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**Mental representations and cognitive processes related to the physical  
world in jackdaws (*Corvus monedula*)**

**PhD Thesis**

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*Az ég kék a fű zöld*

*Szép szárazulatok*

*Óriás tengerek*

*Lelkes állatok*

*Kíváncsi emberek*

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## General Introduction

The comparative study of cognitive processes in different species, comparative cognition, is a rapidly developing discipline, which combines traditional psychological methods with comparative evolutionary and ecological approaches when investigating the origins, mechanisms and functions of cognitive skills. The basic idea of comparative cognition dates from as early as the 1871 book by Charles Darwin, *The Descent of Man and Selection in relation to Sex*. In this book Darwin raises the hypothesis that the difference between the mind of humans and animals is that of quantity and not of quality. Comparative cognition went through drastic development in the last three decades, as the evolutionary and comparative approach became more and more accepted, while cognitive ethology as a new discipline (Griffin 1976) became more and more prominent in the research of behaviour.

Contemporary research in comparative cognition addresses three major aspects of cognition, namely *basic processes*, *physical cognition* and *social cognition* (Shettleworth 2009). Basic processes are not specified by content, but include such fundamental universals as perception, memory, attention, associative and category/concept learning. Further cognitive processes may be divided based on what aspect of the world they are dealing with, i.e. their functions (according to Tomasello & Call (1997) into social and physical cognition. Social cognition has to do with what animals know or can learn about their social environment. This includes processes like imitation and other types of social learning, theory of mind, as well as various aspects of communication. *Physical cognition* deals with organisms' understanding of spatial, causal and characteristic interrelations of objects in their physical world. Some aspects of physical cognition such as time, space and *number* have a long history in experimental animal psychology, while others such as tool use and causal reasoning have emerged only recently. Although animals face a number of problems in the physical domain, undoubtedly, one of the most serious of these is locating and obtaining sufficient food. Many important cognitive skills for many animal species are thought to have evolved in the context of foraging.

In this thesis I assess two aspects of physical cognition in jackdaws (*Corvus monedula*), namely object permanence and quantity related cognition. I found these two object related cognitive skills in jackdaws particularly interesting, as while jackdaws live a relatively "object-centred" life (von Bayern et al. 2007; Schuett et al. 2012), so far they have not been thoroughly investigated. Also, object and quantity related cognition is by nature

closely intertwined, as in the vast majority of comparative studies those are indeed objects, sometimes occluded, manipulated, etc., that are to be “counted”, i.e. quantitatively assessed.

### ***Object Permanence***

Piagetian object permanence is the cognitive or mental “tool” for finding or keeping track of objects, which may be (occasionally) unavailable to the senses. This tracking and finding perceptually inaccessible objects (“object search skill”) is one of the most fundamental paradigms of physical cognition. Object permanence is the ability to form an inner mental representation of the physical world, and to follow object movements, localizing them even in the case when no direct perceptual input is available for the nervous system (Piaget 1954). Object permanence has been named after and introduced by a developmental psychologist, Jean Piaget (Piaget 1954). He has claimed that object search skills emerge in human infants by 18-20 months of age through a fixed series of steps (i.e. 6 stages), with characteristic transitional errors. Very young infants, between 4-8 months of age, although already capable of grabbing objects, seem to lose interest as soon as objects leave their field of perception and show no search behaviour. After the 8<sup>th</sup> month infants start searching and finding disappearing objects (stage 4), but their search behaviour is characterized by a typical error, namely that if they found a hidden item one or more times in a certain location, the infants will keep searching there even if they have witnessed the hiding to another location. As infants in this case persevere in their search, this is called a perseverative error, or A-not-B error. This error disappears typically at the age of 12 months, when infants start searching systematically where they have last seen the object disappear (stage 5). At this stage infants seem to be unable to comprehend invisible displacements, which they come over at the age of 15-16 months (stage 6) and reach the highest developmental stage in the Piagetian system. By that age their search behaviour is coordinated and systematic in multiple invisible displacement tasks as well. More detailed research, however, discovered that at this age infants may not be solving search tasks by mental representation of the hidden item, but they most probably use a simple associative rule. According to this view infants only reach their full representational capacities at the age of 18 months, when they utilize a deductive, rather than an associative method of search (Topál 2009).

To quantify object representation and tracking abilities researchers traditionally used methods in which a desired object suddenly exits the perceptual field. Based on the displayed search behaviour one can make more or less precise inferences about the object

representational capacities of the subject. During their decades of research Uzgiris and Hunt (1975) set up a method (Scale 1), where object hiding/searching trials of growing difficulty constitute a system in which successful search requires more and more developed object representational abilities. Their tasks range from the simplest visible displacements, through multiple visible displacements, and single invisible displacements to multiple invisible displacements.

However, methods based on search behaviour require more or less complex and coordinated motor responses, thus naturally these are not suitable to study object representation at a very early age. For this reason Baillargeon and colleagues (1987) implemented a new method, where infants could be tested based solely on their looking behaviour. In this “violation of expectancy looking time” paradigm infants are hypothesised to look more intently (i.e. longer) at outcomes of experimental situations that are violating their expectancy. The results from studies of object representation using this new method seemed to question the above described stages of development in case of human infants. They suggest that infants as young as 2.5 months of age have expectancies in connection to object permanence (Baillargeon & DeVos 1991; Wynn 1992). The contradiction between the results from traditional search paradigms and looking time paradigms is outlined by the “object permanence paradox” (Meltzoff & Moore 1998).

Most animal species, on various levels of phylogeny, face evolutionary challenges in connection with tracking and finding perceptually unavailable objects. Of course, Piagetian object permanence, i.e. mental representation of objects independent from their perception, requires a quite sophisticated nervous system, and so may not be available to most species. In such species a number of alternative solutions have been invented, such as activation of fixed action patterns or the formation of conditioned responses. Animal experiments are often criticized based on the (high) number of trials. Searching behaviour may only be interpreted as object representation skill, when the number of trials is relatively few (maximum 2-6) (Doré & Dumas 1987).

However, comparative research showed that many neurologically more sophisticated species, mainly primates, other social or carnivorous mammals, and some bird species, like parrots and corvids develop object permanence skills in the same or similar sequence as human infants, only at different speeds (Doré & Goulet 1998). Species may also differ in the final stage reached (i.e. whether they become capable of understanding invisible displacements) and in presence of characteristic search errors, none the less Piagetian object permanence seems to be one of the core universals of physical cognition.

One of the particularly interesting questions in animal studies is whether the so called A not B error phase exists in non-human species. What may cause this characteristic error has been an interesting question to developmental psychologists. Piaget's initial explanation was that infants committing this error fail to separate the existence of the hidden object from the action of their own hand thus regard the object as something that their own action creates. As data multiplied, some other explanations arose, such as that the error is committed due to lack of sufficient working memory, or lack of attention, or perhaps the inability to block a prewired motor response. Based on the contradicting data from "searching" and "looking" experiments, it has been hypothesized that the perceptive and motor systems may not be coordinated and a developmental mismatch of representation and reaction may be present. A novel approach of Longo and Bertenthal (2006) suggest that it is not the repeated and confirmed reaction of the subject that is the cause of this error, but the observation of the hiding action. This action is supposed to prewire a motor response via the mirror neuron system (Rizzolatti & Craighero 2004). Most recently an intriguing paper has been published (Topál et al. 2008), suggesting that in case of infants this so called perseverative search (A-not-B) error may be caused by a pragmatic misinterpretation of the situation. Due to the ostensive-referential signals used by the experimenter, subjects tend to mistakenly identify the hiding procedure as a teaching situation where a "rule" is to be learned, generalizable information is to be gathered.

While natural pedagogy and teaching behaviour is associated solely with humans (Csibra 2007), it has been shown that some corvid species, among them jackdaws, are sensitive to ostensive cues such as the gaze of a conspecific (Bugnyar et al. 2004; Davidson et al. 2014). Jackdaws' direction of gaze, like that of humans, is relatively easy to detect, due to the fact that unlike those of closely related corvid species, their irises are light blue and contrast from grey feathers and black pupil. For this reason, the presence or absence of the characteristic A-not-B phase may be very interesting information to be gained from our studies.

### ***Numerical/Quantity related cognition***

Naturally, real counting and mathematics are the constructs of human culture and are tightly associated with language. None the less, people have long been interested whether animals could count. This interest probably arose from a wider curiosity about animal intellect and how similar or different this might be from our own. Counting, as said before, is thought

to be a characteristically human capacity, thus if such a capacity could be shown in case of animals, one could be tempted to agree with Darwin in that difference between the human and the animal mind is of quantity and not that of quality.

During the past few decades of research it became clear, that animals without language indeed possess basic numerical and/or quantity related capacities. Various studies of comparative psychology showed that animals are capable of making choice decisions based on numerical information, while developmental psychologists have found evidence of numerical cognition in infants as early as a few months of age. From these results emerges the conclusion that numerical competence did not first appear in our own species, but is based on deep biological roots (Nieder 2005).

Research on numerical cognition has changed a great deal in recent times as its theoretical framework, together with definitions and nomenclature, went through a great transformation. Comparative research on quantity related abilities of animals was integrated with investigations of cognitive neuroscience (Feigenson et al. 2004) and research on child development (Brannon 2006).

While the notorious memory of Clever Hans, the horse that allegedly could count (Pfungst 1911), still looms over the field of numerical cognition in animals, researchers now realise that the question whether animals can count is not a very productive one. Besides the obvious oversimplification that lies embedded, it supposes a yes or no answer. However, trying to provide such an answer (i.e. *yes, they can* or *no, they cannot*) will undoubtedly lead to further questions on what the answer actually means and what needs to be demonstrated in order to make such a statement. The transformation of the theoretical framework of numerical cognition is intended to try to work our way around this problem by uniform definitions and unanimous nomenclature, while sharing the understanding that number related cognition includes several core components. Some, but not all of these core components may be shared across species (Shettleworth 2009). Considering the above, the more productive and precise question concerning this issue in animals would be something like “what are the core components of numerical cognition and which of these are shared across species/can be demonstrated in a gives species?”

