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„ Picture-Object Correspondence in Kea "

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Summary

I investigated picture-object recognition in kea (*Nestor notabilis*) in three different experiments by asking subjects to transfer a learned behavior (a discrimination task) from pictures to objects, and vice versa.

Experiment one investigated whether kea could transfer a two-choice discrimination task between pictures displayed on a touchscreen computer and real objects presented on the aviary ground. Results showed strong evidence of object-to-picture transfer in the first few trials of the object-to-touchscreen test session. However, there was no evidence from this experiment for picture-to-object transfer. This was because kea performed significantly better on the object discrimination task than on the touchscreen, so it was impossible to tell whether transfer had occurred, or whether the subjects had simply learned the object task "from scratch". The conclusions for experiment one are twofold. First, kea showed picture-object recognition in the form of transfer of a discrimination task from objects to the touchscreen. Second, as kea very quickly reached significant positive results in a real-object discrimination task, direct discrimination transfer from pictures to objects was not a demanding enough task to test for recognition.

Experiment two addressed outstanding concerns from experiment one. To tackle the lack of evidence for picture-to-object transfer, a reversal-learning procedure was implemented, which is known to be more difficult for kea to solve. To address the concern that object-to-picture transfer only occurred in the first few trials of the touchscreen test session, an operant conditioning box which mimicked the touchscreen was used to test the object condition. This box would hopefully reduce

distracting factors, and make it possible to attain a transfer detectable throughout the entire test session. In fact, results suggest that these procedural modifications were successful, and showed a strong transfer from picture to object which was detectable over the entire test session. However, the operant conditioning box itself proved to be somewhat of a hindrance, as only three subjects of the original thirteen that began training learned to use the box correctly.

Experiment three tested whether kea could transfer between objects and framed photographs, a medium with which they had never worked with before. As in experiment two, procedural variations between mediums were minimized to increase the probability of showing robust transfer. Furthermore, both photographs and objects were presented to subjects in a way they were already familiar with, so a sample size was gained which more accurately represented the group as a whole. Results showed picture-to-object recognition in the form of negative transfer in the first session of the photo-to-object condition. This supported similar results found in experiment two, but with a larger sample size. When taken together with the results from experiment one, it is clear that kea can transfer a learned discrimination task both from pictures to objects, and from objects to pictures.

Based on the results described in this thesis, it is now known that kea can correspond objects and pictures, both when these are presented on a touchscreen and as photographs. Furthermore, the fact that kea were successful in recognizing printed photographs, despite being naïve to these, implies that they are quite flexible in their abilities to recognize different types of pictures. This lends support to the use of pictures in cognitive research with this species.

Zusammenfassung

Diese Masterarbeit beschäftigt sich mit der Frage von Bild-Objekt-Erkennung bei Kea (*Nestor notabilis*). In drei unterschiedlichen experimentellen Settings mussten die Subjekte ein erlerntes Verhalten (Diskrimination) sowohl bei Bildern, als auch bei Objekten, anwenden (Bild-Objekt-Transfer). Dies erfordert eine Übertragung des erlernten Verhaltens von Bild zu Objekt und vice versa (Diskriminationstransfer).

Experiment eins untersucht durch eine Double-Choice-Diskriminationsaufgabe, ob Kea das erlernte Verhalten von Bildern auf einem Touchscreen auf echte Objekte auf dem Volierenboden übertragen können. Die Resultate liefern einen starken Beweis für Objekt-Bild-Transfer in den ersten zehn Wiederholungen der Testung von Objekt-zu-Bildschirm. Allerdings gab es keinen Beweis für Bild-Objekt-Transfer in diesem Experiment. Zusammenfassend brachte Experiment eins, zwei relevante Ergebnisse. Erstens zeigten Kea eine Bild-Objekt-Erkennung. Die Subjekte setzen das erlernte Verhalten der Diskriminationsaufgabe der Objektbedingung erfolgreich in der Versuchsbedingung am Bildschirm um. Zweitens waren die Versuchsbedingungen zur Untersuchung des direkten Diskriminationstransfers von Bild nach Objekt nicht anspruchsvoll genug, um Bild-Objekt-Erkennung nachzuweisen.

Experiment zwei fokussiert auf zwei Probleme von Experiment eins. Um das Problem zu behandeln, dass alleinige Objektdiskriminationsaufgaben für Kea zu leicht zu lösen sind, wurde eine Reversal-Learning-Prozedur eingeführt. Frühere Studien zeigen, dass solche Prozeduren für Kea schwieriger zu lösen sind. Um das Problem zu untersuchen, dass Objekt-Bild-Transfer nur in den ersten zehn Wiederholungen der Testung nachgewiesen konnte, wurde zur Prüfung der Objektbedingung eine Operant-Conditioning-Box verwendet. Hierfür wurde das Aussehen dieses Apparates dem

Touchscreen so weit als möglich angeglichen. Durch diese Modifizierung konnte ein starker Transfer von Bild nach Objekt während der Testung nachgewiesen werden. Allerdings ist hierzu anzumerken, dass von den anfänglichen 13 Subjekten der Trainingsphase des Experiments nur drei Subjekte an der tatsächlichen Testung teilnahmen.

Experiment drei erforschte daher, ob Kea das erlernte Verhalten von Objekten auf gerahmte Fotos übertragen können. Wie in Experiment zwei wurden prozedurale Abweichungen zwischen den beiden Medien reduziert, und weil die Art der Versuchsbedingung allen Subjekten bereits vertraut war konnten mehr Subjekte als in Experiment zwei die Testkriterien erfüllen. In diesem Experiment zeigten Kea Bild-Objekt-Erkennung in Form eines negativen Transfers in der Testung der Foto-zu-Objekt-Bedingung. Dieses Resultat unterstützt die Ergebnisse von Experiment zwei. Durch die erhöhte Stichprobengröße und optimierten Versuchsbedingungen in Experiment drei, sowie den Ergebnissen aus Experiment eins, kann demnach davon ausgegangen werden, dass Kea sowohl Bild-Objekt-Erkennung, als auch Objekt-Bild-Erkennung aufweisen.

Die Ergebnisse dieser Masterarbeit legen nahe, dass Kea eine Verbindung zwischen Objekten und Bildern herstellen und wahrnehmen können. Dies gilt sowohl für Bilder auf einem Bildschirm, als auch für gerahmte Fotos. Außerdem wurde gezeigt, dass Kea gedruckte Fotos erfolgreich erkennen können, auch wenn diese zum ersten Mal präsentiert werden. Dies zeigt, dass Kea in der Erkennung verschiedener Bildarten äußerst flexible Fähigkeiten aufweisen. Des Weiteren unterstützt diese Arbeit, neben der bereits etablierten Verwendung des Touchscreens, den Einsatz von Bildern bzw. Fotos in kognitiver Forschung bei Kea.

Introduction

This thesis will focus on the question of whether kea (*Nestor notabilis*), a rare species of parrot endemic to the mountains of New Zealand, can recognize the objects that they see in pictures. This is a relevant line of research as today pictures are commonly used as stimuli in experiments with kea and other birds, and it is methodologically important to understand what, if anything, these birds perceive in the pictures they are presented with.

In this introduction, I will first explore kea as a species, and then go on to review the cognitive work that has been carried out with them up to this point. Next, as picture recognition is a mainly visual phenomenon, we will summarize what is currently known about vision in birds at the levels of anatomy and physiology, low-level processing, and high-level processing. Finally, we will go through the work that has been done on picture-object recognition in other animals, as a prelude to the experiments carried out for this thesis.

History of kea

Kea in the wild

First described by Gould in 1856, The kea (*Nestor notabilis*) is a large, green parrot endemic to the South Island of New Zealand. Together with the kaka (*Nestor meridionalis*) it forms the genus *Nestor*, and with the kakapo (*Strigops habroptila*) the family *Strigopidae*, which exists only in New Zealand (De Kloet & De Kloet, 2005 ; Diamond & Bond, 1999). *Strigopidae* was the first to diverge, and therefore the oldest, of the three families in the order Psittaciforms (parrots).The ancestor of the

kea, kaka and kakapo was present on New Zealand when it split from the mainland around 100 mya, and diverged into the kakapo and proto-*Nestor* 60-80 mya (Grant-Mackie, Grant-Mackie, Boon, & Chambers, 2003). The kea itself is a fairly young species, having diverged from the proto-*Nestor* only 2.5 mya. However, recent anatomical studies have shown that both the kea and the kaka retain ancestral traits which closely resemble those of the orders falconiformes and passeriformes (Schwing, 2014), which were recently established as the sister orders to the psittaciformes (McCormack et al., 2013; Suh et al., 2011). This suggests that the *Nestor* parrots are the closest living relatives of the proto-parrot, and the most closely related to ancient falcons and passerines. Kea research, therefore, may give us valuable insight into when specific traits and cognitive abilities developed in these three bird orders.

The kea has an average body length of 50 cm and a wingspan of one meter, making it the largest extant land-based bird in New Zealand (Diamond & Bond, 1999). The plumage is mostly green, with bright red and yellow underwings and blue flight feathers. The bright colors are displayed during social interaction, but most of the time these remain hidden and only the fern-green of the body and wings is visible, probably as a defense against their now-extinct predators (Holdaway, 1989). The distribution of kea encompasses the entire range of the Southern Alps, from Fjordland in the Southwest to Nelson Lakes in the Northwest, with West Coast populations breeding down to sea level, as well as a small population on the east coast (Okarito) (Robertson, Heather, & Onley, 2005). Total population estimates are between 1000 and 5000 individuals, and they have an IUCN red list rating of "Vulnerable" (Birdlife International, 2013). They are highly adaptive to seasonal and

changing environments, and exploit a variety of resources throughout their different habitats.

It is perhaps the harsh and variable environment of the Southern Alps that formed the kea into the opportunistic omnivore that it is today (Diamond & Bond, 1999). With their unique bill, made more for manipulating than crushing, as in other parrots, kea access every possible food source their environment has to offer. Although the main part of their diet consists of leaves and buds, they regularly eat herbs, grasses, succulent roots and grubs (Jackson, 1960). They take advantage of seasonal abundances of flowers and berries, and scavenge from local dumps. It is perhaps this scavenging behavior for which they are best known, as it has often brought the kea into contact with humans. They raid dumps and garbage cans, and scavenge carcasses of dead animals. And notoriously, kea are capable of and sometimes do kill sheep (Diamond & Bond, 1999; Temple, 1996). In short, kea will find a way to exploit any and every food source in that they come across.

Kea tend to congregate in groups to forage, and it is in these congregations that their social lives become apparent. Kea have a complex, non-linear social hierarchy, in which access to resources is dependent on age and dominance (Diamond & Bond, 1999; Tebbich, Taborsky, & Winkler, 1996). Adult and juvenile males are the most dominant, the former most likely due to size and strength, and the latter to special privileges afforded juveniles in kea society. Whereas fledglings (< 1 year) are totally dependent on adults for food (Jackson, 1963), juvenile kea (1-3 years) no longer receive any assistance from their parents (Diamond & Bond, 1999). Despite their lack of help and experience, they obtain plenty of food: by simply taking it from other kea, even the most dominant ones. This behavior is oddly tolerated by adults and

sub-adults, although it would normally provoke an attack if displayed by an older bird. When juveniles become sub-adults (3 - 6 years) their behavior shifts in the opposite direction, as adults are no longer willing to share food with them. Sub-adults have to spend a lot of time foraging, and often resort to stealing food from other birds. Upon reaching full adulthood (around 6 years), the individual kea establishes its place in the pecking order through aggressive displays and displacement, and the resulting dominance rank remains relatively stable over time. Once established, however, a kea's rank is not set in stone, and it must continually reinforce its place in the group.

Playfulness and object exploration are probably the traits that have made the kea famous as a charming (yet destructive) icon of New Zealand fauna. Kea show complex play behavior both on the ground and in the air (Diamond & Bond, 1999; Keller, 1975; Kubat & Winkler, 1992 ; Schwing, 2014). This can occur socially or individually, often involves the manipulation and exploration of objects, and is frequently accompanied by a specific play call (Schwing, 2014), which has been shown to induce play in kea which are involved in another activity. Individual play normally involves objects such as stones or sticks, which are tossed into the air, dipped or thrown into water, inserted into other objects, or simply carried around (Keller, 1975). Such behavior may help kea gain knowledge about their environment, and Gajdon and colleagues propose that kea's propensity to create novel object combinations during this type of play encourages abilities to solve complex cognitive tasks, such as spontaneous tool-use (Gajdon, Lichtnegger, & Huber, 2014). Social ground play normally proceeds as a series of tussling, hopping and wing-flapping movements (Diamond & Bond, 1999), whereas aerial play involves two or more birds

taking part in a combination of aerial acrobatics, chasing and mid-air kicking (Schwing, 2014). Aerial play is most likely to occur in areas with a strong updraft. Locations with regular updrafts, such as Death's corner in Arthur's Pass National Park, can become congregation areas for local kea and draw in dozens of tourists daily, looking to see them in action[1]. Play behavior in kea has proven fascinating to observe for lay-people and specialists alike.

Kea are a truly unique parrot species that have both captivated and caused controversy since their first contact with the European settlers in New Zealand. As a member of only two species in the oldest genus of parrots, they provide a rich opportunity for comparative study of parrots and their relatives. Their long juvenile period and playful, explorative tendencies means that they can learn to solve problems and develop cognitive abilities. Furthermore, their ability to navigate through a complex social structure, where each individual's position changes several times throughout its life, is a testament to their social intelligence. In the next section, we will further discuss how kea's intelligence and cognitive abilities have been explored through experiments in the lab and the wild.

Kea in the lab

The first kea came to Austria in 1960's through a wildlife exchange program with New Zealand. The kea group was housed at Konrad-Lorenz-Institut für Vergleichende Verhaltensforschung (Konrad Lorenz Institute for Ethology, KLIVV) in

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[1] In April, 2013, during bad weather, Death's Corner was visited by several cars of tourists per hour. On sunny weekend days, full tour buses stopped by at this tiny parking lot almost hourly (author's personal observations).

Vienna until the Haidlhof Research Station was created near Bad Voeslau, 30 km south of Vienna. The birds have lived at the Haidlhof since its founding in 2010.

The first published behavioral study on this group of captive birds was in the mid 1990's (Tebbich et al., 1996), which triggered a jump in interest in the species. Around 2000, the first large-scale kea project began under the leadership of Professor Ludwig Huber. The kea project consisted of field work with wild kea in New Zealand and experiments with the captive group in Vienna, and focused largely on kea's technical intelligence and social learning skills (Gajdon, Fijn, & Huber, 2004; Gajdon, Fijn, & Huber, 2006; Huber, Rechberger, & Taborsky, 2001; Werdenich & Huber, 2006). Over the next few years, researchers found that captive kea could in fact learn to use tools, although tool use had never been observed in the wild. As a result, the topic of tool use in kea was explored extensively (Auersperg, Gajdon, & Huber, 2009; Auersperg, Gajdon, & Huber, 2010; Auersperg, von Bayern, Gajdon, Huber, & Kacelnik, 2011; Auersperg, Huber, & Gajdon, 2011; Gyula K Gajdon, Lichtnegger, & Huber, 2014). Other research has investigated their abilities to learn and understand abstract concepts (Liedtke, Werdenich, Gajdon, Huber, & Wanker, 2010; O'Hara, Gajdon, & Huber, 2012; Schloegl et al., 2009; Stobbe, Westphal-Fitch, Aust, & Tecumseh Fitch, 2012), and their perceptual capacities (Schwing, 2014).

Kea are highly social birds, and several studies have looked into their social structure and willingness to cooperate with each other on a task. The very first published study on the captive kea in Vienna looked at kea group hierarchy and willingness to cooperate (Tebbich et al., 1996). The kea were presented with a device which required two kea to operate, but only rewarded one of them. The kea were tested both in group situations and in dyads, with results that shed light on their

complex social system: "…in group situations the reward was distributed symmetrically and cooperation was persistent. In dyadic test situations, three individual kea aggressively manipulated their respective subordinate partners to open the apparatus. Their dominance status enabled them to force cooperation." A later study on social attention revealed that age has an effect on how much attention a kea pays to a conspecific. Juvenile kea watched foraging conspecifics of any age, whereas adults ignored juveniles and only watched other adults (Range, Horn, Bugnyar, Gajdon, & Huber, 2008). The information gathered from these studies thus indicates the kea's complex social structure, which takes both age and dominance into account.

