION IN THE ASIAN SMALL-CLAWED OTTER

(*AONYX CINEREA*)

by

JOSEPH T. SVOKE

Under the Direction of Dr. Matthew Grober

ABSTRACT

Color vision can affect our assumptions of an animals' natural history. It can be determined by testing sensory or perception ability, which was employed here. Two Asian small-clawed otters (*Aonyx cinerea*), of opposite sexes, housed at ZooAtlanta, were trained via operant conditioning to discriminate stimuli within 7 tasks, primarily in a two-choice fashion. Varying shades of the colors blue, green and red were tested against varying greys, all which differed in intensity, served as the stimuli for the first 4 tasks. The remaining 3 tasks, the colors were tested against each other. The male reached criterion for the first 6 tasks, indicating an ability to discriminate the stimuli based on color. The female however participated only in 2, and could not achieve criterion as set, though there were indications of discrimination ability. Taken together with sensory work on two related otter species, Asian small-clawed otters possess color vision.

INDEX WORDS: Asian small-clawed otter, Color vision, Operant conditioning, Dichromacy, Color discrimination

PERCEPTION OF COLOR VISION IN THE ASIAN SMALL-CLAWED OTTER (*AONYX CINEREA*)

by

JOSEPH T. SVOKE

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

In the College of Arts and Sciences

Georgia State University

2011

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2011

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(*AONYX CINEREA*)

by

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1 INTRODUCTION

1.1 Background

For animals housed in a captive setting, the presence of color vision can affect aspects of daily husbandry; from operant conditioning to environmental enrichment to exhibit design. If found to exist, it has the potential to improve the quality of care that the species receives. The degree of color vision among species has interested many scientists for various reasons. Different techniques have been utilized to analyze the sensory and/or perceptory systems. Kebler et al. (2003) summarize different techniques for testing either; sensory testing in vertebrates often involves the use of electroretinograms, spectrophotometry, or determining the amino acid composition of the opsin, while perception tests frequently use grey card experiments, monochromatic stimuli, or adjusting broadband stimuli at different intensities.

Originally, it was thought that most mammals are colorblind (Jacobs 1981; Padgham & Saunders 1975; Walls 1942). In recent years, this idea has been shown to be incorrect. The use of operant conditioning methods has been gaining in popularity as a strategy for testing perception, yet historically few experiments have employed this technique (Jacobs 1981). This is an important step because, as Birgersson et al. (2001) suggests, behavioral studies are essential to conclusively demonstrate that an animal is at least dichromatic. Just because an animal has been shown to have all the physical structures for the sensory process to function, such as cones, rods, and a nervous system, this does not mean that they all work in conjunction with each other. By testing perceptual ability, conclusions can be made about wether the photoreceptors axons have (or don’t have) direct synaptic connections to the processing areas of the brain (Pichaud et al. 1999).

Similarly, perception work alone has the potential to be misleading. It has been shown through behavioral testing that some species can discriminate different stimuli suggesting color vision, but sensory work shows that the capacity for it does not exist. This often is influenced by the rods present, and/or the ability to perceive ultraviolet light (Jacobs 1993).

Nevertheless, perception testing is revealing that many mammals have at least dichromatic vision. Behavioral testing has revealed evidence for this within certain species of the Orders: Diprodontia, Scandentia, Carnivora, Artiodactyla, Perrisodactyla, Rodentia, Primates and Sirenia. Trichrimatic vision, however, overall is rare. Most noticeably is its existence in apes, as well as old and new world primates. There are conflicting reports about its status in prosimians (Blakeslee & Jacobs 1985; Jacobs 1993). Trichromatic vision is also suggested to exist in two marsupials, the honey possum (*Tarsipes rostratus*) and the fat-tailed dunnart (*Sminthopsis crassicaudata*) (Arrese et al. 2002). Conflicting results have been reported for the domestic cat with some reporting they are trichromatic (Ringo et al. 1977), whereas others say that there is no active mechanism (Loop et al. 1985).

1.2 Perception Testing

Behavioral assessment of color vision is a growing area of study. Recent use of this technique has extended to species such as the American black bear (Bacon & Burghardt 1976), the giant panda (Kelling et al. 2006), fallow deer (Birgersson et al. 2001), manatee (Griebel & Schmid 1996), tammar wallaby (Hemmi 1999), California sea lions (Griebel & Schmid 1992), and coatis (Chausseil 1992). Within these studies, various operant

conditioning procedures were used, but all relied on variations to 2 or 3 choice discrimination tasks.

An important aspect to note is the need to control for the brightness of the stimuli used. This traditionally has been a problem (Jacobs 1981), but different methods have been developed to handle this. Kebler et al. (2003) summarized that there are three ways to test the perceptual ability of a species: (a) discrimination of a fixed color from a series of grey shades; (b) discrimination of monochromatic colors, which can be changed in intensities; (c) discrimination of two broadband stimuli that can be adjusted such that either one or the other emits more photons over the entire spectrum. Typically these are used in concurrence with associative/discrimative learning originally in a training phase before being applied to testing.

1.3 Asian small-clawed otters (*Aonyx cinerea*)

Asian small clawed otters (ASCO) are one of thirteen recognized species of otters (IUCN 2010). This species has some specialized characteristics that differentiate it from other otter species. Not only are they the smallest of all otters, but they are found to be the most tactile. Also, ASCO's are found to be the most terrestrial though their diet is primarily aquatic. Due to this fact, their visual system may be adapted for life in both terrains, or may be better in one terrain. Due to their natural history duality, ASCO's may be an important species to test, as they could serve as an intermediary species when comparing entirely terrestrial and entirely aquatic species.

Though no published work can be found for the existence of color vision in ASCO's, the effect that aquatic and terrestrial living has on their visual acuity has been studied. Balliet & Schusterman (1971) state that the eye "was emmetropic in air with

adaptations for underwater living", but acuity was functionally the same in both environments. It has also been shown that, with the appropriate brightness of light, visual acuity is equivalent in air and in water, and is only affected under dark lighting conditions where it is better on land (Schusterman & Barrett 1973).

1.4 Mustelids

Generally known as the "weasel" family, Mustelids are subdivided into two subfamilies, Lutrinae and Mustelinae; color vision studies have been attempted in both. This work consisted of either sensory or perception tests, but not both.

For subfamily Lutrinae, work was completed on the sea otter (*Enhydra lutris*) and the European river otter (*Lutra lutra*). The European river otter, with the use of immunocytochemistry, was shown to have many characteristics typically found in diurnal mammals with typical amounts of S- and L-cone densities, and rod photopigments outnumbering that of cones (Peichl et al. 2001). Work by Levenson et al. (2006) sequencing retinal mRNA has shown that sea otters' eyes contain rod pigments with a spectral peak sensitivity of 499 or 501 nm, a M/L cone pigment of 545 to 560 nm, and a S cones with a maximum of ~440 nm, which would imply dichromatic color vision in a blue-green range. The retinal structure and organization of the sea otter has also been documented to be more like that of terrestrial mammals, than to that of aquatic mammals (Mass & Supin 2007). It has been suggested that because of feeding behavior, food type and the heavy use of sensitive forelimbs to catch prey the visual acuity of the sea otter should be relatively similar to that of the Asian small-clawed otters (Estes 1989).

For Mustelinae, five species have been studied. In her review, Ducker (1964) summarized that the polecat (*Putorium putorius*), pine-marten (*Martes martes*), stoat

(*Mustela erminea*), domestic ferret (*Putorius furo*), and the mink (*Putorius lutreola*) all show capacity to see some color. However, Jacobs (1993) questioned these results stating "there is no good way to evaluate the quality of these claims". In other experiments using sensory tests, the mink (Dubin & Turner 1977) and the ferret (Calderone & Jacobs 2003) were shown to have the physiological mechanisms present for color vision.

1.5 Marine and Amphibious Mammals

Amphibious species such as the polar bear (*Thalarctos maritimus*), the pygmy hippopotamus (*Choreopsis liberiensis*), and the river hippopotamus (*Hippopotamus amphibius*) spend time on land and in water, much like the Asian small-clawed otter. The first two, respectively, are believed to have color vision. The polar bear has been examined behaviorally (Ronald & Lee 1981) and anatomically (Levenson et al. 2006), whereas the pygmy hippo has only been examined anatomically and was found to have two separate cones (Peichl et al. 2001). At this time there are limited data for the river hippopotamus. Levenson & Dizon (2003) looked only at the short-wavelength sensitive (SWS) cone for the river hippopotamus. It was shown to be functional, but no conclusions were drawn about the existence of a long-wavelength sensitive (LWS) cone.

Evidence in pinnipeds as a whole is not as clear, because sensory and perception work are conflicting. Sensory work done on a number of different pinniped species suggests monochromacy (Griebel & Peichl 2003; Levenson et al. 2006; Peichl et al. 2001) due to the lack of the S-cone, while only having the L-cone present. However, Griebel & Peichl (2003) mention that four species of seals as well as the southern sea lion were able to pass some discrimination tasks. Griebel & Schmid (1992) also showed that

three individual California sea lions (*Zalophus californianus*) were able to distinguish blue and green from shades of grey. This presents the question that if only one cone is present, how were they able to pass a discrimination tasks? It has been suggested that the rods had some influence in these cases (Griebel & Peichl 2003; Jacobs 1993).

