

Simple Visual Discrimination Training of the Giant Panda (*Ailuropoda melanoleuca*)

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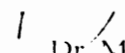
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Simple Visual Discrimination Training of the Giant Panda (*Ailuropoda melanoleuca*)

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SUMMARY

The giant panda (*Ailuropoda melanoleuca*) is a unique and understudied species. In order to remedy this situation, systematic research, especially sensory and cognitive, must be conducted on this rare animal. Other bears have demonstrated color vision and giant pandas have been found to possess the photopigments required for color vision. Therefore, studies of visual abilities are warranted. The present study examined giant panda cognition and visual abilities through the simple visual discrimination training of contrast and color. The purpose of this study was to begin to explore the limits of giant panda discrimination training. Based on past research with bears, it was hypothesized that giant pandas would show the ability to learn these discriminations. One of the subjects did learn to discriminate green from grays and both subjects learned to discriminate both black and white from other shades of gray. Additional insights discovered from the reactions of the giant pandas to the task are also reported.

INTRODUCTION

People rush to zoological societies throughout the world for simply the chance to glimpse the magnificent giant panda (*Ailuropoda melanoleuca*) chomping on a bamboo snack or snoozing the afternoon away. The giant panda is one of the most beloved animals and has been a huge lure of crowds since it was first introduced to American zoos in 1936 (Morris and Morris, 1981). Yet, very little is known about this rare bear, despite its status as one of the most endangered mammals. To remedy this situation, systematic research, especially sensory and cognitive research, needs to be conducted on the giant panda. Information that comes out of sensory and cognitive research can help improve the situation for the giant panda both in the wild and captivity. In addition, behavioral research can provide further support for the theory that the giant panda is a bear.

General Giant Panda Information

The giant panda is nearing extinction, with only approximately 1,000 remaining in the wild, because of the threats of habit destruction, population fragmentation, bamboo die-off, and hunting (Schaller, 1993). The diminishing numbers of giant pandas in the wild every year necessitates a more thorough understanding of exactly what giant pandas are capable of to aid in the production of a training strategy for possible reintroduction programs. The lack of research has also contributed to the decline of panda numbers in the wild. Lu, Pan, and Harkness (1994) examined the rescuing of wild panda cubs thought to be abandoned and determined that these cubs were often merely left alone for a few hours while the mother foraged. These unnecessary rescues, due to a lack of understanding, created a situation where good intentions decreased the number of pandas

in the wild, especially sad because many of these cubs died in captivity. Research on captive giant pandas still has a long way to go. The captive-breeding program has not yet created a self-sustaining population (Zhang et al, 1996, p. 13). Lindburg and Fitch-Snyder (1994) emphasize the need to evaluate reproductive problems with behavior before performing invasive diagnostic procedures. Further research can definitively improve the situation of the giant panda.

The giant panda is a remarkable feat of evolution. It has adapted to the cool, moist climate of the Chinese mountains it inhabits with a warm coat that is oily to repel water. Their unique coloring, and especially the eye patches and ears which resemble another set of eyes, help the solitary giant pandas to notice and avoid each other (Schaller, Jinchu, Wenshi, and Zing, 1985; Morris and Morris, 1981). It also has developed a pseudo-thumb extension of the wrist bone, which increases foraging efficiency because it allows the bear to grasp bamboo stems. Other adaptations to a bamboo diet include the panda's broad, flat molars and strong jaw muscles to crush the tough, fibrous plant material, a tough folded lining in their esophagus and in the beginning of the stomach to prevent injury from sharp bamboo splinters, and their large size.

It is a very astonishing that the panda is adapted to eat bamboo rather than meat. According to Schaller et al. (1985), however, the panda is forced to budget its time between activity to fulfill basic needs and inactivity to conserve energy, because, although natural selection tied the giant panda to bamboo, it did not provide it with the stomach to eat it. The giant panda is a true carnivore and lacks the chambered stomach and microbes to break down and digest the cell walls of bamboo, which provides a low

nutritional return, derived mainly from its cell contents (Schaller et al., 1985). The giant panda has been forced to become a selective and rapid eater because of its digestive tract which, according to Schaller et al., only digests on average 17% of what the bear eats, compared to ungulates which digest near 60-80%. In addition, the giant panda is an inefficient eater despite all of the adaptations it has developed. Unlike the red panda who grinds bamboo leaves to a fine pulp, the giant panda chews for a short amount of time choosing to become a bulk processor as opposed to spending the time required to fully chew the leaves (Laidler and Laidler, 1992).

The Bamboo Bear

The classification of the giant panda has been one of the most hotly debated topics in science since their discovery by the western world in 1869. The early attempts to classify the panda based on morphology and behavior lead to a controversy. In many cases, different investigators interpreted the same data differently, indicating that the early data was insufficient to provide a definite conclusion (Davis, 1964). Schaller (1993) states that, "Science, with its penchant for creating neat categories, had been unable to force the panda into a definite taxonomic position, the animal showing resemblances to both bears and raccoons" (pg. 45). However, recent molecular studies have provided substantial support for the claim that the giant panda is a bear and most modern scientists accept this evidence.

The panda was originally declared to be a bear in 1869 by the French scientist Père Armand David, who was the first Westerner to be shown this unique animal. The controversy began when Père David sent the specimen to his student, Alphonse Milne-Edwards. Milne-Edwards examined the same skeleton and determined that although it

resembles a bear in many aspects, the dentition and bone structure indicated a closer relation to the red panda, and therefore belonged in the raccoon family (Roots, 1989). It was at this stage that the giant panda received a change in its scientific name, from *Ursus* to *Ailuropoda* because of the resemblance to the red panda *Ailurs*. Taxonomists Ray Lankester and Richard Lydekker agreed with Milne-Edwards that this new animal was a form of panda, and they came up with the common name of “great panda,” which was later changed to its current common name, giant panda (Roots, 1989). It is quite possible that if the red panda had not been in the picture, there would have been no question as to the taxonomic classification of the giant panda (Roots, 1989).

After the names of the giant panda were established, the controversy continued, with the debate divided geographically. The English and American scientists tended toward the raccoon school of thought, while European scientists followed the bear school of thought (Davis, 1964); a third school of thought claimed that the pandas should be classified in a separate family (Pocock, 1928; Pocock, 1921). According to Schaller, Jinchu, Wenshi, and Jing (1985), “Each school of thought can point to specific features to support its claims” (pg. 226), which made the debate even more problematic.

On the surface, the giant panda looks like a bear. In fact, the earliest classifications of the giant panda as a bear by the Chinese and Père David were based on looks alone. Unfortunately, this method is inadequate because looks can be deceiving, with many closely related species looking very different based on adaptations to diverse environments (Roots, 1989). Based on comparative anatomy, the bears and the giant panda possess many similarities. These similarities include brain shape (Pirlot, Jiao, and Xie, 1985), body shape, skeletal structure, a keen sense of smell (O’Brien, 2000),

musculature and respiration (Davis, 1964). In addition, the other living bears and the giant panda have similar reproductive behaviors, with both exhibiting multiple births (Roots, 1989), small body weight of young relative to mother and delayed implantation (Laidler and Laidler, 1992).

However, the supporters of the raccoon and separate family theories had plenty of oddities to point out to corroborate their claims. Giant and red pandas both evolved to eat bamboo, so they share many adaptations such as dentition, a pseudo-thumb (Schaller, 1993), and stomach structure (Morris and Morris, 1981). Conversely, they do not share the adaptations specific to eating bamboo stems, since they only eat the leaves. Red pandas lack the thick-walled stomach, radical muscular development, and the mucous cells of the digestive system of the giant panda (Laidler and Laidler, 1992). The two pandas do share similarities unrelated to bamboo. The male genitalia of the giant panda is unlike that of a bear's straight, pointed penis, but is short, s-shaped, and pointed posteriorly which is similar to a red panda's.

Other key differences were based on behavior. Morris and Morris (1981) pointed out scent marking as a difference and claimed it to be "un-bearlike" (pg. 165). Although this behavior is characteristic of red pandas, bears are known to have a very good sense of smell and have been observed scent marking (e.g. Rogers, 1993; Stirling and Derocher, 1993). Other behavioral differences pointed out are vocalizations, bears roar while the panda tends to bleat, and the lack of hibernation in the panda (Morris and Morris, 1981). Giant pandas are able to roar (Schaller et al., 1985). In addition, the sloth bear (Garshelis, 2000) and the male polar bears (Stirling, 2000) do not hibernate, and it is questionable as to whether the sun bear hibernates (Servheen, 2000). The giant panda's

dependence on bamboo, a food source low in nutrients, forces it to eat for a large proportion of the day. Based on the capacity of the panda's stomach, it can only eat enough to be able to sleep for four hours (Laidler and Laidler, 1992). Therefore, it is impossible for the panda to eat enough to build up fat in order to be able to hibernate. Bamboo is also available year-round and consequently the giant panda does not need to hibernate. Accordingly, the lack of hibernation can be seen as an adaptation to its all bamboo diet. Many of the traits that are shared by the red and giant panda, such as the dentition, skull, pseudo-thumb, and behavioral traits, can be viewed simply as adaptations to their herbivore diet, while the others may be primitive carnivore traits that the ursine bears and/or raccoons did not retain (O'Brien, 2000).

Throughout the debate based on morphology and behavior, the giant panda was classified approximately the same number of times as "a specialized member of the bear family, the Ursidae; a specialized member of the raccoon family, the Procyonidae; or that it constitutes a separate family, the Ailuropodinae, either on its own or along with the red panda" (O'Brien, 2000; pg. 34). In 1964, D. Dwight Davis published an extensive comparative anatomy study on the giant panda based on Su Lin, a sub-adult male giant panda that had lived at the Chicago Zoological Park. Mayr (1986) concluded that "the period of uncertainty seemingly ended" (pg. 769) when Davis's work was published. Davis did indeed cover an extensive amount of the giant pandas anatomy and he described potential mechanism to explain the differences from bear anatomy. Mayr states that, "Davis demonstrated the first application of his new concept of evolutionary morphology" (pg. 769). Unfortunately, Davis's detailed study was unable to end the

debate that had raged for almost a century. Many scientists claimed that Davis ignored anatomical evidence that did not support his theory (e.g. Morris and Morris, 1981).

Based on the lack of a definite conclusion from data on morphology and behavior, molecular and chromosomal evidence holds the key to the true identity of the giant panda. The molecular approach examines the “homologous gene sequences and protein gene products (amino acid sequences) of particular species and [constructs] evolutionary relationships from the DNA molecules” (O’Brien, 2000; pg. 28). This method allows for phylogeny to be reconstructed and for the creation of a molecular clock (Ayala, 1982). A molecular clock estimates the timing of evolutionary events based on the idea that mutations during evolution are random but occur in a stable manner, therefore, the longer ago the evolutionary event occurred that divided two species, the greater the difference in their DNA (O’Brien, 2000; Ayala, 1982). These methods are advantageous because the differences are more quantifiable because they are based on units of difference and very diverse organisms can be compared (Ayala, 1982). But, these methods can be inconsistent which necessitates the use of several methods before conclusions can be drawn (Ayala, 1982).