The ability to learn from conspecifics, or social learning, is also important to understanding the social lives of the kea. One study which tested social learning showed that naïve kea could open a complicated locking mechanism faster and more successfully when they had first observed a conspecific demonstrator, suggesting that kea learn by observing others (Huber et al., 2001). Further support for kea as social learners was shown in stick tool use experiments. Only a single kea out of six, Kermit, spontaneously figured out how to use a stick to retrieve a reward from a multi-access box (Auersperg et al., 2011a). In a later study, where stick-tool use was considered in more detail, Kermit demonstrated the technique to the five other birds. This time three additional birds learned to use the stick-tool; one of these, Pick, succeeded after just one demonstration by Kermit (Auersperg et al., 2011b). So it is clear that captive kea are better at solving a complex problem when they have first observed another kea solving it, and that naïve kea can acquire tool-use by observing tool-using conspecifics (Gajdon, Amann, & Huber, 2011).

Research with the kea has shown that these birds have an extraordinarily high level of sensorimotor intelligence. As noted above, they can learn to open complex locking mechanisms, and use sticks as tools. They have proven to be equally competent when confronted with means-end tasks. When presented with a string-pulling test, where a reward was suspended by a string from a perch, "Four keas completed the first trial within a few seconds, by showing only goal-directed behavior, thus executing the solution in a manner that could not be improved upon in nine further trials" (Werdenich & Huber, 2006). All of the kea except one (a fledgling) were successful in the first trial, and solved the task more quickly than any other bird species recorded. The kea did similarly well on the support problem, another means-end task in which an object resting horizontally must be pulled to retrieve a reward (Auersperg et al., 2009). In this experiment, subjects had to discriminate between two slats of wood, only one of which gave access to the reward. In the first condition, the "on problem," the reward rested on one slat and next to the other. All subjects immediately solved this problem by pulling the slat with the reward on top. In the second condition, the "connected problem," a reward rested on both slats but one of the slats was broken. The kea took longer to solve this, but still reached 75% accuracy by the fourth trial. The kea's quick success in both the string-pulling and support problems suggests a good understanding of spatial relationships between objects.

Several studies have focused on the kea's ability to understand abstract concepts, with mixed results. Kea were tested on their ability to choose by exclusion (where two options are given, and one is chosen by excluding the alternative). In this experiment, two bowls were present, one of them baited with food. The experimenter

showed the empty bowl to the kea subject and if the kea chose by exclusion, it would

select the other bowl. In this task, however, kea did not choose the baited bowl

significantly more than chance, suggesting that they were not choosing by exclusion

(Schloegl et al., 2009). However, another study which tested for exclusion

performance showed positive results: "in contrast to Schloegl et al.'s study, the

majority of kea showed a capacity to infer by exclusion the position of a

reward…"(O'Hara et al., 2012, p. 28). The difference being, in this second study, that

the kea were habituated to the handling of cups for several days before testing,

controlling for social impacts of touching covers and the kea's well-known neophilia

and drive to explore. The different outcomes of these two almost identical studies

shows that experimental design, and knowing your subject, is crucial when testing

for understanding of abstract concepts.

Very recent studies, including those described in this thesis, have looked at kea's

problem-solving and learning abilities from a non-technical point of view, using

touchscreen computers and object discrimination tasks as investigative methods.

One study by O'Hara, Huber, & Gajdon, (2014, in review) investigated kea's

performance on a reversal learning task on a touchscreen computer as compared to

one which used real objects. They found that kea took significantly longer on the

touchscreen both to acquire a discrimination task and complete reversal learning,

and suggest that this is caused by a dissociation of reward and stimuli location which

disrupted the learning process (in the touchscreen task the reward was released

from a feeder equidistant from both positive and negative stimuli, whereas in the real

object task the reward was placed directly underneath the positive stimulus). Another

study using the touchscreen tested whether kea could learn a visual artificial

grammar (Stobbe et al., 2012). Here, subjects were trained and tested on two simple patterns which followed the grammatical rules A^nB^n or $(AB)^n$. It was found that, although subjects readily learned to discriminate between the two patterns, there was no evidence that they had learned either underlying grammar. There are currently several ongoing touchscreen studies in the kea lab, and this device is proving extremely useful in uncovering different types of knowledge in the kea.

There is an interesting disparity in the performance of captive kea as compared to wild kea when confronted with similar tasks. When 19 kea were tested on the string-pulling task in the wild, only six were successful in the first trial (Johnston, 1999), as compared to six out of seven captive kea (Werdenich & Huber, 2006). Captive kea are also more focused on complex social learning than their wild counterparts. A wild kea was trained to remove a tube from a pole for reward, a task which required climbing up the pole while moving the tube with the beak simultaneously. This trained kea was then used as a demonstrator for at least 21 other kea. Despite repeated demonstrations, multiple attempts from many birds, and a high level of interest in the apparatus, only two further kea managed to solve the task. According to the authors, "The keas also failed to show clear indications of social learning despite their apparent interest in successful manipulations by a trained conspecific"(Gajdon et al., 2004, p. 69). In a related study the innovation of bin-opening, and the spread of this innovation, was investigated in a group of wild kea in Mount Cook Village, New Zealand. The researchers concluded that it was mainly through trial-and-error, not social learning, that kea could successfully open bin lids (Gajdon et al., 2006). The lower level of success at a means-end task in wild kea as

compared to captive kea, along with the lack of proven complex social learning, is a phenomenon which has yet to be fully explained.

What is clear is that kea are fascinating, intelligent birds, and ideal as a model species in the lab. They are extremely curious, and show an unparalleled lack of neophobia (lack of fear of new objects and situations; Mettke-Hofmann, Winkler, & Leisler, 2002). Kea have proven to be highly motivated subjects in a variety of tasks which involve both sensorimotor and abstract problem solving abilities. Furthermore, their social structure is complex and still not fully understood. In short, we still have much to learn from these charming birds.

Vision in Birds

The topic of this thesis, picture-object recognition, focuses on a visual phenomenon in an avian subject. In order to properly design experiments and interpret data from an animal subject, it is important to understand that subject as well as possible. For that reason, we will review vision in birds, and explore the similarities and differences between bird and human vision.

Anatomy and physiology of the avian eye

A cursory inspection of the eye of any common bird will produce two rather obvious anatomical differences to that of a human's. First is its size; the bird's eye is on average twice as large as that of a comparatively-sized mammal (Howland, Merola, & Basarab, 2004). Second is the presence of an organ in the posterior chamber, the pecten, which is found in no other vertebrate, and serves to oxygenate that area of the eye (Birkhead, 2012; Walls, 1942; Wood, 1917). The other unique features of the avian eye, mainly concerning the retina, come to light only under closer scrutiny.

The construction of the retina in birds, and hence its ability to absorb and discriminate light, is very well developed. Three main types of photoreceptors make up the avian retina: cone, double-cone, and rod cells (Walls, 1942; Wood, 1917). Each of these cell types contains a pigment, which consists of the protein opsin, covalently bonded to a chromophore (this pigment construction remains true for all vertebrates) (Hart, 2001). Rod cells, which only contain one kind of pigment, are used in low-light conditions as they are much more sensitive to light than cones. Double cones are strange constructions, also containing only one type of pigment, which may be important in the perception of non-color information such as texture and motion (Moore et al., 2012). It is in the cone cells where one finds a variety of pigments from cell to cell (Bowmaker, 1977; Hart, 2001). In cone cells, small chemical variations of the pigments create photoreceptor cells which maximally absorb light at different wavelengths. When light is absorbed by two or more cone cells simultaneously, the information from those cells is compared in the brain, and the outcome is color vision: the ability to differentiate light based on wavelength. This is a basic process which creates color vision in birds as well as humans.

However, birds possess an additional feature which allows for more refined color vision: oil droplets. In fact, colored oil droplets can be found in the cone cells of both reptiles and birds, although only those of birds and turtles occur in bright colors like red, orange and yellow (Walls, 1942). Cone oil droplets are "highly refractile spherical organelles located at the distal end (ellipsoid) of the inner segments of the avian cone photoreceptors, and occupy the entire diameter of the inner segment at this site" (Hart, 2001, p. 684). The oil droplets function by filtering out short-wavelength light, therefore refining the light that hits the photo pigment. This reduces

the amount of overlap in the quality of light which falls upon adjacent cone cells, and allows for enhanced color discrimination, among other benefits (Hart, 2001).

As early as the 19th century, it was known that the retina of birds contained these colored oil droplets. Kuehne & Ayres (1878) isolated and described three retinal pigments of the chicken (*Gallus gallus domesticus*). By 1937 it had been determined that those previously isolated pigments were carotenoid in nature (Wald & Zussman, 1937), and several decades later similar pigments were isolated from the pigeon retina (*Columba livia*) (Bridges, 1962). Since then a plethora of knowledge on the makeup of the bird retina has come to light, and this has had a profound effect on our understanding avian vision.

It was discovered in the late 1970's that pigeons possess not three (as humans do) but four visual pigments of single cone cells (Bowmaker, 1977), indicating that pigeons have tetrachromatic vision and can see into the ultra-violet spectrum, thereby exceeding human's color vision capabilities. Microspectrophotometry, the innovative technology that made this discovery possible, subsequently allowed for testing of the absorption range of visual pigments of at least 31 bird species in nine different phylogenetic orders (Hart, 2001). Many of the bird species tested have photoreceptors with different absorption peaks, and evidence is growing that each bird's color vision has evolved to fit its particular ecological niche.

Among the parrots, the color vision of budgerigars (*Melopsittacus undulatus*) has been extensively studied, and they, like pigeons, possess tetrachromatic vision which extends into the ultra-violet range (Bowmaker, Heath, Wilkie, & Hunt, 1997). When the strictly diurnal budgerigar was compared to Bourke's parrot (*Neopsephotus bourkii*), another small Australian parrot species with more

crepuscular habits, researchers found that the color vision of each species was adapted to its respective lifestyle (Lind & Kelber, 2009). Furthermore, a recent study by Knott et al. (2013), which focused on the visual pigments of the crimson rosella (*Platycercus elegans*), discovered two rod opsin pigments which had never been described in any vertebrate. These few studies on the visual pigments of three Australian parrot species have already shown important interspecific variation, and suggest that further research will yield new revelations.

Another important difference between the avian and human eye can be found in the construction of the fovea, a depressed area of the retina which contains a high density of photoreceptors (Birkhead, 2012; Gaffney & Hodos, 2003). Due to this high density of photoreceptors, and the fact that there are no blood vessels present to distort the incoming light, the fovea creates the sharpest point in the visual field. The human eye contains one fovea. However, almost unique among vertebrates, some avian visual hunters have two foveae in each eye: a "shallow" one which is used for monocular, close-up vision, and a "deep" one which is used like a telephoto lens (Birkhead, 2012). Furthermore, the connection between double fovea and good vision has long been known, and Wood, in his 1917 opus on the avian retina, *Fundus Oculi*, states that "Stereoscopic, binocular, single vision in Birds with double foveae … is the most acute, accurate and effective form of eyesight that these or any other animals know…"(p.21).

Bifoveal vision, however, is not the rule among birds, and a variety of forms can be found, probably as adaptations to particular ecological niches (Collin, 1999). Many birds, like humans, possess only one fovea, whereas some few, such as the domestic chicken (*Gallus gallus domesticus*) apparently have none at all (Sillman,

1973). Nor is it uncommon to find a horizontal "visual streak," instead of a round fovea, in seabirds, which is presumably used to detect the horizon (Birkhead, 2012; Sillman, 1973). The Canada goose (*Branta canadiensis*) also possesses a visual streak, but the streak is oblique instead of horizontal, allowing the bird to clearly see both the sky and the ground/horizon simultaneously (Moore et al., 2012). Budgerigars and Bourke's parrots are the only parrot species to date whose retinal topography has been investigated, and both showed a sensitive *area centralis* rather than a discernable fovea (Mitkus, Chaib, Lind, & Kelber, 2014). That such a wide variety of retinal configurations have evolved among bird species is a testament to how important a role vision plays in their survival.

The shape and anatomy of the eyes, as well as the construction of the retina, provides the light-capturing organ which is only the first step in the process of vision. Next, the brain must process the captured light to form an image that corresponds in some way to the outside world, and this is what we will explore in the following sections.

Low-level visual processing

It seems completely natural that, when we open our eyes, the world we see contains objects, and that these objects have edges which make them distinct from their backgrounds (Grossberg, Mingolla, & Ross, 1997; Marr, 1982; Watanabe & Toru, 2012). The objects vary in size and texture, and of course we can see that some are closer to us than others. It may be surprising to learn, then, that the light hitting our retina contains no direct information about where an object ends and the background begins, nor does it tell us which ones are closer and which further away. There is no intrinsic property of light that tells us how fast something is moving, or indeed what

color we perceive it to be. All of this seemingly obvious information about the world around us is actively created by the brain, using as a guide the nerve impulses produced when light hits the retina. Visual perception proceeds in stages, only the first of which involves light hitting photoreceptors on the retina (Cook & Hagmann, 2012; Watanabe & Toru, 2012). This light is then transformed into electrochemical information and transmitted to ganglion cells, where it proceeds to the optic nerve and then to the brain for further processing.

An important stage of this processing is called "early vision" and can be defined as " a set of spatially parallel, preattentive processes that are responsible for taking sensory and dimensional features of different types and rapidly transforming them into perceptual groups of edges, regions, and surfaces"(Cook & Hagmann, 2012, p.43). In early vision, the visual information is split into different processing "streams," and these streams use features such as color and shape to group information (Green, 1991). Methods of testing the early vision process of perceptual grouping have been devised and successfully tested on pigeons, and the results show some striking similarities to humans (Cook, 1992a; Cook, 1992b). It was found that pigeons, like humans, group visual information using features such as color, shape, and regional density, and furthermore that they do it quite quickly (Beck, 1982; Cook, 1992a).

Another fundamental aspect of vision is figure-ground assignment, in which the visual system defines certain areas as objects or figures and other areas as background. This process has been studied by psychologists in humans for a century, and was first described by Edward Rubin in his 1915 doctoral thesis at the University of Copenhagen (in Pind, 2012). Rubin described four "cues" which

influence an image area to be assigned figure status: convexity, small size, surroundedness and symmetry. Later authors discovered more cues, among them lower-region (Lazareva & Wasserman, 2012). The question then arose of whether birds also perform figure-ground assignment, and if so, whether this is done using similar cues to humans. Consequent work with pigeons has shown that they, like humans, tend to assign figure status to smaller and surrounded regions of images (Castro, Lazareva, Vecera, & Wasserman, 2010; Lazareva, Castro, Vecera, & Wasserman, 2006a). Unlike humans, however, pigeons are not predisposed to consider lower regions of an image as figures (Lazareva et al., 2006a). As small size, surroundedness, and lower-region are the only figure-ground assignment cues so far to be tested, there remains much research to be done before we come to a better understanding of this basic visual process.

Depth perception and relative distance from the viewer are further aspects of an image which must be reconstructed during visual processing. There are a variety of cues which give information on depth and relative distance, including binocular disparity, motion parallax, relative size of objects, shading/shadow, texture, linear perspective and occlusion (Spetch & Weisman, 2012). Binocular disparity works because each eye receives a slightly different view of an object, thereby giving 3D depth information. This, of course, only works in a binocular visual field, but many birds have very little or no binocular vision and so must rely on monocular cues. One of these is motion parallax, which relies on movement for depth information. These two mechanisms, however, cannot explain the full range of depth perception cues for several reasons. Binocular disparity only works with objects that are truly three-dimensional, not two-dimensional images like photographs or drawings, because 2D

images provide an identical view to both eyes. Motion parallax can create the illusion of three-dimensionality in two-dimensional movies, but as we are well aware, humans readily perceive depth in still, 2D images, so there must be other cues here at work.

Shading and shadow, linear perspective and occlusion are cues which can create the perception of depth in still, 2D images. There is strong evidence that both human and chimpanzee infants are highly receptive to shading and shadow cues (Imura & Tomonaga, 2003; Imura et al., 2008), and two bird species, pigeons and domestic chickens, have also shown sensitivity to this (Reid & Spetch, 1998; Hershberger, 1970). Linear perspective, on the other hand, seems not to be a very good indicator of depth for pigeons (Cerella, 1977), but this cue has not been tested on any other bird species, and the fact that pigeons are susceptible to the Ponzo illusion (Fujita, Blough, & Blough, 1991) could indicate that they are at least somewhat sensitive to linear perspective.

The final depth cue which has been studied in birds (pigeons and domestic chickens) is occlusion. Occlusion occurs when one object partially blocks the view of another, and can provide information on the objects' relative distance from the viewer (Spetch & Weisman, 2012). When speaking about occlusion, it is necessary to introduce the phenomenon of "amodal completion," whereby a subject perceptually fills in the blocked portion of the object without being able to see it, a normal part of the human visual experience. Chickens were tested on this topic, and it was discovered that not only are they capable of amodal completion (Forkman, 1998 ;Lea, Slater, & Ryan, 1996), but the mechanism they use to accomplish this is quite similar to that of humans (Forkman & Vallortigara, 1999). Pigeons, on the other hand, do not show

good evidence for amodal completion, in spite of multiple tests using different procedures and stimuli types (Aust & Huber, 2006; Sekuler & Palmer, 1992; Ushitani & Fujita, 2005). However, it does seem that pigeons can use occlusion to gain information on the relative distance between objects (Cavoto & Cook, 2006; Nagasaka, Hori, & Osada, 2005). Due to the very different results found for chickens and pigeons concerning amodal completion, research with other bird species will likely find similarly unique outcomes, again underlining the importance of testing a variety of species.