Research completed on exclusively marine species is more straightforward. Griebel & Schmid (1996) demonstrated that the manatee (*Trichechus manatus*), a sirenian, was able to distinguish blue and green from shades of grey. The cetaceans differ, though, in that they are monochromates. Peichl et al. (2001) showed that seven different species in the Order Odontoceti (toothed whales) lack the S-cone. Similar results were seen by Levenson & Dizon (2003) in the species that they tested. This was due to the existence of a nonfunctioning visual pigment protein for the SWS cone opsin gene. The bootlenose dolphin (*Tursiops truncatus*) was tested in both studies as well, reporting the lack of the SWS cone (Levenson & Dizon 2003; Peichl et al. 2001). Fasick et al. (1998) found that there are deletions to the non-expressed SWS opsins, when comparing it to the cDNA of other mammalian species, though they do state that "the dolphin therefore lacks the common dichromatic form of color vision typical of most terrestrial mammals". However, Griebel & Schmid (2002) behaviorally found the potential for dichromatic vision, though the rods probably influenced the results. For the Order Mysticeti, Levenson & Dizon (2003) reported the absence of a SWS cone visual pigment, consequently this Order is believed to lack color vision.

1.6 Purpose

No perceptional color vision work for any species within the subfamily Lutrinae has been published to date. This is also true for the majority of the Mustelidae family.

Sensory evidence exists in two related otter species, however, suggesting the existence of dichromatic vision. This study is the first to test the Asian small-clawed otter using discrimination training. By controlling the intensity of the stimuli presented via a pseudorandom presentation of varying hues of the color and grey, the possibility of choices being made for reasons other than "color" were eliminated in this study.

2 MATERIALS AND METHODS

2.1 Subjects

Four individuals, two males and two females, housed at Zoo Atlanta were trained to participate in the study. This included the dominant breeding pair, male "Moe", born September 1993, and female "Nava Lee", born October 2000. The remaining two individuals were offspring from two separate litters, a female "Harry", born March 2005, and a male "Bugsy", born September 2005.

In all, nine individuals lived within the family group at the start of the experiment. All nine otters routinely take part in training sessions individually with approved keepers. This traditionally occurs during one of their three feeding sessions. These four individuals were selected to participate based on their overall demeanor, and their operant conditioning ability.

2.2 Stimuli and Apparatus

Stimuli were presented as a two choice discrimination task, with one positive and one negative. Positive stimuli consisted of white and 5 shades each of blue, green and red. The negative stimuli consisted of 11 shades of grey, which varied in intensity, for the training task and the first 4 experimental tasks. For the remaining tasks (5-7) grey was not an option as colors were tested versus each other, resulting in green or red

serving as the negative stimuli. Each stimulus was cut to a 13x17 cm rectangle card, and laminated for protection, from an original rectangle of size 22.5x17 cm. The remaining section was later attached to a stick and used as a "station" for the otter. Each rectangle was created from Microsoft Paint Version 5.0 and printed via a color laser printer. Each stimulus card was labeled on the back for identification. The transmission spectrum was determined for all stimuli, via a Spectrascan 650, after lamination (Table 1).

The station consisted of a 0.9 meter piece of 0.6 cm diameter wooden dowel rod (Figure 1) with either white, or the middle shade of blue, green and red (depending on the task) attached with Velcro to one end. This allowed an experimenter to easily present the station in front of their feet, at a level appropriate for the otter, and then being able to remove it without interfering with the otter's line of sight.

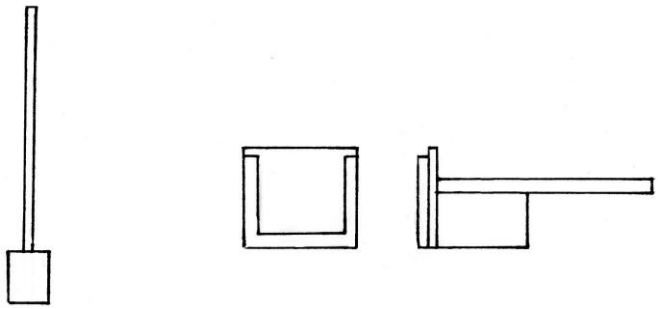

Figure 1 – Representation of the "station" stick and the stimuli holder (front and side view).

Two individual stimuli holders were built (Figure 1) to serve as the apparatus. These were placed on premarked areas of the testing field during each session. The front of each holder consisted of a 15 cm x 15 cm flat board with 0.6 cm metal U-channel on

Table 1 – Overview of the transmission spectra, represented in percent reflectance, for stimuli used at varying wavelengths. Bolded data represents peak reflectance for that stimulus.