In 1956, Charles Leone and Alvin Wiens used a series of serological tests to examine the relationships of the giant panda and concluded that they were closely related to the bears. However, according to Sarich (1973) their use of albumin was problematic because ursid albumin had “accumulated substantially fewer amino acid substitutions than those of other carnivores, thus markedly reducing the resolving power of this molecule in any ursid-related molecules” (pg. 219). He pointed out that their results could come from the fact that conservation of albumin evolution exists in both the giant

panda and the ursids. Using transferrins, which had previously been used to parallel albumin in other carnivore research and did not present the problem of conservative evolution in ursids, Sarich was able to reach the same conclusion as Leone and Wiens. His results even indicated that the red panda split off from the ursids after their division from the procyonids. Both of these studies were evidence that the giant panda was undeniably a bear. Further evidence came from a 1985 study by O'Brien, Nash, Wildt, Bush, and Benveniste. They tested the relationship using three independent molecular and genetic measures; DNA hybridization, electrophoretic mobility, and immunological distance of serum proteins. All of their measures produced evidence that suggested that the red panda split off immediately after the raccoon-bear division, while the ancestors of the giant panda did not split off until immediately before the radiation of the modern bear. Other molecular studies of varying methods, including gel electrophoresis (e.g. Goldman, Giri, and O'Brien, 1989), mitochondrial sequencing (e.g. Ledje and Arnason, 1996; Talbot and Shields, 1996; Ledje and Arnason, 1995; Zhang and Ryder, 1993), both gel electrophoresis and mitochondrial sequencing (e.g. Slattey and O'Brien, 1995), and brain lipids (e.g. Tamai and Abe, 1986) provide additional support for the theory that the giant panda is a bear.

These early studies by Sarich and O'Brien et al. seemed to provide unambiguous evidence that the giant panda is a bear. Nonetheless, there were still a few contradictory findings. Zhang and Shi (1991) found that, in mitochondrial DNA restriction-fragment length polymorphism (RFLP), the giant panda more closely resembled the red panda. However, they state that selection pressure on RFLP is low and convergent evolution may not be the cause of similarities. Another problem is that their analysis lacked an out-

group which makes the conclusions questionable (Hashimoto, Otaka, Adachi, Mizuta, Hasegawa, 1993). The two most compelling lines of defense for the raccoon school of thought came from analyses of chromosome number and hemoglobin.

In terms of chromosome number, Ewer (1973) reports the following diploid chromosome numbers; giant pandas (42), red pandas (36), procyonids (38), spectacled bear (52), and ursids (74). Morris and Morris (1981) report that the numbers of giant panda chromosomes (42) is a direct match with that of the studied raccoons (42), but different from studied bears (56 and 74). At first, these data seemed to challenge the idea that giant pandas were definitely related to bears. Later studies revealed that the differences of the giant panda and spectacled bear from the other ursine bears could be accounted for by simple fissions and fusions. O'Brien and his colleagues in 1985 first demonstrated that despite the different numbers of chromosomes, the banding patterns within the bear chromosomes were closely related. They state that, "Remarkably, nearly every large chromosome of the brown bear could be aligned with a giant panda chromosome arm" (pg. 142). They also found that only two of the banded chromosomes of the giant panda shared recognizable complements in the red panda or raccoons, which once again highlights the relation between the giant panda and the bears. Further studies identified the evolutionary events that produced the ursine chromosome pattern from the ancestral carnivore karyotype and the separate events that produced the giant panda and spectacled bear patterns from the ursine karyotype (e.g. Nash, Wienberg, Ferguson-Smith, Menniger, and O'Brien, 1998; Nash and O'Brien, 1987).

The second major challenge to the bear-giant panda link came from a 1986 study by Tagle, Miyamoto, and Goodman. They examined the α - and β -hemoglobins of several

carnivore families. They found that the hemoglobins of the red panda and giant panda differed from each other by fewer substitutions than to any other carnivore, including the species of raccoon (*Procyon lotor*) and bear (*Ursus maritimus*; polar bear) tested. The minimum mutation distance between the two pandas was found to be seven, while the distance between the giant panda and the polar bear was 11 and the distance between the red panda and the raccoon was 18. They therefore suggest a separate family for the two pandas. Potentially these hemoglobins evolved at a different rate than the molecules studied by Sarich and O'Brien et al. (Mayr, 1986).

In 1993, Japanese scientists reexamined hemoglobin data using a maximum likelihood method because it is robust against the assumption of rate consistency of evolution (Hashimoto, Otaka, Adachi, Mizuta, Hasegawa, 1993). They constructed trees in which the two pandas were more closely related and trees in which the giant panda is linked to the bears. They then produced bootstrap probabilities and found the maximum likelihood tree, which linked the giant panda again with the bears, even on hemoglobin. They claim that Tagle et al. reported only the maximum parsimony tree. They conclude that, "Although there are many uncertainties in [the maximum likelihood] tree..., the placing of the giant panda in close relation to the bear group is clearly robust" (pg. 286). They claim that the hemoglobins of the two pandas may differ in fewer substitutions, but relatively slow rates of substitutions in the pandas, versus the bears, could explain these apparent differences. However, they are unsure why the substitution rates of either the two pandas or the bears would change.

Additional evidence for the giant panda-bear link comes from the fossil record (Zhang and Ryder, 1993). According to O'Brien (2000), the fossil evidence, although

incomplete, aids in the issue of timeline. He states that, "*Agriarctos* is generally believed to be an early ancestor of the giant panda line and occurred during the Miocene, about 15 million years ago. The common ancestor or "missing link" for the non-panda ursids is *Ursavus*, dated at 20 to 18 million years old" (pg. 31). He discusses the comparison of molecular changes of the same genes in bears with primates, with more precise fossil dating, and declares that checking the fossil dates against the molecular bear data leads to "considerable, though not universal, agreement" (pg. 32). He goes on to claim that, "Clearly, paleontological and molecular approaches, when considered together, provide the insight that is needed to resolve this puzzling history" (pg. 32). His conclusions from the combined data are that the New World procyonids and the Old World red panda was an ancient split, which warrants a subfamily designation. The giant panda split from the ursine bears approximately 10 million years after the ursid-procyonid split may also merit a subfamily status, which also suggests the same conclusion for the spectacled bear.

Overall, extensive molecular research along with the more controversial morphological and behavioral data have provided overwhelming support for the theory that the giant panda is a bear. Pan and Lü (2000) state that, "The most recent scientific data, based largely on molecular genetics, makes it quite clear that the giant panda is a bear" (pg. 140). Various molecular techniques have derived the same conclusion, and have resulted in almost identical phylogenetic trees (Mayr, 1986). O'Brien (2000) states that the enigma of the giant panda has supplied scientists with extraordinary opportunity to apply and test the effectiveness of various methods used to identify the relations between species. He declares that, "The lessons learned as a result of this great taxonomic controversy have shown how the combined interpretation of molecular,

morphological, and palentological findings can be used to establish the evolutionary histories of other groups” (pg. 35). The clues may be challenging to unravel, but the combination of genes, anatomy, functional adaptations, and behavior can reveal the relations between animals. In the case of the giant panda, some mysteries still remain over a century after their discovery by the Western world, but the majority of the data warrants the same conclusion. The giant panda is a highly specialized bear who has adapted to the life of an herbivore; it has become the bamboo bear.

Color Vision

Color vision is defined as the ability to discriminate between multiple wavelengths of the visible spectrum independent of their respective brightness (Tansley, 1965). Jacobs (1981) states that color vision is a popular topic due to the fact that color vision “is such a ubiquitous and intrinsically fascinating aspect of man’s visual world” (pg. 1). Jacob claims that in addition to scientific curiosity, interest in comparative color vision is based on the idea that sensory systems are adaptive and explain the variation in color vision across species may potentially allow the integration of “information about color vision with other biological information so as to develop a richer and more complete picture of the natural histories of the species currently inhabiting the planet” (pg. 1).

Animals need at least two different receptor photopigments to be able to possess color vision (Lomas et al, 1998). Walls (1943) claims that color vision is correlated with high visual acuity and the ability to accommodate or maintain a sharp image on the retina. Schiffman (2000) states that, “Although some degree of color vision occurs widely throughout the animal world, not all animals possess highly developed color

vision, nor does there appear to be any clear overall phylogenetic trends” (pg. 117). However, for many animals color is important for mating and camouflage. Animals shown to possess a high degree of color vision include many birds, fish, amphibians, reptiles, arthropods, and most primates. As for other mammals, there is less evidence. Color vision has been demonstrated in squirrels (Jacobs, 1976). Schiffman (2000) adds cats, prairie dogs and maybe elephants to the list, but states that they possess only a limited degree of color vision. It is now postulated that most diurnal animals probably have some degree of color vision. Many animals cannot be classified as completely nocturnal or diurnal, exhibiting activity in daylight, at night, and potentially during twilight. Often these animals use vision extensively and therefore need either special adaptations, such as teleost fish, birds, and frogs, or have retinas with both rods and cones, such as the large terrestrial mammals, which allow for vision in various levels of illumination (Tansley, 1965).

Given the link between giant pandas and other bears, it is logical to examine bear vision to guide a study of giant panda vision. Unfortunately, there have been few scientific studies of bear vision. There have been numerous claims that bears have excellent, or at least adequate, vision. Bacon (1973) states that many claim that the eyesight of the American black bear is poor, but he claims that “this information has been accumulated anecdotally without experimentation or controlled observation” (pg. 93). Shepard and Sanders (1985) state that hunters usually believe that bear eyesight is not as keen due to their highly developed olfactory and hearing senses. They add that, “Much of the anecdotal information on bear vision assumes that the animal approaches strange objects because it does not see them well at a distance, but crows and coyotes do the

same thing and nobody doubts their visual acuity” (pg. 7). Shepard and Sanders (1985) assert that bears tend to be active during the day and night, which is a sign that they have well-developed vision. Although stating that little research has been performed on the sensory systems of bears, Van Valkenburgh (2000) claims that, “Bears appear to rely heavily on their senses of smell and vision when foraging” (pg. 61). In response to the claim that Asiatic black bears had better smell and hearing than sight, Reid (2000) says, “Such comparisons are hard to quantify, but for an animal that climbs extensively and moves in rugged terrain, good vision is no doubt also essential” (pg. 123). Stirling (2000) writes that polar bears likely have eyesight and hearing comparable to those of humans, with a highly developed sense of smell.

There have also been many claims that bears possess color vision, but with little evidence. Shepard and Sanders (1985) state that, “there is evidence of color perception” in bears (pg. 7) and McNamnee (1984) also claims that, “[Grizzly Bears] are by no means color blind” (p. 76). Van Valkenburgh (2000) declares that black bears have been shown to have color vision and “this is likely to be characteristic of all bears, enabling them to recognize edible plant matter, such as fruits and nuts” (pg. 61). Pelton (2000) also asserts that black bears possess color vision, which aids them in foraging for berries among leaves. The main evidence for bear color vision comes from a study by Bacon and Burghardt (1976). They found that black bears could discriminate visual stimuli on the basis of wavelength, with one of their bears learning to discriminate blue and the other learning to discriminate green.

Although little is known about bear vision, even less is known about giant panda eyesight. It seems unlikely that they would have lost the visual acuity or color vision

potentially found in other bears. In addition, Jinchu (2001) found that the eye of the giant panda contains rods and cones, with the rods outnumbering cones, suggesting, but not guaranteeing, that giant pandas possess acute night vision, while still capable of daytime and color vision. However, a highly developed visual system is not necessary for giant pandas in the wild because they live a solitary life in dense forests and rarely encounter another panda (Schaller, Jinchu, Wenshi, and Jing, 1985). Some feel that the giant panda visual system is not well developed and that the pupils consist of visual slits similar to many nocturnal mammals (Schaller, 1993). Indeed, it is believed that giant pandas are able to see well in the dark, which allows them to eat bamboo at night, although they are not nocturnal (Etling, 2000).