The final topic we will discuss under low-level visual processing is the critical flicker fusion (CFF) threshold, or the rate (in Hz, or flashes per second) at which a flashing light is no longer perceived as such, but appears as continuous luminance. Behavioral tests have revealed that both chickens and pigeons have higher CFFs than humans; Chickens have shown a rate as high as 105 Hz (Nuboer, Coemans, & Vos, 1992), pigeons 77 Hz (Hendricks, 1966), and humans only 58.2 Hz (Hodos, 2012). This is relevant in experimental settings that use artificial lights or computer screens, as both have a flicker rate which is calibrated to human vision. Experimenters must take into account that stimuli presented on a computer screen or using a projector may be perceived as flickering to bird subjects, which could have unintended consequences on the results.

In summary, low-level vision is the process by which raw data from the retina is transformed into information which the brain can interpret as images. Among birds, pigeons have been the main research subjects in this area, but chickens have also been investigated. Edges, regions and surfaces are defined using specific visual features, and experiments have shown that pigeons do this in much the same way

as humans. Figure-ground assignment is achieved using visual cues, and tests with pigeons have shown that, while small size and surroundedness are useful cues for figure-ground assignment, lower-region does not seem to be relevant. Both pigeons and chickens use shading/shadow as depth perception cues, and pigeons have shown sensitivity to texture gradient but not linear perspective. Amodal completion of occluded objects is found in chickens at a similar level to humans, but not in pigeons, although they do use occlusion to gain information about relative distance between objects. Finally, there are large differences in the critical flicker fusion threshold between humans, pigeons, and chickens, and researchers should keep this in mind when designing experiments using image projection devices that flicker.

Taken altogether, our knowledge of low-level vision in birds is still in its infancy, and considering the large differences that have been found between the only two avian species which have been tested, we can expect to find even more variation as researchers explore this topic in further detail and with other bird species.

High-level vision

High-level vision, although difficult to define, may be described as the stages in visual processing which begin to analyze the structure of the external world (Cox, 2014). In the study of high-level vision in birds, most research has centered on the themes of object recognition and object categorization, although it has been argued that these aspects are only a small part of visual understanding. For animals in their natural environment, navigation-relevant information could be just as important as recognizing and categorizing objects, if not more so, but those topics will not be covered here. Object recognition and categorization will be the focus of this section,

as these are the pertinent aspects of high-level vision that support picture-object recognition, the topic of this thesis.

Object recognition and object classification are inextricably linked, and are considered an integral part of concept learning in both humans and non-human animals (Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008). However, the task of defining the term "object" is a complicated one, as this can refer to several types of entities (Cox, 2014). Object types can be organized into basic-level categories, superordinate categories, and subordinate categories (Logothetis & Sheinberg, 1996; Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). Basic-level categories, of the three levels, carry the most information and are most easily differentiated from one another (Rosch et al., 1976) and have been termed 'perceptual classes,' as the members share common properties that can be perceived, in our case visually (Zentall et al., 2008). Tests with adult humans have shown that classification of objects into basic-level categories occurs faster and more accurately than at other levels. Furthermore, infants can form basic-level categories from a young age (Eimas & Quinn, 1994), and similar abilities have been robustly shown in non-human primates and other animals (e.g. Herrnstein & Loveland, 1964; Lorenz, 1971). This ability in infants and non-human animals supports Piaget's (1969) proposal that category formation is based on prelinguistic mechanisms, and the assertion that basic-level categorization" and its underlying cognitive processes are generally similar in humans and nonhuman animals" (Zentall et al., 2008).

Superordinate categories are constructed from more than one basic-level category, whereas subordinate categories refer to either individual members of a basic

category, or an even more refined category within the basic level. Whereas basic-level categories are considered perceptual classes, superordinate categories are considered to be 'associative classes,' because class membership is not based on direct perceptual similarity, but on arbitrary and learned associations (Zentall et al., 2008). Evidence for categorization at the superordinate level has been found in pigeons (Olga F. Lazareva, Freiburger, & Wasserman, 2004) and monkeys (Roberts & Mazmanian, 1988). Subordinate categories, on the other hand, could be individual exemplars, or a more specific category than the basic level. In summary, these three levels of object categories make up the basis of concept learning in the object domain for both human and nonhuman animals.

Assigning category membership at the basic level is not an all-or-nothing procedure, but is graded, and based on how closely a certain stimulus resembles the prototype of that category (Logothetis & Sheinberg, 1996). Category prototypes, which are nothing other than central tendencies, are extracted from the features of stimuli sets while an individual is learning that category (Posner & Keele, 1968). Once the prototype of a category has been extracted, a new stimulus is recognized as a member based on its similarity to the prototype, whereas stimuli which are too dissimilar are not classified as members. Research has shown that prototypes are quite real mental entities, (see Strange, Keeney, Kessel, & Jenkins, 1970), and there is much evidence that they are essential elements of basic-level categorization.

Discriminating particular individuals *within* a basic-level category (subordinate-level discrimination; Logothetis & Sheinberg, 1996) is centered around a different recognition system than that used for basic-level categories. This becomes especially apparent in brain-damaged adult humans who are afflicted with certain

types of agnosia, where it has been observed that "agnosic patients can occasionally recognize natural or synthetic objects with distinct shapes that belong to different classes, but they fail to do so when identification of individual entities is required" (p. 613). Research in birds also lends credence to subordinate-level discrimination as being different from basic-level categorization. Cerella (1979) found that pigeons could readily classify silhouettes of leaves into basic-level categories, but had trouble identifying individual exemplars. On the other hand, a wide range of bird species can and do recognize individual conspecifics (e.g Ryan, 1982; Trillmich, 1976; Watanabe & Ito, 1991; Watanabe, Yamashita, & Wakita, 1993). It has therefore been proposed that subordinate-level discrimination, in at least some bird species, is dependent on ecological relevance (Logothetis & Sheinberg, 1996).

While object classification at different levels can account for recognition, distracting factors can get in the way of correct classification, and birds have developed strategies to overcome this. One strategy for recognizing objects, described by L. Tinbergen (1960) and termed "search image," is a phenomenon whereby birds, which are at first deceived by cryptic prey, develop the ability to discriminate them with experience. Although this theory was originally based on observation of wild great tits (*Parus major*), later experiments reproduced the effect in chicks (M. Dawkins, 1971). Additionally, Dukas & Kamil (2001) found that when blue jays (*Cyanocitta cristata*) searched for two types of cryptic prey at the same time, their success rate dropped significantly, and suggested that attention must be limited to a single search image because "from a cognitive perspective , it is advantageous to focus attention on a single difficult task at any given time" (p.197). It seems that

object recognition based on search image is closely related to selective visual attention.

Another strategy for object recognition, which had previously only been observed in invertebrates (Collett, 1992; Collett, 1995) is called active vision, and was discovered in domestic hens in a 2000 study by Dawkins and Woodington. In active vision, the subject follows a pre-determined route or series of eye/body movements when viewing an object or landmark, thereby facilitating recognition without having to store a huge amount of data in memory, the disadvantage being that object recognition is less effective when viewed from novel angles. The authors further mentioned that active vision "appears not to be the solution adopted by primates," (p. 652), and therefore have found another major difference in visual processing between humans and a bird species.

To sum up this section, high-level vision is a collection of processes in which the viewer interprets visual data to gain information about the outside world. We have focused on object recognition, which likely makes up only a portion of high-level visual processing. Objects can be organized into three main types. First, are basic-level categories, in which the category members share perceptual traits, and membership is determined by an exemplars similarity to an idealized prototype. Next are superordinate categories, in which the category members don't necessarily share perceptual traits, but are grouped together based on associative learning. Lastly, subordinate-level categories are either individual exemplars of a basic-level category, or more refined categories, and it is assumed that different processes are responsible for classification at the subordinate level. Finally, two object-recognition strategies have been discovered in birds. The first, search image, appears to be

quite universal across several observed species, and is probably related to selective visual attention. The second, active vision, has only been described so far in domestic hens, but provides a fascinating parallel to an invertebrate visual strategy, and is a strategy which apparently has not been adopted by humans or other primates.

Taken altogether, high-level vision is a huge field of study, and although much progress has been made in this area, many questions remain unanswered, especially where avian vision is concerned. As in the study of low-level vision, the variety of bird species which have been systematically investigated is basically restricted to two, namely chickens and pigeons. However, the body of work relating to pigeons' visual recognition of objects and categorization abilities is huge, and many facets have been studied in great detail. The next steps in broadening our understanding of this field will be to carry out similar investigations in more diverse bird species. Only in this way can we obtain a more complete understand of high-level vision in birds, which, considering the superiority of other aspects of avian vision to our own, could expand both our theoretical knowledge and practical capabilities in the field of vision.

Picture-object recognition

Review: picture-object recognition with a focus on birds

The question of whether different animal species, including humans, can identify three-dimensional objects from two-dimensional pictures is methodologically important in the study of animal behavior as well as psychology. Photographs have often been used as stimuli in experiments to represent objects in the real world (Bovet & Vauclair, 2000). Yet, anthropological research has shown that, cross-

culturally, even adult humans who are inexperienced with photographs may have trouble recognizing the objects they represent (Miller, 1973). Furthermore, a variety of research on the anatomy, low-level processing, and high-level processing of avian vision has shown that birds' visual perception differs from that of humans, and indeed from one bird species to another (see section 1.2 for a detailed review of this topic). Since photographs and movies are made to be viewed by humans, and are calibrated to human color vision, flicker-fusion threshold, etc., birds may perceive something very different from us when viewing these. This underpins the importance of establishing that animal subjects can recognize pictures from objects before conducting research which makes this assumption.

A useful definition for picture-object recognition is given by Bovet & Vauclair (2000), who state that "…we can assume that a picture is recognized when animals react to a picture as they would react, spontaneously or after some training, to the real object." In regard to birds, this definition is supported by Weisman & Spetch (2010), who assert that "in our opinion, studies of direct transfer between three-dimensional objects in the real world and two-dimensional images in photographs or videos provide the best, most direct, evidence that birds see correspondence between a set of pictures and the objects they represent." These authors assume that correct transfer between pictures and objects implies recognition between the two.

There have been quite a few studies over the years to establish picture-object recognition in different species, and these can be divided into those which observe animals' spontaneous behavioral reactions to pictures, and those in which animals show recognition through an acquired behavior such as a categorization task or discrimination transfer (Bovet & Vauclair, 2000). Studies which focus on the former

method generally expose the animal to a still photo or moving image of ecologically relevant stimuli. If the animal reacts to the picture in a similar way to the real thing, it is assumed that recognition has occurred. The stimulus used could be of a conspecific, in which case an appropriate social reaction would indicate recognition. Other possibilities include showing a known predator of the subject, whereby avoidance or alarm behavior would be expected, or prey/food items, whereby a hunting or feeding response would be expected. Primates are popular subjects in this area, and convincing demonstrations of recognition have been shown in three species of macaque, (Kyes, Mayer, & Bunnell, 1992; Plimpton, Swartz, & Rosenblum, 1981;Rosenfeld & Van Hoesen, 1979), as well as in hamadryas baboons (*Papio hamadryas*) (Kyes & Candland, 1984) and squirrel monkeys (Herzog & Hopf, 1986). Other animals which have shown positive spontaneous reactions to pictures include such diverse species as sheep (Vandenheede & Bouissou, 1994; Bouissou & Vandenheede, 1995) anoles lizards (*Anolis nebulosus*) (Jenssen, 1970), red-footed tortoises (*Chelonoidis carbonaria*) (Wilkinson, Mueller-Paul, & Huber, 2013) and jumping spiders (*Maevia inclemens*) (Clark & Uetz, 1990), among others. In these cases, it is highly likely that the animal subjects react to the picture as they do because they have confused it for the real object (Bovet & Vauclair, 2000), a claim which is supported by the fact that in at least one of the tests mentioned above, the animals quickly habituated to the pictures and stopped showing a response to them after "realizing" that they were only pictures (Rosenfeld & Van Hoesen, 1979).

Birds have also shown recognition through their spontaneous reactions to pictures. Domestic cockerels, which normally respond to aerial predators with alarm calls only

in the presence of hens, were induced to alarm call when presented with a predator model and a video projection of hens (Evans & Marler, 1991). In several studies with pigeons, videos of conspecifics have been shown to produce courtship behavior in both males and females (Partan, Yelda, Price, & Shimizu, 2005; Shimizu, 1998). Moreover, female Japanese quail (*Coturnix coturnix japonica*) gave some of the most convincing evidence of picture-object recognition in a mate-preference study. These birds are known to mate more frequently with males that they have a high affiliation with, and furthermore that they increase their affiliation with males which they have previously observed mating with other females (Galef & White, 1998). In a 2003 study, Ophir & Galef showed that female Japanese quail increased their affiliation with familiar males that they had previously seen copulating with other females on video, clearly showing that the females had recognized the particular male on the video. The evidence from these studies strongly suggests that at least three bird species are capable of recognizing conspecifics from pictures, but in all three cases it could be argued that the birds are confusing the picture for the object it represents.

Both mammals and birds have shown picture-object recognition in learned behaviors, and primates, especially the great apes, provide the most convincing evidence for this at a level which could be considered on par with adult humans, i.e. they can name the objects represented in pictures but don't seem to confuse them for the real thing (Bovet & Vauclair, 2000). For example, Gardner and Gardner (1984) showed that four American Sign-Language trained chimpanzees (*Pan troglodytes*) could name the objects represented in pictures shown to them. Additionally, in a 1971 study by Davenport and Rogers, two chimpanzees and one

orangutan succeeded in a cross-modal matching-to-sample task, whereby the apes matched objects which they could touch but not see to a photographic sample. Other primates studied include rhesus monkeys (*Macaca mulatta*), which also succeeded in a visual-haptic matching to sample task (Malone, Tolan, & Rogers, 1980), and olive baboons (*Papio anubis*), which categorized photographs into food and non-food categories, but without confusing the pictures for real food (Bovet & Vauclair, 1998). In more recent studies, tufted capuchin monkeys (*Cebus apella*) showed that they could "match objects to their colour photographs and vice-versa, and that object-picture matching is not due to picture-object confusion" (Truppa, Spinozzi, Stegagno, & Fagot, 2009, p. 140), and lion-tailed macaques (*Macaca silenus*) displayed food preferences for pictures of food on a touchscreen (Judge, Kurdziel, Wright, & Bohrman, 2012). Although these experiments show the impressive abilities of primates to recognize and understand the contents of pictures, they are only a portion of the work that has been done, and researchers continue to make discoveries in this area.

Studies in birds which investigated recognition with learned behaviors have focused only on one species, namely pigeons, but these have proved to be fruitful subjects indeed. The first study to test for direct transfer of a discrimination task in pigeons was by Cabe (1976), who showed transfer between black-and-white photographs and objects in both reversal learning and direct transfer procedures. Similarly, a more recent study showed positive transfer of a discrimination task from complex objects, which were identical except for their configuration, to their pictures on a touchscreen computer (Spetch & Friedman, 2006). However, it may be relevant to mention that both of these discrimination transfer tests were carried out in an operant

conditioning chamber, and the pigeon subjects could only see, not touch, the real objects.

As discussed in section 1.2, classification is considered an important form of object recognition, so many picture-object recognition experiments have looked at pigeons' abilities to classify pictures into different categories. The first authors to investigate this phenomenon in any animal were Herrnstein and Loveland in their 1964 groundbreaking work, where they showed for the first time that pigeons could learn to classify pictures into different categories, and expand this behavior to novel stimuli. These results were later replicated by the authors using pictures of pictures of natural stimuli, and the pigeons ability to categorize pictures of fish, which they had never seen in their environment, led the authors to conclude "…the limited information in a picture is enough for a pigeon to form categories for objects found neither in its, nor its recent ancestors', environment" (Herrnstein & DeVilliers, 1980, p. 88). This very optimistic claim, essentially that pigeons had formed a "fish" category based solely on exposure to pictures, was subsequently criticized, as it was pointed out that the pigeons were most likely using visual cues to distinguish the photographs and had no concept of fish as such (Huber, 1999; Spetch & Weisman, 2012). Consequently, although pigeons may be very adept at classifying photographs into what we would consider natural categories, this does not mean that they are doing so by using concepts in the sense that we understand them.