% Reflectance at Wavelength	Stimuli	Grey 1	Grey 3	Grey 5	Grey 7	Grey 9	Grey 11	Blue 1	Blue 2	Blue 3	Blue 4	Blue 5	Grn 1	Grn 2	Grn 3	Grn 4	Grn 5	Red 1	Red 2	Red 3	Red 4	Red 5
	380	2.90	3.65	11.39	25.62	50.50	80.53	4.23	7.55	8.01	8.72	34.93	5.11	4.07	4.73	7.10	27.64	8.11	6.20	10.49	18.87	46.06
	392	2.98	5.36	13.03	27.97	52.37	86.09	7.81	11.60	12.21	18.11	47.75	4.81	4.78	5.40	9.20	31.41	6.49	6.95	9.61	17.76	49.26
	404	5.20	7.41	15.42	32.60	54.83	86.91	15.10	20.64	24.16	31.79	61.10	6.62	7.32	7.79	12.82	35.67	8.35	8.29	10.19	19.75	51.91
	416	7.04	9.35	18.01	35.11	58.19	88.87	19.64	26.89	31.88	39.83	67.69	8.79	9.47	10.30	15.73	39.13	10.26	10.16	11.99	21.54	52.92
	428	7.21	9.70	18.28	35.73	58.73	89.92	22.25	31.64	39.16	47.02	72.96	8.73	9.77	10.90	16.93	41.25	10.20	10.20	12.08	21.26	52.57
	444	7.27	9.89	18.81	36.79	60.38	90.88	25.75	38.49	49.86	56.84	79.43	9.28	10.44	11.85	19.08	45.06	10.31	10.18	12.05	20.80	52.31
	448	7.34	10.00	18.99	37.09	60.95	91.18	26.32	39.60	**51.54**	**58.28**	**80.14**	9.51	10.75	12.24	19.80	46.06	10.28	10.22	12.13	20.59	51.96
	452	7.33	9.99	19.07	37.30	61.27	91.55	**26.33**	**39.62**	51.53	58.18	79.97	9.67	11.03	12.62	20.41	46.82	10.31	10.14	12.03	20.59	51.68
	456	7.33	10.01	19.08	37.44	61.66	91.76	26.21	39.40	51.07	57.64	79.39	9.88	11.28	12.98	21.05	47.51	10.28	10.20	12.02	20.40	51.40
	468	7.31	10.02	19.16	37.94	62.57	92.15	25.45	37.94	48.43	54.96	77.17	10.77	12.50	14.67	23.35	50.07	10.34	10.20	12.10	20.04	50.94
	480	7.34	10.16	19.50	39.06	94.85	93.47	24.09	35.08	43.22	49.74	73.08	13.95	16.37	19.58	29.15	55.83	10.82	10.66	12.70	20.47	51.00
	492	7.36	10.42	20.09	41.00	68.57	95.32	22.63	31.97	37.66	44.24	68.55	23.05	27.10	32.19	42.04	66.67	11.88	11.72	13.96	22.39	52.48
	504	7.38	10.58	20.51	42.26	71.26	96.53	20.75	28.32	32.23	38.77	63.98	35.52	41.79	49.68	56.47	76.03	12.56	12.41	14.63	23.79	53.30
	508	7.41	10.58	20.43	42.19	71.42	96.57	19.81	26.76	30.17	36.70	62.15	37.39	44.08	52.93	58.33	**76.82**	12.27	12.11	14.22	23.34	52.56
	512	7.42	10.51	20.23	41.85	71.10	96.56	18.70	24.91	27.83	34.29	59.90	**37.84**	**44.72**	54.59	**58.72**	76.62	11.67	11.56	13.49	22.40	51.30
	516	7.40	10.38	19.90	41.26	70.36	96.43	17.41	22.83	25.30	31.64	57.28	36.99	43.90	**54.63**	57.76	75.48	10.92	10.81	12.61	21.19	49.55
	520	7.41	10.28	19.59	40.67	69.68	96.28	16.18	20.82	22.91	29.09	54.72	35.32	42.05	53.50	56.03	73.86	10.25	10.11	11.67	19.92	47.82
	532	7.39	9.84	18.45	38.51	66.95	95.40	12.99	15.72	16.76	22.25	47.41	27.24	32.84	45.36	47.02	66.06	8.89	8.79	10.09	17.37	43.97
	544	7.34	9.48	17.42	36.74	64.04	94.04	10.98	12.53	12.94	17.68	42.13	19.45	23.80	36.18	37.75	57.33	8.85	8.78	10.16	17.59	44.36
	556	7.38	9.24	16.71	35.19	62.36	93.50	9.79	10.44	10.44	14.22	37.24	14.17	17.48	28.80	30.38	49.96	8.74	8.66	10.06	17.32	43.90
	568	7.45	9.09	16.15	33.95	60.60	92.70	9.24	9.43	9.26	12.25	33.87	11.20	13.78	24.00	25.58	44.70	9.03	8.94	10.49	17.87	44.65
	580	7.51	9.30	16.57	34.67	61.33	92.77	9.39	9.50	9.24	12.21	34.24	10.14	12.30	21.84	23.47	42.24	12.59	12.50	15.50	25.01	53.98
	592	7.51	9.63	17.42	36.20	63.39	93.35	9.65	9.75	9.43	12.73	36.02	9.56	11.45	20.50	22.15	40.62	24.13	24.14	33.15	45.00	72.86
	604	7.56	9.81	17.86	36.86	64.43	93.81	9.71	9.71	9.33	12.76	36.44	9.17	10.84	19.43	21.08	39.36	36.93	37.20	57.17	67.25	87.47
	616	7.60	9.91	18.09	37.12	64.98	94.12	9.71	9.63	9.21	12.60	36.36	8.97	10.51	18.82	20.50	38.66	45.29	45.78	77.59	82.82	95.13
	628	7.63	9.96	18.27	37.25	65.52	94.58	9.69	9.55	9.11	12.50	36.30	8.88	10.36	18.48	20.14	38.33	48.94	49.54	88.49	90.01	98.19
	640	7.73	10.07	18.54	37.61	66.50	95.25	9.77	9.54	9.11	12.47	36.33	8.87	10.34	18.41	20.03	38.27	50.49	51.06	93.23	92.99	99.79
	656	7.93	10.37	19.23	38.55	68.10	96.12	10.07	9.85	9.32	12.97	37.50	9.23	10.71	18.94	20.70	39.26	51.52	52.04	95.23	94.02	100.58
	668	8.30	10.81	20.49	40.07	71.23	98.23	10.81	10.42	9.94	13.74	39.36	9.82	11.34	19.69	21.55	40.59	52.55	52.93	95.71	94.64	101.92
	680	8.81	11.29	21.50	41.24	74.31	100.62	11.41	10.83	10.25	14.02	39.79	10.15	11.50	19.58	21.33	41.39	52.91	53.17	95.87	94.71	102.81
	692	8.87	11.72	22.32	42.29	77.20	102.06	11.70	10.99	10.17	13.96	40.34	10.26	11.37	19.35	21.32	41.02	53.12	53.42	96.69	95.49	104.25
	700	9.37	12.00	23.54	43.03	80.78	105.27	12.25	11.34	10.38	14.20	40.26	10.54	11.53	19.01	20.47	41.03	53.64	53.59	96.71	95.40	105.68
	704	9.53	12.34	24.07	43.38	82.26	105.43	12.63	11.67	10.94	14.41	40.39	10.38	11.45	18.54	20.51	40.44	53.60	53.66	96.70	95.47	106.02
	708	9.85	12.55	24.67	44.04	83.67	108.00	13.01	12.03	11.24	14.13	40.98	10.60	11.70	18.42	19.99	41.17	**53.96**	**53.73**	**96.98**	**95.83**	**107.01**
	712	9.90	12.49	24.45	43.35	82.73	106.22	12.96	11.78	10.26	13.44	39.71	10.42	11.45	18.19	19.83	40.67	52.53	52.54	96.98	93.16	104.85
	720	9.55	11.92	24.49	43.36	83.04	106.07	12.68	11.69	11.03	13.65	40.85	10.35	11.38	18.59	20.26	40.11	52.39	52.34	94.37	93.29	104.65
	728	10.19	13.21	25.88	44.08	87.25	108.11	13.75	12.18	11.02	13.97	41.49	10.98	11.44	18.84	20.65	42.88	53.24	52.42	94.96	93.37	107.13
	740	10.40	14.01	29.72	48.86	95.95	116.28	15.39	14.40	13.97	16.56	46.56	12.32	12.43	21.96	23.10	46.83	54.63	54.39	94.61	94.68	109.64
	756	9.93	13.79	30.37	51.61	99.16	111.25	20.17	22.35	21.41	27.81	61.50	21.04	21.94	33.11	34.32	58.33	56.19	55.14	89.16	90.94	102.42
	768	**10.96**	**16.11**	**33.83**	56.76	**111.01**	114.34	33.09	39.92	42.60	48.37	83.35	39.61	43.15	52.18	53.45	81.08	58.06	58.11	88.41	89.15	105.12
	780	8.65	14.84	34.14	**60.55**	109.09	**121.90**	39.83	51.23	57.03	64.04	89.73	51.23	54.84	60.40	61.17	89.47	55.74	56.20	81.58	83.13	102.27

three sides, so that the stimuli could be slid into the apparatus and held in place. Attached to the back was a handle made of 1.3 cm square dowel rod with a piece of 1.3 cm plywood running half the length of the handle. This piece served to keep the stimuli perpendicular to the floor, to reduce any potential glare from overhead lighting. Each holder was positioned approximately 2.3 meters from the "station", and 30 cm apart from each other.

The testing area consisted of one side of the off-exhibit holding space at ZooAtlanta. This area measured 3.35 meters wide by 5.64 meters long, and consisted of a flat upper area (3.20 meters long) and a lowered pool area (2.44 meters long).

2.3 Training

Each otter was trained using positive reinforcement in a non-corrective manner. A non-corrective technique was selected because it has been shown that animals learn faster (Allison 1972) and require fewer reinforcements (Towart & Smith 1966) under this paradigm, which allows for more training to occur during each session. Initially, a pseudoholder (a white board with a handle attached to the back) was created and presented to each subject while it was participating in normal maintenance training. Later, a combination of preexisting and newly trained behaviors were introduced in conjunction with the pseudoholder.

Because the otters did not have a pre-existing remote behavior established, a new behavior, with the given command "select", had to be shaped. To accomplish this, two different behaviors were shaped separately and later chained together for an appropriate response. For the first behavior, the trainer started with placing a regularly used target stick next to the pseudoholder and having the otter target. Next, as the otter moved

toward the target stick, a “select” command was given, while the target stick was lifted away from the stimulus. If the subject touched the stimulus, it was bridged and reinforced. This step was still in very close proximity of the trainer/otter to the pseudoholder. Next, the use of the target stick was slowly eliminated as part of the cue. Following this, the trainer started to move further away from the pseudoholder, employing the use of a directional hand/arm movement with the “select” command. This continued until an appropriate distance was reached, followed by the lessening of the directionality of the cue, until the proper cue was established. This proper cue consisted of a closed fist being opened with splayed fingers, to eliminate any potential directionality, with the addition of a “select” command verbally given.

Secondly the “station” had to be established. This initially was trained via a stick with a white card. The trainer would place it in front of the otter so it could habituate to it. As the otters became more comfortable, they were asked to “hold”, making sure that they were facing the “station” in a relaxed manner. This typically resulted in them lying on their abdomens, while staring forward at the station. Once this was accomplished, both behaviors “hold” and “station” were paired together in close proximity to the pseudoholder.

During this time, the otter had to touch the pseudoholder square with its nose when asked in order to receive food reinforcement. This procedure continued, with the trainer (later experimenter 1) moving farther away from the psuedoholder, until the appropriate distance away was achieved. As the trainer moved farther away, previously trained behaviors “come” and “hold” were added. After touching the square, the otter was asked to “come”, resulting in the otter returning to the trainer. Once at the correct

distance, a second individual (later experimenter 2) was added so the otter could habituate to two people being present, but also allowing for the pseudoholder to be repositioned to various locations within the future testing area. This second individual took a position within the drained pool of the holding area so as to be out of the testing field. The "hold" command was given after the otter "stationed" to allow time for the stimuli to be changed or repositioned.

Table 2 – Examples of predetermined stimuli presentations for a session within the training task, task 4, and task 5.

White vs Grey (Training Task)		Red vs Grey (Task 4)		Blue vs Green (Task 5)	
Grey 10	White	Red 2	Grey 4	Blue 5	Green 1
White	Grey 11	Red 1	Grey 11	Green 5	Blue 3
White	Grey 8	Grey 8	Red 2	Green 4	Blue 3
White	Grey 1	Red 4	Grey 5	Blue 1	Green 1
Grey 5	White	Red 1	Grey 1	Blue 4	Green 5
White	Grey 1	Grey 11	Red 1	Blue 5	Green 3
White	Grey 6	Grey 2	Red 5	Green 4	Blue 4
Grey 10	White	Red 1	Grey 7	Green 4	Blue 3
Grey 1	White	Grey 5	Red 3	Blue 4	Green 5
White	Grey 8	Red 4	Grey 8	Green 1	Blue 1
Grey 11	White	Red 3	Grey 2	Blue 4	Green 5
White	Grey 5	Grey 2	Red 4	Green 1	Blue 2
Grey 3	White	Red 2	Grey 3	Green 5	Blue 5
White	Grey 1	Grey 6	Red 2	Blue 3	Green 3
Grey 4	White	Grey 4	Red 5	Blue 5	Green 4

Before testing could occur, each otter went through a training task requiring selection of the white stimulus from a pseudorandomly chosen shade of grey (Table 2). At this point the actual stimuli holders were used to present the stimuli. During this time, the trainer's posture (i.e. experimenter 1) and line of sight had to be controlled. After giving the "select" command, experimenter 1 looked in a direction perpendicular to the presented stimuli. Experimenter 1 also stood in the same location, which was made possible by using a drain cover as a guide. Selection of the white stimulus (positive

stimulus) was followed by an auditory conditioned reinforcer, or bridge (i.e. whistle), followed by a primary food reinforcer (capelin, smelt or cat food) dropped to the floor in front of the otter. After criterion of 12 correct out of 15 trials (80%) was reached for two consecutive days, the testing phase began.