### ***Core Knowledge Systems***

It has been suggested (Spelke 2000; Spelke & Kinzler 2007; Carey 2009) that humans - instead of a single, general purpose learning system or countless systems, each specialized to

a certain function – possess a small number of separable systems of Core Knowledge. These systems may be described as mechanisms for representing and reasoning about specific types of ecologically relevant entities and events (Spelke 2000). These mechanisms are domain and task specific, and are fairly independent from other cognitive systems. Evidence accumulated in studies of human infants and non-human animals suggests the general presence of five such Core Systems: one serves to *represent inanimate objects* and their mechanical interactions, a second for agents and their goal directed actions, a third for *numerical relationships*, a fourth for spatial layout and geometric relationships and a fifth for social interactions.

Each of these systems focuses on certain principles that set apart the entities belonging to its domain, as well as is characterized by a set of signature limits, allowing identification of a certain system, even in other species. Core knowledge systems are supposed to be shared by other animals and appear to be evolutionary ancient (Vallortigara 2012), making comparative investigation across species possible.

The two core systems which are most relevant to this thesis are the first and the third system mentioned above, namely the core system of object representation and the core number system. In my research I assessed the ontogeny of object representation and search skills (Experiment 1) in jackdaws, and their ability to utilize both the core system of object representation and the core number system (Experiment 2). Thus in the following sections I describe these two systems in more detail.

### *Core System of Object Representation*

Following the early psychological investigations of Jean Piaget (Piaget 1954), where the ontogeny of object representation has been established through studies of object permanence in human infants, research on representations of objects and their numerosity is hard to separate. In infants, numerical competence was believed to be grounded almost exclusively on object tracking processes (Nieder 2005). Decades of research shows that infants build representations of objects as complete, solid bodies that persist over occlusion and maintain their identity through time (Spelke 2000). Thus the core system of object representation seems to obey the spatio-temporal principles of cohesion (objects move as connected and bounded wholes), continuity (objects move on connected, unobstructed paths), and contact (objects do not interact at a distance)t. Karen Wynn (Wynn 1992) used the preferential looking/violation of expectancy method to test 5-months-old infants on tracking objects that moved behind an occluder. She presented infants with correct and incorrect

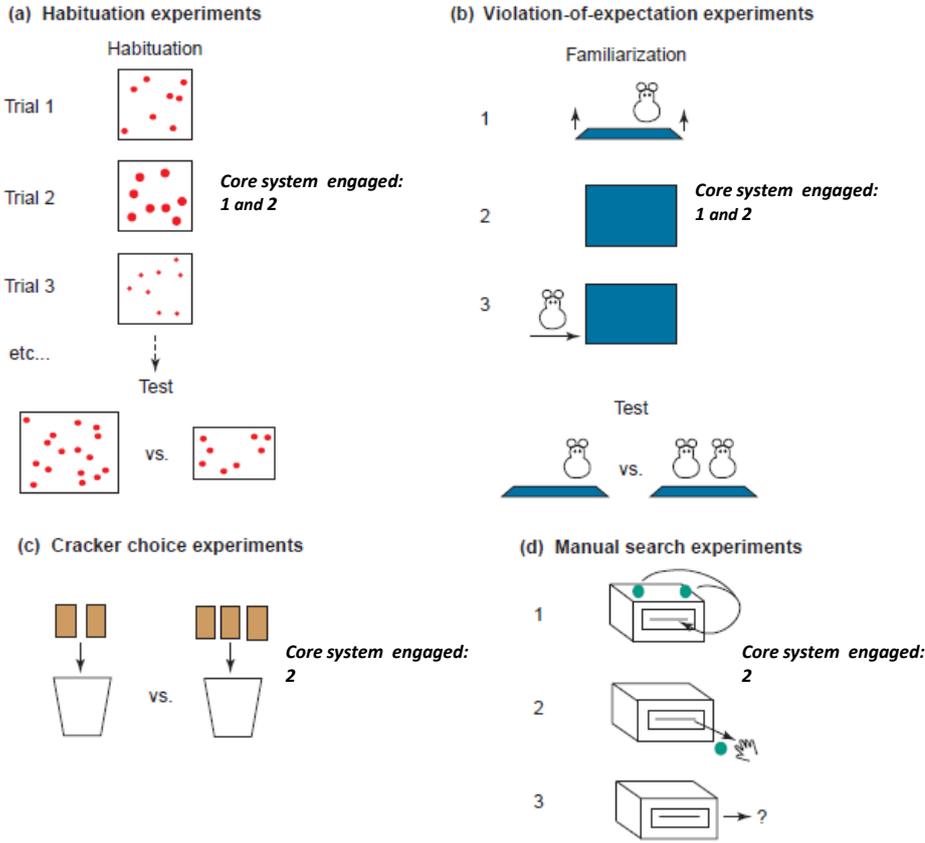
outcomes of a one object plus one object and a two object minus one object situation, where manipulations were made behind an occluder. She found that infants looked significantly longer at the incorrect ones, suggesting that subjects had an expectation of the correct result. Her experiments showed that infants, as young as 5 months of age, keep track of distinct entities over time and space and possess a mechanism for quantifying collections of discrete entities. In further elaboration of her studies it has been shown that infants were truly representing number of items, rather than amount of some other (continuous) property (Simon et al. 1995) and responded to object number rather than to object locations (Koechlin & Mehler 1997). Some further studies (e.g. Feigenson et al. 2002b) using different response systems and different objects corroborated the finding that human infants keep track of objects becoming occluded and construct a representation of the precise number of items in the occluded array. However two very interesting limitations have also been revealed. One limitation is that infants fail to represent number in the case when the occluded items do not “behave” as objects usually do, as for example non-solid, non-cohesive sand piles or piles of blocks (Feigenson et al. 2002a). A second limitation found was that there seems to be a set size limit (i.e. limit to the number of objects to be tracked) which, in case of infants, is around 3. (This limit in case of adult humans and adult monkeys is around 4).

According to Spelke (Spelke 2000) all the accumulated evidence suggests the existence of a core system for representing objects, which is capable of tracking multiple objects simultaneously, which is domain specific, which is subject to a set size limit and is not sensitive to changes in object properties or spatial location. Moreover the same system seems to be present not only in infants, but also in adults (Scholl 2001), in non-human primates (Hauser & Spelke 2004) and probably several other animal species (Vallortigara 2012). Abilities of object representations in some cases are observed without any visual experience in newborn infants (Valenza et al. 2006) and newly hatched chicks (Regolin & Vallortigara 1995). Supposing the system to be constant over human development, one would expect it to be universal, thus also be available to culturally and linguistically distant human groups. Ris

### *Core System(s?) of Number*

Regarding the core abilities concerning number and quantity, discussion remains whether there is only a single core system serving the purpose, or there may be two distinct systems. The reason for suggesting the presence of two systems is the phenomenon that both human and non-human subjects seem to deal differently with tasks on small numbers from

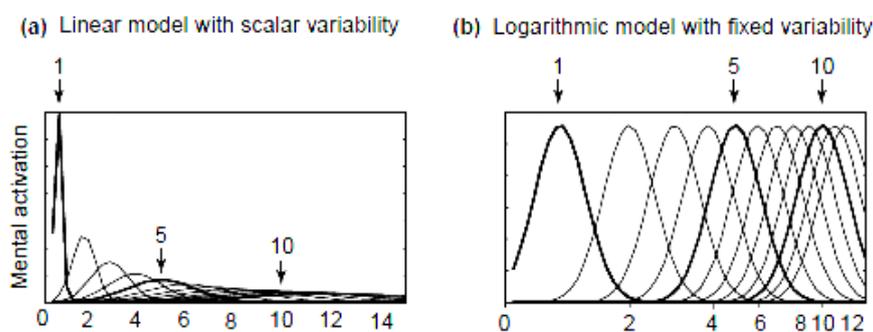
those on large numbers (e.g. Xu 2003). In their review article, Feigenson, Dehaene and Spelke (Feigenson et al. 2004) suggest the presence of two core systems representing number. The studies they cite use different experimental paradigms (please see Figure 1.) and yield evidence for the engagement of either of two core systems.



**Figure 1. Test types used for infant testing and the core systems suggested by results (Drawing adapted from (Feigenson et al. 2004))**

One of these (*Core system 1*) serves approximate representations of numerical magnitude. Many animals, including humans, have been shown to represent the approximate numerosity of large sets of items or events (for a brief review see e.g. (Dehaene 2001). Discrimination in these tests depends on the ratio of the two sets in case of animals and humans alike, in the latter given that conditions discourage/do not allow verbal counting, suggesting a common mechanism. Core system 1 is supposed to be at work for example when 6-month-old infants successfully discriminated 8 vs. 16 (but not 8 vs. 12) dots even when continuous variables were controlled for (i.e. number of items did not co-vary with volume, surface area, contour length, etc.) (Xu & Spelke 2000). Three important factors have

been found to limit these approximate representations. First, infants' discriminations were imprecise and subject to a ratio limit, while (second) precision was found to increase over development, and finally (third) discrimination failed when subjects were tested on small numerosities with controlled continuous variables. These approximate number representations may be explained similarly to models which represent numerosity as an analogue mental magnitude, such as a 'mental number line' (Meck & Church 1983; Gallistel & Gelman 2000). There are two possible mathematical formulations of the 'number line', the linear model with scalar variability and the logarithmic model with fixed variability (see Figure 2.). They both have very similar predictions of increasing 'overlap' of distributions with larger numbers, explaining ratio dependent performance (Feigenson et al. 2004).