Since Herrnstein & Loveland's discovery of pigeons classification abilities half a century ago, a flood of research has come out which attempted to show that pigeons do indeed understand what they see in pictures. For instance, in a 1997 study by Watanabe, pigeons categorized pictures and objects into food and non-food, and

also placed photographs of food and the real objects into the same category, suggesting that they "see pictures as representations of real objects" (p188). Recent studies by Aust and Huber (2006b; 2010) have elucidated that pigeons can not only make a correspondence between pictures and objects, but that they can understand pictures as representations of things in the real world. These authors showed that pigeons who had never seen a human head failed in a categorization task where they had to choose whether a human was present or not in a picture. Pigeons which had extensive experience with humans, on the other hand, succeeded in categorizing the pictures correctly. The discrepancy between the two groups suggests that pigeons were not just using two-dimensional cues to categorize pictures, but that they relied upon their real-world experiences to complete the task.

To this author's knowledge, pigeon are the only birds which have convincingly shown recognition through classification procedures, and further are the only ones which have even been tested for picture-object recognition by discrimination transfer. A single parrot species, budgerigars (*Melopsittacus undulatus*), were tested on facial recognition in pictures of conspecifics as compared to zebra finches and warped synthetic models. Although they picked up the salient features of conspecific faces more quickly than the zebra finches' or synthetic models', there was no direct evidence that they recognized that the pictures contained images of budgerigars (Brown & Dooling, 1992; Brown & Dooling, 1993). Aside from the budgerigar studies, no other bird species has been investigated in this way. While pigeons clearly make an excellent model species for exploring such questions, we cannot necessarily use the results of pigeon studies to make inferences about the capabilities of other bird

species, especially considering the great cross-species variation found in other areas of visual processing and anatomy (see Vision in Birds section for details).

In summary, establishing that animal subjects can recognize the objects portrayed in pictures is a methodological prerequisite for cognitive experiments based on this assumption. Given the large differences between human and avian vision at all levels, researchers cannot take for granted that birds' visual world corresponds to our own. Research to establish picture-object recognition in animals has taken three main forms: observing animal's spontaneous reactions to ecologically relevant pictures, testing for transfer of learned behaviors between pictures and objects, and creating categorization tests which require real-world knowledge to solve. In the first paradigm, such diverse groups as primates, sheep, and spiders have displayed recognition. Among birds, pigeons, chickens and Japanese quail have responded in a socially appropriate manner to pictures of conspecifics, although it can be argued that in all cases of spontaneous reaction to pictures the subject is confusing the picture with the real thing. In the paradigm which investigates transfer of learned behavior between pictures and objects, primates have shown picture recognition that is arguably on the same level with adult humans. Yet again, pigeons are the only birds to be systematically studied in this way, and have shown both the ability to transfer a learned discrimination task between picture and object, and to classify picture stimuli into natural categories. Although early classification experiments could not demonstrate that the pigeons recognized the content of the pictures as being representations of the real world, later, more refined methodologies have convincingly demonstrated that pigeons can use real world experience to classify

pictures. In conclusion, picture recognition is clearly not an ability confined to humans, but has been verified time and again in a wide range of animal species.

Picture-object recognition: research directions and the focus of this thesis

Current research on bird cognition has begun to focus on large-brained species with complex social structures or specific cognitive abilities, such as those found among the corvids and parrots (e.g. Marzluff & Angell, 2012; Pepperberg, 1999; Wascher & Bugnyar, 2013). While exciting discoveries are being made regarding topics like tool use in New Caledonian crows (Hunt, 1996), spatial memory in Clark's nutcrackers (*Nucifraga columbiana*) (Balda, Kamil, & Grim, 1986), and social cognition in ravens (*Corvus corax*) (Bugnyar, 2013), important basic research such as picture-object recognition may be getting left behind in the race to discover the next bird genius.

The information we have obtained from the study of vision in pigeons is invaluable, but focusing on one bird species out of many is not enough. Although the visual anatomy and physiology of many bird species has been researched, low-level and high-level visual processing has been confined mainly to pigeons and chickens, and rather important distinctions have been found even between these two species. As neither pigeons nor chickens are closely related to parrots (Hackett et al., 2008), nor do they share a similar ecological niche, there is good reason to assume that there are non-negligible differences in kea's visual processing. The research undertaken for this thesis will hopefully clarify some of the questions relating to high-level visual processing in kea, and by extension their parrot relatives.

This thesis will describe three experiments which test for transfer of a learned discrimination task between pictures and objects in kea. In the first experiment, described in chapter one, the kea were presented with a real-object discrimination

task on the aviary ground, and a picture discrimination task on a touchscreen computer. In chapter two, we will look at an experiment where the kea had to transfer between pictures on the touchscreen and objects presented in an operant conditioning box which mimicked the touchscreen in many ways. The experiment described in chapter three tests whether kea can recognize pictures in the form of printed photographs. The goal of these experiments will be to provide evidence that kea can recognize pictures from objects and vice versa.

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General Methods

Subjects and housing conditions

The subjects were the kea group at the Haidlhof Research Station in Bad Voeslau, south of Vienna. The group consisted of sixteen kea (*Nestor notabilis*): seven adult females (Coco, Elvira, Hope, Lilly, Plume, Sunny, Willy), eight adult males (Anu, Frowin, John, Kermit, Linus, Pick, Roku, Tammy), and one juvenile male (Paul). Eleven birds were hand-raised (Anu, Coco, Hope, Kermit, Lilly, Linus, Pick, Plume, Sunny, Tammy and Willy), and five were parent-raised (Elvira, Frowin, John, Roku and Paul).

All subjects had prior experimental experience, both with real-object discrimination tasks and touchscreen discrimination tasks (O'Hara, Huber, & Gajdon, 2014). However, subjects were naïve to experiments with photograph stimuli.

The kea were housed together in a large outdoor aviary (52x10x4m) which was equipped with hanging branches for perching, two ponds, wooden sleeping and breeding shelters, feeding tables, and a variety of environmental enrichment which was regularly renewed. Food was distributed three times daily, and consisted of fruits and vegetables, seeds, and an energy food once daily (normally cheese curd, an egg and yogurt mixture, or canned corn). Fresh water was available ad libitum in the aviary.

Apparatus

Touchscreen

Subjects participated in touchscreen experiments by entering a small cabin located inside of the experimental compartment. The cabin was enclosed by a roof and walls on three sides, and contained a standing platform (70.0 x 40.0 x 2.0, WxDxH all in cm) directly in front of a window (27.5 x 20.5 cm) which gave access to the touchscreen and reward tray (see Figure 1).

The touchscreen device consisted of a 15-inch XGA color TFT computer screen (Model G150XG01 by AU Optronics Corp., Taiwan), with a display area of 304 mm x 228 mm (381 mm diagonal) and a resolution of 1,024 x 768 pixels. Attached to the frontal frame of the screen was a 15-inch IR touch frame (Model "CarrollTouch" D87587-001, 15 in.) by Elo (Menlo Park, CA) for detecting responses. The IR grid was located (with a 5 mm gap) directly in front of the safety glass plate, which protects the LCD display from damage and dirt. The monitor and all described components were installed behind a dust-proof, aluminum case measuring 38.5 × 49.5 cm (width x length).

The screen was connected to a modified operant conditioning system described in detail by Steurer et al. (2012). The CPU (based on a Schneider A4F® minicomputer (http://www.mappit.de) with Mini-ITX main board (VIA EPIA1 M10000, with 1-GHz CPU, 2 × USB, 1 × LAN 10/100 Mbit, sound, and VGA on board), 512 MB DDR RAM, a 40-GB 2.5-in. hard disc) and feeding system attached behind the touch sensitive screen were contained in a metal cube measuring 38.5 x 49.5 x 60.5 cm (width x height x depth). The feeding system consisted of a motor, sensor and circular plastic disc with holes, which would rotate one reservoir further, this way releasing a reward below the screen into the small tray (6.0 x 5.5 x 2.0 cm, width × height × depth), whenever a positive stimulus was touched.

The opening for the reward tray was located centrally 10.0 cm below the lower edge
of the screen. The entire touchscreen operant conditioning system rested on a bench
inside of the experimenters' hut, which was situated between the experimental
compartment and a living area inside of the aviary. This hut was modified explicitly
for the purpose of carrying out touchscreen experiments. Openings in the wall to the
experimental compartment exactly fit the touchscreen and reward tray, which
opened and closed via a plastic sliding door and pulley system, and gave the
subjects on the test platform access to the device.

The program used for cognitive testing was CogLab light (version 1.4; see Steurer,
Aust, & Huber, 2012 for detailed description).
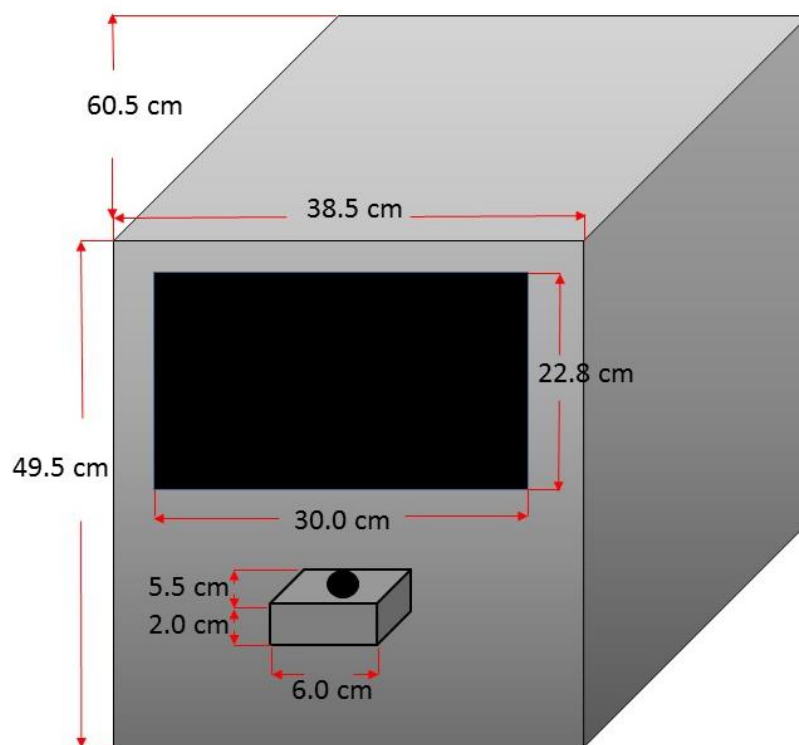
Figure 1. Touchscreen operant-conditioning unit

Stimuli

Touchscreen stimuli

Touchscreen stimuli were digital photographs of objects taken from different angles. These were distributed semi-randomly throughout each session, with each angle occurring about an equal number of times per session. Images were presented on a black background in a fixed position on the screen. Positive and negative stimuli were randomly switched between the left and right sides of the screen for each trial.

General procedure

In all experiments, subjects were trained and tested in a two-choice discrimination procedure, meaning that for each trial the kea was presented with two images or objects and had to choose one before continuing to the next trial. Each session consisted of 20 trials, excluding correction trials on touchscreen. Positive choices were rewarded with 1/8 of a peanut. Test subjects participated in between one and two training sessions per test day, two to three days per week. The training phases were considered complete once a subject had reached criteria. Criteria for each experiment is noted in the chapter in which it is described.

Touchscreen discrimination task

Positive choices were marked by a tone (600.5 Hz) and a reward (1/8 peanut), which was dispensed from a feeder below the screen. Negative choices were marked by a different tone (200.2 Hz) and followed immediately by a correction trial, which was rewarded. There was a between-trial interval of one second for all trials.

Object discrimination tasks

Object stimuli were presented on the aviary ground 1.5 meters away from the subject, with a distance of about 30 cm between the two objects. Furthermore, stimuli were randomly switched between the left and right sides for each trial. Testing and training took place on the ground of the aviary. Birds were separated and visually isolated from the group during testing by a sliding wall. Between trials, subjects were required to wait in a neighboring compartment, separated by a sliding mesh gate, while the experimenter visually obscured and then rearranged the stimuli. Great care was taken that the subjects never saw the experimenter touch the stimuli, to prevent any possible effects this might have had.

Turning or pushing over the object was considered a choice. Rewards were handed to the subject by the experimenter. The experimenter also gave a verbal cue (*brav*, "good job") for a positive choice. Negative choices were neither rewarded nor punished, and subjects were allowed to continue exploration until the correct choice was made, at which point they were rewarded. This is considered an analogue to the correction trials on the touchscreen. Importantly, there was no physical connection between the positive stimulus and reward (i.e. the peanut was not hidden underneath). This ruled out 1) the possibility that the subjects detected the correct choice via smell, and 2) the possible effect of spatial contiguity between stimulus and reward (Miller & Murphy, 1964).

Data Collection and Analysis

Results of object trials were recorded manually by the experimenter. Besides correct/incorrect choice, other information noted was date, time, and whether the positive stimuli occurred on the left or right side.

The touchscreen and object-display box trials were recorded automatically by the CogLab light computer program. Information noted included correct/incorrect first choice, correct/incorrect choice in correction trials, date, time, the position of stimuli on the screen, and the number of pecks on the screen which did not contact the stimuli.

The data analysis program used was IBM SPSS Statistics for Windows, Version 20.0 (IBM Corp, 2011). The particular tests and analyses used for each experiment will be described in the individual chapters, but in general, two-tailed student's t-tests were used to determine significant differences between groups. P-values of < 0.05 were considered significant.

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Chapter I: Direct Discrimination Transfer between Object and Touchscreen

Introduction

Pictures, whether in the form of photographs, projected images, or presented on a computer screen, have been used by researchers investigating the cognitive abilities of animals for decades (for review see Bovet & Vauclair, 2000). The use of photographs with bird subjects began in earnest with Herrnstein and Loveland's 1964 groundbreaking study on pigeons (*Columba livia*), where the authors showed that their pigeon subjects could classify photographs based on whether they contained a human or not. This was the first time that classification of this type had been shown in any non-human animal, and hence a barrage of studies followed, which examined pigeons' classification abilities in every detail (e.g Cerella, 1979 ; Herrnstein, Loveland, & Cable, 1976; Huber, Troje, Loidolt, Aust, & Grass, 2000). Pigeons aptitude for discrimination went well beyond pictures of things with which they had real-life experience, or indeed which could possibly have any ecological relevance to the animals (Herrnstein & DeVilliers, 1980; Watanabe, Sakamoto, & Wakita, 1995). This led some authors to criticize the optimistic claims about what pigeons were truly perceiving when they, for example, identified photographs which contained images of fish (with which the pigeons had no real-life experience), or showed that they could discriminate between Picasso and Monet paintings (a task with no obvious ecological relevance) (Monen, Brenner, & Reynaerts, 1998; Weisman & Spetch, 2010). It became clear that revised methodologies were

necessary in order to figure out whether pigeons could in fact recognize what these pictures portrayed.

A promising method of exploring whether an animal can form a tangible correspondence between pictures and objects is to look for direct transfer between the two. Birds especially have quite different visual capabilities compared to humans, for whom photographs, projected images, and computers screens were designed (see Introduction for a full description of avian vision). Therefore, if bird subjects can show a behavioral correspondence between real objects and pictures, it is likely that they have to some extent overcome the obstacles that picture stimuli inherently present (Weisman & Spetch, 2010).

Along this line of reasoning, several studies have tested for transfer of a learned discrimination task between pictures and objects in pigeons. Cabe (1976) showed that pigeons which were trained on an object discrimination task could transfer this to black and white photographs and silhouettes, but not to line drawings. The results of this study, however, were unidirectional and did not show transfer from pictures to objects. A 2006 study by Spetch and Friedman succeeded in showing bidirectional transfer between real objects and color pictures of these on a touchscreen computer, and that furthermore they transfer to novel, untrained views of both pictures and objects. We can conclude from these two studies that pigeons are capable of recognizing pictures from objects and vice versa, and that this holds for pictures presented in several different formats.

The current experiment was the first to test a parrot species, the kea (*Nestor notabilis*), for picture-object recognition using a discrimination transfer procedure. Up to now, no bird species besides the pigeon had been investigated using such a

procedure, despite the fact that a variety of bird species, most of which are only very distantly related to pigeons, participate in experiments which use picture stimuli (e.g. Bond & Kamil, 2006; Bond, Wei, & Kamil, 2010; Mui et al., 2007). Moreover, both of the aforementioned pigeon studies used an operant conditioning chamber for all experiments, and subjects had only visual access to the real objects. Here, we combined two procedures with which the kea were already familiar: a real object discrimination task where the subjects were required to approach and touch the stimuli, and a touchscreen discrimination task which took place in a touchscreen cabin within the aviary. The kea were additionally tested for transfer to novel views of pictures in the touchscreen training phase. We assumed, as did previous authors, that successful transfer between pictures and objects would provide strong evidence for recognition.