2.4 Testing

The positive stimulus (white, green, blue or red) and negative stimulus (a shade of grey for the first 4 tasks, followed by green or red for the last three) were inserted into the apparatus and presented in a pseudorandom position chosen prior to the start of each session (Table 2). Each position of the stimuli was pseudorandomly chosen so as not to bias any selection method executed by the otter. Alterations were made only to prevent the positive/negative stimulus from occuring more than three times in a row on one particular side. Also, the same stimulus was not to be used more than three times in a row, regardless of its position.

Each session began with the otter stationing in front of experimenter 1 and the apparatus being perpendicular to both. Experimenter 2 conveyed their readiness, by the sound of the stimuli holders being placed on the concrete ground. The otter was then released to make a choice once given the “select” command; at this time the otter was free to move towards the apparatus in any fashion. A selection was determined by the first stimuli touched. It was either scored as “correct” for the positive stimulus and the whistle sounded by experimenter 2, or “incorrect” if the negative stimulus was chosen, and no bridge given. Once a selection was made, the otter was asked to “come” by experimenter 1, resulting in food reinforcement being given for a correct response. The otter was then asked to station via a “hold” command, which allowed for the stimuli to be

changed by experimenter 2 for the next trial. If an incorrect choice was made, no food reinforcement was offered, but the "hold" command was still given.

Seven experimental tasks were to be conducted as follows:

Task 1 - White (positive) versus two grey comparison stimuli (negative) for each trial.
Task 2 - Blue versus one shade of grey.
Task 3 - Green versus one shade of grey.
Task 4 - Red versus one shade of grey.
Task 5 - Blue versus one shade of green.
Task 6 - Blue versus one shade of red.
Task 7 - Green versus one shade of red.

One alteration was made during the experiment for "Harry". Beginning with Task 3, she was able to decide what the positive stimulus was for that particular session. This was determined by the first stimulus that she touched during the initial trial of that session. Because of this, the positive stimulus could have either been the green or grey stimulus.

2.5 Criterion

For the two choice discrimination tasks, criterion was set at 12 correct out of 15 trails, or 80%, with a chance probability of 1.758×10^{-2}. Criterion was set at 11 correct out of 15 trails, or 73%, correct for the three choice discrimination task, a chance probability is 1.807×10^{-3}.

According to binomial distribution calculation, criterion performance will be higher than that of chance performance ($p<0.05$). This criterion was to be reached for two consecutive testing days in order to pass that task.

3 RESULTS

3.1 “Bugsy”

Training Task

Criterion was reached after the completion of 34 total sessions (Figure 2). The final two sessions both ended with 12 of 15 trials correct, or chance probability of 1.758×10^{-2} each. For the last 30 sessions combined, chance probability existed at 7.155×10^{-4}.

Task 1

Criterion was reached after the completion of 22 total sessions (Figure 2). The final two sessions both ended with 11 of 15 trials correct, or chance probability of 1.807×10^{-3} each. For the last 30 sessions combined, chance probability existed at 8.752×10^{-6}.

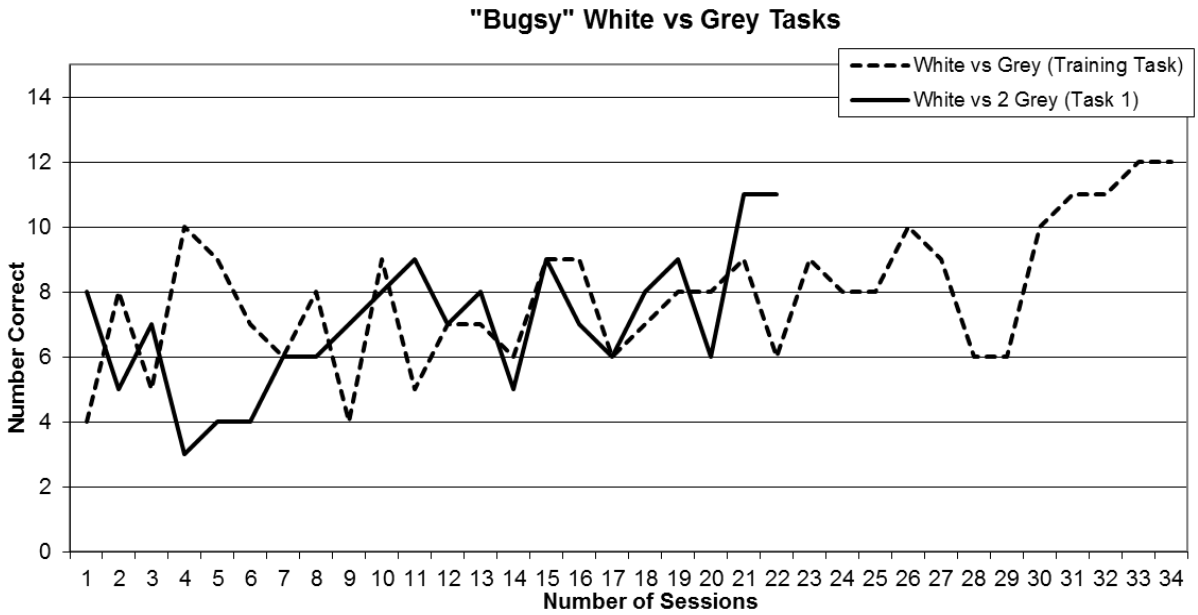

Figure 2 – Number of sessions to reach criterion by “Bugsy” for the training task (white versus 1 grey) and Task 1 (white versus 2 grey).

Task 2

Criterion was reached after the completion of 30 total sessions (Figure 3). The final two sessions ended with 12 of 15 and 13 of 15 trials correct, or chance probability of 1.758×10^{-2} and 3.693×10^{-3}, respectively. For the last 30 sessions combined, chance probability existed at 1.625×10^{-4}.

Task 3

Criterion was reached after the completion of 6 total sessions (Figure 3). The final two sessions ended with 12 of 15 and 13 of 15 trials correct, or chance probability of 1.758×10^{-2} and 3.693×10^{-3}, respectively. For the last 30 sessions combined, chance probability existed at 1.625×10^{-4}.

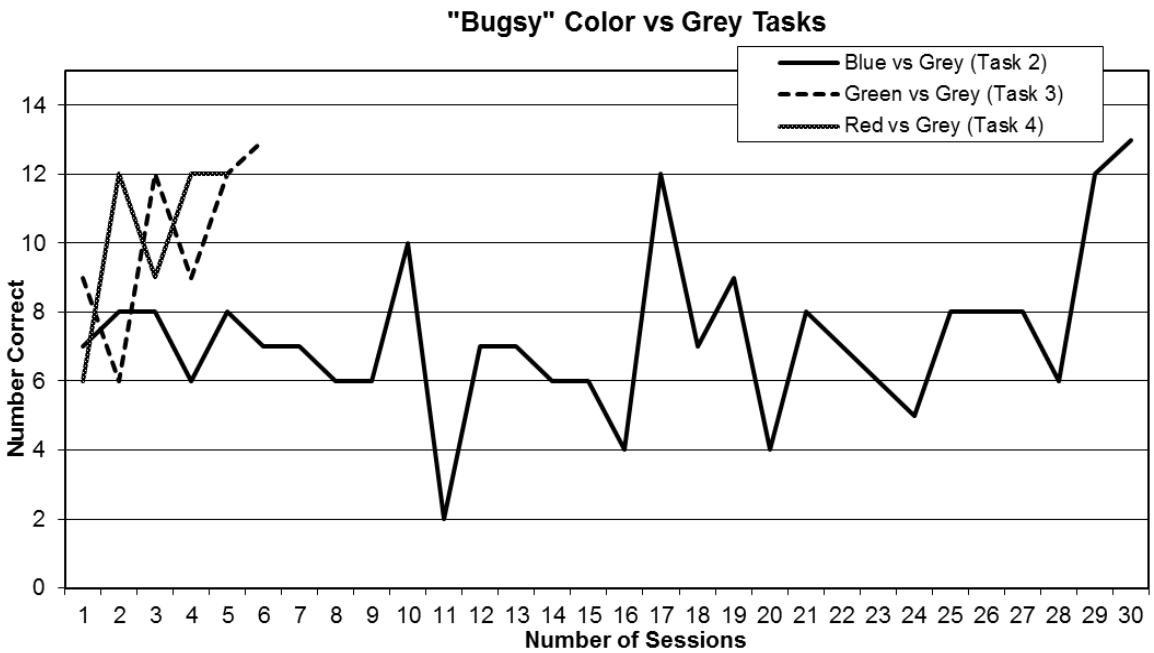

Figure 3 – Number of sessions to reach criterion by "Bugsy" for Task 2 (blue versus grey), Task 3 (green versus grey) and Task 4 (red versus grey).

