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„Reversal learning in the Kea (Nestor notabilis): Comparing the touchscreen to a reality approach“

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"See the animal in his cage that you built,
are you sure what side you're on?..."

NIN, With Teeth 2005
Right where it belongs

For mum…

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Table of contents

Reversal learning in the Kea (*Nestor notabilis*): Comparing the touchscreen to a reality approach

Keywords: Kea (*Nestor notabilis*), discrimination learning, touchscreen, reversal learning, behavioural flexibility

1 Abstract

The ability to shift ones attention from a formally rewarded stimulus to another stimulus is considered an important cognitive adaptation to changes in the environment. One way to experimentally investigate this behavioural flexibility in animals is the method of reversal learning. The kea (*Nestor notabilis*), as a model species for behavioural flexibility, has never before been tested on this topic involving the use of a touchscreen. A recent preliminary study has already concluded that the kea are very willing to participate in touchscreen tasks. So far, however, no study has directly compared the touchscreen approach to a more natural test situation. Therefore, in this study, I investigated the kea's performance in an intra-dimensional reversal task on the touchscreen compared to a corresponding reversal task with real objects. The results draw a significant incongruence between the touchscreen and "reality" task, with far less trials required to reach criterion in the "reality" condition, using solid objects than in the "Touchscreen condition". Furthermore, the learning speed seemed to differ between the two methods used. Correlations between tasks further strengthen the hypothesis that different mechanisms of learning may be underlying the alternate approaches. Age and sex, however, only have limited influence on the reversal performance. These results and the comparison with other studies lead to the discussion about what the reversal learning paradigm is actually measuring and its implication for behavioural flexibility.

Zusammenfassung

Die Fähigkeit die Aufmerksamkeit von einem zuvor belohnten Stimulus auf einen neuen Stimulus zu lenken wird als wichtige kognitive Anpassung an eine sich ständig ändernde Umwelt erachtet. Eine Möglichkeit diese Verhaltensflexibilität experimentell bei Tieren zu untersuchen bietet das Reversal Learning. Der Kea (*Nestor notabilis*), welcher als Modellart für Verhaltensflexibilität gilt, wurde bezüglich dieser Fähigkeit nie zuvor an einem Touchscreen getestet. In einer Vorstudie hat sich herausgestellt, dass die Keas sehr bereitwillig mit dem Touchscreen arbeiten. Jedoch wurden Touchscreenversuche bis zu diesem Zeitpunkt noch nie direkt mit einem ähnlichen "realitätsnäheren" Versuchsaufbau verglichen. Aus diesem Grund habe ich in dieser Studie die Lernleistung der Keas in einer intradimensionalen Reversal Learning-Aufgabe auf dem Touchscreen mit der Leistung einer entsprechenden Aufgabe unter Verwendung von dreidimensionalen Objekten verglichen. Die Ergebnisse zeigen signifikante Unterschiede zwischen den am Touchscreen und in Realität durchgeführten Tests, wobei weitaus weniger Versuche in der realitätsnahen Versuchsanordnung benötigt wurden um ein zuvor festgelegtes Lernkriterium zu erreichen als am Touchscreen. Des Weiteren scheinen sich diese beiden Methoden auch in der Lerngeschwindigkeit zu unterscheiden. Korrelationen zwischen den verschiedenen Aufgaben geben weiters Anlass zur Annahme, dass unterschiedliche kognitive Mechanismen diesen Leistungsunterschieden zugrunde liegen. Alter und Geschlecht scheinen jedoch nur begrenzt Einfluss auf die Lernleistung zu haben.

Diese Ergebnisse und der Vergleich mit anderen Studien aus diesem Forschungsbereich regen zu einer Diskussion an, was das Reversal Learning-Paradigma wirklich misst und welche Schlussfolgerungen es in Bezug auf die Verhaltensflexibilität zulässt.

2 Introduction

Since the beginning of the 20th century scientists have investigated the mechanisms underlying learning and the formation of associations (Pavlov, 1927; Thorndike, 1898). In 1949, Harlow was the first to test monkeys on the Wisconsin General Test Apparatus (WGTA) to investigate the formation of learning sets. In this apparatus the monkeys responded by displacing one of two stimulus objects covering food. The results of Harlow´s experiments indicate that his test subjects began to shift from trial and error learning to what he labelled "insightful learning", meaning that the monkeys were able to transfer from one discrimination problem to the next and therefore improve their learning curves. Harlow explained this phenomenon by the formation of a learning set, which he thought to be an adaption to changing conditions in an animal's natural surroundings. To analyse learning sets on a more complex level he used the discrimination reversal problem. Here an individual basically learns to discriminate two stimuli, with one being rewarded (S+) and another not being rewarded (S-). As soon as an arbitrarily set learning criterion or fixed number of trials is reached, reward contingencies are swapped and the former unrewarded stimulus becomes rewarded and vice versa. With this method Harlow was able to show "insightful" learning in monkeys as well as in three to five year old children.

Since these early beginnings of research on learning and the formation of associations, noumerous studies have been published using reversal learning for the assesment of cognitive flexibility in many different animal species (e.g. rats: Floresco et al., 2008; Göttingen minipig: Moustgaard et al., 2004; corvids: Bond et al., 2007; capuchin monkeys: Beran et al., 2008; rhesus monkeys: Herndon et al., 1997; humans: Kloo et al., 2008; kea: Gajdon, Amann & Huber (in press)).

Most of these experiments mainly follow either of two possible approaches described below:

I. The neurobiological approach: With the use of brain lesion studies researchers aim to focus on the neural basics of behavioural flexibility. In most cases one or more groups of animals are treated with a chemical substance or certain parts of the cortex are directly impaired in order to cause lesions in specific areas of the animals´ brains. The performance of this group then is compared to a control group with untreated animals or a baseline performance (performance of the same group before the treatment) to assess the effect of treatment on the reversal task. The results of several such lesion studies gave insight to the question which parts of the brain are involved in reversal learning (for a review see Watanabe, 2006). In brain lesion experiments, Watanabe

(2006) investigated what kind of cognitive mechanisms and neuronal basis might underlie cognitive flexibility in birds by splitting the acquisition phase into a search and consolidation phase. The study indicates that lesions in the wulst and hippocampus lead to impairments in the consolidation phase, whereas lesions in the basal ganglion (LPO) reveal deficits in the consolidation, but even stronger so in the search phase.

II. The comparative approach: Following Harlow's idea of the formation of learning sets being an adaptation to the natural setting one lives in, it makes sense to compare more or less closely related species differing in their ecology or social complexity. Bond, Balda and Kamil (2007) used this kind of approach to point out the association between behavioural flexibility and social complexity. They used three species of North American corvids differing in the complexity of their social systems. The pinyon jays (*Gymnorhinus cyanocephalus*), a highly social species, showed significantly lower error rates than Clark's nutcrackers (*Nucifraga columbiana*), which are solitary but spatial experts, or the more generalist scrub jays (*Aphelocoma californica*). The authors concluded that animals in highly complex societies have to deal with frequently changing conditions and therefore have to be behaviourally more flexible than animals in less complex societies.

When confronting animals with cognitive tasks it is always essential to take into consideration their ecological background. Regarding the kea (*Nestor notabilis*), some aspects of the ecology of this species might well play a role in their ability to solve a reversal learning task.
The kea (*N. notabilis*) is a parrot endemic to the southern island of New Zealand. It lives in a mountainous to alpine environment that is subject to major changes during seasons. Therefore it has specialised in applying its skills to new circumstances and is a hallmark example of an "open program" species (Diamond & Bond, 1999). Only recently, Gajdon and colleagues (in press) were yet again able to demonstrate the keas´ behavioural flexibility by showing that the parrots rely on social information in a tool use task but abandon it in favour of overt exploration. To be able to behave in such a very flexible and explorative way, a corresponding cognitive setup is a necessity that can be experimentally investigated through reversal learning (Berg, 1948; Robbins, 2007). According to these facts one could expect the individuals to readily shift their attention to the former unrewarded stimulus in a reversal

learning task. However, in a pilot study of Amann et al. (2007) the kea seemed to switch quite fast from a learned stimulus back to chance level performance, but took a long time to learn the new stimulus. A possible explanation for this result can be found in the feeding ecology of the kea. As it feeds on many different plants and parts of plants growing in New Zealand, its feeding ecology may be best defined as extractive forager (Brejaart, 1988). But being an extractive forager, respectively undergoing quite some effort to reach certain roots, it makes sense to stick to a chosen stimulus (e.g. plant), even if not immediately rewarded. Concerning the consolidation phase and new acquisition of reversal learning, this might well affect the behaviour with individuals consistently checking former rewarded stimuli. Therefore, shifting their attention completely to a former unrewarded stimulus and thus having to reverse the discrimination might be a harder task for these animals than the original acquisition. The fact that this species is exposed to environmental changes, but persistent in terms of its feeding ecology, seems to have contradictory implications concerning this species' behavioural flexibility. Therefore it appears justified to further investigate reversal learning in this species.

Not solely the above mentioned ecological factors may influence the outcome of such an experiment. Sperling (1965) has reviewed several publications on reversal learning and resistance to extinction in rats. Sex, strain or age seemed to play a minor role, but among other factors (e.g., amount of food, intermittent reinforcement and single succesive vs. simultaeneous stimulus presentation) the apparatus used (Y-maze: Cole and Abraham, 1962; Siknnerbox: D'Amato et al., 1962; jumpstand: Mackintosh, 1963) can play a significant role in the relationship between amount of acquisition trials and resistance to extinction. For example, all Skinner box studies as well as three studies using runways (mazes) showed greater resistance to extinction the more acquisition trials they got. On the other hand, all experiments resulting in a negative relationship between acquisition trials and resistance to extinction (the more acquisition trials, the less trials were needed for the reversal) used runways.