Methods and procedure

Subjects

The subjects were twelve kea (*Nestor notabilis*): five adult females (Coco, Elvira, Lilly, Sunny, Willy), six adult males (Anu, Frowin, John, Kermit, Roku, Pick), and one juvenile male (Paul). Seven birds were hand-raised (Anu, Coco, Kermit, Lilly, Pick, Sunny, and Willy), and five were parent-raised (Elvira, Frowin, John, Roku and Paul). All subjects had prior experience with both touchscreen and object discrimination tasks.

Apparatus

See description of the touchscreen apparatus under *General methods* section.

Stimuli

Object stimuli

Object stimuli were small toys appropriate for young children (non-toxic). Test and

training stimuli (conditions "Object Known" and "Object Control") were a metal toy

duck and a metal toy frog, which differed in shape, size, color and pattern. The toy

duck measured 10.0 cm in length and 5.5 cm in width at its widest point. The toy frog

measured 6.0 cm in length and 4.5 cm in width at its widest point (Figure 1.1).

Figure 1.1. Stimuli for condition Image Control and stage one of condition Image Known consists of digital photographs of a metal toy frog (left) and a metal toy duck (right), displayed on a black background. The objects from which these photographs were taken made up the stimuli for conditions Object Known and Object Control.

Control Stimuli (condition "Object Unknown") were two wooden toy donuts that

differed in size, shape and color. The orange donut with the hole had a diameter of

4.5 cm, and the beige donut with no hole had a diameter of 4.0 cm (Figure 1.2).

Figure 1.2. Stimuli for condition Object Control consisted of two wooden toy donuts that differed in size, shape and color.

Touchscreen stimuli

Test and training stimuli (conditions "Image known" and "Image control") were photographs of a metal toy duck and a metal toy frog, which differed in shape, size, color and pattern. Images appeared slightly smaller onscreen than the objects they represented. Frog images were all 200 x 150 pixels, or about 5 cm long on the screen. Duck images were 280 x 150 pixels, or about 7.0 cm long on the screen. The width of the image varied based on the angle. The width of the duck varied between 1.75 and 4.0 cm at the widest point. The width of the frog varied between 1.5 cm and 3.5 cm (Figure 1.1).

Control stimuli (condition "Image Unknown") were photographs of a rubber duck and a rubber frog, which differed in shape and pattern. Images were between150 x 200 and 170 x 200 pixels. All control images were about 5.0 cm tall on screen, and varied in width between 3.5 and 4.0 cm (Figure 1.3).

Figure 1.3. Stimuli for condition Image Unknown consisted of photographs of a rubber duck and a rubber frog, which differed in shape, color and pattern.

Procedure

This study tested whether kea could transfer a learned discrimination between two procedures they were already familiar with: touchscreen and real-object discrimination tasks.

Touchscreen-to-object task

Five test (Coco, John, Kermit, Lilly, Roku) and seven control subjects (Anu, Elvira, Frowin, Paul, Pick, Sunny, Willy) participated in the touchscreen-to-object task. Subjects were assigned to the groups semi-randomly, controlling as much as possible for sex, age, and rearing history.

Test subjects underwent the touchscreen training and testing procedure as described in the *General methods* section. Control subjects participated in one pre-training task to become acclimated to working with the experimenter. The pre-training task consisted of one twenty-trial session on the touchscreen. Here the birds were presented with a single image of a shape on the screen, which they had to peck for reward as described above. Pre-training stimulus was a (non-photographic) image of a white cross on a black background.

The training phase for the test group was followed by a generalization test in which two novel views of the stimuli were added to each session, for a total of five angles. In the generalization sessions 10 out of 20 trials contained novel views, which were randomly interspersed throughout the session. Again, criteria was an average performance at ≥ 80% over two consecutive sessions. Once criteria was reached in the training and generalization tasks, subjects were tested on the object discrimination task.

As well as test sessions on the training stimuli, test subjects participated in an object session which involved the same procedure as the object test session, but with novel objects the subjects never seen before (condition Object Unknown). This was to exclude the possibility that the test group was by chance better than the control group in object discrimination.

Object-to-touchscreen task

Six test subjects (Anu, Frowin, Pick, Paul, Sunny, Willy) and five control subjects (Coco, John, Kermit, Lilly, Roku) participated in the object-to-touchscreen task. The five control subjects acted as test subjects for the touchscreen-to-object task, and the six test subjects had acted as the test subjects for that task.

Object discrimination sessions proceeded as described in the *General methods* section Training criteria was an average of ≥80% correct choices over two consecutive sessions. Once training was complete, subjects were tested on the touchscreen task (again, as described in the *General methods* section), where they were presented with photographs of the objects they had been trained on (condition Image Known). They also participated in a control touchscreen session which involved the same procedure as the test session, but with pictures of novel objects (condition Image Unknown). This was to exclude the possibility that the test group was by chance better than the control group in touchscreen discrimination.

Data collection and analysis

Data collection proceeded as described in the *General methods* section for both touchscreen and object conditions. In the both tasks, performance was compared

between the test group (conditions Known), the test group with novel stimuli (conditions Unknown), and the control group (conditions Control).

Data analysis was done on both the first ten trials of each condition, as well as the whole first session. Furthermore, the first and second ten trials of the first session were compared and analyzed in the touchscreen conditions. The first ten trials were compared because it is known that in transfer tasks kea may begin to explore after a few trials (Gajdon, Amann, & Huber, 2011). In both touchscreen-to-object and object-to-touchscreen tasks, data was analyzed using a two-tailed Student's t-test with Bonferroni corrections. P-values of < 0.05 were considered significant.

Additionally, the keas' general performance in the touchscreen task was compared to that of the object discrimination task, in order to see if subjects tended to be better in one medium over the other. Data from untrained object and touchscreen conditions was analyzed, also using a two-tailed Student's t-test. Eleven individuals were included in the untrained touchscreen condition: Coco, John, Kermit, Lilly, Roku, (data from the condition Image Control), and Anu, Frowin, Paul, Pick, Sunny and Willy (data from condition Image Unknown). Twelve individuals were included in the untrained object condition: Willy, Sunny, Anu, Pick, Paul, Elvira (data from training for condition Object Known) and Anu, Frowin, Paul, Pick, Sunny, Willy (data from condition Object Control).

Results

Object-to-touchscreen task

Kea had significantly more correct choices (p < 0.05) in condition Image Known than conditions Image Unknown and Image Control in the first ten trials of the

touchscreen task (Figure 1.4). Subjects in condition Image Known had a mean performance of 73%, whereas both conditions Image Unknown and Image Control had only 38%. There was no significant difference between conditions Image Unknown and Image Control.

When we analyze the first touchscreen session as a whole (Figure 1.5), however, we find no significant differences between any of the treatments. Condition Image Known had a mean performance of 58%, which was only marginally and non-significantly better than conditions Image Unknown and Image Control, with 52% and 46% respectively.
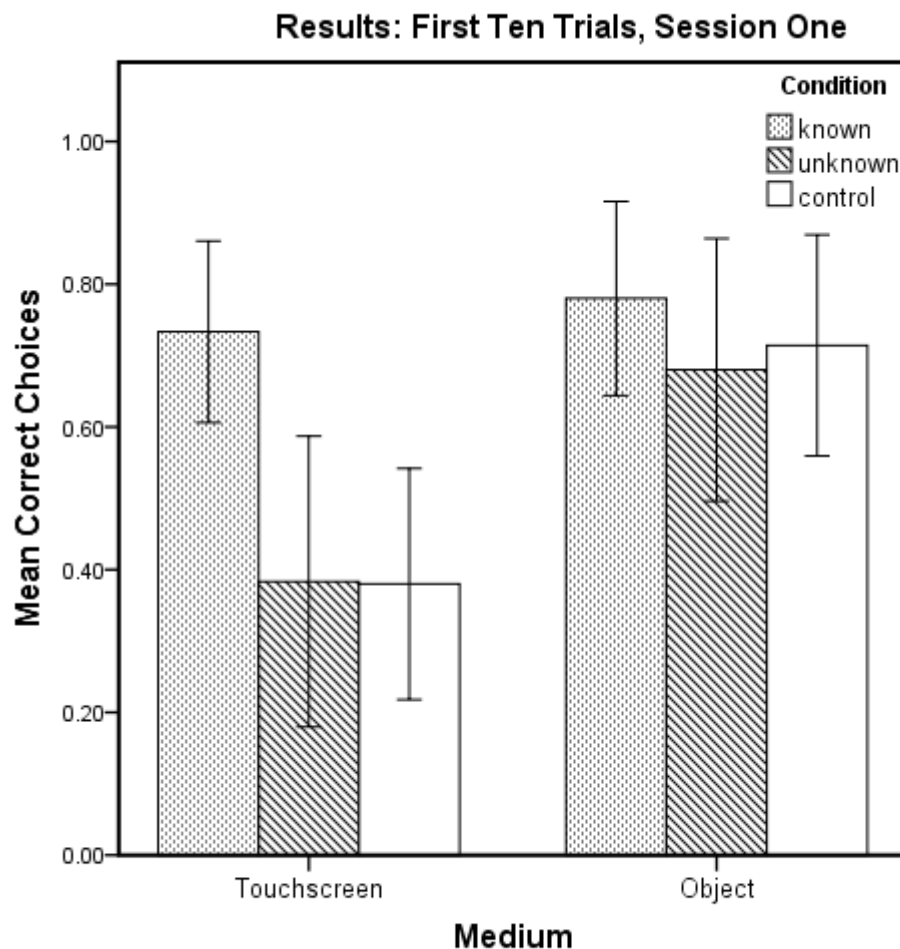
Figure 1.4. Mean correct choices in the first ten trials as a percentage. Condition "known" indicates test group with test stimuli, "unknown" indicates test group with novel stimuli, and "control" indicates control group with novel stimuli. Condition "touchscreen known" (n = 6) is significantly higher than both "touchscreen unknown" (n = 6) and "touchscreen control" (n = 5). There is no significant difference between conditions "touchscreen unknown" and "touchscreen control." Regarding object conditions, we find that there are no significant differences between "object known" (n = 5), "object unknown" (n = 5) or "object control" (n= 7); * p<0.001.
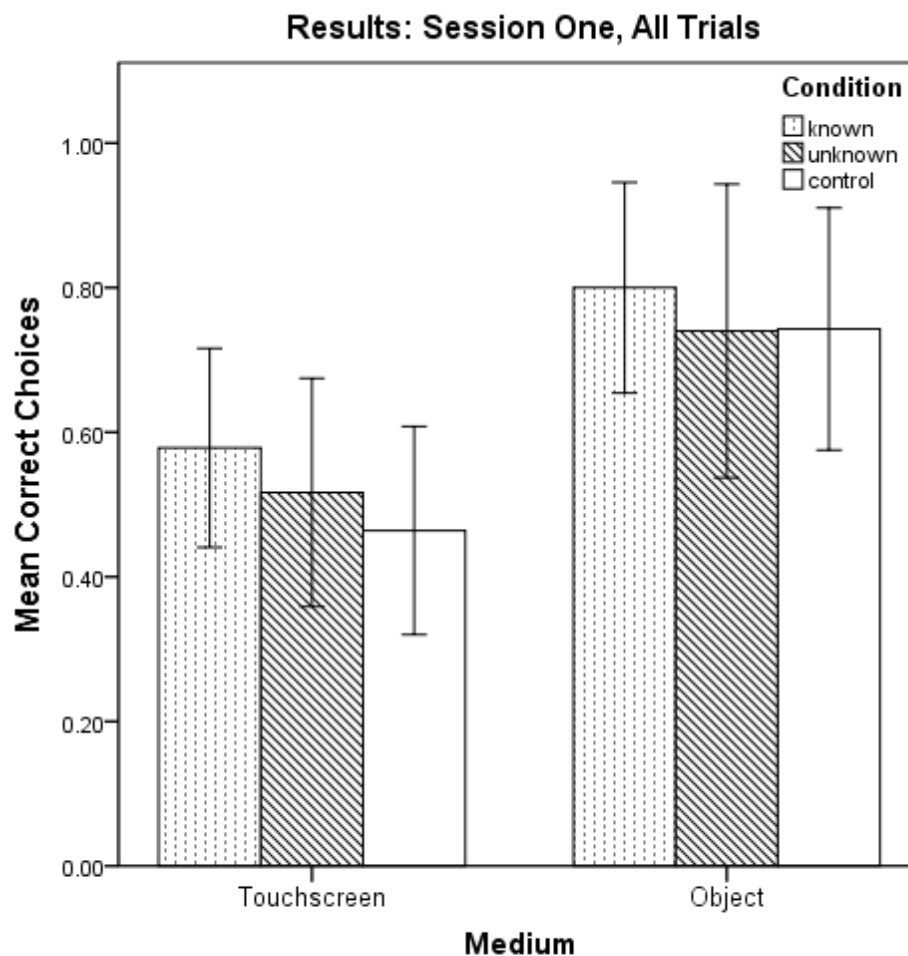
Figure 1.5. Mean correct choices as a percentage for the whole first session. Condition "known" indicates test group with test stimuli, "unknown" indicates test group with novel stimuli, and "control" indicates control group with novel stimuli. Note that significant differences shown in the first ten trials (Fi. 1) are lost when we look at the entire first session of twenty trials. N-values remain the same as in Fig.1.

When we compare the first ten trials with the second ten of touchscreen session one (Figure 1.6), we see that subjects in condition Image Known tend to perform better in the first half of the session. On the other hand, members of conditions Image Unknown and Image Control tend to perform better in the second half of the session. It is important to keep in mind, though, that none of the differences between the first and second ten trials are significant ($p < 0.5$).


Error Bars: 95% CI
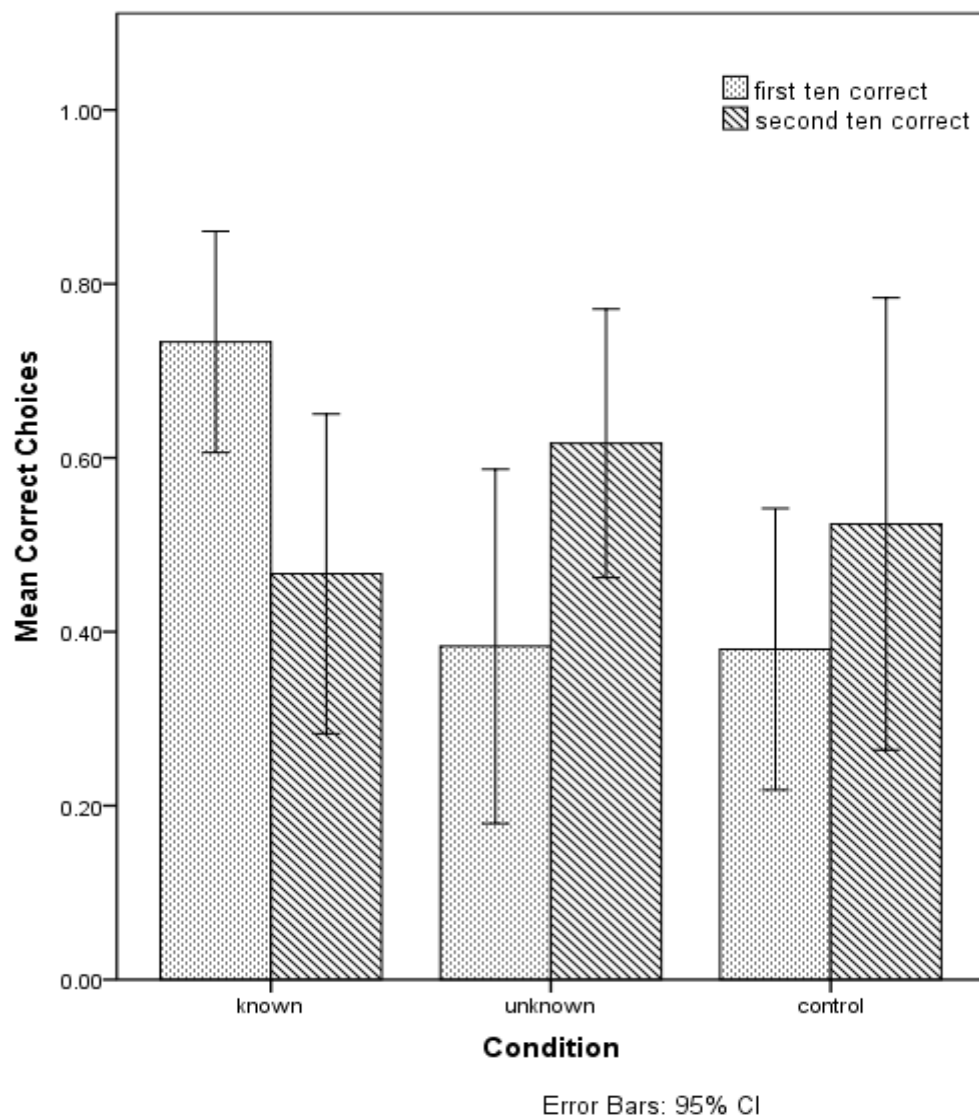
Figure 1.6. The first ten compared to the second ten trials of the touchscreen task. Differences between the first ten and second ten trials are non-significant. However, members of condition "known" tend to perform better in the first half of the session, whereas conditions "unknown" and "control" tend to perform better in the second half of the session. N = 6 for conditions "known" and "unknown," and n = 5 for condition "control;" * p < 0.05.