Task 4

Criterion was reached after the completion of 5 total sessions (Figure 3). The final two sessions both ended with 12 of 15 trials correct, or chance probability of 1.758×10^{-2} each. For the last 30 sessions combined, chance probability existed at 7.155×10^{-4}.

Task 5

Criterion was reached after the completion of 46 total sessions (Figure 4). The final two sessions both ended with 12 of 15 trials correct, or chance probability of 1.758×10^{-2} each. For the last 30 sessions combined, chance probability existed at 7.155×10^{-4}.

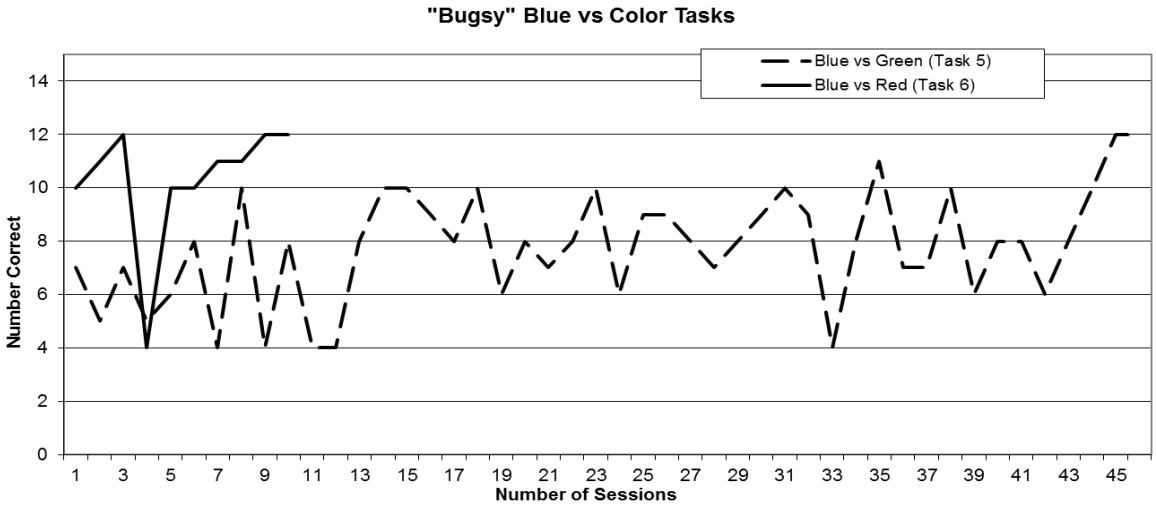

Figure 4 – Number of sessions to reach criterion by "Bugsy" for Task 5 (blue versus green) and Task 6 (blue versus red).

Task 6

Criterion was reached after the completion of 10 total sessions (Figure 4). The final two sessions both ended with 12 of 15 trials correct, or chance probability of 1.758×10^{-2} each. For the last 30 sessions combined, chance probability existed at 7.155×10^{-4}.

Task 7

Criterion was not reached based on previous set requirements after 34 sessions (Figure 5). Because of time constraints and the lack of behavioral evidence that "Bugsy" was able to distinguish shades of green from the shades of red, testing was stopped.

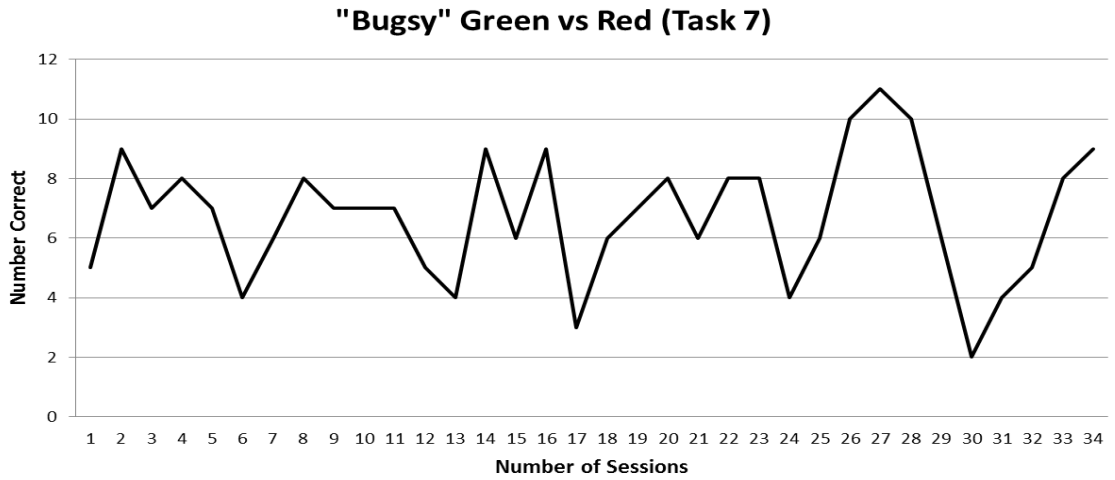

Figure 5 – Number correct for sessions that "Bugsy" participated in for Task 7 (green versus red).

3.2 "Harry"

Training Task

Criterion was reached after the completion of 4 total sessions (Figure 6). The final two sessions both ended with 12 of 15 and 13 of 15 trials correct, or chance probability of 1.758×10^{-2} and 3.693×10^{-3}, respectively. For the last 30 sessions combined, chance probability existed at 1.625×10^{-4}.

Task 1

She was not asked to participate in this task because of changes to the formatting of the experiment based on "Bugsy's" earlier reactions. The original three-choice task was abandoned for what was seen as a more favorable two-choice discrimination task.

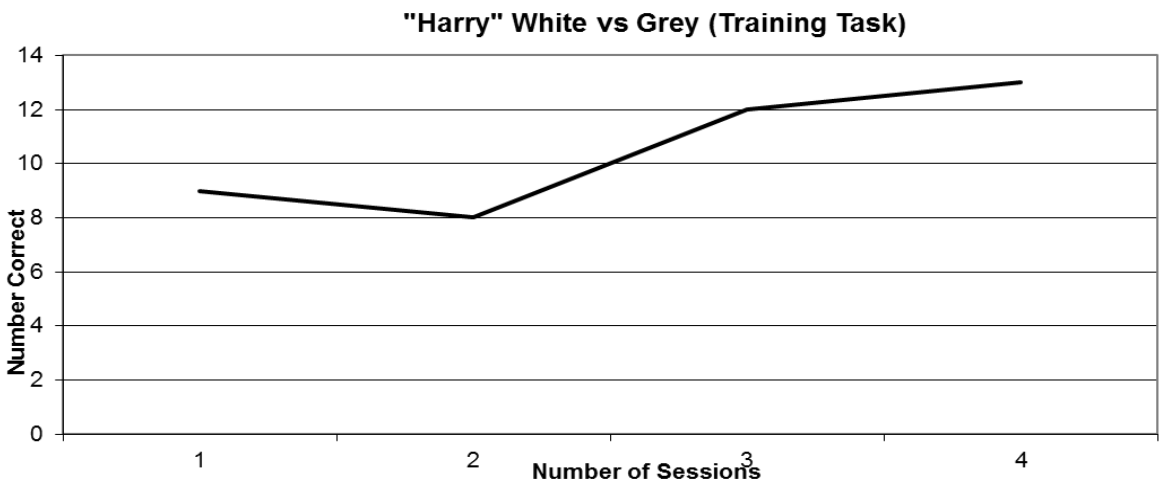

Figure 6 – Number of sessions to reach criterion by "Harry" for the training task (white versus 1 grey).

Task 2

Criterion was not reached based on previous set requirements after 48 sessions (Figure 7). Based on no observational or experimental evidence that she was learning that blue was the positive stimulus, this task was abandoned in hopes that another task would yield a more positive result.

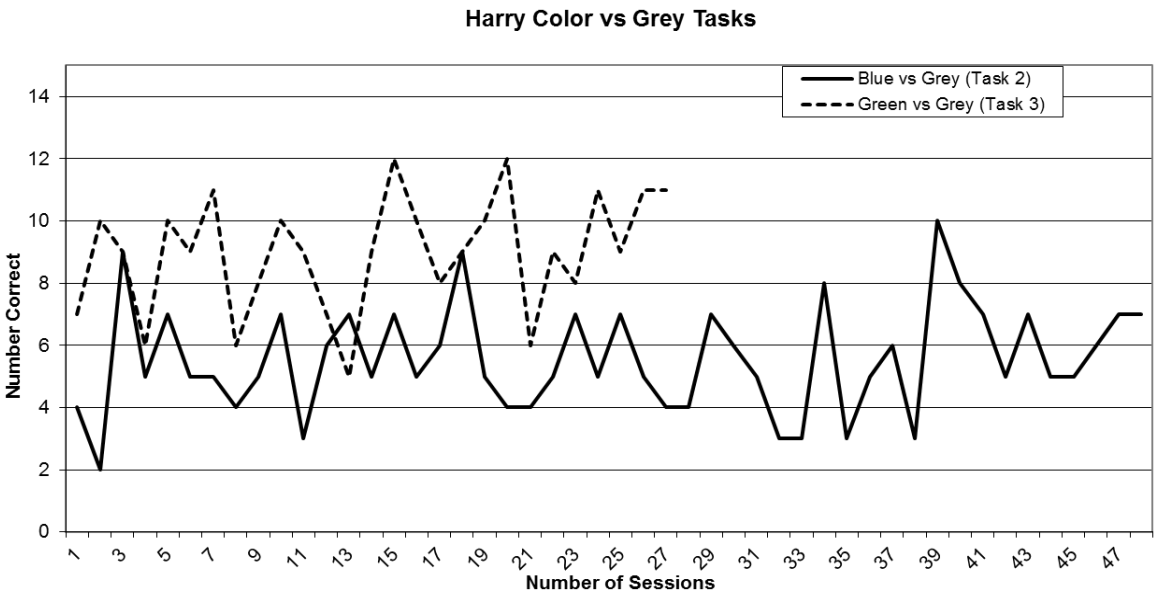

Figure 7 – Number correct for sessions that "Harry" participated in for Task 2 (blue versus grey) and Task 3 (green versus grey).