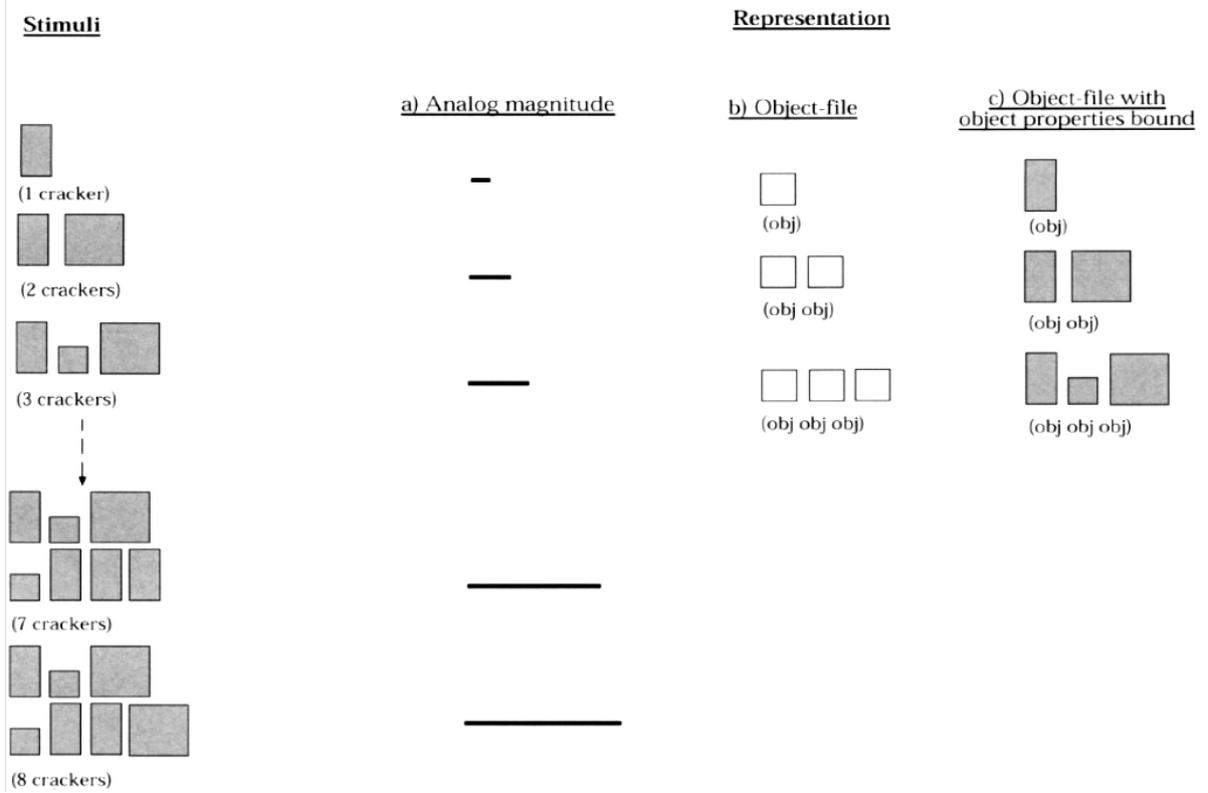


**Figure 2. The two competing mathematical models of the mental number line showing mental activation as a function of numerosity (Drawing from (Feigenson et al. 2004))**

According to the above, this core system is supposed to be capable of noisy representation of approximate number, is constant across modalities and variations in continuous properties, showing a signature ratio limit. In humans this core system is suggested to become integrated through development with the symbolic counting system used by humans via linguistic competence later in enumeration and computation.

The other core system suggested by Feigenson and colleagues in 2004 (*Core system 2*) serves precise representations of distinct individuals. This system is supposed to be used for keeping track of the precise small number of individual objects as well as representations of their continuous quantitative properties. This system/model best explains results from for example the experiment where 10 and 12 months old infants were given a choice between two small quantities of hidden crackers (Feigenson et al. 2002b, see figure 3.). Performance in these tasks was very different from those observed with large numerosities, as it did not depend on numerical ratio of the sets, but rather on the absolute number of the presented items, with an upper limit of 3. Infants in this experiment also seemed to code and compute

the total continuous extent of the arrays, as in a control choice of one large vs. two small crackers they opted for the one large cracker over the two small ones. This sensitivity of core system 2 to continuous variables has been observed in other paradigms as well (Clearfield & Mix 1999; Feigenson et al. 2002a). The signature limits of this system are also consistent across tasks and modalities. Subjects fail to represent more than 3 items, and cannot make a correct choice for more in case continuous variables are controlled for. This second core system of number seems to correspond with ‘object file ‘ models of representation of number (Kahneman et al. 1992).



**Figure 3. Three different models of representation of stimuli**  
**(Drawing adapted from (Feigenson et al. 2002b))**

However some researchers recently put forward a strong argument for the presence of only one system for numerical representation (Jordan & Brannon 2006; Cantlon et al. 2010). Cantlon and colleagues (Cantlon & Brannon 2007; Cantlon et al. 2010) found strong evidence that both 3-year-old children and non-human primates spontaneously recruit the analogue system of numerical representation for small and for large numbers alike. In their

experiments, children's judgement of small numbers was modulated by numerical ratio to the same degree as that of large numbers. The numerical ratio effect is considered to be the signature of the analogue magnitude system, thus they argue that children by the age of 3, represent the numerical quantity of small sets via an analogue magnitude mechanism. The same results have been found previously in case of non-human primates (Cantlon & Brannon 2007). While they cannot rule out the possibility that younger children and infants deal with small numbers via the object file system, as reported earlier (e.g. Feigenson et al. 2002b, 2004) they strongly suggest that children (and non-human primates) use a single representational system for small and large quantities.

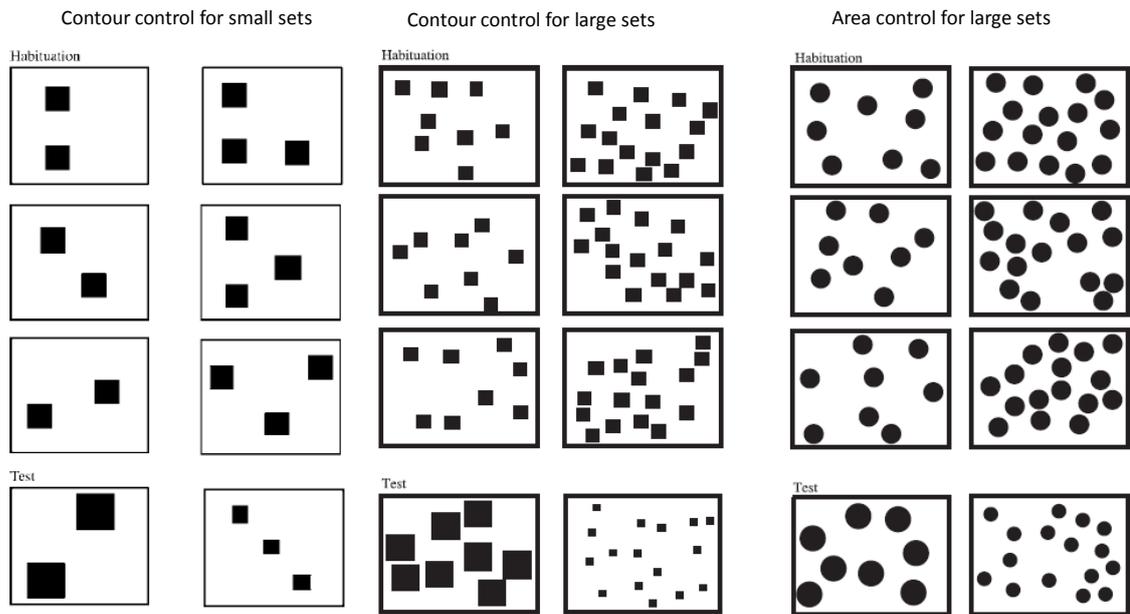
Elizabeth Spelke, in her 2000 (!) article on core knowledge systems (Spelke 2000), put forward a very interesting alternative. Her view on the question is particularly elegant, and her implications seem very logical. When trying to consider what mechanism might underlie infants' representations of large numerosities and how does it relate to the mechanism that underlies infants' representations of small numbers, a logical hypothesis would be that indeed it is the same (and only) system. However, Spelke does not support this hypothesis, as she says there are three sets of evidence suggesting that a separate system is dealing with the representation of small and large numerosities. Performance with small and large numbers is subject to different limits (small-set size/large-ratio) (1), performance with small numbers is robust over occlusion (*this will bear special significance concerning our second set of experiments!*), while this is not the case with large numbers (2), performance with large numbers is robust over variations in continuous qualities, while this is not the case with small numbers (3). Based on these, Spelke suggests that *two core knowledge systems* are at work in these experiments. One is the *number system*, representing sets and their approximate numerical values, and another, the *object system* representing and tracking objects and their characteristics, which is supposed to be in use when dealing with small number of items. Both these systems are domain and task specific, and are independent from each other. As to our question whether one or two core systems are involved in representation of numerical attributes, based on the above, we can answer that there are indeed two, but two core knowledge systems and not two core systems of number representation. According to this idea the *core object system* (which is not inherently quantitative, but can be used to judge quantity through one-to-one comparison of objects and object features (Cantlon et al. 2010)) is responsible for the precise representation of small numbers of individual objects ('object files'), while the *core number system* is responsible for representation of large, approximate numerical magnitudes of sets ('analogue magnitude').