Touchscreen-to-object task

Kea showed no significant differences in mean correct choices in any of the object conditions, regardless of whether the first ten trials or the whole session were analyzed (Figures 1.4 and 1.5). Condition Object Known had a mean performance of 80% over the whole session and 78% over the first ten trials. This was not significantly higher than conditions Object Unknown (74% whole session, 68% first ten trials) or Object Control (74% whole session, 71% first ten trials).

Performance differences based on medium

Kea performed significantly better ($p < 0.05$) on the untrained object conditions than the untrained touchscreen conditions (Figure 1.7). Subjects performed at chance levels in the first session touchscreen task (mean 49% correct) whereas the mean performance in first session of the object task was significantly higher at 74% correct ($p < 0.05$).
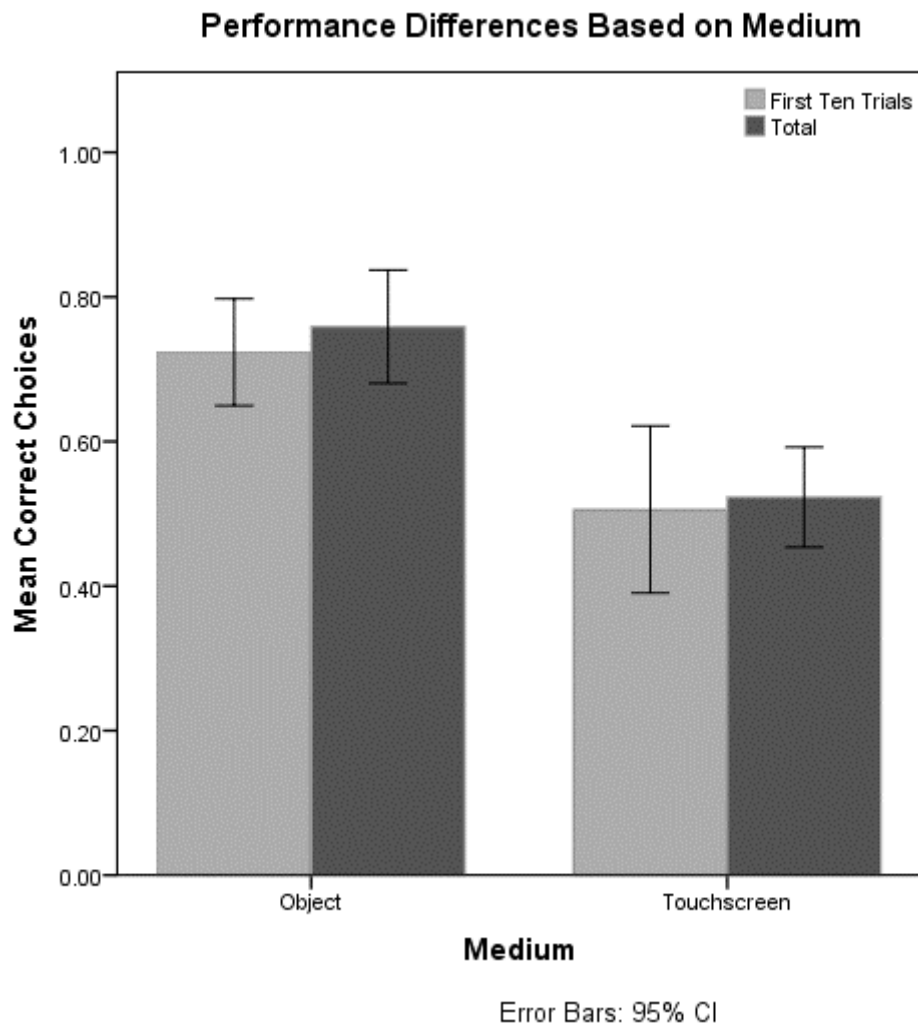
Figure 1.7. The mean correct choices of session one of the touchscreen and the object discrimination tasks, looking at first ten trials as well as the session as a whole. Performance differed significantly between the two tasks (p < 0.05). N=11 for the touchscreen condition and n=12 for the object condition.

Discussion

Kea show evidence of picture-object recognition in the form of the positive transfer of

a learned discrimination task in the first ten trials of the touchscreen test session.

These results support the notion that kea can recognize pictures from objects,

although it is not clear whether this is a transfer of two-dimensional aspects or true object recognition. These findings can be compared to the performance of pigeons on similar tasks (Cabe, 1976; Spetch & Friedman, 2006) and they suggest that the touchscreen can indeed be a good method of representing real objects when testing the cognitive abilities in kea.

However, after the first ten trials, test performance drops, making the evidence for transfer less robust. A similar phenomenon has been observed in kea before by Gajdon and colleagues, who showed that kea were capable of social learning by watching a conspecific solve a tool use task, but quickly abandoned the technique they had learned by observation in favor of exploration (Gajdon et al., 2011). In the current study, subjects may have similarly begun to explore new strategies after a few sessions, which would explain the high performance in the first ten trials, followed by chance-level performance in the second ten trials of the touchscreen test session.

Differences in the presentation of the stimuli could have been a factor which caused heightened exploration in the second ten trials. The first presentation difference was the testing location: on the aviary ground vs. in the touchscreen shelter. The next was the stimuli configuration. In the object condition, stimuli were presented flat on the sand, whereas in the touchscreen condition they were displayed vertically at the kea's eye-level on a black background. The differences in location and configuration in the two conditions may have weakened the association between test and training stimuli in the later trials (Miller & Murphy, 1964). Studies which tested for transfer of learned discrimination tasks in pigeons, which performed more consistently than the kea, always took place with the subject inside of an apparatus which presented both

pictures and objects in the same location and configuration (Cabe, 1976; Spetch & Friedman, 2006).

The results of the touchscreen-to-object task were inconclusive, and from this experiment we cannot say whether kea can transfer from pictures to objects. In the object task, there were no significant differences between known object and object control conditions. In fact, the object control groups performed so well on the task (some individuals achieved 90% correct in the first session) that it was not possible to find a learned transfer in the test group. This indicates that an object discrimination task is not challenging enough to test for transfer in kea.

To get a clearer picture of how well kea can transfer between pictures and objects, experiments two and three will test for learning transfer using revised procedures. Both will use a reversal learning procedure to test for negative transfer in order to create an adequately challenging task. Experiment two will present the object stimuli in the same location and configuration as the touchscreen. Experiment three will test for transfer between framed photographs and objects, both presented on the aviary ground.

A final result of this experiment worth mentioning is that kea perform much better in the first session of object discrimination tasks than touchscreen discrimination tasks. This collaborates the findings of O'Hara and colleagues that kea require more trials to reach criterion in touchscreen than in solid object tasks because rewarding is spatially dissociated (O'Hara, Huber, & Gajdon, 2014). The present study shows that there is more to the story than just spatial dissociation, though, as there was no spatial connection between stimulus and reward. Further experiments are needed to find out what factors are responsible for this discrepancy.

In conclusion, this experiment showed that kea can transfer a learned discrimination task from solid objects to images on a touchscreen, providing evidence for object-to-picture recognition. However, it was not possible to show touchscreen-to-object transfer using the current procedure. Furthermore, this study clearly supports earlier findings that kea learn discrimination tasks with solid objects significantly faster than with touchscreen images, although the reasons for this discrepancy cannot be ascertained from the data presented here. Further discrimination transfer experiments will be described in the following chapters, which will look more closely at kea's abilities in this area. Hopefully this study, and those that follow it, will provide a methodological basis for using the touchscreen to represent real objects when working with kea and other parrot species in the future.

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Chapter 2: Discrimination Transfer between Touchscreen and Object-Display Box

Introduction

In this chapter, we will address two outstanding concerns from chapter one: first, the lack of evidence for picture-to-object transfer, and second, the fact that object-to-picture transfer only occurred in the first ten trials of the first touchscreen test session. In chapter one, we showed that kea can transfer a learned discrimination task from real objects to pictures on a touchscreen, thereby providing evidence for object-to-picture recognition. However, in that experiment it was not possible to show transfer in the other direction, i.e. from pictures to objects, because kea are so adept at object discrimination tasks that they can perform well above chance level even in the first session. This created a ceiling effect, and the naïve control subjects performed just as well as the test subjects, making it impossible to clarify whether the test subject had transferred knowledge from the touchscreen, or simply learned the object discrimination "from scratch".

In the current chapter, we will describe an experiment which tests for transfer between pictures and objects using a reversal-learning task, a procedure known to be more difficult for kea to solve. O'Hara, Huber, & Gajdon, (2014) showed that, both in real-object and touchscreen conditions, kea perform significantly lower in the first session of a discrimination task with reversal learning than in a task with novel stimuli, and that furthermore it takes them more sessions to reach criteria. This is a phenomenon that has not gone unnoticed in the literature, and the two studies which

tested for picture-object recognition in pigeons by means of a discrimination transfer procedure used both direct transfer and reversal learning (also called "negative transfer") (Cabe, 1976; Spetch & Friedman, 2006). Following these researchers, we assume that negative transfer has occurred in a reversal learning task if a subject performs significantly lower in the first session(s) and/or takes significantly longer to reach criteria than in a discrimination task with novel stimuli. Negative transfer between objects and pictures provides strong evidence for recognition, as it indicates that the subject had to first "unlearn" the original task before acquiring the new one, a process which would not occur without correspondence between picture and object stimuli.

To address the concern that transfer only occurred in the first ten trials of the touchscreen test session, we tested the object condition using an operant conditioning box which mimicked the touchscreen as closely as possible. This reduced possible distracting factors between the object and touchscreen conditions, such as differences in testing location, object configuration, and reward acquisition. These variations, which were present in experiment one, may have may have weakened the association between test and training stimuli in the later trials (Miller & Murphy, 1964), and perhaps by controlling for them we would be able to attain a strong transfer which was detectable throughout the entire test session.

In summary, the experiment described here used a learned two-choice discrimination task to test for transfer between pictures and objects, as in experiment one. However, it differed from experiment one in that we tested for negative transfer with a reversal learning task, as opposed to direct transfer. Furthermore, object stimuli were presented in an object-display box which allowed only visible access to

the stimuli, controlling as much as possible for distracting factors between touchscreen and object conditions. We assumed that kea recognize pictures from objects, and vice versa, if they showed negative transfer between the two.

Methods and procedure

Subjects

The subjects chosen for this experiment were 13 kea (*Nestor notabilis*): six adult males (Anu, John, Kermit, Linus, Pick, Roku), six adult females (Elvira, Hope, Lilly, Plume, Sunny, Willy) and one juvenile male (Paul). One adult female (Lilly) dropped out in the pre-training phase, and only three of the remaining birds met criteria to move on to the testing phase (Elvira, Linus, Sunny). All subjects had prior experience with touchscreen discrimination tasks, but had never before used the object-display box.

Apparatus

Object-display box

The object display box used in experiment two was built by the experimenter, and designed so that the front display and reward tray fit exactly into the touchscreen window, whereas the back attached to the touchscreen device itself. It consisted of a large wooden frame (49.5 x 60.0 x 62.0, WxDxH all in cm) which in front held a plexiglas display, stimuli compartments, and movable shelves. The shelves were supported all the way to the back of the frame, where it attached to the touchscreen.

Subjects could access the box in the same manner as the touchscreen (see above). The front display was a 35 x 25 cm piece of plexiglas painted black, with two

transparent, movable windows 9 cm from the top, 8 cm from the bottom, and 6 cm from the center of the screen. These windows were located on the black plexiglas display approximately where the picture stimuli would be displayed on the touchscreen. Behind the transparent windows, the object stimuli rested on an attached clear plexiglas shelf, and were secured to this shelf by magnets. The viewing angle of the stimuli could be adjusted by manually turning them on the magnets. The stimuli were located inside of small, painted-black plexiglas compartments (8.5 x 6.5 .8.5, WxDxH all in cm) which were open at the top to allow the experimenter access, and which had slits in the back through which the movable plexiglas shelf, on which the objects rested, could pass. Lights were fixed 9 cm directly above the stimuli shelves (see Figures 2.1 and 2.2 for detailed schematics).

The shelves which held the object stimuli were in total 52.0 cm long, and in their resting position ended directly in front of the touchscreen, so that when pushed slightly they made contact with the screen. Subjects were required to push on one of the clear windows to make a choice, whereby the shelf contacted the touchscreen, which then recorded the choice and gave the appropriate auditory feedback. It was up to the experimenter to arrange the stimuli in the box display to match the positive/negative touchscreen display. When the subject made a correct choice, the experimenter manually dropped a reward into the reward tray, which measured (6 x 8.5 x 2, WxDxH all in cm) and was made of aluminum.

All cues for the configuration of the object stimuli were displayed on the touchscreen for the experimenter (i.e. the viewing angle, display on the left or right side), and had to be manually configured by the experimenter between trials. The subjects' view

was blocked between trials by a large black piece of posterboard which slid in front of the display.

Figure 2.1. Object display box, top view. The front of the box consists of a large wooden frame which in front holds a Plexiglas display, stimuli compartments, and movable shelves. The shelves were supported all the way to the back of the frame, and came to rest directly in front of the touchscreen so that when pushed they made contact and allowed the computer to log the subject's choice.

Figure 2.2. Object display box, front view. The front display was a piece of Plexiglas painted black, with two transparent, movable windows. Behind the transparent windows, the object stimuli rested on an attached clear Plexiglas shelf inside of small, painted-black Plexiglas compartments (8.5 x 6.5 .8.5, WxDxH all in cm) which were open at the top, and which had slits in the back through which the shelf could pass. Lights were fixed 9 cm directly above the stimuli shelves.

Touchscreen

The touchscreen apparatus is described in detail in the *General methods* section.

Stimuli

Object stimuli

Object stimuli were small toys appropriate for young children (non-toxic). Pre-training stimuli were a plastic tiger (8.0 x 3.0 x 1.5 cm) and a plastic rhinoceros (6.5 x 3.0 x 1.5 cm) which differed in shape, color and pattern (Figure 2.3). Test stimuli for the touchscreen-to-object condition were two children's block toys (3.5 x 2.5 x 2.5 cm), one green and one yellow, which were identical in all aspects except color (Figure 2.4). Training stimuli for the object-to-touchscreen condition were also two children's half-circle shaped block toys (3.5 x 2.0 x 3.0 cm), one light blue and one light green, which were again identical in all aspects except color (Figure 2.4). Object stimuli were presented to the subjects in the object-display box.

Figure 2.3. Pre-training stimuli were a plastic tiger and a plastic rhinoceros, which differed in shape, color and pattern.
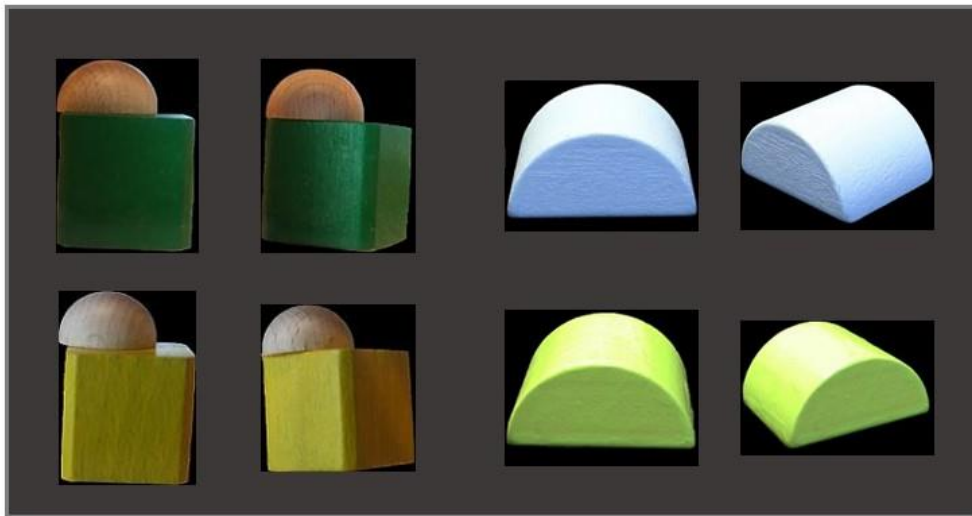
Figure 2.4. Touchscreen-to-object condition stimuli, shown left, were two children's block toys, one green and one yellow, which were identical in all aspects except color. Object-to-touchscreen condition stimuli, shown right, were also two children's block toys, one light blue and one light green, which were again identical in all aspects except color. For the touchscreen tasks, stimuli were photos of these objects from two different angles.