Task 3

Criterion was not reached based on previous set requirements after 27 sessions (Figure 7). Though correct responses were more favorable than the previous task (Task 2), no consistent evidence was present that she was able to retain information about what the positive stimulus was. Also, because of time constraints, testing was stopped.

"Harry" had the option during this task to choose the positive stimulus for each session, determined by the first stimulus touched. Based on this, she selected green as the positive stimulus 24 out of a possible 27 sessions, a chance probability of 2.46×10^{-5}.

3.3 "Moe"

"Moe" was completely trained for the behavior, but no data could be obtained from him because of vision concerns that developed.

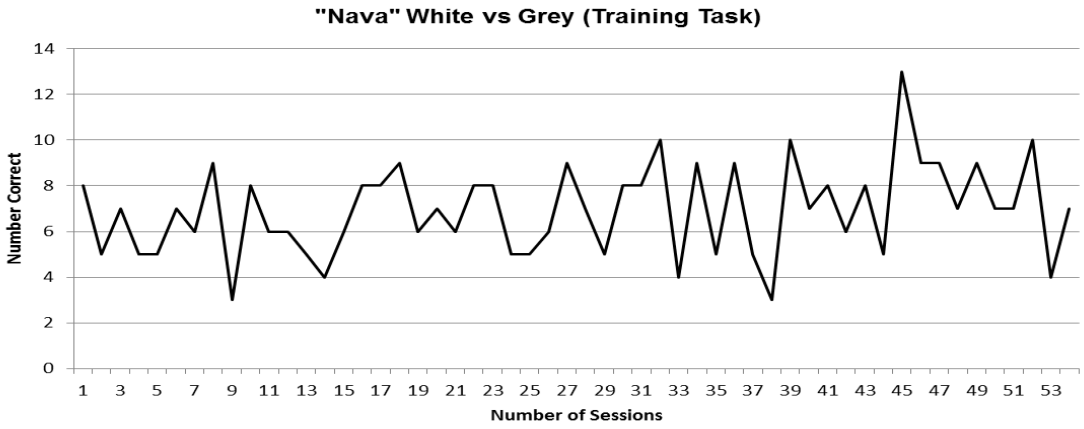

Figure 8 – Number correct for the session completed by "Nava" during the training task.

3.4 "Nava"

"Nava" was never able to fully complete the requirements to reach appropriate criterion for the training task. Overall, she was asked to participate in a total of 54 sessions (Figure 8). During this time, she was only able to reach criterion during one

session, getting 13 out of 15 correct. The following testing date she only was able to achieve 9 correct, resulting in a failure.

4 DISCUSSION

4.1 “Bugsy”

By first completing the training task, white versus shades of grey, it showed that he had the ability to discriminate between different stimuli through an operant conditioning method. Thus, there was the potential to participate in a color discrimination task. By “Bugsy” passing 6 experimental tasks, it showed that he was able to discriminate between the stimuli, probably by differences in color. The movements and placements of the experimenters were controlled, thus allowing him to attend to differences in the stimuli. As mentioned earlier, the importance of controlling for differences in the intensity of the stimuli is highly important. This was done by varying the hues of the stimuli presented, resulting in ever changing intensities (Figure 9 and 10). The size and placement of the stimuli in the surroundings were also controlled

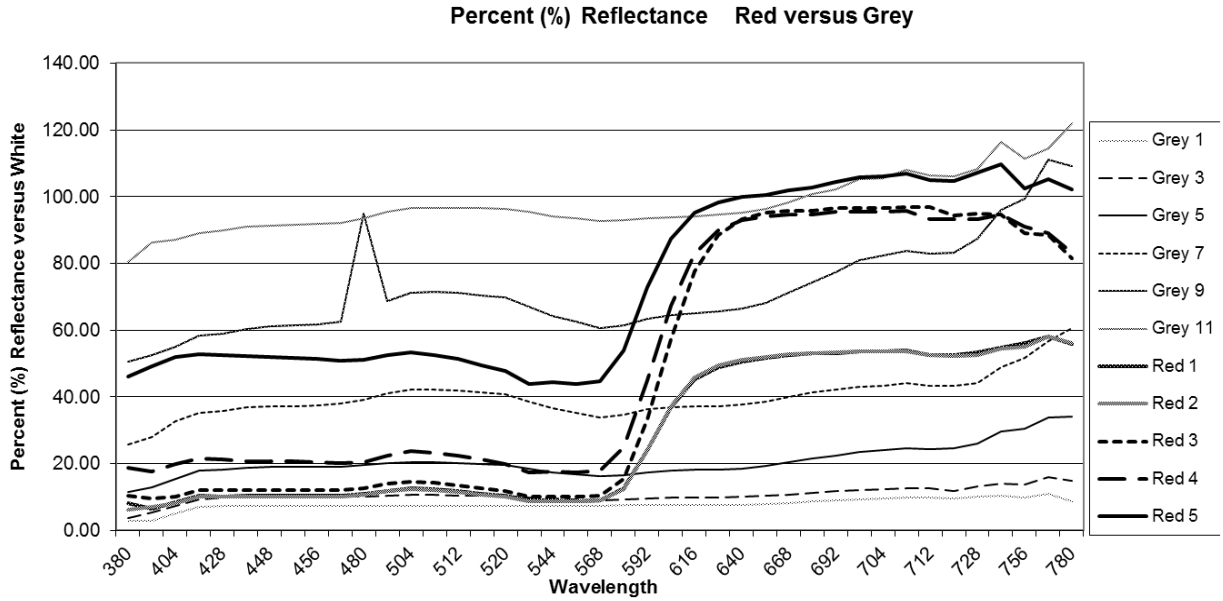

Figure 9 – Transmission spectra relationship between the red and grey stimuli used within each session of Task 4, based on their comparison to white.

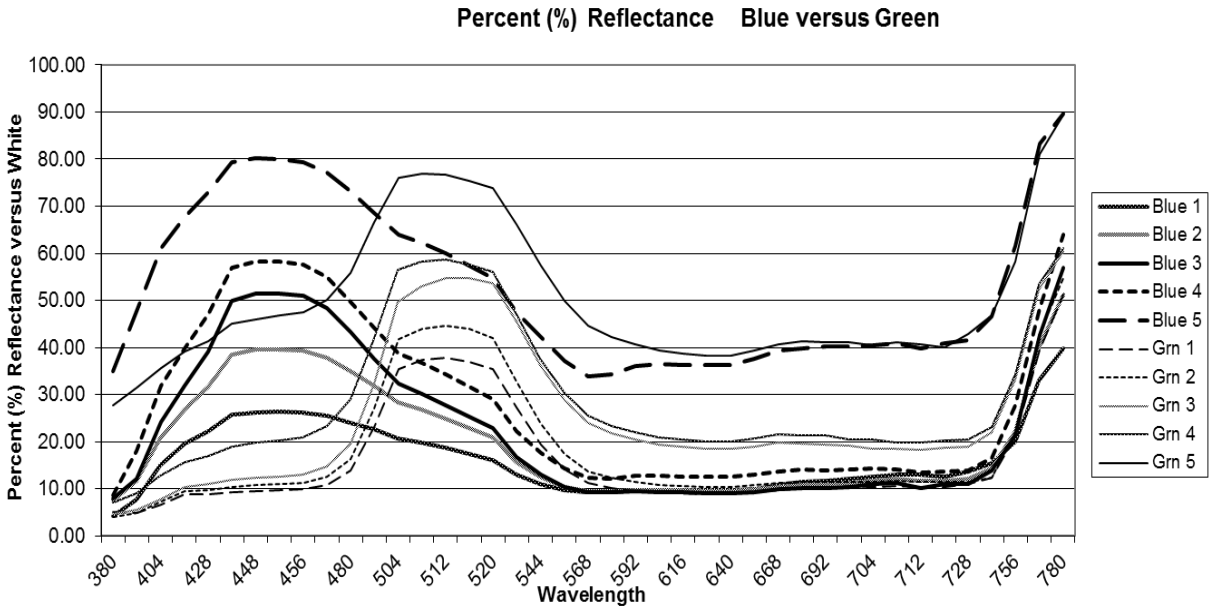

Figure 10 – Transmission spectra relationship between the blue and green stimuli used within each session of Task 5, based on their comparison to white.

making color the pertinent cue.