In the last few years the use of touchscreens has been implemented more and more into cognitive sciences and therefore more or less replaced the use of pecking keys. The touchscreen proved an especially functional tool to investigate certain behaviours of the kea and even the underlying mechanisms (O'Hara and Gajdon, unpublished data), because it is mostly automated and therefore massively increases standardisation as well as data collection efficiency. However, it is still contentious how comparable experiments with real world

objects and experiments with object representations on screen actually are. Studies dealing with this question were so far mainly based on picture-object-equivalence, which has been studied thoroughly in pigeons (Watanabe, 1997; Watanabe, 2000; Specht & Friedmann, 2006, Aust et al. 2006) and nonhuman primates (Fagot et al., 2000).

To be able to tackle the question of the actual ecological relevance of a touchscreen reversal task, we aimed to compare the kea's performance on the screen with a task involving the use of solid objects, comparable to the touchscreen task. This study is the first in which kea were confronted with a reversal learning task on the touchscreen. In a preliminary study, we constructed a special computer terminal using a well-proven pigeon system (designed by M. Steurer) and created a rather simple discrimination task. All individuals very quickly interacted with the touchscreen and managed to perform significantly above chance in the discrimination task after only few sessions. In critical test-trials neophilia towards new stimuli seemed to have less influence (O'Hara and Gajdon, unpublished data) on the screen than in recent experiments conducted in a more natural approach (Kubat, 1992). These findings suggest that 3-dimensional objects, probably because of their additional haptic dimension as well as reward connectedness, might have an additional enhancing effect for showing such neophilic behaviour.

The main aim of this study is not to investigate the different underlying causes responsible (distribution of food, inter trial intervals, perception of stimuli, etc.) for divergent results in the two conditions (Touchscreen vs. the use of Solid Object), but rather to investigate if the touchscreen and a task with three-dimensional solid objects might involve different learning processes. We hypothesize that a reversal task conducted on the touchscreen might rather necessitate inhibitory control (Watanabe, 2006) and less behavioural flexibility (Watanabe, 2006), which might be a key issue when dealing with 3-dimensional objects. As mentioned above, from the ecological standpoint the kea has to be very flexible due to rapidly changing environment, but might lack the inhibitory control because of its feeding ecology (being an extractive forager). Following this hypothesis and these ecological facts, I propose that the kea should perform better in the Solid Object condition and the Touchscreen condition being the more "difficult" procedure.

One other indication the pilot study of O'Hara and Gajdon (unpublished data) revealed was that different strategies might have been used to discriminate between stimuli, depending on the age of the individuals as well as their sex. It seemed as if the adult kea is more vulnerable

to win-stay errors than juveniles are. The win-stay/loose-shift strategy is said to be a sophisticated method to overcome problems and even hypothesized to outperform tit for tat in a prisoner's dilemma (Nowak and Sigmund, 1993). Subadult individuals on the other hand, might have to learn to acquire this kind of strategy yet, so to speak learn to learn (Harlow, 1949). An effect of age on cognitive functions has been found in several species, including humans (Albert et al., 1988). In the course of individual development, cognitive abilities incline (Weed et al., 2008), but younger individuals may also lack inhibitory control and therefore be worse than adults in learning to reverse (Haddad et al., 1976). On the other hand investigating further aging, a cognitive decline may also occur (Bartus et al., 1978; Lai et al., 1995; Herndon et al., 1997; Voytko, 1999; Schoenbaum et al., 2002; Joly et al., 2006). In the pilot study, only very few individuals (N=8) have been tested, thus we could not claim a significant effect of age on the discriminative strategies used. In the current study we therefore also wanted to test if age as well as sex has an effect on the discriminative strategies of the kea, which could, to our knowledge for the first time, give insights to ontogenetical development of the kea´s learning abilities.

3 Material and Methods

3.1 Test subjects

The experiments were carried out with 20 captive individuals of *N. notabilis* (see Table 1) at the Konrad Lorenz Institute for Comparative Ethology (KLIVV) in Vienna. The animals were housed together in a large, environmentally enriched group aviary (15m x 10m x 4m), that could be divided into three equally sized compartments. The birds were weighed on a weekly basis and received a diet of fruit, vegetable, protein and seed every day, to compensate their corrected basic metabolic rate of 202.9 kcal/kg per day (Bryant, 2005). Drinking water and bathing opportunities were available ad lib. Eight birds had previously participated in discrimination experiments on the touchscreen, but had not received any reversal learning tasks on the touchscreen yet. The other individuals were completely naïve to the touchscreen prior to this experiment and therefore received pre-training (see 3.3.3.1 Touchscreen Training). All, but one individuals have participated in a reversal task involving solid objects conducted by Amann et al. (2007).

Table 1: Individuals participating in this experiment with their names and short names in brackets; prior touchscreen experience is coded "training" if they had only had habituation and "discrimination" if they had participated in the pilot-study; which image was used for the training is shown under habituation, the starting condition tells which stimulus (one or two) set is used and whether the individual started in the touchscreen or reality condition

Name	Hatched	Sex	TS experience	Habituation	Starting condition
Anu (An)	2007	♂	Training	House	Screen_1
Bruce (Br)	2002	♂	Discrimination	Triangle	Screen_2
Coco (Co)	2007	♀	Training	D	Screen_1
Frowin (Fr)	2004	♂	Training	Square	Screen_2
Hope (Ho)	2007	♀	Training	Hexa	Real_1
Kermit (Ke)	2004	♂	Discrimination	House	Screen_1
Knut (Kn)	2000	♂	Training	Triangle	Real_1
Lilly (Ly)	2007	♀	Training	Triangle	Real_1
Linus (Li)	2004	♂	Training	W	Real_2
Luke (Lu)	2003	♂	Discrimination	Circle	Screen_2
Mismo (Mi)	1999	♂	Training	Circle	Real_1
Pick (Pi)	2004	♂	Discrimination	D	Screen_1
Plum (Pl)	2007	♀	Discrimination	Slice	Screen_1
Roku (Ro)	2008	♂	Training	D	Real_2
Rosa (Rs)	2001	♀	Discrimination	Square	Real_1
Rudy (Ry)	2007	♀	Training	W	Real_2
Sunny (Sy)	2007	♀	Training	Slice	Screen_2
Tammy (Ta)	2007	♂	Training	W	Real_2
Willy (Wy)	2007	♀	Discrimination	Triangle	Screen_2
Zappel (Za)	2004	♂	no		Real_2

3.2 General procedure

The experiment was seperated into two conditions:

- The "Touchscreen condition", in which the animals had to touch visual stimuli presented on a computer screen in order to receive a reward.
- The "Solid Object condition", in which the kea had to turn over plastic cups to reach the reward hidden underneath.

In each condition the individuals had to complete two phases (the acquisition and the reversal phase), in each of which they had to achieve a learning criterion of 85% correct first choices in two consecutive sessions. In the acquisition phase the animals had to discriminate between the two stimuli shown and choose the rewarded stimulus (S+). In the following reversal phase the test subjects were required to choose the former unrewarded stimulus that now was rewarded.

Two different sets of stimuli were used and the stimulus set in the "Solid Object condition" being the alternative one used in the "Touchscreen condition", meaning that an individual was never offered the same stimuli in both conditions.

Which stimulus set was to be used (as well as what condition was conducted first) had been pseudo-randomly assigned to each individual, but counterbalanced between groups of age and sex. One session consisted of 20 trials and not more than two daily sessions were offered to an animal. A trial was repeated until the correct choice was made, but only counted as correct if the first choice was correct. Correction trials were defined as trials needed until the correct stimulus was chosen. A correct choice was rewarded with an eight of a peanut seed.

3.3 The Touchscreen condition

3.3.1 Apparatus

To interact with the touchscreen the individuals had to enter a cabin, located in the experimental compartment of the aviary, with a platform to stay on (70x40cm). During an experiment only one bird was allowed to be in the experimental compartment. I fixed a board above and two flaps to its sides to avoid reflections on the screen (Fig. 1). Attached to the touchscreen-CPU was an automatic feeder that distributed rewards immediately after pecking the correct stimulus. The delivery-opening was located 10 cm centrally below the screen. The software used for this experiment is called "CogLab light© v1.4" (developed and programmed by M. Steurer, Austria).

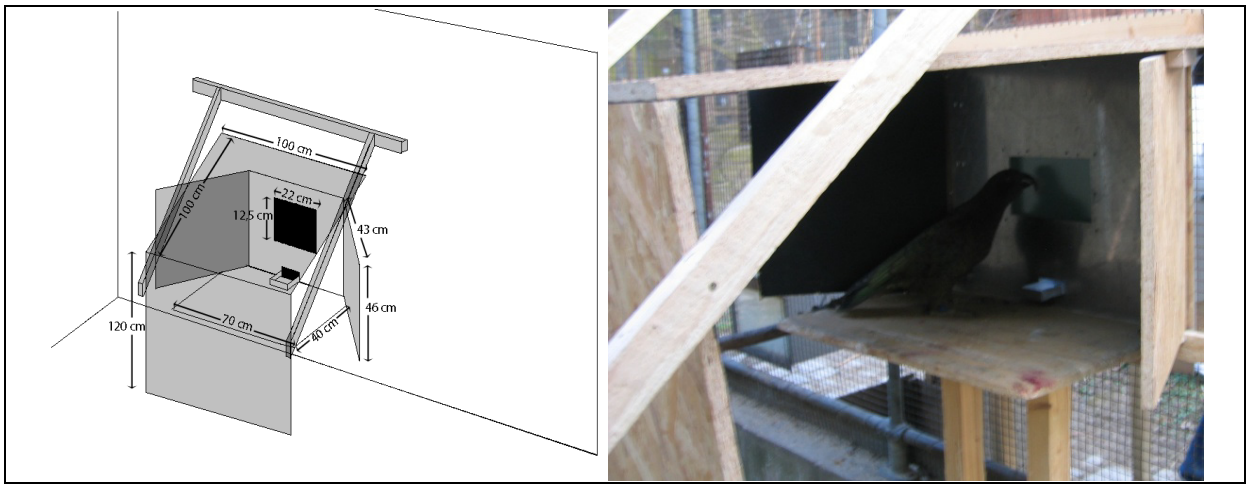

Figure 1: left: Apparatus and its dimensions: touchscreen with feeding tray below (black); right: photo of kea in action on the touchscreen; the inner sides of the screens painted black to reduce reflection of sunlight;

3.3.2 Stimuli

Two sets of stimuli were used with two images in each set. The images were photographs of the appropriate stimuli in the Solid Object condition, but slightly edited by Photoshop© Elements v.6.0 to remove the background (see Fig. 2).