### ***Mental representation of objects and their attributes***

A further subject of extensive debate is the question regarding how exactly objects are represented, what attributes are encoded, and what is the relative salience of these attributes. It has been hypothesised that the “small number representation system” (may it be the core object system or a separate object file system, perhaps ‘core number system 2’) encodes various attributes simultaneously and in connection with a given object or set of objects, such as contour length, total surface area, number of items, etc., (much like “object files with object properties bound” figure 3.). This system keeps precise track of small numbers of individual objects together with information on continuous quantitative properties (Feigenson et al. 2004). This is supposed to be the reason why small number discriminations fail when continuous variables are controlled for (Clearfield & Mix 1999; Feigenson et al. 2002a; Xu 2003).

As mentioned before, in a choice task, the relative salience of these co-represented attributes is debated. For example some researchers claim that, in case of children, representation of cumulative surface area or contour length is more primary and develops earlier than the representation of number (Clearfield & Mix 1999; Feigenson et al. 2002a). Others seem to have found evidence of this in non-human animals as well (Davis & Memmott 1982; Davis & Pérusse 1988; Seron & Pesenti 2001). This hypothesis calls numerical representations as basis of quantity discrimination a ‘*last-resort*’ strategy.

This hypothesis however has been disputed since by numerous studies, for example that of Cordes and Brannon (2009). They present the results from three experiments intended to test whether infants indeed prefer to represent continuous variables over number, in which they pit number vs. continuous extent as basis for decision.



**Figure 4. Example of stimuli used to pit continuous extent against number**  
 (Drawing from (Cordes & Brannon 2009))

Their results suggest that representing discrete quantity is not a last resort for human infants; they do not find continuous properties more salient than number, and finally that number is spontaneously represented by young infants, even when other cues are available. Similar results have been found in case of great apes (e.g. Tomonaga 2008), monkeys (Cantlon & Brannon 2007), and various other animal species (Rugani et al. 2009, 2010b; Agrillo et al. 2011; Scarf et al. 2011).

However, research on the relative salience of numerical and non-numerical information seems to suggest, that the parallel mental coding of several attributes of a set aides to make an optimal choice, as under natural conditions numerical and non-numerical attributes co-vary. For example chimpanzees' choices were found to be affected by total area and density of items, however their effect could not alone explain performance, suggesting that relative numerosity difference was used as a discriminative cue (Tomonaga 2008). In

sum, it seems safe to hypothesize that relative quantity judgements may be based on both numerical and continuous attributes as redundant cues.

Finally, it is definitely worth to mention in this section that although so called “relative numerosness tasks” or “natural choice procedures” , where food items are involved, are based on the idea that subjects (naturally) aim to maximize the number of food items and thus maximize the overall food volume, this might not always be such a clear case. Chimpanzee studies have shown (Boysen et al. 2001; Beran et al. 2008) that subjects are biased to select the set with the biggest individual item, even if this array contains the less total amount of food. This is a very interesting phenomenon, as it is hard to understand, why any animal would be inclined to opt for the biggest item at the expense of overall intake. Beran and colleges speculated several possible explanations in their discussion, including the possibility of the biggest item bearing the highest consummatory impulses, difficulty in combining multiple stimulus properties, rapid responding through the use of a usually profitable “shortcut”, or perhaps an effect of usual competition for food on behaviour.

Beran, Evans and Ratliff (Beran et al. 2009) found that not only magnitude, but contiguity and wholeness also has an effect on choice behaviour optimal reasoning. Their study showed that chimpanzees undervalued the total amount of food in sets where items did not appear to be whole, thus showing suboptimal responding preventing maximal food intake. This result will bear significance regarding the final control situation of our quantity related experiment, when a choice between one large and three small pieces were offered, equalling in volume.

### ***Cognitive skills - Spontaneously available or result of rigorous training?***

On the waves of the recent “revolution” of comparative cognition, where research is now conducted on considerably more species than before, many impressing results have been published on the cognitive capacities of certain animals. However, a clear distinction has to be made between capacities that can be “taught” to subjects through (sometimes) thousands and thousands of training trials, and those skills that are readily available to an animal living under natural circumstances. In the first case the results mean that the capacity to “develop”, or the potential, might be present in all members of a given species, but only some extensively trained individuals may fulfil this potential. In the latter case any individual may be expected to express the given capacity.

In regard of any reported success it is always of value to ask how dependant the results might be on previous experience of the subjects (e.g. Hanus & Call 2007), or perhaps training in some special (however unrelated) skill. A very good example of this (alongside of course of the many symbol-trained chimpanzees using Arabic numerals and lexigrams, computer touch-screens, etc. (e.g. Savage-Rumbaugh et al. 1986; Boysen & Berntson 1989; Beran et al. 2000; Matsuzawa 2009)) is Alex, the African grey parrot (*Psittacus erithacus*) of Irene Pepperberg “who” was trained to use English vocal labels for shapes, colours, numbers, materials, etc. (e.g. Pepperberg et al. 2000). Alex has been reported to possess outstanding object related (Pepperberg et al. 1997) and numerical skills (Pepperberg & Carey 2012) (even understanding the zero concept (Pepperberg & Gordon 2005), but question remains whether his capacities were connected to his vocal labelling and/or lifelong training, or these skills are readily available to any adult African grey, only are difficult to pinpoint, due to the restricted means of communication.

Interestingly Pepperberg reported at least one object related skill, “insightful” string pulling (see in (Heinrich 1995), the demonstration of which is not improved, but impaired by vocal communication. She found that birds which had little training in referential English requests (i.e. I want X) were much more successful in this task than those who could simply request the suspended item. These language trained subjects engaged in requesting the experimenter to give them the reward, and failed to obtain it themselves (Pepperberg 2004).

Over the past few decades, a number of birds (e.g. pigeons, budgerigars, large parrots, canaries, magpies, ravens) and many mammals (e.g. rats, racoons, dolphins, dogs, several species of monkeys and apes) have been reported to successfully perform numerical tasks after extensive training. However, regarding these experiments, question remained whether animals might be merely responding to well-known stimuli, which they were accustomed to during their training. A breakthrough experiment (Brannon and Terrace 1998) however has shown that monkeys (*Macaca mulatta*) are able to transfer their trained numerical knowledge to novel numerosities. Two subjects have been trained to order sets of 1-4 objects in an ascending order. Non- numerical stimuli were controlled for. When tested with novel numerosities 5-9, the monkeys responded correctly, touching the sets in an ascending order, without any reinforcement. This is a very important result, as it shows that the subjects had acquired true understanding of cardinalities and their sequential arrangement.

Laboratory results have been on occasion criticized on being “laboratory artefacts” which bear little relevance under natural circumstances. To address this issue some research to follow (mainly that of Hauser and colleagues) have been performed under natural

circumstances, using wild (semi-free ranging) subjects (*Macaca mulatta*) (Hauser & Carey 2000; Sulkowski & Hauser 2001; Flombaum et al. 2005). Data was collected from several species and result showed that many species of animals indeed make good use of numerical information under natural conditions.

In summary it seems that controlled laboratory investigations and field studies complement each other in that members of many animal species are numerically competent and use numerical information to make optimal choices in their environment, natural or artificial.

### ***Cognitive skills – In place at birth?***

Preverbal human infants of just a few months of age may be tested on their object and quantity related cognition, mainly utilizing the violation of expectancy-looking time paradigm, which takes advantage of the phenomenon that subjects tend to look longer at unexpected outcomes than at expected ones. Such studies have shown that infants may possess knowledge about hidden objects that the traditional Piagetian studies have suggested. According to Piaget, Stage 4 object permanence (i.e. actively recovering a fully hidden object) emerges at approximately 8-12 months of age (Piaget 1954). Baillargeon and colleagues, however found evidence of Stage 4 in case of infants as young as 3.5 month old (Baillargeon 1987). As described earlier in connection with the A-not B error, there is discussion on the possibility of a knowledge-action mismatch in the performance of pre-verbal human infants in object search tasks. For elaboration of this discussion please see the article of Meltzoff and Moore (Meltzoff & Moore 1998).

Infants of only a few months of age have been shown to have the capacity to represent quantity (for a recent review see (Feigenson et al. 2004). Using the habituation-dishabituation protocol, infants as young as 5 months of age have been shown to engage in rudimentary arithmetic (Wynn 1992). Subjects looked significantly longer at a numerically inconsistent outcome, which support the notion that infants have a capacity to understand simple arithmetic ontogenetically very early.

However, as human infants, as well as the young of other altricial species, have a very limited behavioural repertoire, contemporary comparative cognition sometimes uses precocial bird models (usually domestic chicks (*Gallus gallus*)) to assess whether some cognitive capacities are inborn. The origins of both object permanence and numerical cognition have been studied in domestic chicks.

It has been shown that 2-day-old chicks already master some aspects of Stage 4 object permanence (i.e. recover a fully occluded object), however they are shown to be unable to predict where the occluded object will reappear from its direction of movement prior to occlusion. None the less, chicks have been shown to possess an object concept that maintains a representation of the object when no direct sensory cues are available (Regolin et al. 1995; Vallortigara 2006).

Numerical cognition seems also to be apparent early in development. Newly hatched chicks have been tested on their sensitivity to number vs. continuous extent. When objects were similar, chicks chose the set with the larger number of items, independent from the number of objects they have been reared with. Furthermore, when chicks were reared with objects which differed in their attributes such as colour, size and shape, and then tested with yet novel objects controlled for continuous extent, they chose the set comprising the same number of items that they had been imprinted with (Rugani et al. 2009, 2010b). The early availability of small numerosity discrimination suggests that this ability is in place at hatching (Rugani et al. 2008), as well as is basic arithmetic skills (Rugani et al. 2009) and mapping the number line left to right (Rugani et al. 2010a).