These last three factors are some of the key elements that Padgham & Saunders (1975) discuss, mentioning that the appearance of color can depend on the luminance level of the color, the field size, the color of the surroundings as well as the luminance of the surroundings. This last point was one factor that could not be fully controlled for as the quality of the light within the building was influenced by two skylights above the testing area. This could have slowed some learning if the stimuli were muted by the quality of the ambient light, but in general this factor did not hamper learning over the span of testing.

“Bugsy” did not pass Task 7 (green vs. red) within 34 sessions. It is hard to infer if he would have been able to pass this task if testing was continued. The sensory work completed on two related otter species showed the red cone to be lacking (Levenson et al. 2006; Peichl et al. 2001). Given this and the results of this task, ASCO’s also probably

lack this conal pigment. Thus, we do not know what color the subject perceives when presented with the red stimuli. It is possible that many of the cones being stimulated were green in nature, therefore causing confusion between the two stimuli.

"Bugsy's" general behavior allowed for testing to be a fairly smooth process. He would continually return to experimenter 1, to "hold", before making another selection when given the command, no matter how many he selected incorrectly. Hunger seemed to be one of the greatest challenges to overcome. While learning what the positive stimulus was, if he would make repeated incorrect choices, he would behaviorally start to emit a humming noise, as well as clench his front paws into fists. This typically would be followed by a very quick selection when released, lacking concentration (indicated by his head position) onto what he was choosing. This quick selection method was also seen in the beginning of sessions, if hunger was an issue (i.e., being fed later than normal). To control these issues, experimenter 1 was allowed to ask unrelated previously trained behaviors outside of the testing field. This change appeared to help focus his attention, and thus allowed for more rewarding trials to be conducted.

It was observed that "Bugsy's" selection method changed throughout the tasks. During the training task, he developed a behavior of initially running towards the stimuli on his right, potentially only evaluating one stimulus before making a decision. If he was to select the stimuli on his right he continued to run straight towards it, then touch it. If he was choosing the stimuli on his left, he would make an exaggerated turn to his left, most often occurring within 30 cm of the stimuli on his right. To aide in his selection method, both experimenter 1 and the stimuli were separated further apart from an initial distance of 1.83 m to the final 2.3 m, to help more clearly define the subject's choices.

This method of selection continued in the earlier stages of Task 1, but was not going to be a successful tactic, as there were now two stimuli to his left. By the end of the task he was still running more towards his right, but was more centered between the right two stimuli, as well as turning earlier in his run. This learning period of adjusting to the presence of three stimuli is most likely why it took him 22 sessions to complete the task, even though the positive stimuli was the same as the training task.

Task 2, and the following 5 tasks, were all originally designed as three-choice discrimination tasks, but were reduced to two-choice tasks because of "Bugsy's" reaction at the beginning of the original Task 2. At this point white was no longer an option. So, he had to learn what the new positive stimulus was. He began to show signs of confusion, as initially he would not always make selections, vocalizations became louder, and his posture became tenser. There was a hope that by making the "station" the same color as the positive stimulus the learning process would occur faster and cause less confusion for the otter. However, this connection was never noticed. To try to make this a more positive experience overall, and reduce experimental time, the task was changed from a 3 choice to a 2 choice task. This change did seem to reduce the negative reactions observed. While testing Task 7, the same changes in body posture and vocalizations were present, possibly suggesting an inability to distinguish the stimuli.

After Task 2 was reduced to a two-choice task, the subjects method of selection changed, such that he had a more central run towards the stimuli. This occurred throughout the color versus grey tasks (Task 2-4), but he later reverted back to the right-sided runs once colors were tested against each other (Task 5-7). Also, early in learning what the new positive stimulus was for Task 2, he started to "cheat" on his selections of

the stimuli on his left. He would appear to be making a choice on his left, but would never actually touch the stimuli, which was the criterion for selection. Instead, he would run by the left stimulus' right side and stop. Since no immediate bridge was received, he would then turn to his right and go and touch the stimulus on the right. He later connected these two behaviors by forming a continuous arc, not selecting a stimulus in the end. This only occurred if he was heading for the left stimuli. If he was going to select the right stimuli, he ran directly towards it and touched it without turning. To try to combat this, the two stimuli were separated further apart, from about 20 cm to 30 cm. Though it never fully stopped the behavior, it did cause him to start touching the stimuli on his left again.

During the process of testing Task 5, "Bugsy" started to develop a routine of alternating his choices based on side. He would, as an example, started off by selecting the stimulus on his right, followed by his next choice being on his left, then back to the right, etc. This became a very predictable practice. This behavior may be similar to a procedure known as spontaneous alternation behavior (SAB), in which choices are alternated with no reinforcement to continue. SAB has been said to occur within discrimination-learning experiments (Dember & Richman 1989). In order to reach criterion, though, he would have to break this pattern of selection, which did eventually happen.

Upon examining the tasks in groups based on common characteristics, it is evident that comparable tasks took fewer sessions to pass (Table 3). This fact was also noted in studies involving the giant panda (Kelling 2006) and the coati (Chausseil 1992). "Bugsy" was able to cue into some characteristic, most likely a color cue, and remember

it for the following tasks. The training task and Task 1 both had white as the positive. Here, “Bugsy” was able to pass the later task in 12 fewer sessions, even though there was

Table 3 – Grouping of tasks into comparable characteristics for all tasks passed by “Bugsy”

White as Positive Stimulus		Grey as Negative Stimulus		Blue as Positive Stimulus	
Trail	Sessions Completed	Trail	Sessions Completed	Trail	Sessions Completed
Training Task	34	Task 2	30	Task 5	46
Task 1	22	Task 3	6	Task 6	10
		Task 4	5		

a change in stimuli number present. Task 2, 3 and 4 all had grey as a negative stimuli. The two earlier tasks also had this trait, but now an individual color served as the positive, which now required him to learn to go to blue instead of white. Task 2 took him 30 sessions to complete. However, Task 3 and 4 only took 6 and 5 sessions, respectively, even though they used different colors as the positive stimuli. It can’t exactly be said what he learned, whether it was to go to a color, or to avoid grey. Tasks 5 and 6 both had blue as a positive stimulus, but now another color (green and red) as the negative, which once again required a learning period. He started off with a long testing period of 46 sessions to pass Task 5, but that was followed by only 10 sessions for Task 6.

When closely analyzing “Bugsy’s” incorrect responses on the tasks, on the two sessions that he passed as well as the four preceding sessions, there was not a significant error pattern associated with any particular shade of color or grey. There were some trends, but nothing significant. It was reported for the manatee (Griebel & Schmid 1996) as well as the domestic cat and civet (Ducker 1964) that as the grey stimuli became lighter, there was more difficulty in obtaining correct responses to the color. “Bugsy” showed a trend for selecting the four lightest shades of grey (those closer to white) incorrectly rather than the positive colored stimulus. He was also more likely to select grey over the darker shades of the color.

4.2 “Harry”

Much like “Bugsy”, hunger seemed to be the greatest challenge to overcome with “Harry”, and similar practices were used to deal with it. Unlike her brother, her general behavior is more aggressive and therefore more challenging. After a couple of unrewarded wrong selections, she would often attempt to bite or chase either experimenter. She also would not return to experimenter 1 immediately, but would maneuver within the testing area away from the experimenters. Experimenter 1 had to quite often lead “Harry” back to the proper position using the stationing stick, so that she could be sent again resulting in more time consuming testing sessions versus “Bugsy’s” sessions. This behavior decreased over time to a point where she rarely would attempt to bite anyone near the end of Task 2.

The training task was completed in a very short period of time (4 sessions) which was probably caused by differences in teaching the “select” command and well as a greater length of time being exposed to stimuli before testing. One of the main differences was that the second stimulus was introduced more randomly, and the grey cards were altered more often, limiting exposure to only a certain shade. Probably the greater factor was the duration that the training occurred over. This was not intentional, it occurred because the family structure broke down as well as a major illness occurred within the family group. Both occurrences caused a ceasation of training followed by a need to almost completely retrain the “select” command, though she was quick to relearn the steps involved.

Task 2 was abandoned after 48 sessions as there was no indication that she was learning to select the color. Probably like “Bugsy”, there was a need to have a learning

period as the parameters for a correct response now had changed. Initially, a side bias was evident, though not particular to the right or left side overall. When this did not result in a reward, she started to run towards the stimuli with her head raised, in a position that did not appear to allow her to attend to the stimuli. It was possible that she was trying to get some sort of cue from experimenter 2 instead of studying the stimuli. To combat this, experimenter 2 started to take two steps to the side so that she could not simultaneously touch a stimulus and look at experimenter 2, forcing her to pay more attention to the stimuli. At this time she started to develop a selection method much like "Bugsy" in which she would run to the stimuli on her right, then turn at the last moment to select the left stimuli if that was her choice. This method continued when participating on Task 3.