Instead, pandas tend to be polycyclic, with peaks in the early morning and late afternoon. Overall, Schaller et al. report a probability of activity in the daytime of 0.64 and 0.58 during the night. Laidler and Laidler (1992) report that the low capacity of the giant panda's stomach forces it to feed throughout the day. Given the rapid passage of bamboo through the panda's system, with bamboo traveling completely through the system in about eight hours (Dierenfeld, Hintz, Robertson, van Soest, and Oftedal, 1982), the giant panda can only sleep around four hours at a time without awakening to "a very empty stomach. Given the poor quality of the panda's diet and its need to maintain a steady trickle of nutrients into its system, an empty stomach is not the minor inconvenience it might be to most carnivores – it is a matter of survival" (Laidler and Laidler, 1982; pg. 101). Therefore, the giant panda is forced to feed and sleep in shifts throughout the day and night. With these activity trends, giant pandas could be

hypothesized to possess the well-developed eyes of an animal that is active during daylight hours.

Although giant pandas rarely encounter another animal, no animal is completely solitary. Giant pandas interact during breeding and mothers and cubs spend up to two years together. With home ranges being small and overlapping to some degree, “occasional meetings...[are] almost inevitable” (Schaller et al., 1985; pg. 155). Giant pandas use visual signals as a means of communication. Giant pandas may use their coloring as a warning pattern and would therefore need better vision than nocturnal mammals (Morris and Morris, 1982). They communicate with body postures (Schaller et al., 1985) and visual markings, such as bark stripping and clawing (Laidler and Laidler, 1992; Schaller et al., 1985). In light of the use of visual signals, it seems probable that giant pandas have acute enough vision to distinguish the signals of others. But giant panda vision has not been studied, leaving only speculation. No conclusions on the visual acuity of giant pandas can be drawn until further research has been performed. Therefore, a bad performance on a visual task could reflect stimulus perception problems instead of a cognition limit.

A similar lack of evidence on equine vision led Timney and Keil (1992) to perform a visual discrimination task. They state that, “It is difficult to provide a quantitative estimate of visual acuity based solely on anatomical, physiological, optical or anecdotal evidence” and that the purpose of their study was to use “behavioral techniques to obtain the estimate” (pg. 2289). There is also some question as to the visual acuity of the giant pandas and this study has a similar goal, but Timney and Keil used sine wave gratings, and this study will utilize color stimuli.

Animal Cognition

Animal cognition is an important field to study because survival depends on a certain level of aptitude. Studying animal cognition may help humans in their interactions with animals, especially captive. A large proportion of animal cognition research has been focused on the great apes because of their relation to humans and laboratory animals because of their convenience. Although this research is very important because we need to understand the minds of animals to better manage and breed them; many other species have been neglected. One species that is severely understudied is the giant panda.

Animals learn from experience. Roitblat and Weisman (1986) feel that, "Perhaps the most striking feature of living organisms is their responsiveness to environmental events" (pg. 3). Kamil (1998) points out that "we know that cognitive processes can have adaptive outcomes: remembering where food has been stored, singing effective songs, finding the way back to the hive" (pg. 10). Animals reveal cognitive skills through their capacity to adapt to their environments. The behavior an animal exhibits can be viewed as an indicator of its level of knowledge in a certain environmental situation. Learning potential is useful to measure because learning is necessary for the survival of many animals in the wild.

Animals that forage, such as the giant panda, depend on cognitive abilities to deal with problems faced in acquiring food. Griffin (1984) has found that "in the natural world food is seldom available in such abundance that an animal can satisfy its needs without considerable effort" (pg. 48). Griffin (1992) also claims that, "Locating suitable food is one of the most widespread and pressing problems faced by animals" and most

wild animals spend a majority of their awake hours obtaining food (pg. 28). According to Tomasello and Call (1997), "For many animal species the most pressing problems arise in locating and obtaining food. It is thus widely accepted among behavioral scientists that many important cognitive skills for many animal species evolved in the context of foraging" (pg. 25). They claim that there are two important problems; locating and manipulating food to make it edible. Animals must also identify food and quantify the amount available. Rogers (1997) also discusses the importance of foraging, stating that, "The need to forage for food is considered to be a driving force for increasing the cognitive complexity (or cognitive capacity) of the brain" (pg. 72).

Many may think that the herbivore has an easy plight, to simply roam around and forage. In fact, many scientists base theories of intelligence solely on social complexity and ignore theories of extractive foraging. Rogers (1997) writes that, "Some people argue that ungulates (horses, cows, sheep, and so on) have had no pressure to evolve higher cognitive powers because they do not have to go out in search of food in the same way that species with more specialized diets must" (pg. 73). However, Rogers claims, even ungulates do not eat every single blade of grass that they find; instead they select a favorite and search for those blades. Griffin (1992) sums up the situation by saying:

It is seldom an easy matter of wandering about nibbling whatever vegetation is encountered. Not all plants are equally nutritious by any means and even grazing animals that appear to need nothing but abundant grass do pick and choose just which patches are most worth cropping. Many herbivores must pay considerable attention to signs that food is

available from particular plants, and the tactics they employ often call for at least simple levels of learning and perhaps conscious thinking. (pg. 28)

Griffin (1984) alleges that even an earthworm displays some sort of strategy in its foraging attempts. When the soil it swallows is not nutritious enough, it moves to a more productive area.

Eisenberg and Wilson (1978) examined the relation between feeding strategies and relative brain sizes of several bat species. They found that cranial capacity correlated with feeding strategy, and insectivores, which had to isolate small pockets of resources, had larger brain to body mass than frugivores. They “submit that a foraging strategy based on locating relatively large pockets of energy rich food that are unpredictable in temporal and spatial distribution necessitates the use of a complicated information storage and retrieval system involving input from several sense organs” (pg. 750).

Many theories of cognitive ability have been based solely on social complexity. Conversely, Maple (1980) cites the orangutan as an intelligent, yet solitary animal. He states that orangutans are able to perform many tasks as well as chimpanzees and gorillas and have demonstrated tool use. They are solitary animals, claims Maple, “due to their dependence on dispersed patches of fruits without threat of predation” (pg. 20). Theories of intelligence based on social complexity fail to account for the intelligent orangutan, as extractive foraging theories do. Griffin (1992) points out that he has not observed a close correlation between foraging behavior and phylogenetic group, and has noticed resourceful foraging strategy in some so-called “lower” animals.

Ursine bears must eat a lot of a scarce resource rapidly to survive, thereby needing elaborate and adaptable foraging strategies. Giant pandas feed on a plant that is

readily available year-round, but they are limited by their digestive system and potentially could need adaptive behavior in order to forage efficiently. In addition, despite the abundance of bamboo, it varies in nutritional value, and the panda may be a very selective feeder (Schaller et al., 1985). Although the relative brain size of a giant panda is similar to other carnivores and only slightly above some bears (Gittleman, 1994), if animal cognition truly evolves for the role they fill in their environment, the daunting task a foraging giant panda faces points to a possible high level of cognitive ability.

Kamil (1998) claims that “cognitive processes are strongly influenced by ontogeny” (pg. 8). Animals evolve for the role they fulfill. The limits of what an animal can learn vary greatly by species. Even different primate species have different learning strategies (Rumbaugh and Pate, 1982). There can never be a single theory of learning or a single IQ test for all species. It is essential that all animals are tested based on an understanding of their niche in their environment.

Discrimination Training Basics

According to Stebbins (1970) animal psychophysics can be defined as “an area of research in which the primary concern is with the behavioral analysis of sensory function” (pg. 1). One method to begin studying the basics of animal psychophysics is simple discrimination training, in which the animal is trained to differentially respond to stimuli. Using this method, it is possible to determine whether an animal can perceive a certain stimuli. In cases in which it is unclear as to whether the animal can perceive any form of the stimuli, it is useful to assess the basic sensory abilities before attempting to determine the thresholds.

Animals discriminate in the wild; one stimulus will lead to a different behavior than another. Examples of animal discrimination in nature are ungulates picking favorite grasses (Rogers, 1997) or herbivores selecting patches of vegetation worthy of consuming (Griffin, 1992). Efficient foraging requires learning and discrimination. If an animal could not learn patterns for where to locate food or discriminate between edible and not edible, it would waste a lot of time on unimportant objects (Griffin, 1984). A more specific example is the classification of vocalizations of own species versus other species of territorial songbirds (Shettleworth, 1998). Giant pandas in the wild discriminate and are selective feeders because of the limits placed upon them by their digestive tract. They must be able to pick out the most nutritious pieces and patches of bamboo (Schaller et al., 1985), despite the fact that they eat a very abundant food.

Discrimination studies in the laboratory can parallel natural discriminations and can shed light on the adaptability of the animal because “studies of reward and punishment tell us something of how an animal can be made to change its ways” (Barnett, 1967, p. 173). Laboratory studies can indicate the limits of what an animal can learn if the animal is tested with ecologically relevant tasks. Garcia, McGowan, and Green (1972) support this idea, stating, “so long as we observe the beast locked in his narrow ecological slot, we may never find out what he is able to learn, or more importantly, what he is not able to learn” (pg. 37). Often laboratory tests yield surprising results that are not seen in the wild. For instance rats have been shown to possess the ability to count, a skill which would most likely be useless in the wild (Shettleworth, 1998). However, one should not conclude an animal is incapable of learning simply

because it cannot learn a certain task presented. The problem may simply be an arbitrary task.

It was once thought that discrimination learning-set tasks were the ideal method to measure and rank animal intelligence, mainly because the percent correct increased from the rhesus to the chimpanzee. Learning sets are defined in Slotnick and Katz (1974) as “learning to learn... [and occur] when training on a series of discriminations of the same general class results in progressive improvement in solving each subsequent problem” (pg. 796). Unfortunately, the results did not turn out to be that simple. The results were often surprising, with chickens and mink performing well (Fobes and King, 1982) and rats, who are easily trained in mazes and such, performing very poorly (Slotnick and Katz, 1974). When Devine (1970) tested the effects of chromatic versus achromatic color stimuli and whether the cebus or rhesus monkeys were trained to criterion or to six trials per problem, he found significant effects of stimulus attributes and training procedure. He suggests, based on his results, caution when making generalizations about the intellectual abilities of species from learning set (LS) studies because they “are at best tentative until more is known concerning the optimal stimulus and procedural variables in LS formation” (pg. 66).

Similar problems with discrimination studies have been found in many species, including dolphins and rats. The dolphin has a highly developed auditory system. Dolphins generally fail visual tests, but they perform analogous to a primate tested visually when they are tested using auditory stimuli (Herman and Gordon, 1974; Herman and Arbeit, 1973). Dolphins have been shown to be able to imitate, learn rules, classify objects, learn relationships, and associate symbols with objects (Howard, 1991). Rats

have also provided ample evidence that a standard training procedure fails to encompass the abilities of all species. Rats are more sensitive to certain connections (i.e., Garcia, McGowan, Green, 1972). They easily learn that taste can predict illness and noise/light can indicate a shock, but are not as likely to learn the other combinations. These results are very logical considering that in the wild noise would tend to signal pain from a predator and illness would frequently be preceded by an unusual taste. Rats also have very poor vision. Garcia, McGowan, and Green state that “the rat, a nocturnal feeder with poor vision, dependant upon its excellent chemical analyzers, cannot accomplish [the] feat of directly associating visual cues with delayed illness” (pg. 37). Slotnick and Katz (1974) demonstrated that rats can reach an asymptote of near errorless performance within eight problems if operantly trained using olfactory cues. They note that the results of their study are important “not only because they demonstrate that rats can acquire a learning set for odor stimuli comparable to those achieved by primates in response to visual stimuli, but also because of the rapidity with which the learning occurs” (pg. 798). They conclude that the results of their study are probably due to the fact that rats are predisposed to attend to odors and associate odor cues with reinforcement, but they caution that it is still difficult to compare results because of the difference in training procedures when testing visual versus olfactory stimuli.