Figure 2: The two sets of stimuli used in this experiment, chosen to be easily distinguishable with regard to colour and shape

3.3.3 Procedure

3.3.3.1 Touchscreen-Training

The training phase consisted of two sessions of 35 trials each. As reward a maximum of 12 peanuts was delivered to the animals (whole, half quarter or eighth pieces – randomly distributed). The Inter-Trial-Interval (ITI), in which the screen went black, was set to one second. As soon as a bird left the platform and did not return to the touchscreen within 10 min, the session was aborted and restarted from the point of the abortion on the following day. In the first phase of habituation the animals were presented with a stimulus that consisted of a simple geometric figure (like a circle, triangle, etc. as shown in Table 1), 140 x 140 pixels in size. These images were shown centrally on the screen in the first eight trials and also included additional stimulus/local enhancement through a moving mouse cursor. After this initial phase the image was presented at a randomized position and with the mouse cursor hidden for the rest of the session (27 trials). For the second habituation session these conditions remained unchanged, except that only a total of 4.25 peanut seeds were delivered during this session (an eighth peanut per trial).

3.3.3.2 Discrimination learning (Acquisition) and Reversal:

After completing the training each bird was confronted with a new set of stimuli (Fig. 2). After pecking on a centred trigger-stimulus (to retrieve exact response latencies) the actual stimuli were presented. These stimuli were located on the medium horizontal axis of the screen, one a third of the screen´s length from the left frame and the other one two thirds of the screen´s length from the left frame. The side on which each stimulus was shown was semi-randomly assigned (one left, one right). To prevent the individuals from developing side-preferences, correction trials (CT) were delivered after each incorrect choice until the correct stimulus was pecked. Correction Inter-Trial-Interval (CTIT) was set to two seconds. A peck on the positive stimulus (S+) was rewarded by delivery of an eighth piece of peanut. Additionally, every choice was also paired with an acoustic feedback. For this purpose, we recorded the sound of knocking on the real stimuli, which sounded slightly different for each stimulus due to different shapes. After meeting the learning criterion of 85% correct first choices in two consecutive sessions the rewarded response stimulus was reversed so that the former rewarded stimulus became the unrewarded. The acoustic feedback though kept bound to the specific stimuli and did therefore not necessarily correlate with a reward.

3.3.4 Data collection

The CogLab program automatically logged date and time when the experiments were conducted, as well as the number of correct first choices per session and number of correction trials (=number of errors per trial). Additionally, the location of the stimuli was recorded and the frequency of touching the screen without hitting an image (pecks on screen). I subtracted the latency of touching the trigger-stimulus from the exact timing of a response to a stimulus to calculate the decision time.

3.4 The Solid Object condition

3.4.1 Apparatus

Two coloured plastic icons were placed in the sand on the floor of the aviary, centrally within a circle trenched in the sand (100 cm in diameter). They lay 40 cm apart from each other on an imaginative line in a right angle to the bird´s normal approach way in order to be able to clearly identify which stimulus was chosen.

Figure 3: Picture of the setup in the Solid Object condition

3.4.2 Procedure

3.4.2.1 Training:

Because of the explorative nature of these parrots, they readily investigated the cups, so that nearly no training was needed in this condition. If there was no response in the very first trial, a piece of peanut was placed in the centre of the circle, right between the stimuli. This was (except in one case) enough enhancement to get the animals interested in the stimuli.

3.4.2.2 Discrimination learning (Acquisition) and Reversal:

The reward (an eighth peanut) was placed beneath the S+, so to retrieve it the individuals had to turn over the correct stimulus. Lifting the non rewarded stimulus was considered an error, but the trial continued in analogue to the correction trials of the Touchscreen task until the correct stimulus was turned and the reward retrieved.

After each trial the animal was instructed to leave the experimental compartment and the stimuli were rebated and rearranged for the next trial behind an opaque barrier by the experimenter. To avoid any biases both stimuli were touched and slightly moved. Again the position (right or left) of the stimuli were pseudo randomized, but to avoid the development of a side preference, presentation on the same side did not exceed three consecutive times.

3.4.3 Data collection

Each trial was videotaped and reanalyzed in case of uncertainty of mistakes or latencies. The date as well as the side of the positive stimulus and the number of errors per session was noted. I timed the entering into the experimental compartment using a commercial stopwatch, and also the entering of the circle, the first choice and – if occurred – further choices, as well as total trial time. As decision time I defined the time from entering the circle to the first lift of a cup.

3.5 Statistical analysis

Trials to criterion were defined as the number of trials until the last error occurred before an individual had reached the learning criterion. In each condition (Touchscreen / Solid Objects) and phase (acquisition / reversal) trials to criterion were tested for normality with a Kolmogorv-Smirnov test. To test for differences of stimuli sets as well as sequence groups (first Touchscreen, then Solid Object condition as sequence group 1 or vice versa as sequence group 2) a multiple factor analysis of variance was conducted in each phase and condition. Because which condition an individual was offered first (that is which group it was in) differed for trials to criterion in the reality acquisition phase, the two groups had to be analysed separately for influences of sex, age and which condition was used. Therefore, a Repeated Measures ANOVA was conducted for each sequence group, with the phases (acquisition vs. reversal) and condition (Touchscreen vs. Solid Objects) as within subject factors and sex and age as between subject factors.

To check for relations between trials required to reach criterion and errors in the different phases and conditions a Spearman rank order correlation was conducted. Since I found

correlations between trials to criterion and errors, I used only trials to criterion for further statistical analysis.

To analyse the course of the learning curves during the first two sessions and reveal differences between conditions and phases, the mean number of errors was calculated for the first five trials and the last five trials in each session. Furthermore, the improvement during a session was calculated by subtracting mean errors of first five trials from mean errors in the last five trials. To calculate the improvement between two sessions the mean errors of last five trials of the previous session were subtracted by the mean errors in the first five trials of the following session. Only the first two sessions could be analysed in this manner, because some individuals did not need more than two sessions to reach criterion. Therefore, data from all individuals were available only for session one and two of all conditions and phases. These data then were tested for normality via Kolmogorov-Smirnov test and, since they could not be fitted to normal distribution, phases and conditions were compared by a Wilcoxon signed rank test for beginning of session 1, improvement within session 1, improvement between session 1 and 2, beginning of session 2 and improvement within session 2.

All statistics were performed with the statistics package SPSS (version 10).

4 Results

Due to health problems of two individuals (Mi and Za) and because of four failed attempts to habituate one individual (Ro) to the Solid Object condition, these three animals had to be excluded from the experiments.

4.1 Number of trials to criterion

As trials to criterion and total errors are strongly correlated in each of the tasks (see Table 2 for exact correlations coefficients) and because the analysis of total errors showed very similar results as trials to criterion, only the latter analyses are presented here.

I first checked for differences between groups (first touchscreen, then reality as group 1 or vice versa as group 2) and stimulus sets in each of the four tasks (phases by conditions). Only the two-way ANOVA of the Solid-Object-Acquisition-task revealed an unexpected significant difference of acquisition (trials required until reaching criterion) with a main effect of the group (group: $F_{1, 15}= 10.682$; $p< 0.01$; stimulus-set: $F_{1, 15}= 3.311$; $p= 0.092$). There was no interaction effect of these two factors (group*stimulus-set: $F_{3, 13}= 0.063$; $p= 0.805$). As shown in Figure 4, the individuals that had previously participated in the Touchscreen condition required only half or less trials to reach the criterion than individuals which were in the Solid Object condition first.

Because of this difference further analyses were performed separately for individuals that first started with the Touchscreen and individuals starting with Solid Objects.