### ***Corvid cognition – Comparable to Primates***

In the last few decades an increasing amount of evidence seems to suggest that intelligence (i.e. complex cognition) has evolved independently in several groups of vertebrates, other than primates, such as cetaceans (Marino 2002), canids (Miklósi et al. 2004) and perhaps most remarkably in some birds, such as parrots and corvids (Emery & Clayton 2004b; Seed et al. 2009).

In recent years corvids have been reported to be successful in domains which, in the animal kingdom, were thought to be uniquely found in apes, such as tool use and manufacture (Weir & Kacelnik 2006), travelling mentally in time and space (e.g. de Kort & Clayton 2006) as well as advanced social cognition (Bugnyar & Heinrich 2005). Emery and Clayton, in their 2004 review article (Emery & Clayton 2004b) cite evidence that at least four nonverbal cognitive tools are displayed by both corvids and apes. They propose that these four cognitive tools are the corner points of complex cognition. The first such tool is *causal reasoning* (i.e. understanding causal relationships by which physical or social agents operate) that has been found for example in the tool use and manufacture of New Caledonian crows (*Corvus moneduloides*) in the physical domain (Kenward et al. 2011), and in tactical deception shown

by ravens (*Corvus corax*) (Bugnyar & Kotrschal 2002) both similar to that of chimpanzees (Hare et al. 2000, 2001). The second is said to be *imagination* (i.e. currently perceptually unavailable situations are formed in the mind) displayed for example by ravens in the context of string pulling (Heinrich 1995), followed by *flexibility* (i.e. flexible action upon information and/or flexible learning strategies) as shown by western scrub jays in an experiment where perishable food items were also to be cached and recovery decisions had to be flexibly altered accordingly (Clayton & Dickinson 1998) and finally *prospection* (i.e. simulation of possible future events in the mind) as shown for example by ravens in the food caching/pilfering context (Bugnyar & Heinrich 2005).

The complex cognitive abilities that have been convincingly demonstrated in some corvid (and psittacine) species and the strong similarities to mental abilities of non-human primates may be striking at first glance considering the vast evolutionary distance between mammals and birds (over 280 million years). Moreover, apart from the other trivial morphological differences, birds' neuroanatomy seems to differ greatly from that of primates, as birds show a relative absence of cortical structures (Güntürkün 2005).

Although birds do not have a 6-layered neocortex, there is now a consensus among neuroscientists (Jarvis et al. 2005) that the avian pallium has neo-cortex like cognitive functions and thus the avian and mammalian brain shows substantial homologies. Emery and Clayton (Emery & Clayton 2004a) report a comparative analysis that has been performed to investigate the forebrain : brainstem ratio of 140 bird species as well as the neocortex : brainstem ratio of 63 mammalian species in order to reveal the patterns of relative size. The result of this analysis showed that when the forebrain: brainstem ratio of corvids and parrots is compared to other avian species the pattern of difference closely resembles the pattern of difference of neocortex: brainstem ratio between great apes and other mammals.

The functional equivalent of the primate prefrontal cortex in birds is suggested to be the hyperstriatum ventrale (HV) or the neostriatum caudolaterale (NC). Comparative analysis of the volume of four regions of the forebrain in 6 species of birds (1 corvid (*Corvus corone*) and five other) has revealed that the HV and neostriatum of the corvid species (*Corvus corone*) was indeed larger than predicted by body size (Emery & Clayton 2004a).

To summarize, primate and corvid brains may differ significantly in size and structure, however similar specialization and development of certain regions is evident. None the less fundamental structural differences outnumber the similarities, thus it has been suggested that the relationship of corvids and primates represent a case of divergent evolution regarding their neuroanatomy, however a convergent evolution regarding mental processes. The function of

cognition is to be able to produce flexible adaptive behaviour in a complex and variable physical and social environment. Corvids and apes may well have been exposed to similar evolutionary pressures (Seed et al. 2009), such as surviving and reproducing in a complex and unpredictable environment. Cases of convergent evolution make it possible to identify similar evolutionary pressures and thus those proximate mechanisms that produce complex cognition in two or more lineages. Phylogenetic comparative psychology (MacLean et al. 2012) aims to reveal the degree to which phylogeny predicts cognitive abilities, if cognitive abilities are correlated with ecological, social or perhaps anatomical factors, and may search for evidence on what the ancestral state of a certain ability may be. Phylogenetic methods may also predict the species which may most effectively be used to test a given evolutionary hypothesis (de Kort & Clayton 2006).

### ***Food Storing - does it make a difference in the brain?***

Corvid cognition (as described just above) is, in many cases, shown in a food caching context. It is enough to recall the amazing spatial memory system of Clark's nutcrackers (*Nucifraga columbiana*), storing up to 33000 food items in several thousand cache sites underground and retrieving those with outstanding accuracy several months later (Balda & Kamil 2002). In the social domain, let us mention observational learning or 'tactical deception' (Bugnyar & Kotrschal 2002), visual perspective taking (Bugnyar & Heinrich 2005), or gaze following (Bugnyar et al. 2004) of ravens (*Corvus corax*) also shown in a storing/pilfering context.

Early comparative studies of the avian hippocampus and its role in spatial memory (i.e. recovery of cached food items) have shown a three way association between food storing behaviour, spatial memory and enlargement of the hippocampal complex (Shettleworth 2003). For example Sherry and Vaccarino (1989), when comparing the volume of the hippocampal complex and the telencephalon of 3 food-storing families (chickadees, nuthatches and jays) and 10 non-storing families and sub-families of North American passerines have found that the hippocampal complex is larger in food-storing birds than in non-storing birds. Furthermore, as storing families are not more closely related to each other than they are to non-storing families, they suppose that this greater size is the result of evolutionary convergence. Healy and Krebs (Healy & Krebs 1992) measured the volume of the hippocampal region relative to body mass in seven species of corvid (*Cissa erythrorhyncha*, *Corvus corone*, *Corvus frugilegus*, *Corvus monedula*, *Garrulus glandarius*, *Pica pica*,

*Pyrrhocorax graculus*). Their results showed a positive correlation between hoarding capacity and the relative volume of the hippocampus.

The above approach, suggesting that food hoarders have a larger hippocampus than non-hoarders (called ‘neuroecology’), is widely accepted, however is not shared by all researchers in this field. Bolhuis and Macphail (2001) pointed out three main problems with the suggested correlation, namely that it may not only be the hippocampus that is important in spatial learning and memory, that food hoarders were not shown to be superior in other spatial learning and memory tasks, and that no correlations have been found between behavioural difference and hippocampal volume. In their 2008 review Brodin and Bolhuis (Brodin & Bolhuis 2008) give a very good summary of this debate and suggest ways to further investigate this question.

However, if there is a difference in the volume of the hippocampal complex between hoarders and non-hoarders, this will raise an interesting question. Is this difference only reflected in spatial memory (and related accuracy in cache recovery) or perhaps in other object related cognitive abilities? At least we know that spatial memory is not restricted to remembering where food has been stored, but it is more general, so it is safe to say that dependence on stored food has been a selective pressure in the direction of advanced spatial cognition, but not in a domain specific way (Balda & Kamil 2002).

Thus the proposition that the study of the performance of a non-storing corvid species, such as the jackdaw (*Corvus monedula*), in cognitive tasks, may bring interesting new results to the field and perhaps bring more insight into what part of corvid cognition may have – or may not have - been influenced by the selective pressures of dependence on stored food.

### ***The Legacy of Otto Köhler***

Finally in this section of introduction to my thesis I feel the need to mention the scientific work of Otto Köhler (1889-1974), German ethologist. My reason for doing so is not only the fact that he conducted and supervised a series of controlled experiments that established the representation of number as a cognitive process in animals (Boysen & Capaldi 2014), but also the sentimental fact that he used (among many other bird species, of course) jackdaws (*Corvus monedula*) as subjects.

After his early research on microorganisms and certain general problems of ontogeny and genetics his research interests were strongly influenced by the young discipline of ethology. He became the founder and co-editor of the scientific journal, *Zeitschrift für*

*Tierpsychologie* (now called Ethology) in 1936, together with Konrad Lorenz. His studies of “counting” in animals have started with a student paper (Fischel 1926) and produced an outstanding theoretical review in 1943 and ended with an English paper in 1957. Previously, there had been decades of attempts to show that animals were able to count, but there was always some deficiency in the experimental procedure which rendered the results questionable. It was the outstanding achievement of Otto Koehler and his colleagues to produce convincing results, under controlled circumstances, which showed that animals, mostly birds, can “think un-named numbers”—that is, they have a pre-linguistic number sense; to some extent, “they think without words” (Hassenstein 2010). This is an achievement with which Otto Koehler’s name will always be linked.

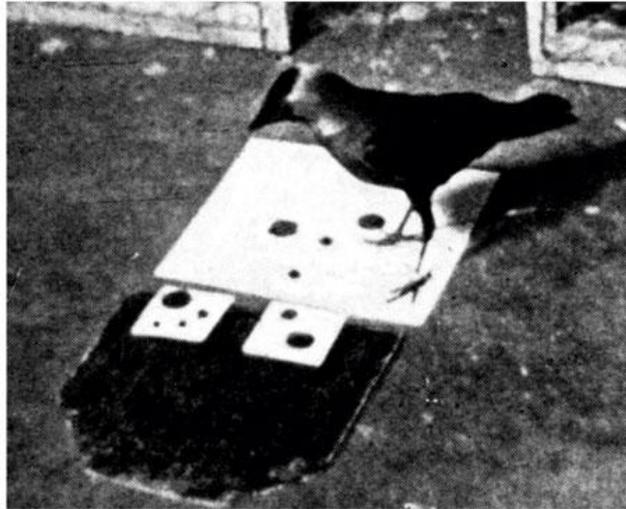
His experiments with jackdaws included a matching-to-sample task in which one of the jackdaws was particularly successful. After looking at an array of patches on a "sample" card, the bird had to remove the lid from one of two reward pots, which had the same number of marks, as the sample card. One bird, that performed best on this task, could match the numbers of items on the sample card and the comparison lid even when the configuration of patches and their sizes differed (both between and within trials), so that the only common feature was their number.