Touchscreen stimuli

Touchscreen stimuli were digital photographs of the objects used in the test and training phases of the object discrimination task as described above. Photographs were taken from two views; one view was arbitrarily chosen as the front, and the second view was taken with the object turned 30 degrees to the right. The pictures were displayed on a black background, and appeared on the computer screen to be the same size as the real objects. For the touchscreen-to-object task, pictures of the green block measured 114 x 155 pixels and 126 x 128 pixels, and pictures of the yellow blocks measured 107 x 151 pixels and 127 x 137 pixels. For the object-to-touchscreen task, pictures of the light blue blocks measured 185 x 141 pixels and

161 x 125 pixels, whereas those of the light green blocks measured 168 x 135 and 187 x 130 pixels (Figure II).

Procedure

Object-display box pre-training

All subjects went through a pre-training phase to habituate to using the object-display box. The pre-training procedure was a two-choice discrimination task (twenty trials per session, plus rewarded correction trials) with real objects presented behind the movable object-display windows (see *General methods* section for description and schematics). Subjects were required to push on one of the movable windows to make a choice, which was logged by the touchscreen computer attached to the back of the box. Objects were randomly switched between the left and right sides of the display box between trials to help control for side-preferences. All stimuli manipulation and rewarding was done manually by the experimenter between trials while the display was visually obscured.

Pre-training criteria was an average of 80% correct over two consecutive sessions. After meeting criteria, subjects were moved on to the touchscreen-to-object training phase.

Touchscreen-to-object task

Three subjects, Elvira, Linus and Sunny, reached pre-training criteria and therefore could participate in the next phase. The training phase of the touchscreen-to-object task was a standard two-choice touchscreen discrimination task as described in the *General methods* section. The first three sessions of the training phase were considered the "acquisition period", and the last three the "acquisition achieved"

period. Training criteria was ≥85% over three consecutive sessions with a minimum of five total sessions. Training was continued for all three test subjects until the last one had reached criteria. This was to ensure that a subject which took longer to reach criteria did not have an advantage over other subjects due to more exposure to training stimuli.

Once all subjects had reached criteria, they were given a reversal learning test on the object-display box, meaning that the positive photograph stimuli from the touchscreen training now became the negative object stimuli, and vice-versa. The test procedure was again a two-choice discrimination task as described in the *General methods* section and above under *Object-display box pre-training.* Subjects were tested until they reached criteria of ≥85% over three consecutive sessions. As in the training phase, the first three sessions of the test phase were considered the "acquisition period", and the last three the "acquisition achieved" period.

Object-to-touchscreen task

The object-to-touchscreen procedure was identical to that of the touchscreen-to-object, but began with an object-display box training phase which was followed by a reversal learning test on the touchscreen. Object training criteria was ≥85% over three consecutive sessions with a minimum of five total sessions, and only two subjects, Linus and Sunny, met this criteria and were moved on to the touchscreen test. Subjects were then tested until they reached criteria of ≥85% over three consecutive sessions.

Data collection and analysis

Touchscreen and display-box data (for all pre-training sessions) was recorded automatically by the CogLab light software as described in the *General methods* section.

Due to construction in the touchscreen hut, the object-display box could no longer be attached to the touchscreen computer after touchscreen-to-object test session one for Linus and Sunny, and touchscreen-to-object test session two for Elvira. After this, all object-display box data was recorded manually by the experimenter. The experimenter recorded the following information: session number, date, time, side on which positive stimuli was presented, and correct/incorrect choice.

Statistical analysis was done in IBM SPSS version 20. Performance differences were analyzed for the mean of the first three sessions of each task (acquisition period) and the last three sessions of each task (acquisition achieved) to see if subjects performed significantly lower in the acquisition phase of the test condition than in the control condition, which would suggest reversal learning. Furthermore, I looked at whether subjects took more sessions to reach criteria in the test condition than the control, which would also provide support for reversal learning. All conditions were compared using a two-tailed student's t-test with Bonferroni corrections, and p-values of < 0.05 were considered significant.

Results

Touchscreen-to-object task

The mean performance on the acquisition period of the touchscreen-to-box transfer was significantly lower than control (test: 32%, control: 63%; n = 3) in a two-tailed student's t-test with Bonferroni corrections, suggesting that reversal learning had

occurred in this task (Figure 2.5). Subjects also took more sessions to reach criteria in the touchscreen-to-object transfer than in control (Sunny: 6 sessions test, 4 control; Linus: 9 sessions test, 3 control; n = 2), but this was not significant, probably due to small sample size.
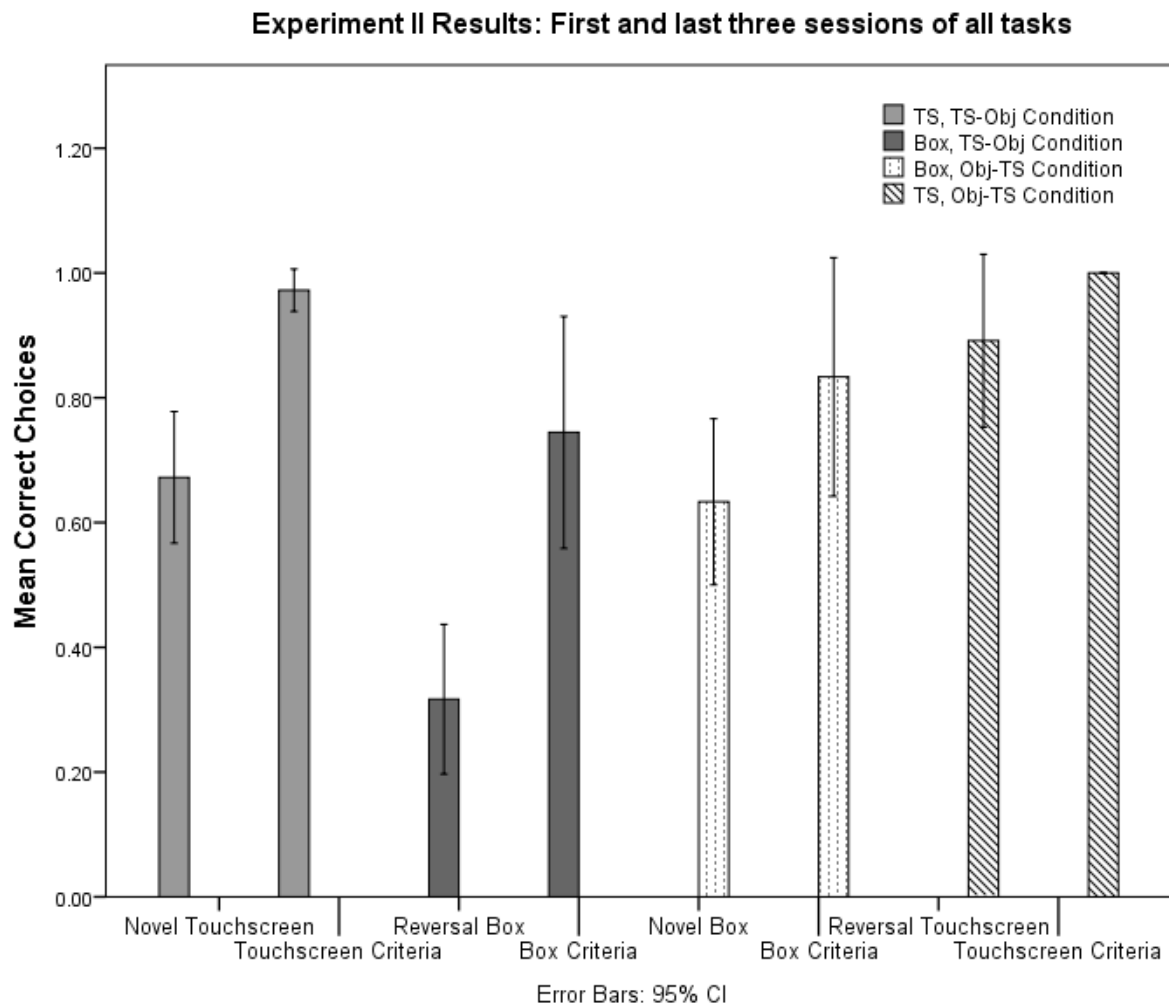
Figure 2.5. This graph shows the results of experiment 2 chronologically, from left to right. Condition "Novel Touchscreen" is the mean performance of the first three sessions of a discrimination task with novel stimuli, and "Touchscreen Criteria" is the mean last three sessions of that task. "Reversal Box" is the touchscreen-to-box transfer task, and "Box Criteria" again the last three sessions. "Novel Box" is an object display box discrimination with novel stimuli, and serves as the control condition for "Reversal Box." "Reversal touchscreen" is the box-to-touchscreen transfer condition, for which "Novel Touchscreen" serves as the control. "Reversal Box" is significantly lower than "Novel Box" ($p < 0.01$, n = 3).

Object-to-touchscreen task

The mean performance in the acquisition phase of the object-to-touchscreen transfer was not significantly different than control (test: 89%; n = 2; control 67%; n = 3) nor did subjects take more sessions to reach criteria. Surprisingly, subjects performed higher in the object-to-touchscreen test condition than in control, although only two birds participated in that test condition (Linus and Sunny) because the third subject, Elvira, failed to meet training criteria. Due to these results, the object-to-touchscreen task does not show evidence of reversal learning.

Discussion

Subjects showed evidence of picture-to-object recognition in the form of negative transfer from pictures on a touchscreen to objects in an operant conditioning box. The transfer was robust over the first three sessions of the transfer task, in contrast to experiment one where transfer was only evident in the first ten trials. Interestingly, there was no evidence of transfer in the object-to-touchscreen task, which is the opposite of what we found in experiment one. Furthermore, though different stimuli were used for test and control conditions, it is unlikely that this can account for the performance differences on the tasks, as all stimuli were very similar.

The fact that transfer was robust over the first three picture-to-object test sessions suggests that, in experiment one, variations in the picture and object tasks were indeed distractors for the kea, causing them to explore for a new solution after a few trials. By controlling for testing location, stimuli configuration, and rewarding method, the kea remained focused on the task, and transferred the behavior they had learned

on the touchscreen to the object display box. Furthermore, experiment two showed that a reversal learning procedure is an effective method of demonstrating transfer in kea.

It is not clear why the kea failed to transfer from objects to the touchscreen in the current experiment, especially considering that they had already achieved this in experiment one. As only two individuals participated in the box-to-touchscreen task, it is likely that the small sample size created results which would not be representative for a larger group. Testing more subjects would have greatly strengthened the results of this experiment, and may have shown transfer in the picture-to-object direction, or at least elucidated to some extent why this was not the case.

In the next chapter, we will discuss an experiment which was designed to tackle the challenges presented by experiments one and two. First, to minimize the distracting factors that affected kea's performance in experiment one, experiment three will control for variations in procedure such as testing location and rewarding method. Next, as in experiment two, it will use a reversal-learning task, which has now proven to be an effective method of testing for transfer. Last, the kea will not have to learn to use a new apparatus in experiment three, but will be tested in a methodology which is already familiar to them. Thus, more subjects will likely meet testing criteria than in experiment two, creating a larger sample-size and stronger results.

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Chapter 3: Discrimination Transfer between Framed Photographs and Objects

Introduction

So far, kea have demonstrated object-to-picture recognition in the form of direct discrimination transfer (experiment one), and picture-to-object recognition in the form of negative discrimination transfer (experiment two).

However, those experiments presented several challenges. First, in experiment one, it was not possible to show picture-to-object transfer due to a ceiling effect created by kea's proficiency at quickly solving object discrimination tasks. Furthermore, the object-to-picture transfer in that experiment was only apparent in the first ten trials of the test session, presumably due to variations in the procedures of the two discrimination tasks, which distracted the subjects and caused them to explore for a new solution. In experiment two, we attempted to control for variations in testing procedures between the two mediums by presenting the object stimuli in an operant conditioning box. Moreover, we used a reversal-learning procedure to test for negative transfer, which created a more difficult task for the subjects, controlling for the ceiling effect in experiment one. These modifications allowed us to show robust transfer from picture to object, but also greatly decreased the sample-size, as only few kea achieved mastery of the operant conditioning box. It was perhaps a consequence of this small sample size that we could not show transfer from object to picture in experiment two. What is called for next is an experiment which, first, controls for procedural variation between the picture and object mediums, and

second uses a methodology with which subjects are already familiar, thereby ensuring an appropriate sample size.

Experiment three tested whether kea could transfer between objects and framed photographs. Procedural variations between mediums were minimized by controlling for testing location, stimuli configuration, and manner of rewarding. Furthermore, as the photographs were presented in the same way as the objects, a method with which all subjects were already familiar, there was no need for them to use an unknown apparatus, thereby increasing the likelihood that more subjects would meet testing criteria. By taking these factors into account, we increased the probability of showing robust transfer, and gained a sample size which more accurately represented the abilities of the group as a whole. Additionally, the strength of the connection between pictures and objects was tested in a phase of the experiment not performed previously. Here, the subjects were presented with the original training pictures after completing the object reversal phase, in order to see if the connection between objects and pictures was strong enough to "override" a previously learned positive association.

The major difference between the previous experiments and the current one was the use of photographs to represent pictures, as opposed to the touchscreen. Although, to human eyes, both photographs and computer screens may seem equally suitable ways of displaying pictures, there are dissimilarities between these two which may greatly affect how birds perceive them (Weisman & Spetch, 2010). For example, computer screens constantly refresh at a rate which is imperceptible to humans, but to birds they may in fact appear to flicker, as both pigeons and chickens have been shown to have a higher flicker-fusion threshold than humans (Hendricks, 1966;

Hodos, 2012; Nuboer, Coemans, & Vos, 1992). Flickering could create difficulties in perceiving equivalence between pictures and objects, a challenge not presented by photographs. Alternatively, the kea group at Haidlhof has extensive experience using the touchscreen, making this a familiar medium, whereas the current experiment was the first to use photographic stimuli. This experiment therefore also tested whether the method of picture display, touchscreen or photograph, would have an effect on the kea's ability to transfer between the two.

Methods and procedure

Subjects

The subjects chosen for this experiment were ten kea (*Nestor notabilis*): six adult males (Anu, John, Kermit, Roku, Tammy), four adult females (Coco, Hope, Lilly, Willy), and one juvenile male (Paul). Three birds, John, Paul, and Roku, were parent-raised, whereas the rest were hand-raised. Of the ten subjects that began pre-training, one dropped out for health reasons (Tammy). Of the remainder, six met pre-training criteria and were included in the training and testing phases (Anu, Coco, Hope, John, Kermit, Willy).

Stimuli

There was one positive and one negative stimulus for each phase (pre-training, training and testing). One of the two stimuli was randomly assigned to each subject as positive. Being a reversal learning procedure, the positive stimulus in the training phase was switched to the negative stimulus for the testing phase.

Pre-training stimuli

Pre-training stimuli were simple, two-dimensional black shapes (a hollow triangle and a solid square) on a white background. These were held onto a wooden frame by Plexiglas and screws. The frames were made in such a way that they stood vertically by being partially buried in the aviary sand. Frames measured 15.0 x 11.5 x 1.5cm, (see Figure 3.1 for pictures of frames) and the images measured 4.5 x 4.5cm, not including the white background.

Photograph stimuli

Training stimuli were two photographs of wooden blocks (blocks are described under Object stimuli). These photographs measured 10.0 x 10.0cm, and were displayed in frames as described above. The photographs were taken with a high-definition digital camera on the aviary ground in natural light, and were printed life-sized. This was to reproduce the visual impression of the real objects as closely as possible (Figure 3.1).
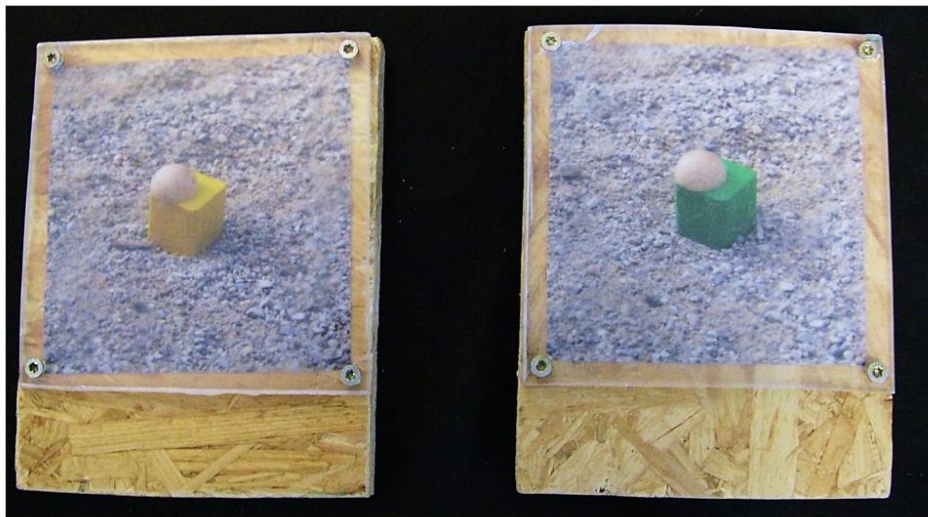
Figure 3.1. The stages of experiment three. Stage one (top); subjects were trained in a two-choice discrimination task with photographs. Stage two (middle); subjects were presented with and object discrimination task with the objects from the photographs, but the S+ was reversed. Stage three (bottom); subjects were presented again with the original photographs, but this time the stimuli from the object condition was rewarded.