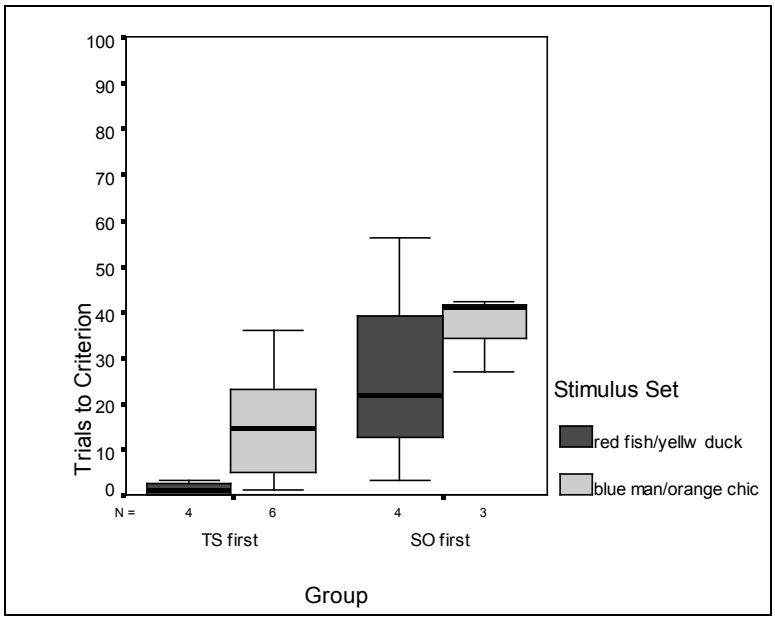

Figure 4: Mean number of trials required to reach criterion for sequence groups and stimulus sets used for the reality acquisition

Table 2: Correlations between total number of incorrect first choices and number of trials required to reach criterion in the same tasks (top four correlations) and correlations of trials required to reach criterion between different tasks (bottom four lines)

			Trials Touchscreen Acquisition	Trials Touchscreen Reversal	Trials Reality Acquisition	Trials Reality Reversal
Spearman's rho	Errors Touchscreen Acquisition	Correlation Coefficient Sig. (2-tailed) N	0.566 **0.018 *** 17	-	-	-
	Errors Touchscreen Reversal	Correlation Coefficient Sig. (2-tailed) N	- - -	0.726 **0.001 *** 17	-	-
	Errors Reality Acquisition	Correlation Coefficient Sig. (2-tailed) N	- - -	- - -	0.670 **0.003 *** 17	-
	Errors Reality Reversal	Correlation Coefficient Sig. (2-tailed) N	- - -	- - -	- - -	0.837 **0.000 *** 17
	Trials Touchscreen Acquisition	Correlation Coefficient Sig. (2-tailed) N	- - -	0.501 **0.041 *** 17	0.445 **0.074 t** 17	0.048 0.855 n.s. 17
	Trials Touchscreen Reversal	Correlation Coefficient Sig. (2-tailed) N	- - -	- - -	0.177 0.498 n.s. 17	0.031 0.907 n.s. 17
	Trials Reality Acquisition	Correlation Coefficient Sig. (2-tailed) N	- - -	- - -	- - -	0.345 0.175 n.s. 17
	Trials Reality Reversal	Correlation Coefficient Sig. (2-tailed) N	- - -	- - -	- - -	- - -

*: significant; t: tendency; n.s.: not significant

4.1.1 Trials to criterion for subjects starting on the Touchscreen first

I performed a Repeated Measure ANOVA containing within subject factors condition and phase and between subject factors age and sex. This analysis revealed a significant effect of phase ($F_{1, 8}$= 47.781; p< 0.01) and condition ($F_{1, 8}$= 27.141; p< 0.01) as well as an interaction effect of phase with condition ($F_{3, 6}$= 8.284; p= 0.024). The between subject factors on their own showed no significance (age: $F_{1, 8}$= 0.636; p= 0.451; sex: $F_{1, 8}$= 0.323; p= 0.588) but an interaction with condition and age ($F_{3, 6}$= 5.732; p= 0.048) as well as condition, phase and sex was to be found ($F_{5, 4}$= 6.221: p= 0.041). As shown in Figure 5, over all more trials are required in the Touchscreen condition than in the Solid Object condition. The reversal of the Solid Object discrimination required about as many trials as the Touchscreen acquisition and the increase of trials from acquisition to reversal was bigger on the Touchscreen than in the Solid Object condition.

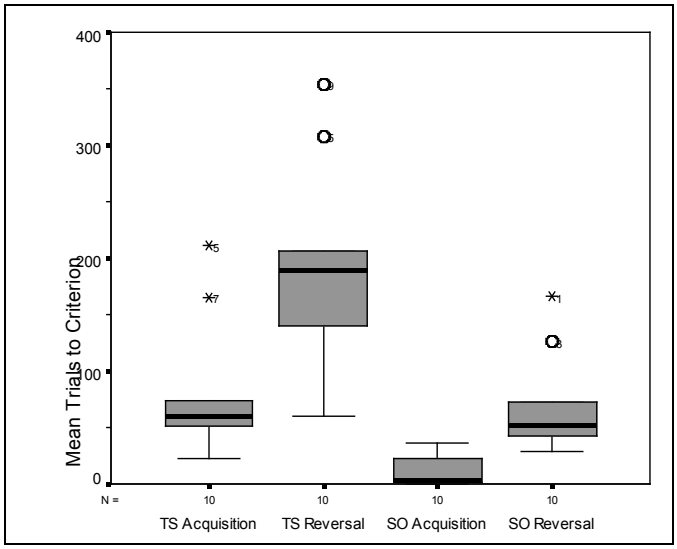

Figure 5: Mean number of trials to criterion comparing the phases and conditions of the individuals first presented with the Touchscreen

The interaction plot of condition and age (Fig. 6) shows only a small decrease in trials required to reach criterion for subadult individuals in the two conditions. In contrast adults decrease significantly by more trials from the Touchscreen to Solid Object condition.

The interaction of condition, phase and sex is depicted in Figure 7. In the Acquisition (Fig. 7, a) it takes males and females the same amount of trials for the acquisition in the Solid Object task. But while males require six times as many trials in order to discriminate stimuli on the touch screen, females require more than ten times as many trials to do so. For the reversal (Fig. 7, b) males reach criterion after about half the trials required by females in the Touchscreen condition. With solid objects, on the other hand, females accelerated to very few trials required, whereas males take almost as many trials as in the Touchscreen condition.

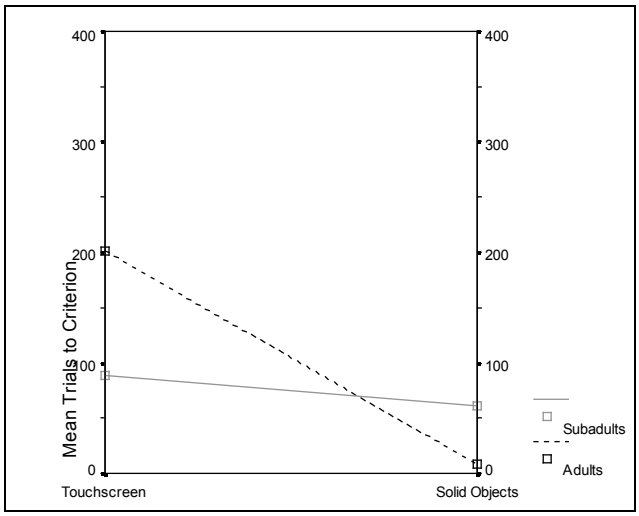

Figure 6: Interaction plot of within subject factor Condition with between subject factor Age for individuals starting on the Touchscreeen

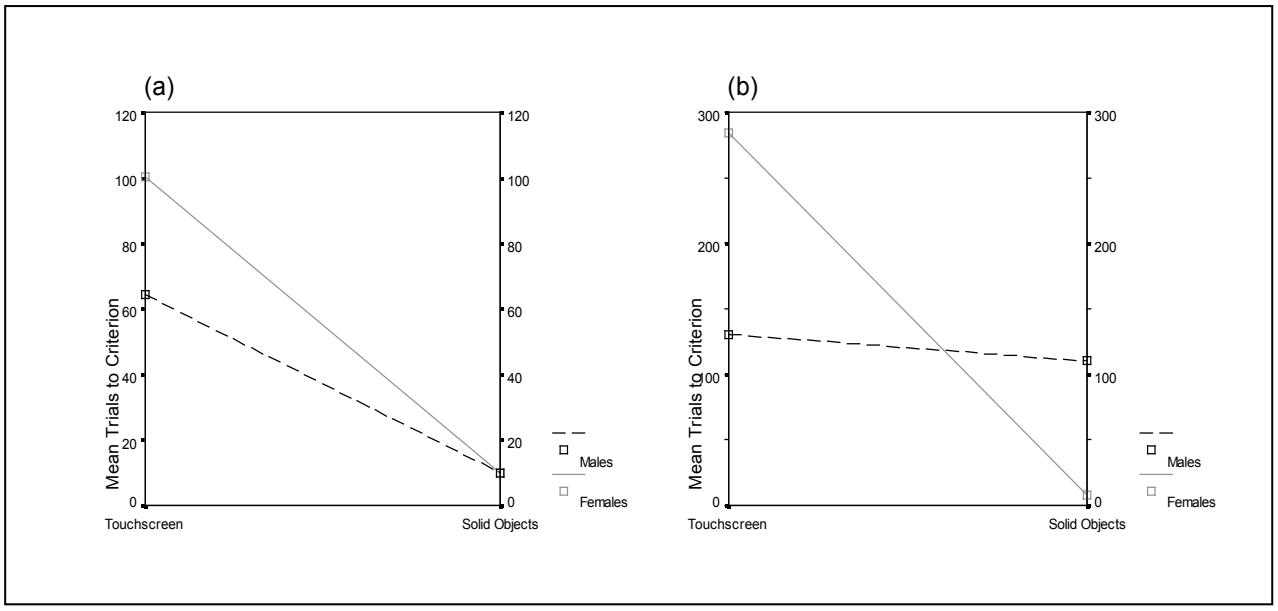

Figure 7: Interaction of within subject factor condition and phase and with between subject factor sex for individuals starting on the Touchscreeen; (a) showing interaction of sex and condition for the acquisition phase; (b) interaction of sex and condition in the reversal phases

4.1.2 Trials to criterion for subjects starting with Solid Objects first

The second RMANOVA investigated the same within and between subject factors as in chapter 4.1. for individuals starting with solid objects. Also for this sequence group significant main effects were to be found between phases ($F_{1, 5}$= 34.308; p< 0.01) and conditions ($F_{1, 5}$= 34.109; p< 0.01). Also an interaction effect of these two factors were found (phase*condition: $F_{3, 3}$= 27.984; p< 0.01). Between subject factors age and sex themselves had no effect, nor were there any interaction effects involving these factors. As illustrated in Figure 8, the trials required to reach criterion in either phase of the Touchscreen condition exceeded trials needed for the corresponding phase in the Solid Objects condition. A rather equal amount of trials were required for the acquisition in the Touchscreen as for the reversal in the Solid Objects condition. As in the other sequence group, the gain of trails from acquisition to reversal in the Touchscreen condition exceeded the corresponding raise of trials in the Solid Objects condition, which reflects the interaction effect of phase and condition.