Another one of Koehler’s tasks that involved jackdaws consisted of taking the lids off pots until a specific number of hidden food items had been retrieved, after which the remaining pots in the row would be empty. The important feature of this experiment was that on successive trials, the same number of food items was differently distributed.

From these and many other studies, Köhler concluded that the tested species have at least a limited ability to discriminate objects or events on the basis of their numerosity and inferred that these animals have some way of internally tagging the items they have seen or responded to. Koehler was careful to say that animals do not seem to count in the way that an adult human, rather, he argued that animals learn what he called "unnamed numbers", so that four items might be represented by a series of inner marks or tags. He also noted that different species showed remarkable similarities in the limits of their ability to discriminate numerosity (Köhler 1941).

Similarly to Darwin and several other ethologists, Koehler assumed that there is continuity between animal and human mentality. His primary interests were learning and thinking without language. His studies on “un-named numbers” and “un-named thinking” brought Koehler conveniently to some reflections that are anthropologically relevant. Köhler was particularly interested in animal and human communication, and he tried to discover

some basic patterns of “language” in various species. He maintained that there are prototypes of human communication in animals. Generally, his aim was to close the traditional gap between animals and humans and to show that any specific human ability has roots in some capacities displayed by animals (Rilling 1993).



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# Aims and Hypotheses

## Object Permanence

Within the framework of this Thesis, as a **first** step, I aimed to gather some basic data on the development and final stage of object permanence (OP) in jackdaws (*Corvus monedula*), while checking for the presence of characteristic errors (such as the A-not-B error mentioned in the Introduction). The development of OP has been previously studied in four food storing corvid species, magpies (Pollok et al. 2000), ravens (Bugnyar et al. 2007), Eurasian jays (Zucca et al. 2007) and western scrub-jays (Salwiczek et al. 2009). Apart from gathering data on yet another corvid species, which has its merit in its own right, I was also interested in the fact that jackdaws store little or no food in the wild. This species lives a very ‘object centred’ life, as well as has a sophisticated social system (de Kort et al. 2003), so any deviations from OP development of storing species could be interpreted in the caching/non-caching context. As mentioned briefly before, within the old world corvids, the jackdaw (*Corvus monedula*) is known to cache little or not at all, and have a relatively small hippocampus, thus this species is often presented as a ‘typical non-storing species’ (Clayton & Krebs 1994; Pollok et al. 2000; Kort et al. 2006). It is important to note however, that all the close relatives of jackdaws actually cache, which may lead us to speculate that it may be more parsimonious to hypothesize that the common ancestor was a food storer (caching being a homology in corvids), in which case jackdaws secondarily lost their caching behaviour, as an adaptive specialization, where, for some reason, this species became less and less dependent on hoarded food (de Kort & Clayton 2006).

### *In summary:*

#### **Aims**

- Gathering missing data on the development and final stage of OP in jackdaws with the same method as in related, but caching species, such as the magpies
- Check for characteristic A-not-B error phase
- Clarify final stage with additional experiment

- Contrast development rate with that of closely related species, the magpie

**Prediction**(Pollok et al. 2000):

- Non-caching jackdaws will be found to develop slower than caching magpies
- Difference will be found in final stage reached

**Hypothesis**

- As common ancestor is suggested to be a cacher, and OP has functions in other contexts, we *do not* expect development rate to be slower or final stage different

**Quantity related studies**

Once the basic data on ontogeny of OP has been collected and our jackdaws became young adults, I started on a series of studies on quantity related abilities. As described earlier in the Introduction, ‘counting’ and ‘number’ related abilities in animals had a long history in comparative research, initially trying to find the roots of our own sophisticated mathematical thinking. Since the beginnings, many species have been reported to show some level of ‘quantity related’ processing, from fish through apes. However results from corvids were few and far between (Köhler 1941; Zorina & Smirnova 1996; Smirnova et al. 2000), and while the field of number related research in non-verbal subjects has grown immensely, data on corvid species did not seem to proliferate. As mentioned earlier, jackdaws seemed promising subjects in quantity related experiments, not only as Otto Koehler published some positive results in this species, but also based on their social structure (colony breeding, etc.) and foraging techniques. Also, as described earlier in detail, corvids were reported some cognitive abilities paralleling primates in other contexts (Emery & Clayton 2004b).

Having the data from the OP experiments, I supposed that jackdaws readily form mental representations of objects temporarily out of view. In a brief baseline experiment I also established that subjects showed a general, strong preference for more food over less food, as naturally expected. Based on these two facts I decided to use a special case of relative quantity (formerly termed numerosness) judgements, where the items were placed into opaque containers one-by-one, thus the entire set was never visually available to the subjects.

In this case jackdaws needed to keep track of the quantity during the one-by-one additions. These types of procedures have been used in case of monkeys (Hauser & Carey 2000) and apes (Beran et al. 2009) previously, so positive results could mean yet another point where corvid cognition resembles that of primates.

We find that corvid species are considerably underrepresented in quantity related cognition studies in birds. This is in particularly true for non-caching corvid species. While a fair amount of studies have been published lately on quantity related cognition in non caching non corvids, for example gray parrots (*Psittacus erithacus*) (Aïn et al. 2009; Pepperberg & Carey 2012), domestic chicks (*Gallus gallus*) (Rugani et al. 2009, 2011; Fontanari et al. 2011; Vallortigara 2012) as well as pigeons (*Columba livia*) (Scarf et al. 2011) and even some on caching non corvids, North Island robins (*Petroica longipes*) (Hunt et al. 2008; Garland et al. 2012), only two papers came out, already some time ago on caching corvids, namely hooded crows (*Corvus cornix*) from the same laboratory (Zorina & Smirnova 1996; Smirnova et al. 2000).

To my knowledge, there has been no research on this topic with non caching corvids, such as jackdaws since those of Otto Köhler (please refer to section in the Introduction). Thus, for the sake of filling in at least a bit this hole in the existing data, and also as we had good reason to hypothesise that jackdaws may have enhanced quantity related abilities due to their ecology, we started our experiments, as will follow below.

### ***In summary:***

#### **Aims**

- to investigate quantity related abilities in non-caching jackdaws, adding some interesting data on corvids in the physical cognition domain
- by using opaque containers and one-by-one placement where subjects have to rely on mental representations as in Hauser et al. (2000) with rhesus monkeys, apes (Beran 2004; Hanus & Call 2007), or capuchin monkeys (Evans et al. 2009)
- by using a non-corrective method in order to minimize possible training
- to control for temporal factors

## **Hypothesis**

- jackdaws will be able to discriminate larger set sizes based on mental representations of the sets
- without any quantity related training
- jackdaws' performance will be comparable to that of rhesus monkeys, apes and capuchin monkeys

# Experiments

## *Experiment 1:*

### *Ontogeny of Object Permanence in the Jackdaw* (Ujfalussy et al. 2013)

#### *Introduction to our Object Permanence study*

In the physical world that we share with countless organisms, both animate and inanimate objects tend to move through space. The ability to follow these appearing, disappearing and perhaps reappearing objects is of unquestionable advantage to virtually any organism, indeed it is crucial for any animal's survival. When following the movement of an object, an individual may rely on a number of signals, visual, olfactory, auditory (Etienne 1984). However when an object disappears without leaving such perceptual cues, following its movements requires some cognitive tools, such as mental representation of the object as a distinct entity and the ability to understand that objects continue to exist, even when temporarily out of sight of the observer.

As briefly mentioned earlier, in children object permanence develops over the first two years of life in a staggered manner. Piaget (Piaget 1954) has shown that children develop their understanding about temporarily invisible objects in distinct stages, which each correspond with a specific age. Before children start to search for an object that they have seen disappear, they are still in stage 1 according to Piaget. At stage 2 children become capable of visual pursuit a moving object, while at stage 3 they can retrieve a partially covered object. At the beginning of stage 4 infants are only able to find a hidden object if a grasping movement has been initiated at the time of disappearance (stage 4a), while later (stage 4b) this condition is no longer a prerequisite to recover the object (single visible displacement). However, in stage 4b, infants remain unable to solve a sequential visible displacement (where the object is fully visible during the manipulations). They are prone to the so-called A-not-B error, as they search for the object where they previously found it even though they saw the object hidden in another location. In stage 5 the A-not-B error has disappeared and infants solve problems with a sequential visible displacement (stage 5a) and successive visible displacement (stage 5b). In stage 6, infants master first (stage 6a) problems with a single invisible displacement (when the object is hidden first in the hand or in a container and then is moved behind a cover). Then, in

stage 6b, problems involving sequential invisible displacement and successive invisible displacements are mastered.

Object permanence is a fundamental cognitive skill that may serve as basis for more complex cognitive mechanisms in animals as well as humans. Moreover the comparative study of infant development and animal cognition might be very useful in gaining information on the nature and evolution of cognition (Gómez 2005), while it is undoubtedly important to keep in mind the possibility that similar abilities in different species may be based on different mental mechanisms. The presence of object permanence capacity has been extensively studied in many species, including several avian species (Etienne 1973; Dumas & Wilkie 1995; Funk 1996; Pepperberg et al. 1997; Funk & Matteson 2004). Some of these studies (Doré & Goulet 1998; Gómez 2004) have revealed that many species develop object permanence skills in the same sequence as children, only at different speeds. Though in some aspects criticised by some researchers (Bower 1982; Doré & Dumas 1987; Baillargeon 1987), the Piagetian framework has been recognized as a very useful tool tracking the existence of the developmental stages, and also for comparative research, as the tasks involved may be administered with minimal variation to very different species, so differences revealed cannot simply be explained by different experimental procedures (Pepperberg 2002).