Herman and Arbeit (1973) state that the true goal of comparing the cognitive ability of species “is the production of the maximum skill level achievable, and this requires favorable conditions of stimulus control” (pg. 392). A single definition for the complicated construct of intelligence cannot be reached; therefore it is inappropriate to expect a single test for all species. Different species fill different roles in their

environment and evolve special abilities and behaviors to fill those roles (Howard, 1991). It is impossible to simply rely on the test designed for the rhesus monkey. Even if a certain species performs well on the standard test, the results may not be the limit of its ability. Despite the many shortcomings of the standard visual discrimination tasks, they are a useful starting point. They can provide much needed information about the sensory abilities of the animal. Visual discrimination was the starting point when McCain and Stepter (1968) began studying discrimination in the black rhinoceros (*Diceros bicornis*). Despite the rumor that these animals are slow learners and lack visual acuity, they were able to train the rhinos to a plateau of 80% correct in twenty-one days. These procedures help define the limits of a species' ability and point researchers in the best direction to proceed for an understudied species.

Many species exhibit similar confusions in discrimination training. The octopus and rat show similarities in training difficulties such as confusing mirror images of a diamond and triangle after being trained to discriminate a triangle and a square (Sutherland, 1969). Sutherland uses these data to postulate that "there has been strong convergent evolutionary pressure towards the production of similar mechanisms of pattern processing in the visual system of widely different species" (pg. 389). Because these training procedures have been used in various ways on most species, there are a wealth of data to which one can compare the results of a species that has been understudied, such as the giant panda. The pattern of results observed can be compared to many species and the similarities and differences can help point to how the tests should be altered in the future. For instance, past studies that have lead to improved results for species with similar patterns can provide possible alterations to the study used, such as

changing stimuli, nature of response required, reinforcement, apparatus, or procedures. Savage, Rick, Brangan, Martini, Pugh, and Miller (1994) used this strategy when testing African elephants. They also tested the sea lion, which they claim has been well studied on the complex task they were using as a context for the performance of the elephants. They were able to conclude that both were able to perform the task and found that sea lions needed fewer trials to reach criterion, while the elephant demonstrated learning that is more gradual. They interpreted their results in the light that elephants are herbivores and may be less visually adept.

Studies by Swaisgood and colleagues provide evidence that giant pandas can discriminate the individual scents of different conspecific individuals (e.g. Swaisgood, Lindberg, and Zhang, 2002; Swaisgood, Lindburg, Zhong, and Owen, 2000; Swaisgood, Lindburg, and Zhong, 1999). They examined the discriminations in the habituation-discrimination paradigm, by investigating the change from diminished responses, or habituation, to increased response, or discrimination, when the scent sample of a new individual was placed in the enclosure or by preference and behavior tests. The earlier experiments were harder to interpret because of the interaction of sex and novelty in scent interest. Subjects of both sexes had a clear preference for novelty in male scent, but the difference was not as large for female scent. These studies provide evidence that giant pandas can learn discriminations, but giant pandas have not been tested on visual discriminations.

It would be useful to have a more basic understanding of giant panda discrimination and sensory abilities to be able to interpret studies such as these. In the case of discriminations, the simplest are location (right versus left) and visual contrast

(black versus white) discriminations (Bitterman, 1976). These discriminations require tracking one item consistently. Once giant panda discrimination is better understood at a more basic level, studies can be performed to determine the limits of giant panda discrimination learning and how the bears react to more complex situations.

Given that giant panda cognition and color vision are relatively new fields, it makes sense to start at the absolute beginning and examine simple discriminations. Training experiments are a useful method in studying visual abilities of animals (Jacobs, 1981; Tansley, 1965), despite the drawbacks of being time-consuming, tedious and that they require a great deal of control. Animals are often able to pick up on other cues, allowing them to appear to be able to discriminate colors when in fact they are using another cue, such as brightness (Jacobs, 1981). The conclusions of early color vision experiments are often questioned because they did not control for brightness. The brightness problem is especially hard to deal with due to the fact that animals may have different spectral sensitivity than a human and therefore, a great amount of experimental work is required to determine the actual sensitivity of the animal. In addition, potential fluctuations in thresholds make a precise determination of brightness equality impossible (Jacobs, 1981). The most frequently used strategy to deal with the brightness problem, and the one used in this experiment, is to make brightness an irrelevant cue by presenting the color with enough grays to prevent discrimination by brightness alone. Even this strategy can become a tedious task (Jacobs, 1981).

For this study, the procedures selected are crucial, because changes in methodology may alter the results of the experiment (Stebbins, 1970). One must develop a procedure that substitutes for verbal instructions. Many of the procedures used in

laboratory studies with animals such as pigeons, rats, or moneys are inappropriate for studying the giant panda. Therefore, simply adapting a method for widely used experimental animals is not enough (e.g. Berkley, 1970), a unique procedure had to be created for this unique animal.

This study is a systematic replication of Bacon and Burghardt's (1976) study of color discrimination in black bears, with modifications to accommodate testing giant pandas. Bacon and Burghardt found that black bears could discriminate visual stimuli on the basis of wavelength. One of their bears learned to track blue and the other learned to track green. In terms of reinforcement, it is essential to select a preferred food. Bacon and Burghardt's bears were given raisins, but the giant pandas tested in this study did not eat raisins and they had worked for leaf-eater biscuits and fruit in other studies (personal observation). In their study, they were able to use manipulatable feeders and actually enter the juvenile bears' enclosure. Neither of these procedures could be used with the giant pandas. For the apparatus, it was designed to remain outside of the enclosure and benefit from already trained behaviors that could be shaped into a procedure. The number of hues and control of brightness cues in the color phases matched those used by Bacon and Burghardt. Bacon and Burghardt used a correction procedure, potentially because it was difficult to stop their bears from making a second response. This study used a non-correction procedure because although there is still some mixed evidence, non-correction has frequently been found to be a more efficient method (e.g. Allison, 1972; Riopelle, Hill, and Rector, 1967; Towart and Smith, 1966).

This study included simple discrimination based only on brightness or contrast. The purpose of this study is to begin to decompose the limits of giant panda visual

discrimination ability. The study is divided into two phases of training: contrasts and color. The first phase was conducted to gather empirical evidence that giant pandas could be trained using the chosen method and that they can learn a visual discrimination task. The second phase of this study was conducted to determine if giant pandas can distinguish color and whether they can be easily trained using visual stimuli through behavioral techniques. The hypothesis was that the giant pandas would come under differential control of brightness in the contrast phase and wavelength in the color phase.

METHOD

Subjects

The subjects for this study were 1.1 giant pandas (*Ailuropoda melanoleuca*), Yang Yang and Lun Lun, that reside at Zoo Atlanta. The animals are housed in an indoor holding facility at night, but are housed on exhibit from approximately 9:00 a.m. to 5:00 p.m. every day in either an indoor day room or an outdoor enclosure. The animals were tested in an indoor shift area designed to fit a squeeze cage (hereafter referred to as “squeeze cage”) or a cage with moveable sides that immobilizes animals by squeezing in the sides to allow for injections at a close range. Using this squeeze cage area allowed for constant lighting for all sessions. The subjects were tested before they went out on exhibit between 0730-0830.

Stimuli

The stimuli consist of green and gray (ranging from white to black) color squares. The color squares were created using MSPaint and a color laser printer. Five shades were created for green (with transmission peaks around 510), with 18 shades of gray, including white and black. The transmission spectra for each color were plotted using a

spectrometer (see Figures 1 and 2; Bacon and Burghardt, 1976; Muntz and Conly-Dillon, 1966) to ensure that there are shades of gray that are brighter and dimmer than all of the shades of each color.

Apparatus

The apparatus was composed of two pieces (see Figures 3 and 4). The top of the apparatus consisted of a board (4.5 feet by 8 inches by $\frac{3}{4}$ inches) which held a removable PVC rod which held up to four stimuli. Attached to the PVC rod were up to four small “chip” clips, which allowed the stimuli to be changed easily and permitted performing several trials without needing to shift the panda out of the squeeze cage.

The bottom of the apparatus consisted of a board with holes drilled through to allow for the insertions of PVC pipe extensions. The PVC pipes were capped on the end that extended into the panda area to remove sharp edges. The other side had a bolt to prevent the subject from being able to pull the pipe through the mesh. The pipes had extensions to allow them to all be pushed into or pulled out of the den at the same time.

The top board or part of the squeeze cage blocked the trainer’s and/or volunteer’s eyes so that the subject could not receive cues from the trainer or volunteer. Therefore, the trainer had to judge the subject’s response by the movement of the PVC pipe extension. The boards were attached to the mesh wall of the den, with only the PVC pipe extensions reaching through to the subject’s side of the mesh.

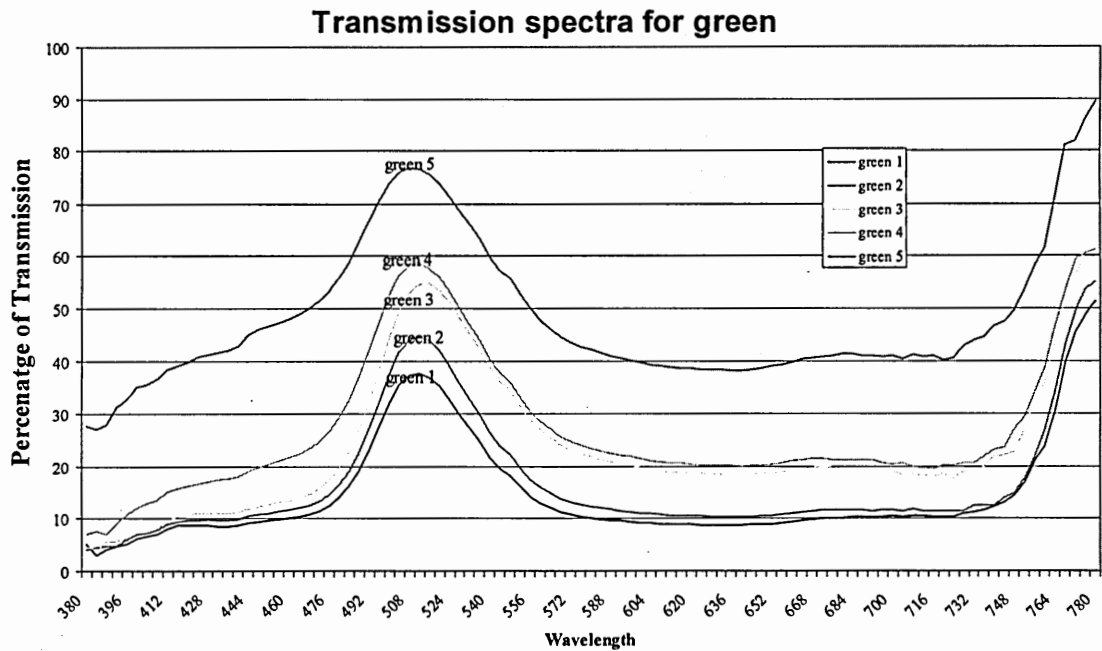


Figure 1. Transmission spectra for the five shades of green (Green 1 is the darkest and green 5 is the lightest shade) in comparison to the white card used in the study.