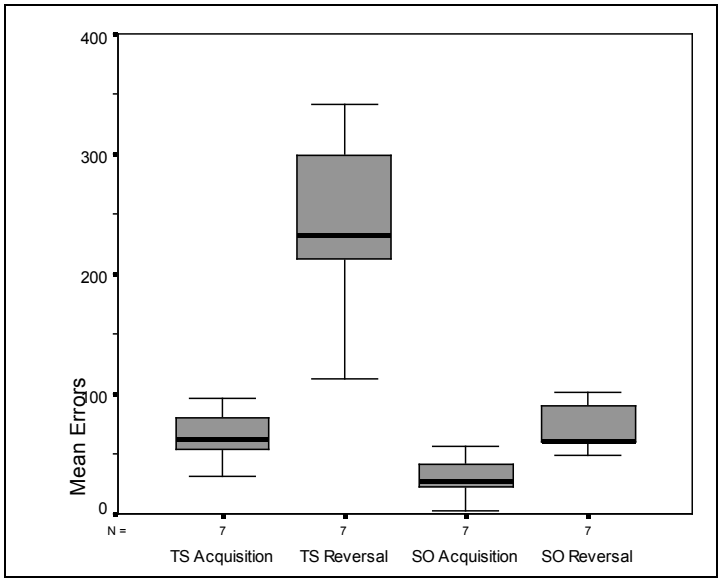

Figure 8: Mean trials to criterion comparing the phases and conditions of the individuals first presented with Solid Objects

4.2 Comparing progress of trial to trial performance between conditions

Figure 9 shows the number of individuals making a mistake in each trial of the acquisition phase and compares the Touchscreen and the Solid Object condition as Figure 11 does for the reversal phases in both conditions. Figure 10 shows the individuals' means of errors they did in the first five (beginning) and last five (end) trials for the first and second session in the acquisition phase of each condition, as Figure 12 does for the reversal phase.

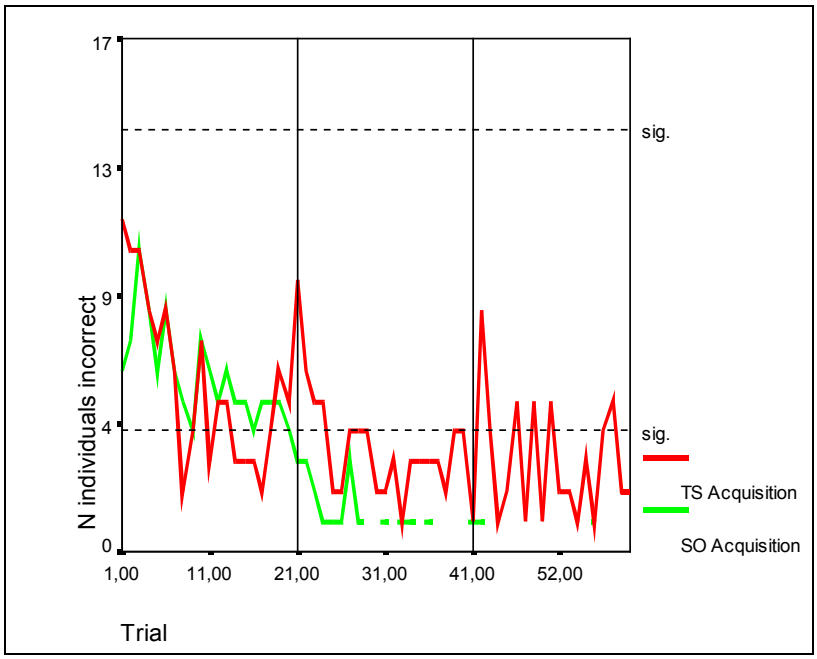

Figure 9: Number of individuals making incorrect choices in the acquisition of different conditions within each trial; dotted lines note significant binomial deviation of chance; vertical lines indicate the beginning of a new session

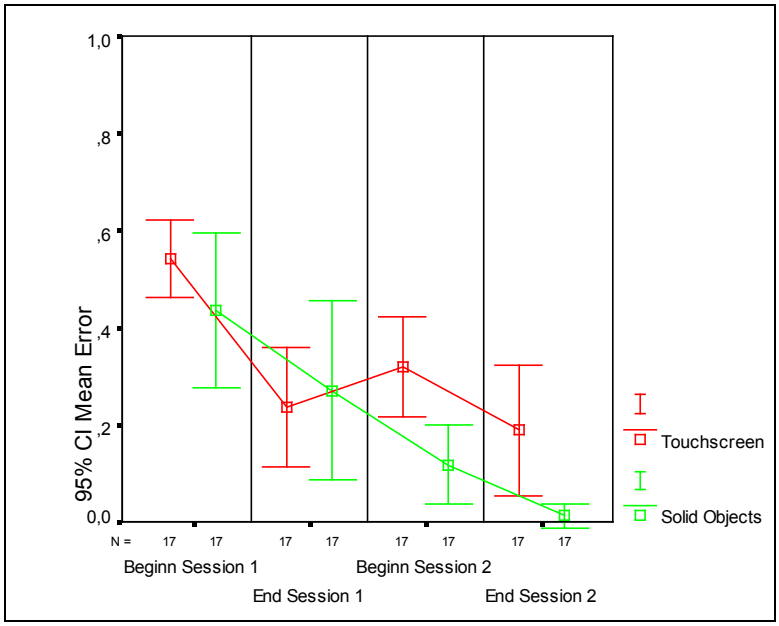

Figure 10: Comparison of mean errors in first five trials (Beginning) and last five trials (End), with 95% confidence intervals indicated by whiskers, of Session one and two for the acquisition in the different conditions; the slope of the lines giving an impression of different improvement within and between sessions

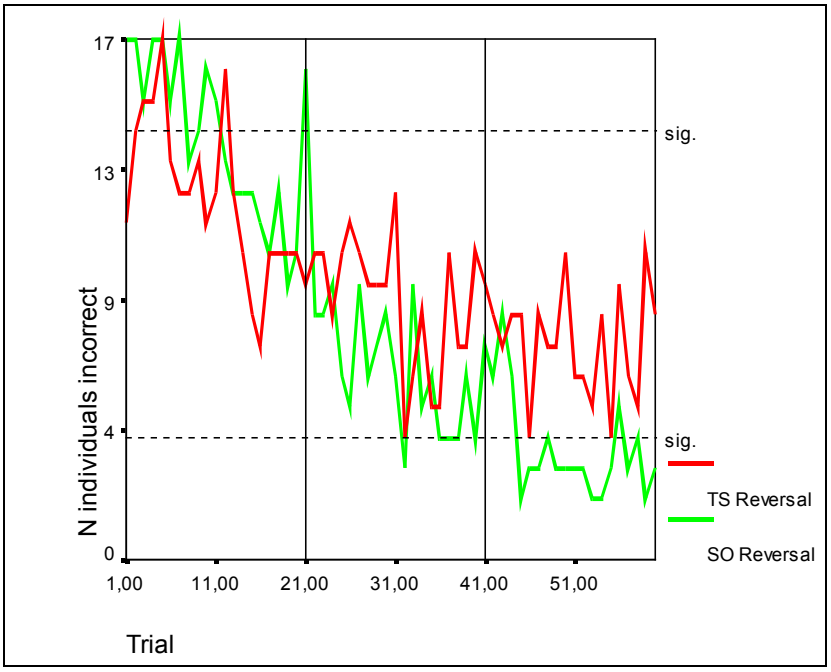

Figure 11: Number of individuals making incorrect choices in the reversal phases of different conditions within each trial; dotted lines note significant binomial deviation of chance; vertical lines indicate the beginning of a new session

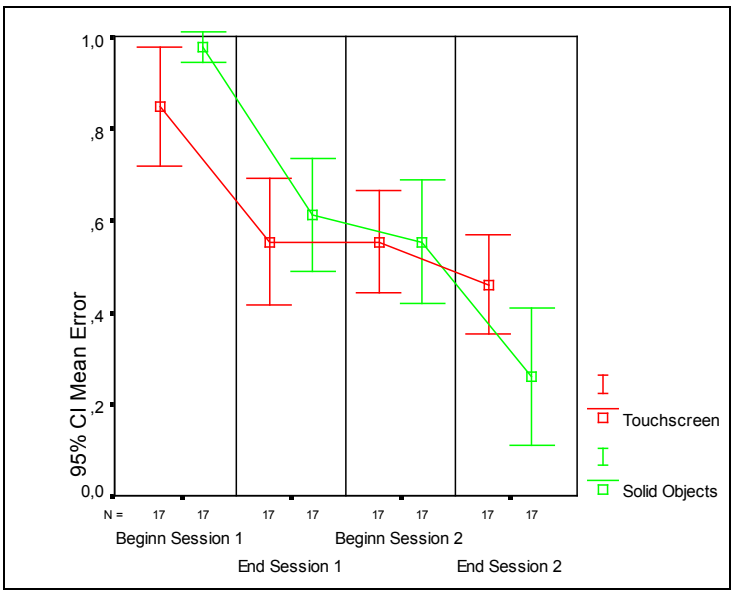

Figure 12: Comparison of mean errors of first five trials (Beginning) and last five trials (End), with 95% confidence intervals indicated by whiskers, of Session one and two for the reversals in the different conditions; the slope of the lines giving an impression of different improvement within and between sessions

4.2.1 Acquisition in both conditions

In the first session of the acquisition the two conditions seemed to generate similar results. Individuals started in both conditions at about chance levels and proceeded to significant levels according to binomial test at least in some trials in the second half of the session. This was underlined by a Wilcoxon signed rank test comparing the individuals mean errors of the first five trials, not differing between the conditions (see Fig. 10; Z= -1.427; p= 0.154, N= 17). There was no significant improvement from the first to the last five trials within session one. However, there seemed to be a strong trend for a difference between conditions in their improvement from the last five trials of session one to the first five trials of session two (see Fig. 10; Z= -1.893; p= 0.058, N= 17). Subjects decreased in their performance on the touchscreen, while performance with solid objects remained rather the same. This yielded a significant difference between conditions of the subject in the first five trials of session two. Here subjects performed significantly worse in the Touchscreen condition than in the Solid Object condition (see Fig. 10; Z= -2.846; p< 0.01, N= 17). As shown in Figure 9, almost no individual committed an error in the Solid Object condition anymore, whereas this still happened frequently in the Touchscreen condition. Therefore, further improvement was almost impossible for Solid Object, but it also did not occur in the Touchscreen condition, resulting in a significant variation of error rates between conditions at the end of session two (see Fig. 10; Z= -2.724; p< 0.01, N= 17).