Corvid cognition is generally considered quite advanced. As described before in more detail, it may even parallel primate cognition in several aspects (Emery & Clayton 2004a). Most of the intriguing evidence of these highly specialized mechanisms come from studies conducted in a food-storing context (e.g., Balda & Kamil 1992; Clayton & Krebs 1994; Bednekoff & Balda 1996a, 1996b; Heinrich & Pepper 1998; Dally et al. 2005). These studies show that food-storing corvid species have an excellent spatial memory, some are capable of recalling cache sites even many months after the cache was made, moreover some can recall also the type of item cached at the particular places as well as when the cache was made, suggesting the presence of “episodic-like memory” (Clayton & Dickinson 1998). They also seem quite capable of handling the social aspects of caching, as there is a growing amount of evidence in corvids for phenomena such as gaze following (Bugnyar et al. 2004), visual perspective taking (Bugnyar & Heinrich 2005; Dally et al. 2006) and tactical deception (Bugnyar & Kotrschal 2002). The capacity to remember numerous cache sites for sometimes extended periods of time, in sum excellent performance in studies of spatial memory, has been associated with a relatively larger hippocampus in food-storing corvids (Healy & Krebs 1992).

Considering all this information on a wide range of food-storing species, we know surprisingly little about the cognitive capacities of non-storing corvids. Jackdaws are one of the few Old World corvids caching very little or no food, and have been shown to have a relatively smaller hippocampus (Healy & Krebs 1992) than their caching relatives, which might affect their performance in spatial memory tasks. Scheid and Bugnyar (Scheid & Bugnyar 2008) have shown that food caching ravens are much more efficient in observational spatial memory tasks than non-caching jackdaws. However, very little attention has been paid to how these differences may affect other related cognitive abilities. Among many others, the development and final stage of object permanence has so far only been studied in food storing corvids. Eurasian jays (*Garrulus glandarius*) (Zucca et al. 2007) and ravens (*Corvus corax*) (Bugnyar et al. 2007) have been shown to have Stage 6 competence, while magpies (*Pica pica*) (Pollok et al. 2000) also reached Stage 6, while showing a particular anomaly.

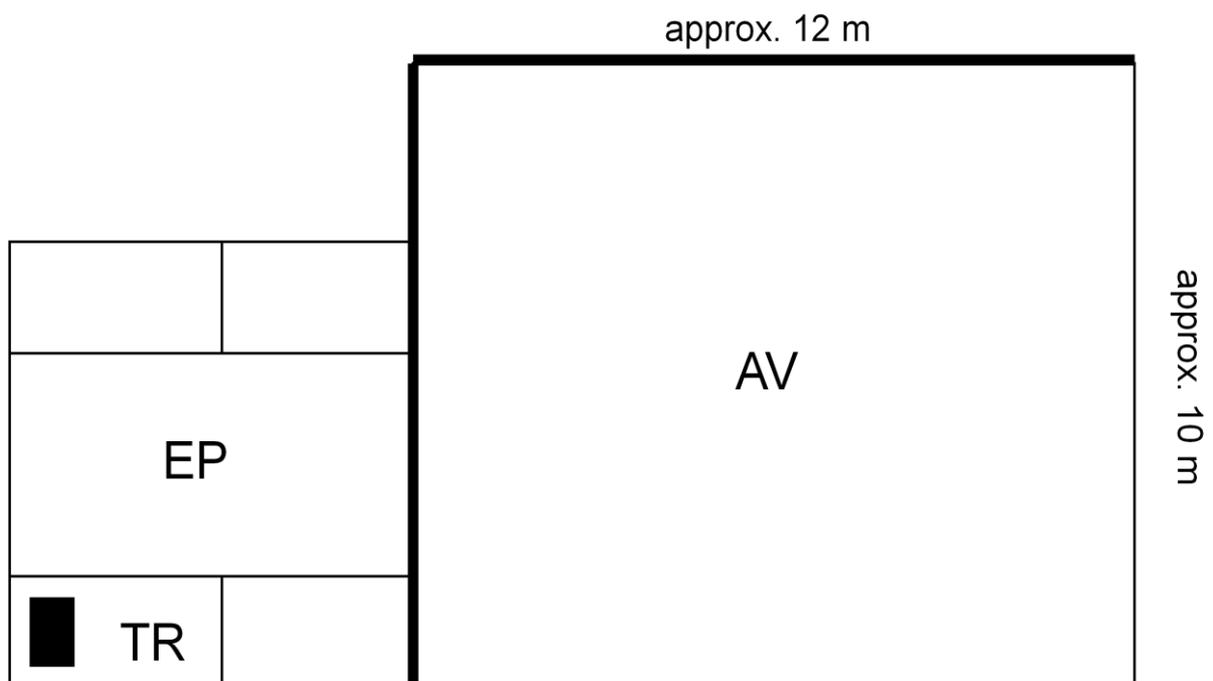
To assess the ontogeny of object permanence and the final stage reached in a non-storing corvid species we have conducted a series of experiments on 19 hand-raised jackdaws (*Corvus monedula*). In order to obtain comparable data to recent studies on caching species (Pollok et al. 2000; Zucca et al. 2007; Bugnyar et al. 2007; Salwiczek et al. 2009) we have used the same methodology, namely the “Scale 1” series of tasks from Uzgiris and Hunt (Uzgiris & Hunt 1975a) (see also Pepperberg et al. 1997 and Pepperberg 2002) and one additional test, the so called “Shell game” to further assess the question of stage 6 competence (Sophian & Sage 1983; Sophian 1985). Despite criticism of this method, mainly on the “face-to-face” nature of the testing and the possible training of subjects (habituation or learning) in the course of testing, we have decided in favour of using it primarily for the sake of comparability. None the less we have addressed the critical issues, minimized the chance of possible cueing and tested for any possible effects of training. Apart from comparability, another positive aspect of “Scale 1” is that specific subsets of these tasks directly correlate with Piagetian stages, but provide finer divisions of these stages, possibly yielding more detailed information.

## **Method**

### ***Subjects***

We have hand-raised 20 young jackdaws (*Corvus monedula*) to participate in this and some other experiments starting in the spring of 2005. The hand-raising and the testing took

place at the Konrad Lorenz Research Station in Grünau, Austria. The jackdaws were taken from nests in Stralsund and in Baden-Württemberg, Germany, with appropriate licences, in between the age of 13 and 20 days post hatch. After their capture they were kept in cardboard boxes, 2, 3 or 4 birds together, lined with hay and kitchen towels, until they fledged at between 26 and 31 days of age. A few days after fledging they were moved to a spacious outdoor aviary, approximately 12 metres by 10 metres and about 4-5 metres high. The aviary was fully equipped with perches, sheltered shelves, a tray of bathing water, and the floor was covered by natural vegetation. A small experimental complex, consisting of 5 compartments, was connected to the main aviary by a wooden door and a wooden window, so the experimental areas could be fully visually separated from the main aviary (for rough plan of the premises see Figure 5). The floor of the experimental complex was covered with fine grained gravel. During most of the day, when no testing was in progress, the birds were free to roam in the entire main aviary and the experimental complex as well.



**Figure 5. The jackdaw aviary and the experimental rooms.**  
**AV=main aviary, EP=experimental parts, TR=testing room**

While still in the nest, the birds were fed with a wet mix consisting of ground beef, hardboiled egg yolk, cottage cheese and a commercially available dry insect mix. Bird vitamins and ground cuttlebone were mixed into the food. On hot days additional water was provided through syringes. After moving to their outdoor aviary the birds continued to be fed on this mix, but gradually other various foods were introduced such as fruits, vegetables, pasta, rice, potatoes, milk products, mealworms, crickets and dry cat food as treats.

All of the subjects participated in object permanence testing except as noted below, for exact number of subjects in each task, please see Table 1. One very shy bird, Dominique, had to be excluded from testing before task 5, as it became extremely reluctant to enter the experimental complex. From this point on the total number of subjects was 19.

To assess criticisms of “Scale 1” concerning training and learning throughout the testing procedure we divided our subjects randomly into 3 groups. The subjects of our first group ( $N=8$ ) were tested on all tasks. The subjects of our second group ( $N=5$ ) were tested on only every second task from task 4 onwards (namely on tasks 6, 8, 10, 12 and 14), while in the third group ( $N=6$ ) subjects skipped tasks 5-9, and resumed testing on task 10. All birds ( $N=19$ ) were tested on Task 15. The aim of this experimental design was that if there is a training effect altering the age at which a certain task is passed, then we should be able to find a difference in the performance of our groups, due to the different amount of testing.

A total of 10 subjects ( $N=10$ ) participated in this Task “S”, the Shell Game, five from Group 1, one subject from Group 2, and four from Group 3.

## ***Procedures***

### **Tasks**

The test series of “Scale 1” has been designed so, that it’s tasks increase in difficulty and are meant to be administered one after the other, i.e. when one task is passed, the next, more difficult task is to be presented. Subjects’ responses were coded correct only in case they have responded exactly according to criterion (see below).

#### *Stage 2 (visual pursuit)*

**Task 1:** Subject succeeds in this task if it is able to track an object moving slowly around the bird in a horizontal plane through an arc of 180°.

**Task 2:** A moving object disappears behind a screen. Success is demonstrated in this task if the bird looks at the point of disappearance or returns its glance to the starting point, after several presentations.

Stage 3 (*simple visible displacements-partial hiding*)

**Task 3:** An object is partly hidden under a single cover that is laid on the table. The criterion of success is met when the subject obtains the object either by pulling it from under the cover or by removing the cover and then taking the object.