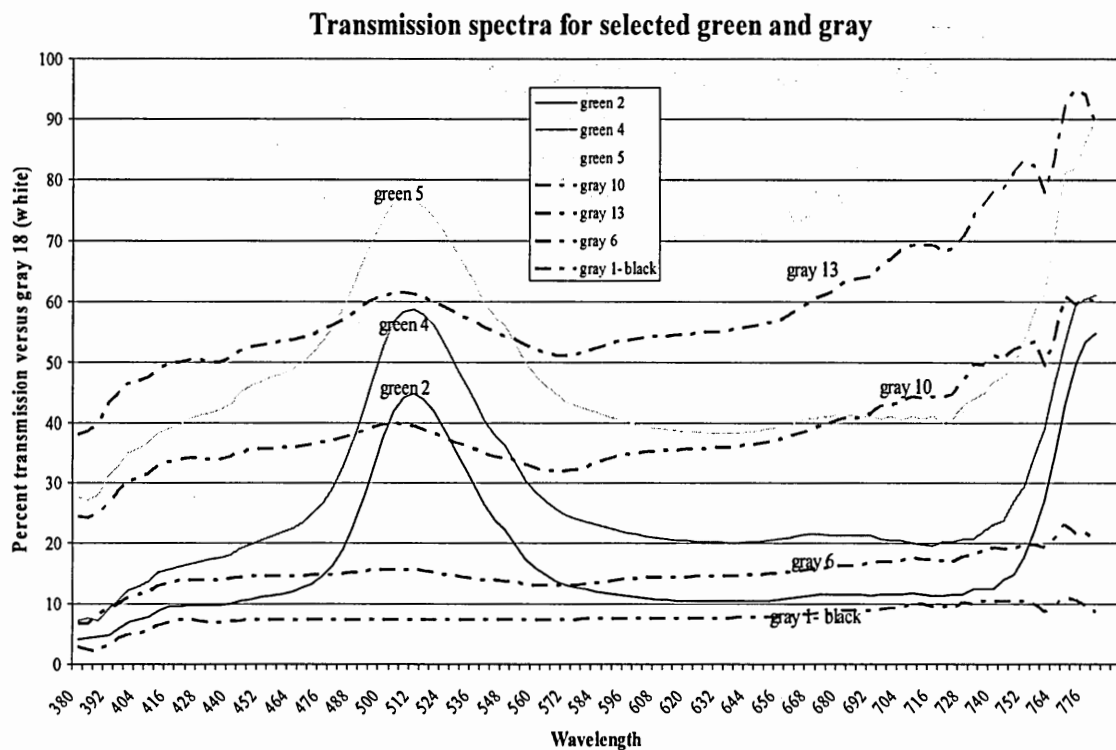


Figure 2. Transmission spectra for selected green and gray cards versus the white card used in the study.

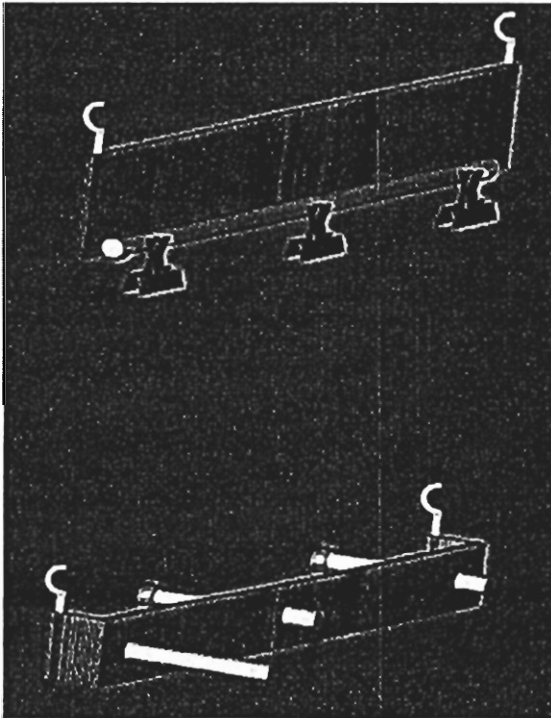
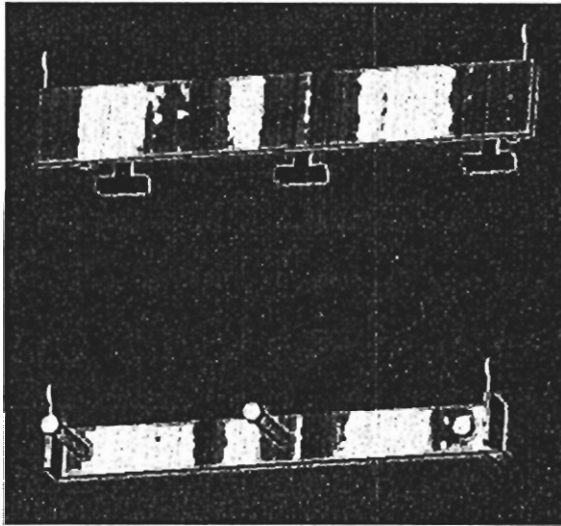


Figure 3. An illustration of the apparatus from the view of the subject (3a) and the trainer (3b). Only the PVC pipe extensions extending into the panda's side of the mesh. The apparatus is in two pieces, with a bar across the top allowing for the stimuli to be removed and placed simultaneously and extensions on the PVC pipes allowing for them to be extended into the panda's side or be pulled onto the trainer's side individually or simultaneously.

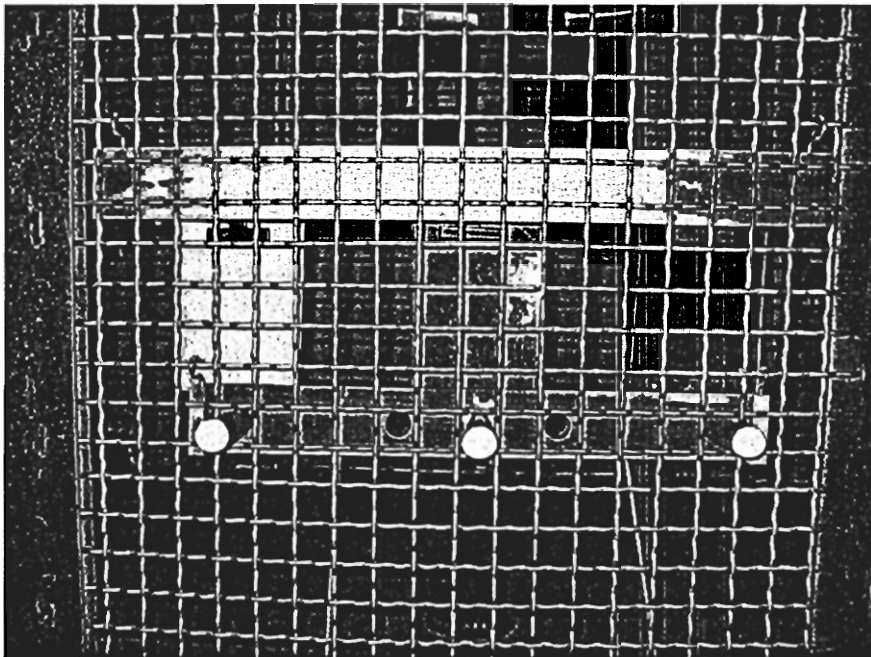
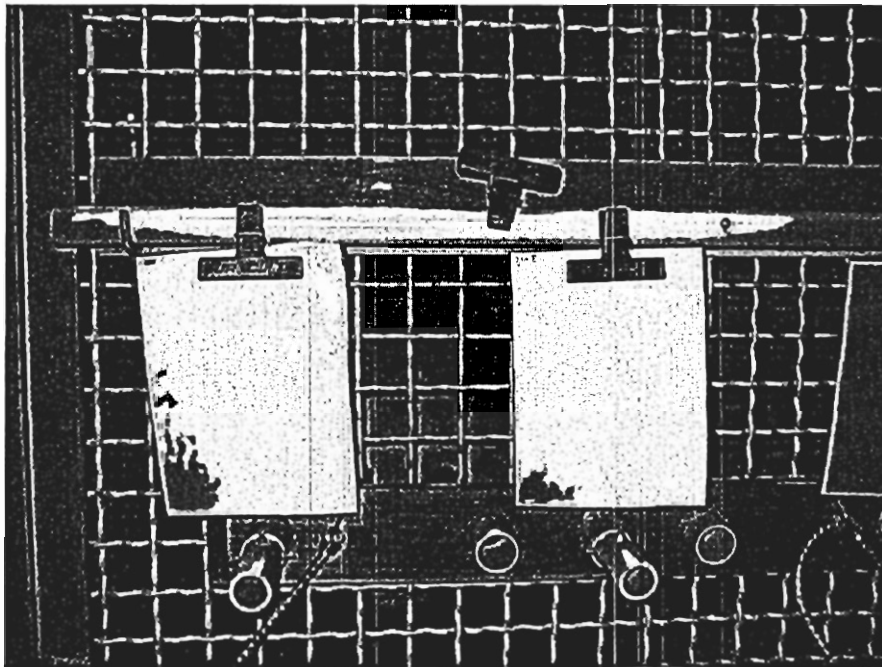


Figure 4. Pictures of the apparatus from the trainer's side (4a) and from inside the squeeze cage area, giving the panda's view of the black card, white card, and an intermediate gray card.

Habituation to setup

Before the experiment began, the subjects were habituated to the set-up and reinforcement procedure in a pilot study to test how they would react to the apparatus. The initial training, which began on May 6, 2002, was performed by the panda keepers. The pandas had been previously trained to present their paw when requested; therefore the “paw” command was used and shaped into a “push” behavior, which entailed pushing the PVC pipe extension through the mesh with their paw. In the beginning, the pandas were allowed to push any pipe and gradually the behavior was shaped so that they pushed the pipe to which the trainer pointed. Once the “push” behavior was established in early June 2002, the subjects were shown only the positive stimulus, as discussed in Borgese (1968). In this study, the first positive stimulus was white.

Training Procedure

The procedure used was a non-correction discrimination, which is different from the correction procedure used by Bacon and Burghardt (1976). Trials began with the panda being required to touch their nose to a wooden rectangle “remote” target when the cue of “remote” was given. Once the panda offered the “remote” behavior, they were given the cue to “push” which indicated that they should walk over to the pipes and respond by pushing one pipe through the mesh. The trainer judged the accuracy of the response by the movement of the stimulus holder via the PVC pipe extension. If the response was correct, the trainer produced a clicking sound using a clicker (conditional reinforcer) and provided reinforcement, which consisted of leaf-eater biscuits (50 grams daily) and fruit (approximately 100 grams daily, which included some combination of banana, apple, and pear for both pandas with sweet potato added for Yang Yang) through the mesh and the next trial began once the panda returned to the remote after the

“remote” cue was given. If the response was incorrect, the subjects were required to return to the “remote” and hold there for an inter-trial interval before the next trial could begin.