4.2.2 Reversal in both conditions

As obvious from Figure 11, performance in the Touchscreen and Solid Objects condition seemed to differ already in the beginning of session one. Whereas the individuals seemed to stick to the wrong stimulus when confronted with solid objects, surprisingly not all of them made a mistake on the touchscreen in the first trial. The Wilcoxon signed rank test confirms a trend towards less errors made in the Touchscreen condition in the beginning of the session (see Fig. 12; Z= -1.845; p= 0.065, N= 17). During the first session, errors reached the maximum on the Touchscreen in the following trials, just to decline as about the same rate as in the Solid Objects condition. Therefore improvement within session one over all failed to produce significant differences. Neither was a difference to be found between conditions when comparing change from the last five trials of session one to the first five of session two. The beginning of session two also did not show differences between conditions. Even though numbers of errors went high above chance levels in its first trial of the Solid Object condition, they droped back to an expected range in the following trial. Therefore, when comparing improvement from the first to last five trials in session two, finally a tendency for difference began to emerge again (see Fig. 12; Z= -1.701; p= 0.089, N=17), resulting in a strong trend to differ in conditions for the last five trials of this session (see Fig. 12; Z= -1.936; p= 0.053, N= 17). From Figure 11 it seems obvious that this difference prevailed throughout session three except for the beginning, when individuals making errors with Solid Objects reached the levels of the Touchscreen condition. In the following trials of session three, the number of individuals making errors in the Solid Object condition mostly stayed below binomial significance, while about half of the individuals chose the incorrect stimulus on the Touchscreen.

4.2.3 Trial 21

One of the most striking differences to be found between conditions reveals itself in trial 21, the first trial of session 2. Comparing Figures 9 and 11, it is obvious that in the first trial of the second session eight individuals out of seventeen chose the incorrect stimulus in both phases of the Touchscreen condition as is expectable from a random distribution. In the acquisition with solid objects only three individuals went for the incorrect stimulus which significantly differs from chance according to a binomial distribution (p= 0.013, N=17). Therefore the assumption for the reversal with solid objects would have been that individuals choose better than random or at least at chance level as in the Touchscreen condition. However, only one individual chose the correct stimulus. This significantly differed from chance performance

(p< 0.01, N= 17). The birds performed significantly worse in trial 21 even when testing with the expected frequency they showed in the previous trial that was the last one of session one (frequency: 0.59; p< 0.01, N= 17).

4.3 Correlation of trials to criterion in the different tasks

As apparent from Table 2, trials to criterion correlate between the acquisition and reversal phase of the Touchscreen condition. Also the trials required for the acquisition with solid objects correlate with the acquisition in the Touchscreen condition. There is no correlation between acquisition and reversal in the Solid Object condition, or between reversal learning in the two conditions (Fig. 13).

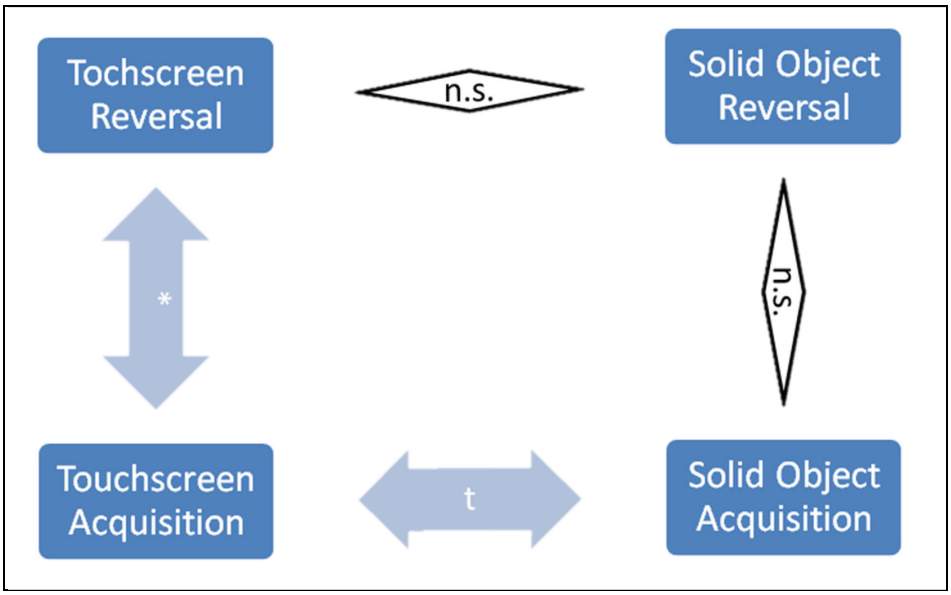

Figure 13: Diagram of relation between correlating phases and conditions; * indicating significant correlation, t indicating a trend to correlation, n.s. showing no significant correlations

5 Discussion

Testing the ability of reversal learning in kea both on the touchscreen and with real-world objects revealed several similarities and differences between the two conditions:
Firstly, in both conditions reversal learning took longer than the acquisition process. Secondly, acquisition curves matched in both tasks during the first session. However, the birds required more trials to reach the learning criterion in the Touchscreen condition than in the Solid Object condition. Interaction effects of other factors than phase (age and sex) with condition were found only in sequence group 1. The sequence of conditions in which the groups were tested only influenced the acquisition phase in the Solid Object condition. Trial to trial progress differed between conditions from the second session onwards. Contrary to acquisition of both conditions and both phases in the Touchscreen condition, there was neither a correlation between the reversal and acquisition with solid objects, nor between the reversal tasks of the two conditions.

In the following I will discuss possible reasons for these differences in order to evaluate the mechanisms that are involved in the two conditions. I will also address the question how kea perform in comparison to other bird species in the reversal learning paradigm. Finally, I will sum up what the present study can contribute to the question what reversal learning is measuring in the two conditions, where it can provide insights for the study of animal cognition in general and what the future research questions might be.

5.1 Comparing acquisition and reversal learning in the two conditions

5.1.1 Differences between conditions

Even though birds´ olfactory senses seem to be underestimated and it is known that the kea also may rely on smell (Steiger et al., 2008), olfaction did not seem to play a role in this task when considering the performance in the first trials of the reality reversal (see Chapter 4.2.2).
So if olfaction did not account for the difference between conditions, what else may have caused these differences?

1. Spatial dissociation of the reward

   The reward was always placed underneath the Solid Objects and therefore in close proximity of the stimulus. In the Touchscreen condition the reward was always delivered at the same distance from each stimulus. Spatial dissociation is known to

lead to a reduction in learning speed (Brown, 1994; Toelch et al., 2007). Furthermore, additional sensory modalities (e.g. haptic dimension) may differentially influence the formation of associations in the two conditions (Uwano et al., 1995).

2. Experience

   The kea are known for and have been tested extensively on their sophisticated physical intelligence (for a review, see Huber & Gajdon, 2006). Therefore they are quite proficient with solid objects. This may especially be the case for adult individuals (see 5.1.2). The fact that sequence group effects (which condition was tested first) were found, i.e., individuals being generally faster in the reality condition after completing the task on the touchscreen than if it was the first task (Fig. 4) might indicate that some kind of task transfer has taken place. This transfer might have occurred only in this direction because the Solid Object condition seems to be easier and therefore a transfer may be less masked by the difficulty of the task itself. Seasonality (e.g. influence of weather conditions, temperature, etc.) could also account for the sequence effect in the Solid Object acquisition, but seems very unlikely because no such effect was found in the Touchscreen condition.

Despite the plausibility of these arguments, differences generated by experience or through spatial dissociation of the reward would at the most be of quantitative nature.

5.1.2 Interaction effects with condition

The interaction of phase and condition shows that overall more trials are required in the Touchscreen condition. But since far more trials were necessary for the acquisition in the Touchscreen condition, it suggests that this condition posed the more challenging problem. Put into perspective though, the relative increase of error-rates for each condition seems quite similar (see 5.2).

Interactions between age and condition in the "Touchscreen first" group (Fig. 6) suggest that adults improved their performance significantly more than subadults from Touchscreen to Solid Objects. This kind of age effect was not to be found for the group tested with Solid Object first. The fact that subadults required less trials than adults on the touchscreen (at least for sequence group one) supports the assumption of an impact of pre-experience (see 5.1.1). However, it contradicts the hypothesis that subadults lack inhibition any more than adults. Of course subadult individuals have less experience with objects than adults. Though when set in

a novel situation (novel to both age groups), subadults perform just as good as or even better than adults, whereas adult individuals may respond more conservatively.