Object Stimuli

Test stimuli were two commercially produced wooden blocks for young children (non-toxic). The two blocks were identical in all aspects except color; one block was yellow and the other green. The blocks measured 3.5 x 2.5 x 2.5 cm (Figure 3.2).

Figure 3.2. The object stimuli were wooden blocks made for children, and were identical in all aspects except color. Stimuli were presented on the aviary ground.

Procedure

This study tested whether kea could transfer a learned discrimination task from printed photographs to real objects using a reversal learning procedure.

Photo-to-object task

Subjects participated in a pre-training two choice discrimination task to habituate to working with framed photographs. The pre-training task was very similar to that described under *Object discrimination task* in *General methods*, with a few modifications. Photographs were presented standing vertically on the aviary ground, and a choice was made when the subject pushed over a frame. Correct choices were rewarded as usual, but when an incorrect choice was made by pushing over

the wrong frame, the subject was directed to return to the waiting compartment. The subject was then allowed a correction trial, where it could push over the remaining frame and was subsequently rewarded. Pre-training criteria was an average of ≥ 80% correct over two consecutive session.

After pre-training, subjects moved on to the training phase, where they were presented with the framed photographs as described under *Photograph stimuli*. The training phase had a stricter inclusion criteria of ≥85% accuracy over three consecutive sessions, with a minimum of five training sessions in total. All six subjects included in the training phase met training criteria.

Once subjects had reached criteria, they were given a real-object reversal learning test, meaning that the positive photograph stimuli from the photograph training now became the negative object stimuli, and vice-versa. The test procedure was again a two-choice object discrimination task as described in the *General methods* section. Subjects were tested until they reached criteria of ≥85% over three consecutive sessions, with a minimum of five sessions in total (identical to training criteria). All six subjects included in the testing phase met criteria, after which they were moved on to the final testing phase.

Object-to-photo transfer

The final testing phase was a single-session transfer from the real objects to the original photographs. This done to find out if the connection between objects and pictures was strong enough to override the original learned task with the photographs. In the object-to-photo transfer phase, subjects were given a single 20-trial session with the original training photographs. This was a direct object-to-photograph transfer test, so the rewarded photo was the same as the rewarded test

object. If the kea had complete picture-object equivalence, they should now choose

the positive stimuli from the test phase and should show a strong positive transfer.

On the other hand, if the kea perceived some important difference between the

objects and the photographs, then they would recognize and choose the positive

stimuli from the training phase, thereby showing a negative transfer (Figure 3.3).
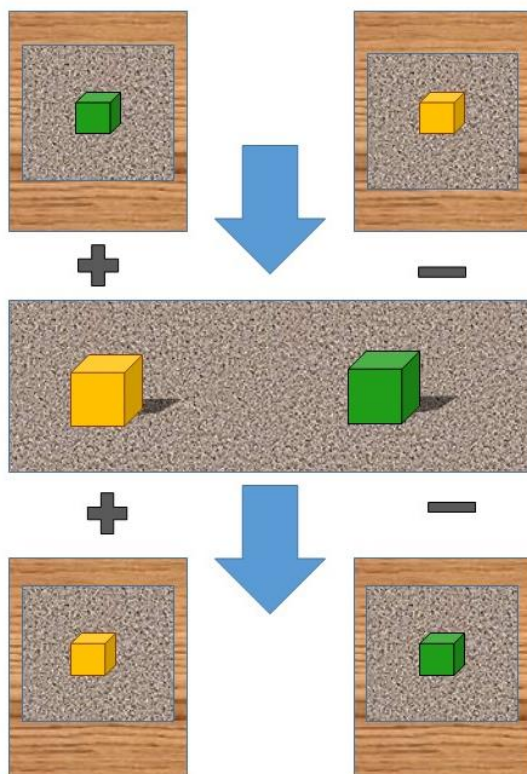
Figure 3.3. The stages of experiment three. Stage one (top); subjects were trained in a two-choice discrimination task with photographs. Stage two (middle); subjects were presented with and object discrimination task with the objects from the photographs, but the S+ was reversed. Stage three (bottom); subjects were presented again with the original photographs, but this time the stimuli from the object condition was rewarded.

Data collection and analysis

Results were recorded manually by the experimenter as described in the *General*

methods section.

Data analysis was done in IBM SPSS version 20. A Shapiro-Wilk's test was performed to test for normal distribution of the data. Independent samples Mann-Whitney U tests were carried out to test for significant differences between the first session of test (Picture-object Reversal, Object-to-picture transfer) and control conditions (Novel Photo, Object Control).

Results

The data was shown to be non-parametric according to the Shapiro-Wilk's test.

There was an sample size of six for all test and control conditions. The independent samples Mann-Whitney U test showed that Photo-Object Reversal was significantly lower than Object Control (p = 0.001, mean values 66% and 91%, respectively), suggesting transfer from the photo to the object task. (Figure 3.4)

Object-photo transfer was significantly lower than Novel Photo (p = 0.000[1], mean values 18% and 76%, respectively), suggesting a strong connection between the original photo task to the Object-photo back-transfer task. Two individuals, Willy and Kermit, chose the former, now unrewarded S+ for 100% of the object-photo transfer trials, and another, John, chose this for 90% of the trials.
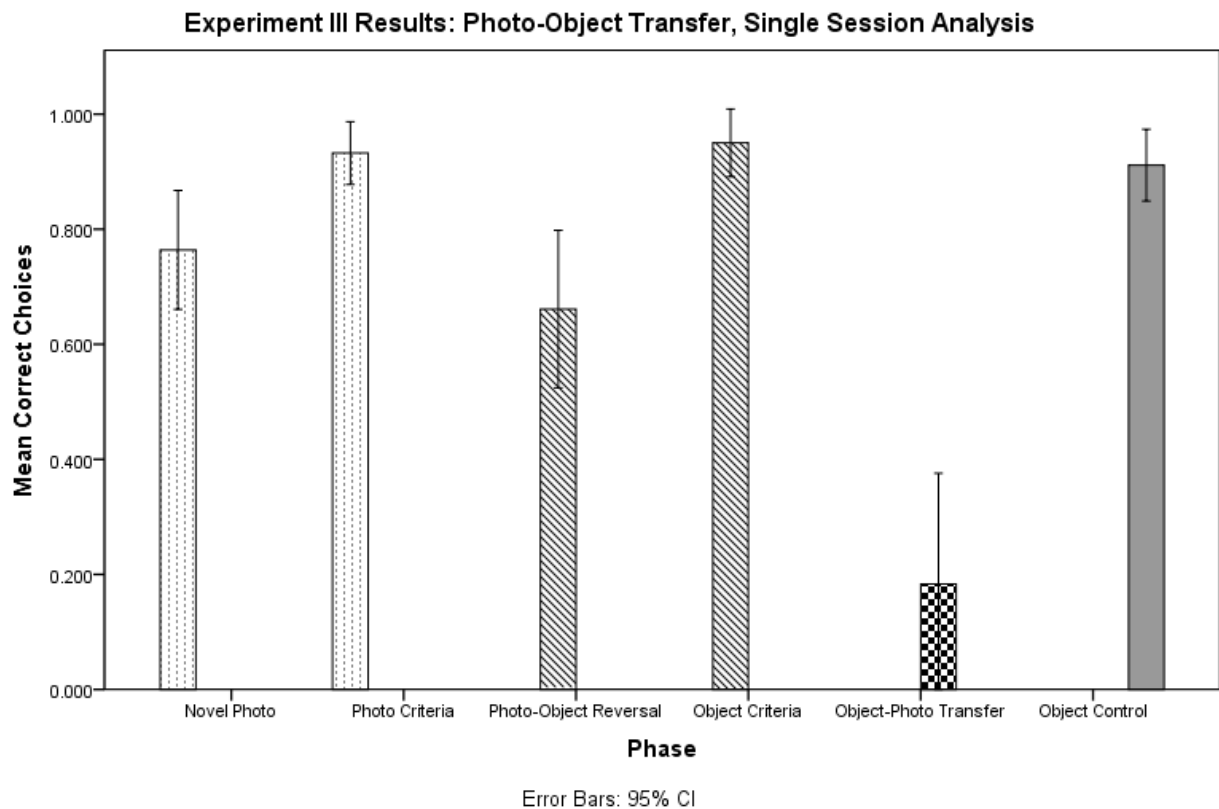
Figure 3.4. The results of experiment three presented chronologically. Starting from the left, "Novel Photo" represents the first session of the photo discrimination task, and "Photo Criteria" the last session of that task. "Photo-Object Reversal" represents the first session of the photo-to-object transfer task, with S+ reversed, and "Object Criteria" is the last session of the object task. "Object-Photo Transfer" is the session where subjects are presented with the original photograpsh after having completed the object-reversal task, and the S+ from the object condition is rewarded. "Object Control" is a novel object task, and is the control session for the photo-object reversal condition. Novel Photo serves as the control condition for Object-Photo Transfer. Photo-Object reversal is significantly lower than Object Control (p = 0.001), suggesting negative transfer from photo to object. Object-Photo Transfer is significantly lower than novel photo (p = 0.000[1]), suggesting negative transfer from the original photo task, not positive transfer from the object task (n = 6 for all conditions).

Discussion

Kea showed picture-to-object recognition in the form of negative transfer in the first

session of the Photo-object Reversal condition. This provides support for similar

results found in experiment two, but with a larger sample-size, and helps complete

the story which began in experiment one, where subjects showed only object-to-

picture recognition. Furthermore, the current experiment demonstrated that kea can recognize both pictures displayed on a touchscreen and framed photographs.

After subjects completed the photo-object reversal task, the strength of the connection between the photos and the objects was tested by confronting them with a discrimination task using the original training photos. This was to find out if they would try to solve this by direct transfer from the objects, or if they would recognize the photo discrimination as a known task and choose the S+ from the photo training phase. The latter proved to be the case, and the subjects strongly chose the S+ from the original photo task despite the fact that this was now unrewarded. Although the kea had shown that they recognized the objects from the photos, the reversal-learning object task did not interfere with their performance on a known task with photos of those objects.

A possible explanation for this lack of interference is that the kea, while showing recognition, did not confuse the objects with their pictures. In cases of picture-object confusion, we would expect the subject to react to a picture exactly as it would to the real object. For example, in a recent study red-footed tortoises showed that they could distinguish between pictures of food and non-food, but could not distinguish between pictures of food and the real thing (Wilkinson, Mueller-Paul, & Huber, 2013), suggesting the tortoises had confused the pictures with the real objects. In this study, kea could have shown picture-object confusion by relearning the task so completely in the transfer phase that, when presented with the pictures again, they would react to them as if they were the objects. This was not the case. The kea clearly differentiated between the picture and object mediums, but were still able to transfer from one to the other.

Experiment three concludes the empirical portion of this thesis. In the final

discussion section, we will explore the results of these three experiments in the

context of the relevant background literature. We will also discuss what our findings

mean for future research.

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General Discussion

There are three levels of picture-object recognition according to Bovet and Vauclair's extensive review of the topic (2000). The first level is an animal's ability to distinguish salient features of the picture. The second is the ability to establish a correspondence between pictures and objects, which can be shown for example by transferring acquired behaviors between the two mediums. The third level is picture-object equivalence, and can be shown by bi-directional transfer or cross-modality matching. However, picture-object equivalence may or may not involve confusion between the two, and it is important to establish whether this is the case if we are to have a proper understanding of an animal's capacities in this area. The three experiments described in this thesis tested for bidirectional transfer of a learned discrimination task between pictures and objects, thereby investigating whether kea are capable of the third level of recognition, picture-object equivalence.

Experiment one showed that kea can transfer from solid objects to pictures on a touchscreen, but the transfer was only measurable during the first few trials of the test session, after which the subjects apparently began to explore new solutions, a behavior previously observed in kea by Gajdon and colleagues (Gajdon, Amann, & Huber, 2011). Furthermore, experiment one failed to give evidence of picture-to-object transfer because the control groups performed so well on the object discrimination task that a ceiling effect was created, and it was not possible to tell if test subjects had transferred knowledge from the touchscreen to the object task. Kea performed significantly higher on the object task than the touchscreen task, which is in line with findings of O'Hara, Huber, and Gajdon, (2014). This indicated that a

direct picture-to-object transfer task was not challenging enough to test for discrimination transfer in kea. Due to this, and the fact that transfer from object to touchscreen was only robust in the first ten trials, a revised procedure was implemented for the next experiment.

Experiment two was designed to create a more challenging task which would clearly show transfer, and control for possible distracting factors which might cause the kea to explore for a new solution after only a few test trials. To make the transfer task more challenging, a reversal learning procedure was implemented and recognition was indicated by negative transfer from pictures to objects and vice versa (Cabe, 1976; Spetch & Friedman, 2006). To control for possible distracting factors such as testing location, stimuli configuration, and rewarding method, an operant conditioning box which mimicked the touchscreen as closely as possible was built to display the objects. These revisions to the procedure were effective, and we could successfully show picture-to-object transfer, which could be robustly measured over several testing sessions. However, the operant conditioning box proved difficult to master for many birds, and only three subjects met training criteria and could participate in the experiment. The difficulty the kea displayed in using the operant conditioning box suggests that they were using cues besides the provided stimuli to try and solve the task. The small sample size meant that results were weaker, and it was not possible to show object-to-picture recognition. Consequently, a third experiment was designed which took into account the challenges presented in experiment one, but used a procedure with which the kea were already familiar in order to obtain a larger sample size.

Experiment three investigated whether kea could recognize pictures in the form of framed photographs, a medium with which they were unfamiliar. We controlled for distracting factors by carrying out both photo and object discrimination tasks on the aviary ground, and rewards were given to the subjects by the experimenter in both conditions. As in experiment two, a reversal learning procedure was used, as this had proved an effective challenge, and recognition was indicated by negative transfer. Additionally, in experiment three we implemented an extra step, namely we presented the original photograph stimuli to the subjects after they had completed the photo-to-object transfer task. This was to find out whether the subjects would choose the "new" S+ from the object task, or stick to the "old" S+ from the photo task. The results showed that kea did indeed transfer from photograph to object, but that they overwhelmingly chose the original S+ from the photo task and not the S+ from the object task. A possible interpretation of this is that the kea did not confuse the objects with their pictures, despite being able to transfer between them.

Taken altogether, experiments one through three showed that kea can transfer from objects to pictures and vice versa, which means that they achieve the third level of picture-object recognition: equivalence. Furthermore, results from experiment three may imply that they do not confuse pictures with objects.

Methodological Implications and Future Work

Based on the results described in this thesis, it is now known that kea are capable of corresponding objects and pictures, both when presented on a touchscreen and as photographs. Furthermore, the fact that kea were successful in recognizing printed photographs despite being naïve to these implies that they are quite flexible in their

abilities to recognize different types of pictures. This lends support to the use of pictures in cognitive research with this species.

However, the fact that kea can transfer a learned discrimination task between pictures and objects does not provide evidence for internal representation, only correspondence. For example, we cannot say whether kea recognize pictures at the basic category level, i.e. that when they see a picture of an apple that they recognize it as such. Therefore, the work presented in this thesis does not necessarily support the use of pictures as representations of objects, although it provides a strong basis for future work which investigates such questions.

Logical follow-up studies to the current ones would include those which investigate in more detail the relationship between pictures and objects, and those which look for abilities to categorize pictures at the basic, subordinate and superordinate levels. For example, experiments which observe kea's spontaneous reactions to ecologically relevant pictures, such as food or conspecifics, would help clarify the question of whether the kea simply confuse pictures with objects, or whether they differentiate between the two while still seeing correspondence between them. Additionally, in a similar setup to Watanabe's 1997 experiment with pigeons, kea could be tested on their abilities to categorize pictures of food and real food into a single category, and then additionally be asked to discriminate between the pictures and the real objects. Such a design would provide strong evidence that kea see pictures as representations of objects, while showing an absence of picture-object confusion.

Kea are now the first parrot species to definitively show picture-object recognition, so the results described here can be useful in comparative studies with other parrot species. Finally, while there remains much to be learned about the details of picture-

object recognition in kea, and researchers must still proceed with caution when using

picture stimuli in their experiments, the work done for this thesis provides a

promising start for further research in this area, and shows that this can be a relevant

and fruitful path of investigation.

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Curriculum Vitae

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