A behavior that Yang Yang performed more than Lun Lun was pushing a second pipe, usually the correct pipe, after an incorrect selection. In the rare cases in which the subject pushed the correct pipe before the trainer or volunteer could pull it in, the trainer would occasionally click to indicate that the response was correct, but the trial was still treated as an incorrect response, receiving no primary reinforcement and requiring a hold on the remote. Initially, if the subject pushed a second pipe there was never a response from the trainer, which increased the frequency of behavior labeled as “frustration,” consisting of pacing, bleating, and other stereotypic behavior. The approach of indicating whether the second response was correct or not was used more during the sessions in which the subjects were performing poorly and receiving little reinforcement.

During part of the study, the pandas developed a tendency to correct the last response by returning to the pipe that was correct on the last trial. Therefore, occasionally, the same trial was repeated with only the pipe for the positive stimulus extended through the mesh or in trials that they were able to make a second response, its correctness was indicated by a click or buzz in an attempt to decrease the tendency to correct the last response by allowing them to correct it before the next trial began. When the pandas were not receiving enough reinforcement to prevent “frustration,” they were sometimes given cues for simpler behaviors, such as “target” and “paw,” during a session to allow them to acquire some reinforcement. After each trial, the trainer or a volunteer recorded the subject’s first response and set up the stimuli for the next trial.

Initially, four locations for the white and three grays were used to prevent learning based on stimulus position. However, the size of the mesh on the squeeze cage limited the spacing of the stimuli and therefore made the stimuli hard to distinguish. Consequently, the apparatus was altered to allow for three even spaced pipes and stimuli. Training was also changed to stages instead of introducing all negative stimuli at one time. Once the panda reached the training criterion of 100% correct on positive stimuli only, one gray was added until the panda reached a training criterion of 80% correct for three consecutive days.

In the beginning of each phase the pandas tended to perform poorly, which led to longer training sessions because of the time required for the intertribal interval. In an attempt to decrease any effects from the length of the study and maintain the positive enrichment benefits, the sessions were reduced to approximately 10 trials until the panda reached a training criterion of 80%. This change was performed in order to keep the sessions shorter. Once the subjects reached the training criterion, sessions were increased to 20 trials per day for a testing criterion of 16 correct responses out of 20 trials for three consecutive days in a row, for a total criterion of 48 out of 60. Occasionally, session durations were reduced if the panda was not being attentive. Session durations were adjusted a few times to allow the session to end with a correct response.

Training Phases

Contrast Phase: The first phase of this study, which began on July 20, 2002, was contrast discriminations with white as the positive stimuli. After the subjects learned to respond only to the positive stimulus and not push in pipes without a stimulus above them (July 27, 2002 for Yang Yang and August 2, 2002 for Lun Lun), the negative stimuli (black

and grays) were added and location on the apparatus was randomly decided for all stimuli (see Appendix). Borgese (1968) claims that after being exposed to only the positive stimulus and being rewarded for responding to it, the animal will tend to choose the positive stimulus when the pair is offered. Therefore, this procedure should be more efficient than introducing all stimuli at one time. To begin with, there were three negative stimuli and the positive stimuli, which produced a chance level of 25%. Due to the change to the apparatus on November 17, 2002 because of spatial limitations, chance was increased to 33%. Testing criterion remained 80% for three consecutive days.

Reversal Training: When criterion was reached for the first contrast phase (November 29, 2002 for Yang Yang and December 30, 2002 for Lun Lun), the subjects were reversal trained, meaning the positive choice was switched to black. This phase was performed because it provides evidence that the pandas did not learn the discrimination based on an unintentional cue if the reversal of the positive stimulus leads to a drop in performance. Training was attempted on black versus two grays, but because of time limitations, the criterion for the reversal training was lowered to black versus gray. Therefore, chance for the reversal training was 50%. Both subjects passed this phase on April 9, 2003.

Color Phase: Phase two consisted of color discriminations. The first positive color for both pandas was green, selected for its ecological relevance since it is the color of the food that pandas eat. Both subjects were initially trained on green versus two grays, but green only training was added when subjects selected the same pipe for up to 90% of the trials. The criterion for green only was 80% for three days with 20 trials a day or 100% for one session. When the subjects passed green only (April 23, 2003 for Lun Lun and

May 8, 2003 for Yang Yang), both were trained on green versus gray. Some sessions with green and two grays were attempted in mid-May and mid-July to test if training on green versus two grays might be more efficient, and on August 26, 2003 training on green versus two grays was resumed. Lun Lun passed green versus two grays on October 26, 2003. Yang Yang ceased eating the reinforcers and his training was suspended.

For color training, the positive color was paired with shades of gray that are brighter and dimmer than the positive stimulus, determined using a spectrometer. In this way, the animal had to track several shades of one color, and was unable to perform these discriminations based on brightness cues because the positive color will be presented as brighter and dimmer depending on the trial. This method has been used with other animals to render brightness an irrelevant cue (e.g., Bacon and Burghardt, 1976; Muntz and Cronly-Dillon, 1966, Birgersson, Alm, and Forkman, 2001).

RESULTS

Data Analysis

Data were examined graphically to analyze the patterns of responding. Data were also compared to chance, which was determined through a binomial distribution, since correct and incorrect choices are binary, mutually exclusive and exhaustive events. Using a criterion of 80%, the probability of the subjects getting 16 or more trials correct out of 20 consecutive trials is 2.51×10^{-5} if there are three stimuli (chance equals 33%) and 5.91×10^{-3} if there are two stimuli (chance equals 50%) and the possibility of selecting the pipe without a stimulus is ignored. Extending the probability to three sessions in a row at 80%, the probability of the subjects getting 48 or more trials correct out of 60 consecutive trials is 1.54×10^{-13} for three stimuli and 1.59×10^{-6} for two stimuli. Therefore, criterion

performance for all phases was statistically above chance performance (all p values are well below .01).

Habituation to Setup

Both subjects had been trained to present their paw on the command “paw,” which allowed rapid training of the push response. Lun Lun had more problems than Yang Yang, her initial response was to bite the pipe and she also tried to pull or slap at the pipe. Both subjects were able to learn to push the pipe in a month. At that point, the pandas were shaped to push only the pipe that had the white card above it. At this step, the subjects began to push all the pipes in order because they had often been trained to do so before the white card was presented. Both subjects were required to learn to push white only to a criterion of 80% for three sessions in a row. Yang Yang (121 trials) learned to push white only quicker than Lun Lun (246 trials). Both pandas performed at 100% for at least one session.

Contrast Phase

Once criterion was reached on white only, three grays were added. Both subjects were trained on white versus three grays for almost 100 trials, but then both pandas went through a phase in which they did not eat and became very difficult to train. Yang Yang ended up having to have a tooth removed. They were retrained to criterion on white only and then trained on white versus one gray. Once Yang Yang reached criterion on white versus one gray, he was trained on white versus three grays. However, due to space limitations on the apparatus, it became obvious that four stimuli were too crowded and the apparatus was changed to accommodate presenting only three stimuli at a time. During this period, the subjects were occasionally trained in their dens to prepare for the

arrival and use of the squeeze cage. However, they were unable to stay on task well enough to perform even white only in the dens, most likely because of the large differences in the procedure such as different approach directions and distractions such as bamboo. It was determined that the squeeze cage could be removed from the squeeze cage walkway to train. In terms of white versus two grays, Yang Yang passed after 317 trials (see Figure 5) and Lun Lun passed after 250 trials. Visually examining the data reveals that Yang Yang performed above chance for all of the white versus two grays trials, whereas Lun Lun had two early sessions that were actually below chance. In addition, Yang Yang's performance was found to be more variable than Lun Lun's.

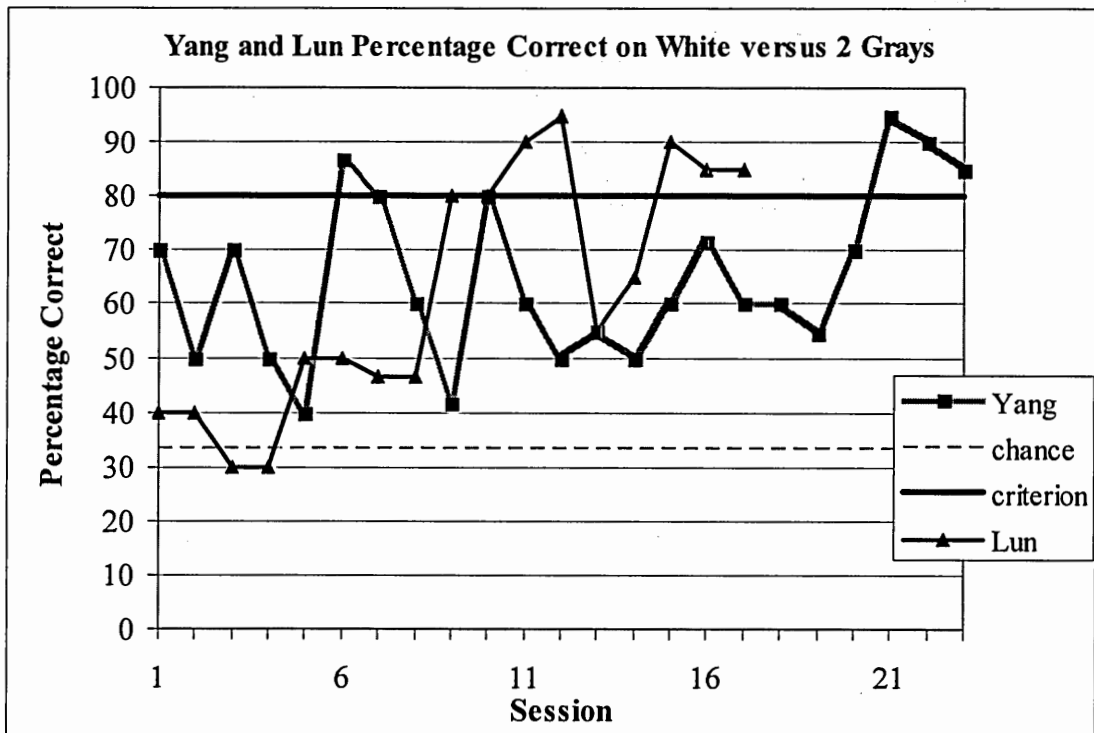


Figure 5. Percentage of correct trials for Yang Yang and Lun Lun on white versus two grays trials. The first sessions in which Lun Lun is above criterion consisted of only 10 trials and therefore were not enough for her to move to the next phase. Lun Lun passed in fewer trials (250) than Yang Yang (317).

Reversal Training

Once the subjects passed white versus two grays, they were initially trained on black versus two grays. Due to confusion and poor performance, they were then trained to a criterion of 100% on black only and black versus two grays was retried. After 200 trials without much improvement, the pandas were switched to black versus gray. This discrimination took four months, with Yang Yang requiring 824 trials and Lun Lun requiring 822 trials (see Figure 6). Therefore, once the subjects passed this stage of training it was decided to move on to color discrimination.