The interaction of sex, phase and condition may be a first hint towards the lacking of a mechanism on the touchscreen that quite clearly occurs in the Solid Object condition. Persistency seems to be very much dependent on the socio-ecology of a species (Winkler & Leisler, 1999; Gajdon, 2007). In this respect, females seem to be more persistent in the reversal involving solid objects. Further this mechanism may override other mechanisms accounting for differences. Definitely one has to be cautious when inferring results solely from touchscreen tasks.

5.1.3 Progress of trial to trial performance

Baring in mind the factors discussed in chapter 5.1.1, one would expect a greater improvement of discrimination learning in the Solid Object condition than in the Touchscreen condition already during session one. Yet there was no significant difference in improvement to be found between the two conditions. Interesting deviations only begin to show in change of performance from the end of the first to the beginning of the second session. The first trial of the second session pinpoints major differences between conditions: while failure of improving in the Touchscreen condition can be explained by less consolidated learning due to reasons outlined above (see 5.1.1), the deviation from chance and opposing performance in the two phases of the Solid Object condition indicates fundamentally different effects of learning intermediate session 1 and 2. The nearly complete preference for the negative stimulus in trial 21 of the Solid Object reversal and its steep decline in the very next trial suggests that the individuals already have recognized the former reward contingency and therefore prepared to act according to changed reward contingencies. But they favoured the option of briefly checking the former rewarded stimulus.

Due to this different performance in the first trial of the second session and the lack of different improvement within the first session one can assume additional mechanisms occurring in the Solid Object condition (see also Gajdon et al., in press) that are non-existent in the Touchscreen condition. I suppose that these mechanisms are related to information acquisition and affordance learning: the physical containment of the reward in the formerly positive stimulus provides a rather different setting in the Solid Object condition than in the Touchscreen condition for the affordance of the cover in the sense of Byrne (1998). Because the kea are extractive foragers of cryptically embedded and seasonal food sources (Brejaart, 1988) it seems adaptive to revisit potential food sites.

5.1.4 Correlation between tasks

When testing correlations between tasks we expected a link between acquisition and reversal of the Touchscreen as well as acquisition in the Solid Object condition. As expected, performance in one of these tasks allows predictions about the outcome in another of these tasks. The Solid Object reversal on the other hand does not appear to be dominated equally strong by the same proximate mechanisms. Therefore the Solid Object reversal in the kea stands out as not being part of this correlative assembly.

Based on these preceding elaborations regarding the interaction effects, fundamental differences in trial to trial performance and exclusive status of the Solid Object reversal concerning correlations with other tasks, additional factors (such as experience) and perhaps cognitive mechanisms are effective especially in the Solid Object condition. Therefore it appears justified to assume not solely quantitative, but also qualitative differences between reversal learning with solid objects and on the touch screen.

5.2 Comparing reversal learning studies

Of course it is always highly interesting but nevertheless difficult (for reasons of different criteria and methodologies) to compare studies. When comparing the kea with other bird species as in Table 3 (modified from Tebbich et al. 2010), it becomes obvious how methodology can influence the results. The kea reflects both extremes. No species in this comparison is faster in the acquisition (of the Solid Object condition) and at the same time needs more reversal training (in the Touchscreen condition).

Even though in all studies the same testing paradigm has been used, of course still main methodological differences remain. But since other studies investigated acquisition and reversal in either a skinner box (equivalent to the Touchscreen condition) or a Solid Object condition, the relative difference between acquisition and reversal is more relevant than absolute number of trials. Figure 14 illustrates the problem of concluding from the keas' difficulty in solving the reversal problem (chapter 5.1.1) to other species. Whether similarities in trials to criterion of both phases in corvids are accounted for by their extraordinary flexibility or rather their difficulties in the acquisition remains unknown. Intriguingly, the woodpecker finch, an extractive forager like the kea, exhibits the greatest relative deviation among the Darwin finches. This finding is in line with the persistency hypothesis for extractive foragers. If a lack of flexibility or perhaps also persistency accounts for the great relative divergence between phases for pigeons remains unclear without further investigations. Like in keas, a trial by trial analysis may provide further insight.

Table 3: A comparison of the performance of species comparing mean trials (with s.e.) to criterion and mean errors (with s.e.) in the Reversal for different methods; data shown for pigeons, three corvid species, three Darwin finch species and the kea; (modified from Tebbich et al., 2010; original data for pigeons: Lissek et al., 2002; corvids: Bond et al. 2007; Darwin finches: Tebbich et al. 2010)

Species	N	discrimination				reversal				errors reversal			
		Touchscreen/ skinnerbox	s.e.	"Reality"	s.e.	Touchscreen/ skinnerbox	s.e.	"Reality"	s.e.	Touchscreen/ Skinnerbox	s.e.	"Reality"	s.e.
Pigeon *C. livia*	8	40				168				99			
Corvid species													
Pinyon jay *G. cyanocephalus*	5	149,6	33,6			155	28,3						
Western scrub jay *A. californica*	5	136,8	20,9			191	35,7						
Clark's nutcracker *N. columbiana*	5	122,4	8,18			142,6	3,6						
Darwin's finch species													
Small tree finch *C. parvulus*	8			41,1	18,4			76,3	13,8			37,4	6,8
Woodpecker finch *C. pallida*	16			39,8	2,7			95,6	5,4			56,4	4,8
Medium ground finch *G. fortis*	8			56,1	9,2			93,7	12,5			46,4	7,9
Kea *N. notabilis*	17	73,1	11,8	18,4	4,3	213,5	20,7	70,7	8,5	79,0	9,6	35,1	5,6

Independent of condition (Touchscreen or Solid Objects), the kea shows the greatest relative divergence between phases among the listed species. This seems to put the assumptions made in chapter 5.1 into perspective. In either condition special mechanisms appear to be responsible for the relative divergence being larger than in any of the other species listed. Therefore both conditions may be used for comparative means. But following this line of argument the kea would be one of the most inflexible species according to the ability of changing associations. Questioning the flexibility of this species though would contradict the common perception concerning this species' flexibility in other cognitive or behavioral domains (Diamond & Bond, 1999; Diamond & Bond, 2004; Werdenich & Huber, 2006). This underlines the necessity for a discussion of which mechanisms are really measured by the reversal learning paradigm.

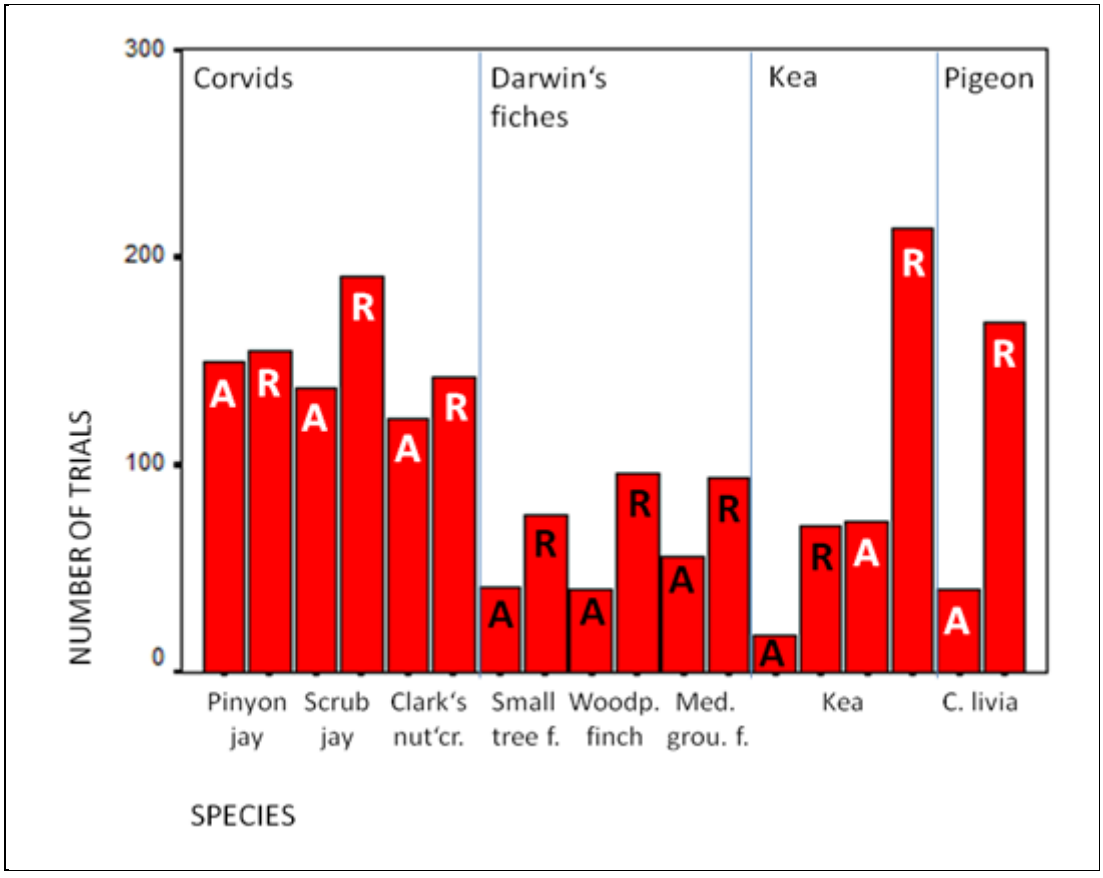

Figure 14: Mean number of trials recquired to reach criterion comparing different species; A indicates the acquisition phase, R indicating the performance in a reversal phase; whith letters show performance derived from a skinnerbox procedure, dark letters code trials needed in an rather Solid Object-like condition

5.3 What is measured by the reversal learning paradigm

Many recent studies have investigated reversal learning as a measure of cognitive or behavioural flexibility in different species (e.g. rats: Floresco et al., 2008; Göttingen minipig: Moustgaard et al., 2004; capuchin monkeys: Beran et al., 2008; dogs: Boutet et al., 2005; rhesus monkeys: Herndon et al., 1997; humans: Kloo et al., 2008; kea: Gajdon, Amann & Huber (in press)). Bond et al. (2007) have defined the ability to adapt to alternations of acquisition and reversals as indication of behavioural flexibility. Tebbich et al. (2010) have claimed to measure the ability to inhibit previously successful responses as a part of many components of behavioural flexibility. From lesion studies it is known that the prefrontal cortex (PFC) plays a major role when investigating key components of behavioural flexibility (Tait & Brown, 2007). Lissek (2002) concluded that the Neostriatum Caudolaterale (NCL), which in birds is the functional equivalent to the mammals PFC, is involved in extinction of obsolete information rather than acquiring new information. This suggests at least two different mechanisms that influence behavioural flexibility.