Though she was never able to reach set criterion for Task 2, there was still evidence that she was able to perceive a difference in the stimuli. "Harry" was able to reach criterion in the reverse; she went to grey (the negative stimuli) 12 out of 15 times for two testing days in a row, during trial number 32 and 33 (Table 4). Even though she was only getting rewarded for going to the blue stimulus, she would still routinely choose the grey instead. This would strongly suggest that she identified there was a difference in the stimuli. The same controls were in place during testing as with "Bugsy", so her selections seemed likely to be linked to color difference.

At the beginning of Task 3, it was decided that "Harry" would have the chance to select what the positive stimulus was for that particular session. This change was made based on her greater affinity to the grey stimuli during Task 2, on the assumption that if

Table 4 – "Harry's" selections, in bold, for session 32 and session 33 of task 2.

Harry Task 2: Blue vs Grey			
Session 32		Session 33	
Blue 2	**Grey 6**	**Blue 1**	Grey 1
Blue 4	Grey 2	Blue 3	**Grey 7**
Grey 2	Blue 2	**Grey 7**	Blue 4
Grey 11	Blue 3	**Blue 3**	Grey 8
Grey 11	Blue 2	**Grey 9**	Blue 4
Blue 2	**Grey 2**	**Blue 1**	Grey 5
Grey 10	Blue 1	**Grey 2**	Blue 1
Grey 9	Blue 4	Blue 4	**Grey 7**
Blue 5	**Grey 11**	**Grey 8**	Blue 5
Grey 4	Blue 5	Blue 2	**Grey 8**
Blue 4	Grey 11	Blue 3	**Grey 5**
Grey 9	Blue 4	**Grey 5**	Blue 5
Grey 4	Blue 1	Blue 3	**Grey 8**
Blue 3	Grey 10	**Grey 11**	Blue 1
Blue 2	**Grey 6**	Blue 4	**Grey 5**

she received a reward for selecting the grey then she would continue selecting it. In general, this did not occur. Out of the 27 sessions tested, she only selected grey initially 3 times. This was a significant number of times that she went to green first which could indicate that she comprehended, over a period of time through continuous reinforcement, to go to green to get a reward. Her last two sessions provide some evidence for this possible understanding, as well. In both she achieved 11 of 15 correct, though one had the positive stimuli as green and the second as grey. Individually, the sessions were just above chance performance (5.923×10^{-2}), though combined the chance performance existed at 8.062×10^{-3} (22 of 30 correct). This last statistic actually occurred two other times during the task. Taken all together the data appears to indicate that she was able to distinguish the stimuli. Potentially, as Bacon & Burghardt (1976) stated in their analysis of the American black bear, she was making "correct, but not consistent, choice".

The hardest challenge faced during this task was that she would often return to her side preference at some point during the testing session. What caused this confusion is not exactly known. It was noticed that the shorter the time period between each trial, the more likely she would continue to select the positive stimulus. If there was a delay, this would most often cause her to return to her side bias.

During this time, she was able to reach criterion for one testing day on two separate occasions, showing that she could perform above chance. During these two sessions, she seemed be evaluating both stimuli before making a selection. At times, she would move her head from side to side while running towards the stimuli, while other times she would nearly or completely stop to observe them before selecting. On the following testing day the results were not favorable. On one occasion, the session was abandoned because of the refusal to make selections halfway through. While on the second occurrence, she only got 6 correct relying heavily on side bias.

Based on the data obtained on “Harry”, there is some favorable evidence that she was able to determine choices based on color, though it did not meet previous set criterion. Possibly the criterion that was set was too difficult for her to pass on a reliable basis, or the reinforcement was not great enough to maintain a favorable reaction. The side bias may have been her default choice in most cases, influenced by her standard operant conditioning sessions. Most of her known behaviors, outside of this study, rely on her to position herself in specific ways, or go to certain areas of the holding facility when asked. If she was not sure of an answer or not paying full attention, this may have caused the bias in a selection as location was previously was a rewarded behavior.

4.3 “Moe”

“Moe” quickly learned the overall general behavior of the “select” command, by leaving experimenter 1 and selecting a stimulus. Right before the addition of the second stimuli (i.e. the training task), a noticeable cloudiness developing in both his eyes. After a medical examination, it was determined that he was developing bilateral cataracts. Due to compromised vision, he was dropped from the study.

4.4 “Nava”

Though “Nava” learned the overall concept of leaving experimenter 1 and selecting a stimulus, she was only able to reach criterion on one testing day. There were a few behavioral irregularities with her that made testing challenging, and eventually resulted in her removal from the study. As Griebel & Peichl (2003) state, a negative result may not always be that the animal, in this case, has color vision, but rather it may not have “understood” or “attended to” the task. It is inconclusive where “Nava” fell within these parameters, as possibly the reward was not enough incentive to participate or the sessions may have been too long to keep her attention.

During her participation, there were two main blocks of testing data. She was tested for 43 sessions, before a 3 1/2 month delay was encountered, followed later by 11 more sessions. At the beginning of these two blocks, her general behavior was not atypical for an animal learning a new behavior. A right side preference in general was observed for her. If looking at chance probability, of the 54 sessions completed, 26 sessions did not contain a side preference. Of those 26 sessions, 13 existed in the last 15 sessions that she completed. Many of those that were not significant had a particular side selected 11 or 10 times, and so choices were still weighted towards one side. This may

have suggested that she was breaking her side preference technique, but her general behavior was breaking down at the same time. Eventually, both times, she started to refuse to select a stimulus.

If “Nava" was asked to continue to participate, she would eventually remove herself to a corner of the testing area and refuse to participate. Ultimately her behavior reached a point t which she avoided the trainer completely. Griebel & Schmid (1996) note that one of their manatees also stopped cooperating during testing, and was removed from the study, but no note was made about her behavioral change. In addition, if “Nava” selected the negative stimuli, and thus no bridge was given, she would often behave as though she selected a correct response. This change in behavior had not occurred previously in general training sessions outside of this experiment. Based on her behavior and the fact that “Harry” had passed the training task, “Nava” was removed from the training task.

4.5 Overall Conclusion

When comparing the natural history of the Asian small-clawed otter, sea otter and the Eurasian river otter, the ASCO would be the most likely to retain color vision based on their greater terrestrial activity, a connection made by other researchers. Peichel et al. (2001) makes this connection when discussing why whales and some seal species have lost the ability for dichromatic vision. They adapted to an aquatic environment, which lacked the rich spectral properties of a coastal area. Adaptation to an aquatic coastal environment was also suggested to be the factor as to why California sea lions, a pinnidped, were able to discriminate blue and green from shades of grey (Griebel & Schmid 1992). The M/L cone pigment sensitivities of pinnepeds have also been shown

to be closer to terrestrial carnivores than to the aquatic bottlenose dolphin (Levenson et al. 2006). Griebel & Peichl (2003) state that dichromatic vision should be present in those species that are active during the daytime and are likely to use aerial vision, traits that the ASCO's possess. As Kevan & Backhaus (1998) state, "color vision systems mostly seem to make the best of the natural photic environments and are attuned to the perception of a wide variety of objects of importance, and their backgrounds."

Concluding that an animal has (or doesn't have) color vision is a complicated practice because there is a need to examine both the sensory and perception systems. It is, as Roth et al. (2007) state, difficult to actually know how a dichromatic species recognizes any color within their "colour space". Ducker (1964) suggests that it may not be correct to call it color vision, but should be referred to as a "reaction to certain spectral colours". We commonly discuss color vision in human terms, but we really don't know how other species actually recognize color. This idea is supported by work done with the ring-tailed lemur (Blakeslee & Jacobs 1985), as an example. If they have trichromatic vision, it is not the same as humans have because the lemurs' thresholds are shifted higher in the color spectrum. So, comparing a species to humans or non-human species to each other may actually be misleading.

It is suggested that color in dichromatics is perceived in a continuous scale (Hemmi 1999; Roth et al. 2007; Wachtler et al. 2004), where a neutral point as previously defined does not exist. Instead of being perceived as grey, the neutral point may actually be seen as a chromatic color. Previous reports state that the neutral point is where equal amounts of the long wavelength sensitive and the short wavelength sensitive cones are stimulated, causing a grey (or white) light to be seen. On one side of this neutral point is

where a certain color would be stimulated, whereas on the opposite side a second color would be recognized. Nevertheless, if a neutral point could be identified, it would help to clearly state that a species is in fact a dichromate.

The reason for the differences in performance between the individuals tested here is hard to conclude. There are probably a number of factors that affected the results. These individuals have definite differences in the nature of their general behavior, which could affect learning aptitude, motivation, or attention. Living in a social group, individual Asian small-clawed otters may rely more on social learning to solve problems and to learn new techniques, as independent learning could be limited. The sexes may also recognize the same color differently, which has been suggested for the spider monkey (Blakeslee & Jacobs 1982), as an example. Or potentially, the method used in this study was not an ideal set-up for testing this specific question in ASCO's.

Based on the perception data obtained on "Bugsy", passing 5 varying tasks that involve color as a positive stimulus, and comparing these results to the sensory work on the sea otter and European river otter, it can be said that Asian small-clawed otters, as well as most likely all otter species, have the ability to see color. They are likely dichromates like many of the mammalian species that have been tested, which is potentially behaviorally supported by the problems seen in passing Task 7 (green versus red). The data on "Harry", though not conclusive, adds credence to this species' ability to see color. These conclusions help to support the idea that many mammals are not colorblind, like previously thought.

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