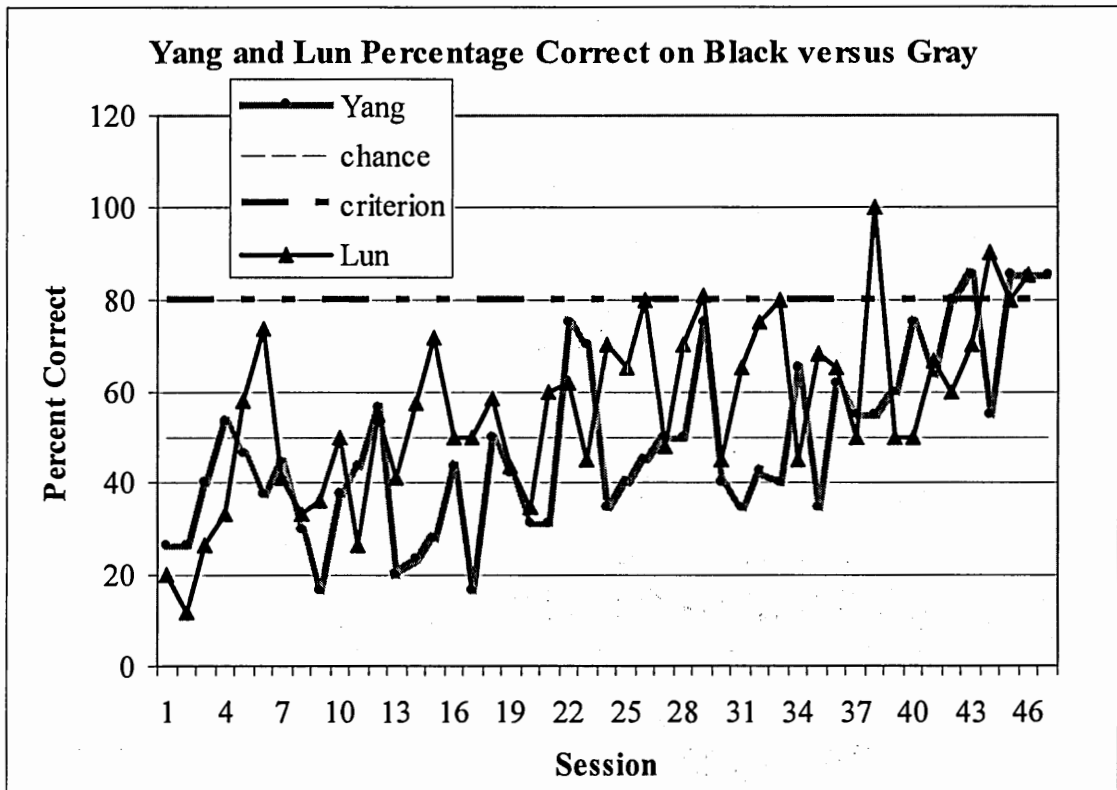


Figure 6. Percentage of correct trials for Yang Yang and Lun Lun on black versus one gray trials. Both giant pandas took approximately the same number of trials, 822 for Lun Lun and 824 for Yang Yang, to pass the criterion.

Color Phase

Both subjects were initially presented with green and two grays with the hope that green would stand out enough to make training more efficient. However, both pandas were having difficulties and training on green only and green plus one gray were added. All trials of green versus two grays are reported in totals. Yang Yang ceased eating all of the reinforcers and was unable to complete the color phase. Lun Lun reached criterion after 860 trials (see Figure 7).

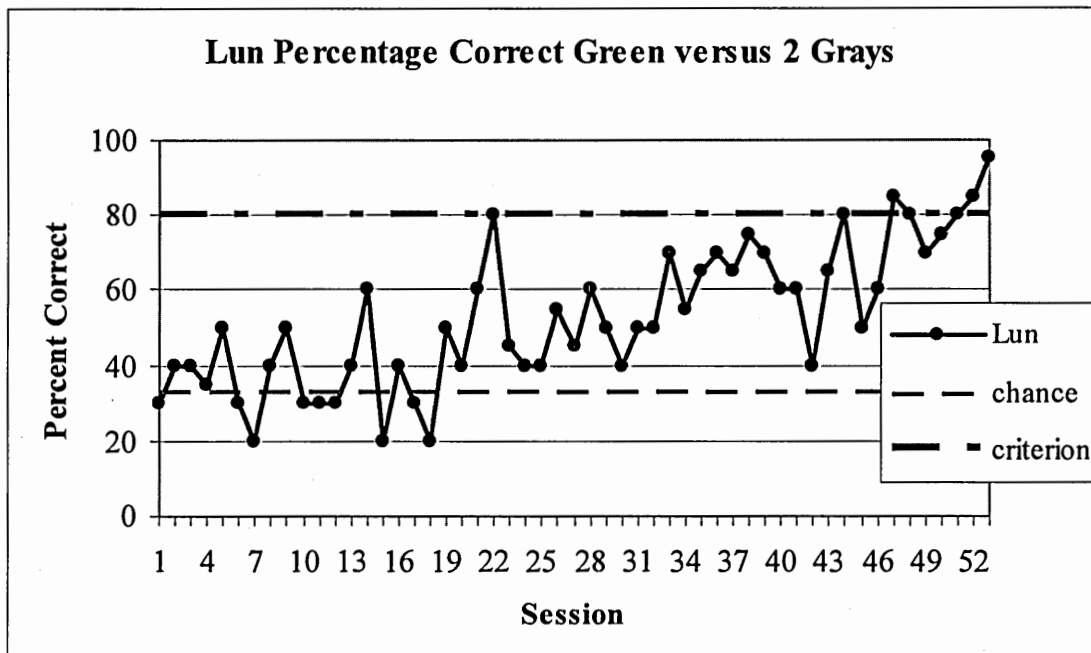


Figure 7. Percentage of correct trials for Lun Lun on green versus two grays trials. Lun Lun required 760 trials to reach criterion.

Interesting Findings

There were three interesting findings that were unrelated to color vision. The first was that the two giant pandas used different paws to perform the task. Yang Yang used his left and Lun Lun used her right. This difference, along with Lun Lun's tendency to run into the pipes when approaching from the left led to setting up the procedure so that the subjects approached from different sides. The finding of paw preference is interesting in the light of a current study at Zoo Atlanta and in China that has found paw preference in eating bamboo (Snyder, unpublished data).

The second interesting finding was the emotional responses of the animals, especially during the times in which they did not feel well or during breeding season. Both animals displayed what could be called frustration in humans. They paced in the squeeze cage and often bleated. Lun Lun would also retreat to leaning on a wall and repetitively lick her chest, a stereotypic behavior she performs, especially when she is stressed or has biscuits in her teeth. During times in which he was supposed to be holding on the remote, Yang Yang also began chewing on or near the mesh and bobbing his head. Both pandas would also raise their paw on the mesh, potentially presenting some behavior for which they would be reinforced and released from the hold. Once the animals displayed these behaviors, it was difficult to get them to return to the task. The greatest display of "frustration" came from Yang Yang. In one session he was performing very well. He only missed one trial out of the twenty of the session, and after he missed that one trial he bleated and walked away briefly. It is unclear as to whether this display was directed at me for buzzing him or himself for missing the trial, but the message was transmitted.

The third finding of note was that the subjects tended to approach the task differently. Yang Yang was more motivated to receive reinforcement than Lun Lun, and the actual pushing behavior seemed to be intrinsically reinforcing for Yang Yang. Perhaps because of that appearance, he seemed to try everything until reinforced, whereas Lun Lun appeared to latch on to one strategy that was often incorrect and she would often select one pipe and return to the remote. Yang Yang was usually more prepared to perform the task and easier to get to change when he developed unnecessary or hindering behaviors.

Difficulties during Training

The difficulties in training these unique creatures offer some insight into their behavior. Both subjects developed the tendency to push the pipes in order, related to the fact that they were often asked to push all the pipes in order to allow for more efficient responses. It was very hard to disrupt this behavior when the white card was added. Another noteworthy difficulty was that when the giant pandas would release themselves before the trial was ready and give the correct response, they almost always gave the incorrect response if asked to repeat the trial. The lack of reinforcement after a correct response rendered them unable to repeat the trial correctly.

There were several problems related to attentiveness or motivation, for lack of a better term. It was postulated that the animals were too hungry in the morning since their last fresh feeding of bamboo had been the night before. Potentially, the reinforcers of fruit and leaf-eater biscuits were not as strong of a reinforcer in light of the intense need for bamboo, despite the high nutritional value of the reinforcers. Therefore, training was attempted in the afternoon when the giant pandas were brought off exhibit so that the

dayrooms could be cleaned and fresh bamboo provided. However, the subjects had often just awakened from a nap or were pulled away from eating and were likely just as hungry as in the early morning. They performed just as poorly as in the morning sessions. For that reason, afternoon training, which was more difficult for the keepers, was discontinued.

Often the subjects seemed unwilling to actually look at the stimuli and select a pipe. It occasionally seemed that they decided which pipe to push before walking toward the apparatus. This behavior was more apparent in Lun Lun who would often walk over to the apparatus with her head down and lift it to pick the pipe in front of which she was standing. Forcing these animals to wait while trials were being prepared was problematic. When grays were first added, the slow pace made a large difference in performance and displays of "frustration." The waiting led the subjects to push the closest pipe in the earliest trials. A similar behavior that they developed was to pick favorite pipes, not necessarily the closest, and push only that pipe. When it was attempted to never present the positive stimulus on that pipe, Yang Yang began switching favorites between pipes. This pattern continued several cycles and forced the presentation of the positive stimulus on the favorite pipe occasionally to prevent him from switching favorites. Lun Lun would even go so far as to place her paw on the correct pipe and then remove it and push her favorite.

Both subjects developed a behavior which could be labeled as correcting their responses. They would select an incorrect response and on the next trial select the pipe that was correct on the trial before. This inclination led to a horrible performance on the entire session. Lun Lun would often exhibit this behavior after she was in the later stages

of learning a phase. She would enter a session the day after a good performance and not look up to select the correct pipe on an early trial, which would lead to near chance performance on the day after above criterion performance. This correction behavior suggests that a future study of memory may be warranted. The subjects would select the pipe that was correct from the last trial even when the intertribal interval was increased and/or they were asked to present other trained behaviors in an effort to distract them.

DISCUSSION

Evidence of at least adequate visual abilities and color vision in the giant panda has been provided by this study. Jacobs (1981) suggests that the integration of this information with other biological data about giant pandas aids in the crusade to “develop a richer and more complete picture of the natural histories of the species currently inhabiting the planet” (pg. 1). This evidence of visual acuity and color vision fits with the higher level of activity of giant pandas during daylight hours (Schaller et al., 1985) and the presence of cones in the giant panda eye (Jinchu, 2001). In addition, the evidence of visual acuity suggests that giant pandas are prepared for the rare encounters with other giant pandas and visual communication, such as coloration and bark stripping and clawing (Laidler and Laidler, 1992; Schaller et al., 1985).

The large amount of difficulty present in obtaining this evidence suggests that the giant panda may not readily use color as a cue in foraging. Similar results have been found with the domestic cat. Although the cat possessed cones, early experiments could find no evidence for color vision. Jacobs (1981) states that extensive training is required in order to demonstrate color vision in the cat and it “is like other species in which color vision is not highly developed or, possibly, does not provide a very compelling source of

environmental information” (pg. 130). Potentially color is not as useful to these bears as other cues, such as location. Future studies should farther decompose the limits of color vision; potentially other studies may better tap into its ecological significance. Perhaps giant pandas would respond better to color vision using a go-no go procedure.

Additionally, the tendency to attempt to use location as a cue for discrimination suggests that this apparatus may be useful for studies based on location, such as preference testing.