One is adaptive response updating. Monterosso et al. (2010) argued that reversal learning procedures test adaptive response updating when reward contingencies are altered. But for an extractive forager of cryptic, seasonal food sources it does not seem "adaptive" not to recheck the former rewarding option. Still it appeals adaptive to act behaviourally flexible upon this option. The absolute amount of trials or errors until the criterion is reached does not seem to be the ideal measure of behavioural flexibility in this case, since other socio-ecological factors like persistency might have a very strong overriding effect. Intriguingly Darwin finches also are known to be very flexible according to their feeding behaviour (Tebbich et al., 2010), even though they exhibit a relatively large divergence between phases (Fig. 14).

The analysis of trial by trial progress in the beginning of the reversal seems to be more sensitive towards behavioural flexibility when reward contingencies are reversed. In this respect the kea exhibit more flexibility to react to reversed reward contingencies, especially in the Solid Object condition, as compared to a classical analysis of trials to criterion. Following this line of argument and combined with the conclusions of chapter 5.2, this suggests that flexibility, concerning responses towards reversed reward contingencies, requires an analysis of the learning progress during the first session in a Solid Object condition. At least this seems preferable to an arbitrary criterion defining a fully completed reversal.

Cognitive flexibility is a key issue for complex cognition and is fundamental for expansion of knowledge, change of learned behaviour and innovation. Precursors of cognitive flexibility may be environmental intelligence and social intelligence (Watanabe, 2006). To be behaviourally flexible is especially advantageous for species living in a fluctuating, unpredictable environment.

Furthermore Lefebvre and Bolhuis (2003) discussed the importance of behavioural flexibility for innovation. Figure 15 gives a summary of innovation embedded into a socio-ecological framework. From this diagram it becomes clear how behavioural flexibility might be correlated to factors like colonisation success, evolutionary diversification, scramble competition, perhaps slower development and the relative size of the isocortex.

In conclusion, the findings of this study clearly show that it is necessary to investigate how individuals achieve a task and consider the effect of general dispositions and surrounding conditions, rather than solely comparing final achievements. This aspect has so far received only scant attention in comparative studies.

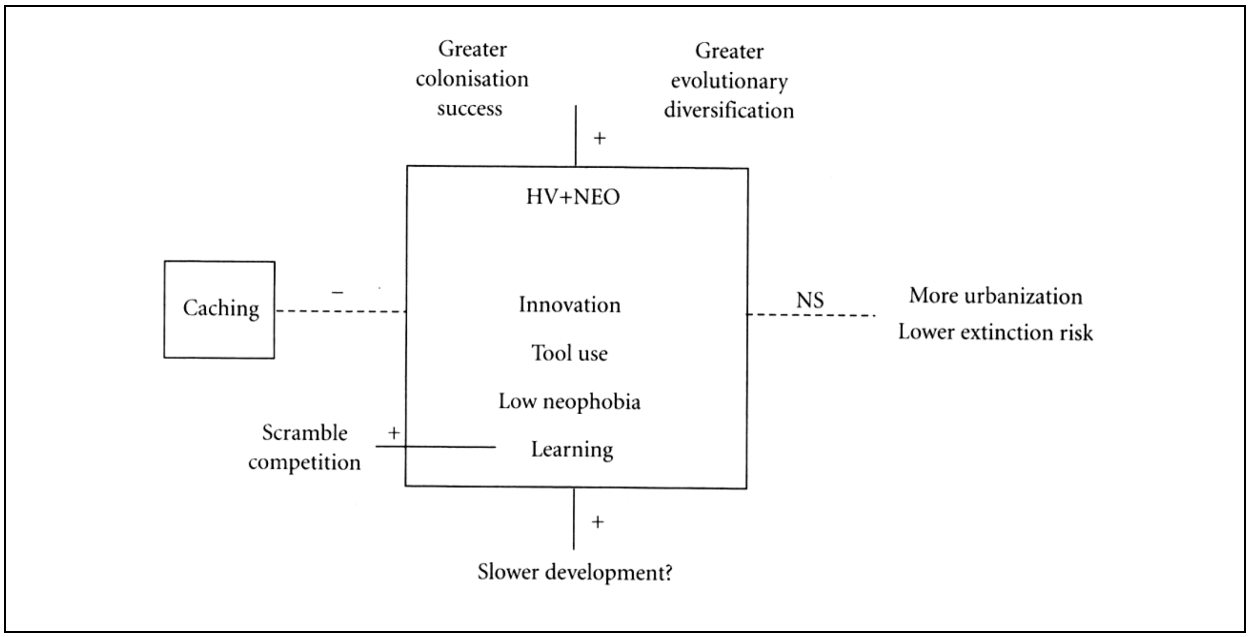

Figure 15: Relationships between feeding innovations and cognitive neuronal ecological developmental and evolutionary variables in birds. Full lines indicate a positive association; the stippled line with the minus sign indicates a negative association; the stipled line with NS indicates a non-significant relationship. HV + NEO: hyperstiatum ventrale and neostriatum (taken from Lefebvre and Bolhuis, 2003)

5.4 Future research

This is - to my knowledge - the first study directly comparing two commonly used approaches towards measuring an animal's cognitive abilities. Therefore further research concerning the methodological difference may contribute largely to several questions that have emerged from this study. But it also may help to understand discontinuities when comparing previous studies using these methodological approaches.

Questions that have emerged on the one hand concern basic methodological differences like:

- Pre experience of the animals

  As already discussed in chapter 5.1.1., the touchscreen represents a new testing environment for keas, confronting them with abstract, ruled-based learning problems. Therefore it would be extremely interesting to test the individuals of this study again, after they had extensive experience in different tasks on the touchscreen.
- Spatial dissociation of the reward

  To control for reward connectedness in a follow up experiment the reward could be delivered at a fixed location equally distant from stimuli in the Solid Object condition.
- Stimulus perception

  Influences of stimulus sets used may refer towards a colour preference for red objects (since it seems very unlikely that the kea have a preference for fish-shapes). On the other hand the red stimulus didn't have an impact on the performance in the touchscreen condition. This raises questions for further studies concerning the kea's colour perception of stimuli presented on screen and at the same time underlines the necessity of performing preference tests prior to conducting any discriminative experiments.

As well as potential different cognitive mechanisms involved in the different task with varying ontogenetically development.

One reason why the overall difference among age groups (see 5.1.2) could have been weakened is that at the time of testing the subadult individuals were at the brink of adulthood (after Diamond & Bond, 1999). It would thus be very interesting to repeat this study with even younger individuals in comparison to adults.

On the other hand this study has also raises fundamental questions about the interpretation and processing of results derived from the reversal learning paradigm. Therefore further comparative studies should additionally evaluate trial to trial performance in different species taking into consideration their socio-ecological, environmental and ontogenetical background. These analyses might shed further light on the measurement of behavioural flexibility.

The aim of this study was not so much to investigate the differences of methods in depth, but rather to point out that these differences exist. With the touchscreen being a very good and conservative way of exploring associative learning, one should bear in mind that assumptions based solely on this methodology may often underestimate an animal's mental capacity and therefore not necessarily reflect the ecological relevance of a created task.
This study also presents comparable data for the kea's performance in a reversal task, a species showing great competence in behavioural flexibility. Though many of the questions raised remain unanswered I believe this study contributes to science by offering a method to compare studies using different methodological approaches and raising the discussion of what really is measured by the reversal learning paradigm and it's assumptions concerning behavioural flexibility.

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7 Curriculum Vitae

Personal Details

Born on the 24th of November 1982
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Employment

06/2010-11/2010	**University of Vienna,** **Department of Cognitive Biology;** **Technical Assistant** ▪ Construction work for the Haidlhof research station ▪ Construction work of metal aviary elements
10/2009– 06/2010	**University of Vienna,** **Department of Cognitive Biology;** **Scientific Assistant** ▪ Assistant project management ▪ Data collection ▪ Animal health supervision
06/2004 – 07/2004	**CONNEX UND PARTNER MARKETING UND WERBEAGENTUR GMBH;** **Promotion agent** ▪ Promotion work ▪ Driver
10/2001 – 09/2002	**Red Cross Upper-Austria;** **Civil servant** ▪ Paramedic ▪ Ambulance driver

Education

10/2002 – currently	**Zoology at the University of Vienna** ▪ Study focus: Cognitive biology ▪ Additionally: Human ethology ▪ Diplomathesis: „***Reversal learning in the Kea (Nestor notabilis): Comparing the touchscreen to a reality-approach "***
02/1993 – 02/2001	**BG, BRG Wels,** **Realgymnasium mit naturwissenschaftlichem Schwerpunkt** ▪ High school with focus on natural sciences