Color vision studies may also be useful in providing additional evidence of the relations between bears, raccoons, red pandas, and giant pandas. Raccoons are acknowledged to have excellent visual acuity (Zeveloff, 2002; Cole, 1912), but are thought to have weak or absent color vision (Zeveloff, 2002; Davis, 1907). Therefore, with this evidence giant pandas and ursine bears have both been found to possess color vision, whereas raccoons do not. However, many of the raccoon studies were performed with outdated methods and some that actually found evidence on color vision are claimed to have not controlled for brightness (Davis, 1907). Therefore, further studies are needed on more bear species, red pandas and raccoons, but sensory abilities are one avenue that warrants future examination.

The black bears in Bacon and Burghardt’s (1976) study required very different lengths of time because they used one subject to evolve the procedure and tested the second on a predetermined procedure. The first bear required 31 sessions with between 16 and 19 trials per session, for a total of approximately 550 trials. The second bear required only twelve sessions for approximately 210 trials. Goldfish are able to learn color discriminations to a criterion of 90% in under 100 trials (e.g. Muntz and Conley-Dillon, 1966). Elephants, which are believed to have poor daylight vision, were claimed

to learn gradually when they took a maximum of 330 trials to reach the criterion of ten consecutive correct responses on a visual object discrimination study. Therefore, it was hoped that the giant pandas, which had been successfully trained using positive reinforcement techniques, would be able to learn each discrimination in around 500 trials. The giant pandas did learn the discrimination, but slower than desired. Both subjects learned the discrimination with white as the positive stimulus in well under 500 trials, however, performance was much slower on the black and green phases, with both phases requiring over 800 trials to reach criterion. The training was often tedious with the giant pandas progressing slowly and presenting many training challenges. They were not adaptable. Change, such as the change in positive stimulus from white to black resulted in terrible performance. During this study many issues arose such as decreased feeding and a toothache, but other sorts of change were met with similar results. The subjects never demonstrated learning sets, they never learned to learn, but instead were worse with the reversal and change to color training. Potentially they could have begun improving with reversals if given more training. Despite all the issues faced, the giant pandas were able to learn the discriminations if given enough trials. Basic discrimination abilities were demonstrated in this unique species using a unique testing procedure adapted for them.

Because the rate an animal learns in a certain situation is dependant on many factors, such as characteristics of stimuli, nature of the response required, motivation, reinforcement, testing apparatus, and training procedures; it is hard to determine what causes slow acquisition (Warren, 1974) and it cannot be attributed to sensory or cognitive limits. Subtle changes in the procedure may lead to large improvements in performance.

In this case, the subjects did not perform as well as anticipated and the task may not be ecologically relevant or the conditions may not have been optimal to test the subjects. Devine (1970) points out that, “Implicit in species comparisons is the assumption that the task and procedure used does not markedly favor any one species” (pg. 62). It is essential to view results that are not optimal in light of the fact that the test itself may not be optimal for the species and its perceptual processes. Simply because results of one study are not ideal does not indicate a lack of cognitive competence or sensory abilities. The apparent hunger in the subjects may have made the reinforcers or biscuits and fruit not as valuable in light of the intense need to consume bamboo. Although others have found that “motivation for leaf eater biscuits as reinforcers seemed to be high” (Bloomsith, Jones, Snyder, Singer, Gardner, Liu, and Maple, 2003; pg. 333), perhaps their strength varies based on hunger level. Scientific tests of reinforcer strength in giant pandas may aid future training studies.

Although the evidence of color vision in the giant panda is exciting in its own right, Jacobs (1981) states that it is important to go further and determine the answer to “more interesting questions of color vision” (pg. 21). He goes so far as to claim that, “we now know that the possession of color vision is so widespread that merely establishing its presence in one more species is only of moderate interest” (pg. 21), unless color vision is found where it is not predictable or absent where it is anticipated. Therefore, future studies should look at whether giant pandas are di- or trichromatic and test their spectral sensitivity. However, Jacobs (1981) later contradicts himself and states that color vision is understudied in many species, especially mammals, and many studies that have been

performed were flawed, which makes comparisons difficult. Therefore, it would be useful to apply this procedure to other bears in order to be able to make comparisons.

Overall, this study led to many remarkable discoveries of a unique species. The difficulties faced in this training may guide future studies. The emotional response seen provides insight into the personalities of two pandas and may be an interesting area to study in the future. The fact that performing the task well by actually looking up and selecting a stimulus seemed to require more effort than the subjects were willing to give is also interesting. The lack of “motivation” to do the task along with the lack of patience highlights the difficulty of training these animals if they are uncooperative or if the task is too demanding or not demanding enough. The paw preference is notable because of the data on panda paw preference in feeding (Snyder, unpublished data) and the interest in vertebrate, and especially nonhuman primate, paw preference and its potential relation to asymmetry in cerebral function (e.g. Walker, 1980). The giant panda is unique in its ability to use the pseudo-thumb to precisely manipulate bamboo and could potentially possess lateralization of motor performance. Comparative analyses focusing on paw preference in animals other than the nonhuman primates, such as the giant panda, may help shed light on development of hand preference in humans and whether it is genetic or ontogenic in origin (e.g. Annett and Annett, 1991; Denenberg, 1981). One of the most incredible results of the study was the indication of a remarkable memory based on the tendency to correct the previous response. Future studies should definitely tap into this potential resource and decompose its true nature.

The difficulty of the task for the giant pandas indicates that it was most likely a challenging task. Therefore it has some value as a form of behavioral enrichment. In

addition, the behaviors labeled as frustration were rare during the study and were also present at other times, such as when waiting to begin the task or to go out after completing the task or even during times in which they were forced to wait unrelated to the task. Lun Lun would also repetitively lick her chest after her morning feeding of biscuits, so potentially this behavior is related to the biscuit remnants in her teeth. In fact, although they both displayed behavioral indications of frustration, the subjects habitually chose to participate even though they were not forced to do so, indicating that it was a positive experience. The few refusals came during the periods of decreased food consumption, in which the subject would often begin the task and then refuse the reinforcement and walk away to the shift door and refuse to come back to the task, or during breeding season, during which Lun Lun preferred to scent mark and Yang Yang preferred to investigate her markings than perform the task.

Swaigood, Ellis, Forthman, and Sheperdson (2003) state that an enriched environment includes opportunities for animals to work for food. Hare, Ripsky, Battershill, Bacon, Hawk, and Swaigood (2003), cite the importance of providing mental challenges to giant pandas. Accordingly, this task can be viewed as a positive experience despite a few kinks. These kinks may be unique to the animals tested, but they can provide insights about trying to work with giant pandas in general. Once the subjects walked away from the task, it was difficult to compel them to return, so a time-out may be helpful to allow them to display frustration and become willing to reapproach the task. In terms of Yang Yang's pacing and bleating, if he was allowed to walk around the squeeze cage area for two to three repetitions he would often come back to the remote and begin the task again. It is unclear as to the true meaning of these frustration

displays, but it is most likely more beneficial to attempt to prevent them. Performance on these types of tasks will not always be high; therefore, it is essential to provide giant pandas with easier methods to receive reinforcement if the task is new or too challenging to allow for much reinforcement to prevent them from leaving the task and displaying frustration. Of the several methods attempted during this study to prevent frustration, frequent reinforcement by simpler tasks tended to be the most effective.

The evidence provided that giant pandas can see color may help provide for other forms of enrichment using that ability. Hare et al. (2003) claim that, “Natural sensory abilities and behaviors seen in the wild offer an excellent guide for developing enrichment strategies to meet specific goals” (pp. 402-403). The level of visual acuity and color vision displayed in this task allows for visual forms of enrichment. Swaisgood et al. (2003) states that an enriched environment includes “a diverse array of novel objects to stimulate play and exploration” (pg. 347). This study and further studies that examine color vision will allow for novelty through different colors or other visual characteristics.

This procedure also allows for expansion into other modalities, mainly olfactory and auditory. Many species’ performance on discrimination tasks is confounded by their dominant sensory modality and using this procedure on other modalities for the pandas could help provide empirical evidence for a dominant modality. Giant pandas have been shown to rely on olfactory cues in mate selection and have demonstrated the ability to habituate to an individual’s scent (Swaisgood, Lindburg and Zhou, 1999). Swaisgood, Lindburg, Zhou, and Owen (2000) provides evidence that giant pandas can discriminate conspecific scents based on sex and reproductive status through differential responding to

odors left by males, nonoestrous females, and oestrous females. It is also possible to use vocalization playback to experimentally test discrimination ability for auditory stimuli, which giant pandas use to communicate at close range.

Another problem inherent in the design is the small sample size. With one male and one female giant panda, differences could be caused by sex differences. All the typical problems of small n designs are present, such as random effects and individual differences. Jacobs (1981) also claims that color vision may vary within a species and studies with limited sample sizes may miss important variations or make misleading conclusions. To remedy the sample size problem, the study should be taken to China or other zoos in the United States to increase the sample size to a more reasonable number.

The coordination of this study could also have potential conservation benefits, such as aiding in developing a training program prior to reintroduction. Although the captive population is not self-sustaining, reintroduction has already been discussed. Schaller (1993) reprints excerpts from a 1989 World Wide Fund for Nature plan for conservation of the giant panda. The plan states that the ultimate goal of breeding in captivity should be to reintroduce animals into areas that were formally inhabited or areas that have been rehabilitated. It cites that there have been no captive releases, but there have been some successful reintroductions of wild-born pandas. It claims that since pandas recognize bamboo as food in captivity and since they have a simple lifestyle, little training should be necessary. On the other hand, captive born animals may have difficulty establishing home ranges and dealing with other challenges found in the wild. Studies of adaptability in giant pandas may help in forming a training plan to aid in the adjustments needed.

Additional evidence on the importance of learning in giant pandas may help stress the importance of allowing captive giant pandas to remain with their mothers longer. It is currently the practice to remove the cubs at about six months to allow the mother to cycle sooner, despite the fact that wild giant panda cubs usually remain with their mothers for two and a half years. One wild cub was even found to learn from another male. Zhi (1993) reports that the cub was forced to leave at two and a half years and lost his confidence. He became tentative and unsure, trying to find his own territory. He then became attached to an older male and Zhi states that, "Hu Zi, who had spent years learning from his mother, now passed hours watching and following the more experienced male" (pg. 63). Cognitive studies on giant pandas can help move toward the goal of improving well-being in captivity. It is crucial to gain an understanding of how intelligent giant pandas are and the scope of their abilities to improve their management in captivity. Evidence on giant panda training and intelligence can be used to design studies to examine the importance of learning in the early years, which may lead to important changes in the management of captive giant pandas.

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Appendix: Sample Trials where S⁺ is green, used with Lun Lun on October 17, 2003.

1	gray 16	green 3	gray 1 7
2	gray 12	gray 5	green 2
3	green 1	gray 3	gray 15
4	gray 9	green 4	gray 13
5	green 5	gray 8	gray 16
6	gray 4	gray 6	green 4
7	green 3	gray 10	gray 9
8	gray 7	green 2	gray 17
9	gray 5	gray 18	green 3
10	gray 14	green 1	gray 2
11	gray 9	gray 3	green 5
12	green 4	gray 6	gray 10
13	gray 15	green 3	gray 5
14	gray 7	gray 14	green 2
15	gray 3	green 4	gray 1
16	green 5	gray 3	gray 4
17	gray 5	gray 12	green 5
18	gray 9	green 1	gray 15
19	gray 16	gray 4	green 5
20	gray 1	green 3	gray 10