Stage 4 (*simple visible displacements-complete hiding*)

**Task 4:** An object is completely hidden under a single cover laid on the table. The criterion of success is met if subject removes the cover and picks up the object. Search was only allowed to begin when the hiding process was completed.

Stage 5 (*simple and complex visible displacements-multiple covers*)

**Task 5:** Two covers, A and B, were used. The object was hidden three times under one cover (A in the case of 10 birds and B in the case of the other 10), then was hidden under the other cover. Criterion performance was immediate search under the cover where the object has been last hidden. Errors in this task, namely continued search under the first cover (so-called A-not-B errors) characteristically precede stage 5 competence in human infants.

**Task 6:** Two covers, A and B, were used, and the object was hidden alternately under the two different covers. Criterion performance was to search immediately under the cover where the object was last hidden.

**Task 7:** Three covers, A, B and C, were used. The hiding place of the object varied between the three covers. Criterion performance was to search immediately under the cover where the object was last hidden.

**Task 8:** In this task the object was held visibly in the hand of the experimenter and was passed successively under two of the covers and then was finally hidden under the third cover. Success in this task is demonstrated only if the subject searches directly under the final hiding place. Searching in the order of the hiding is incorrect.

**Task 9:** In this task the three covers were laid on top of each other and the object was hidden under them, so to meet criterion the subject had to remove all three superimposed covers to obtain the object. This task is meant to test the subjects' persistence.

Stage 6: (*invisible displacement tasks, in which only the implementing cover is visible, thus inferential abilities are required to track object*)

**Task 10:** One standing screen (set up perpendicular to the plane of the table) and a small non-transparent container were used. The object was placed into the container, then the

container with the object inside was moved behind the screen and the object was hidden there. Finally the empty container was shown to the bird. Criterion performance was indicated if the subject checked the container, then retrieved the hidden object from behind the screen, or went straight to the screen to retrieve the object.

**Task 11:** Two standing screens (A and B) and a small non-transparent container were used. As in task 5, the object (only this time concealed in the container) was hidden three times behind one screen, and then hidden behind the other screen. The hiding was similar in other ways to the hiding in task 10. Success is demonstrated by the subjects if they immediately start searching behind the screen where the object was hidden.

**Task 12:** The container concealing the object was moved behind one of the two screens (A and B), alternating by trial, where the object was then hidden. The hiding was similar in other ways to the hiding in task 10. Criterion performance was immediate search behind the screen where the object was hidden.

**Task 13:** The object travelling in the container was hidden behind one of three screens (A, B or C). The hiding was similar in other ways to the hiding in Task 10. Criterion was immediate search behind the screen where the object was hidden.

**Task 14:** Three screens (A, B and C) were used. The object was placed visibly in the palm of the experimenter, who then closed her hand thus concealing the object. The closed hand was passed behind two screens then finally the object was left behind the last screen. The empty hand was shown to the subject. The sequence of the displacement was either ABC or CBA. The criterion was searching all screens in the same order as the hand moved and finding the object under the last screen. If the subject has previously found the object under the last screen in this situation, going only to the last screen and finding the object was also acceptable.

**Task 15:** Very similar to task 14, except that it is a “trick”, as the object was left under the first screen visited by the closed hand, but the hand moved on, leading the subject to believe that the object will be hidden under the last screen. The criterion here was to search the screens in reverse order. For alternatives in the interpretation of performance in this task, please see Results and Discussion.

**Task S (“Shell game”):** We also tested our birds on a task, testing for attention, spatial cognition and different memory types, as well as object permanence abilities, similar to the one suggested by Doré et al. (Doré et al. 1996). This procedure was initially introduced in infant studies by Sophian and Sage (Sophian & Sage 1983; Sophian 1985). Three non-transparent containers were used in this task, with the object visibly hidden in one of them.

After hiding the object the experimenter visibly changed the position of the baited container relative to the other two. Task S included seven trials, in five of which the baited container changed its relative position, while in the remaining two the baited container remained in place and another container was moved to a different position, so unlike the first five trials, the subject had to choose a container that remained in place in order to obtain the reward. These two trials were intended to control for stimulus/local enhancement. Exact manipulations involved in the trials of Task S are shown in Figure 6.

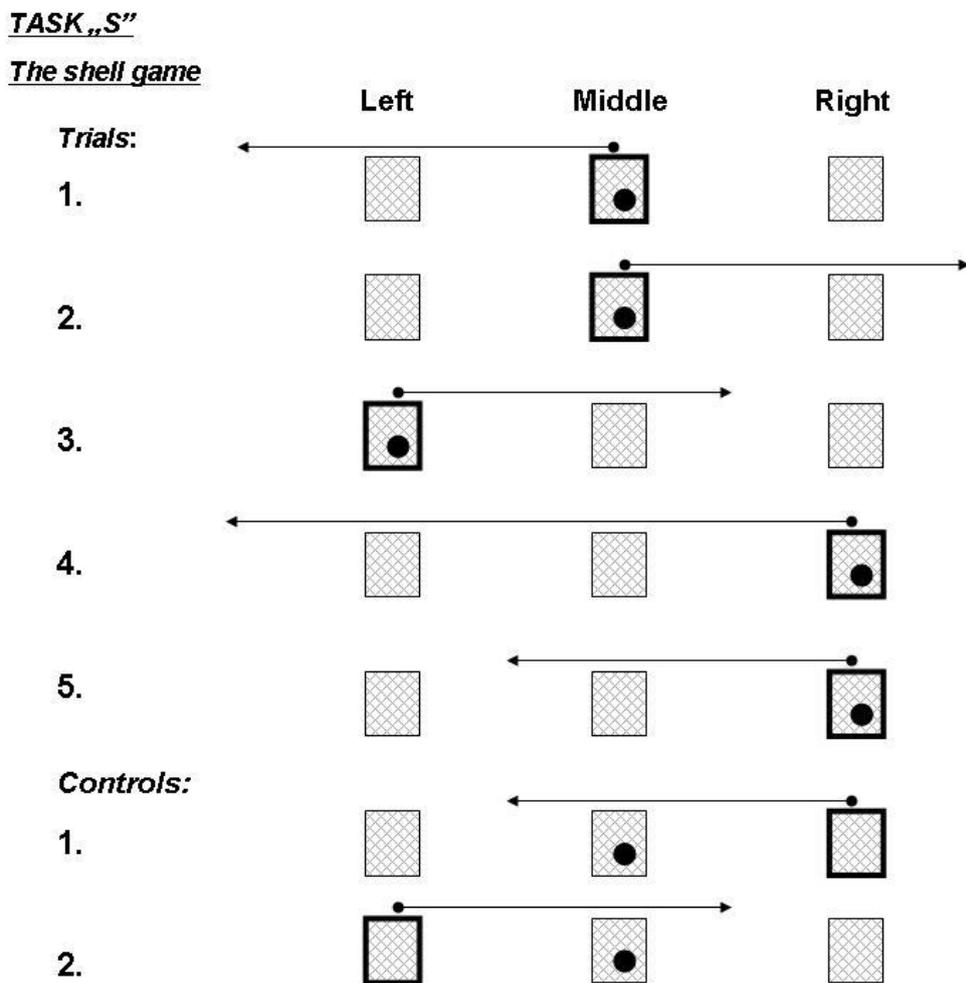


Figure 6. Trial and control situations in our Task S, the Shell Game. In trials the baited containers moved to change their relative position, while in the controls the baited container remained in the same place and empty containers moved. (Dots indicate baited containers, dark outlines indicate moving containers.)

## *Apparatus*

When we started our experiments, our subjects were still in the nest-boxes and were unable to feed on their own. Apart from this they were unable to ingest relatively large and hard items, which would have been suitable to use as search items. For this reason we have started testing with non-food objects, namely pieces of shiny tin foil (approx. 1 cm by 3 cm) in which the birds were particularly interested. After task 4 was passed we found that our birds became less interested in non-palatable objects, but were increasingly motivated by cat food treats, so we used these treats as search objects from that task onward. We used brown cardboard squares (10 cm by 10 cm) as screens. They were slightly bent and crumpled in the middle to give full coverage, so the baited screen provided no visual cue to the position of the hidden object. All the screens used were identical without any markings. Where several screens were used, they were placed approximately 30 cm from each other. On tasks testing invisible displacements we used a small brown cardboard container (5 cm by 4 cm by 3 cm) and the screens were set up perpendicular to the plane of the table, as we found it easier and less confusing to subjects to pass behind them with the container, rather than trying to pass under them. For the shell game we used 3 small cardboard containers similar to that used previously in invisible displacement tasks.

Although the relative importance of the sense of olfaction to birds seems to vary greatly between avian species (e.g. Harriman & Berger 1986) and for example Gagnon and Doré (Gagnon & Doré 1992) argue that odour cues are unimportant even for creatures with an olfactory sense as sensitive as dogs', we wished to control for this possibility due to such criticism in connection with Scale 1 (Pepperberg et al. 1997). In order to do this, when starting to use food as search items, we stored all the objects used in the tasks in actual physical contact with the search items (cat food), so that all objects acquired the odour of the treats, to avoid the possibility of olfactory cueing.

## *Procedure of testing*

Testing began 12 days after acquiring the birds (at age 25-32 days old), when they were still in their nest-boxes, prior to fledging. The testing for the first tasks (1, 2 and in some cases 3) was conducted while the subjects were still in their nest boxes. After the birds moved to their outdoor aviary (ages 21-36 days post hatch), the testing was conducted in one of the

compartments of the experimental complex on a table (100 cm by 70 cm) put there for this purpose.

Testing sessions took place every day when the weather allowed, but subjects were never tested on a particular task on two consecutive days and in general we attempted to expose each individual to a given task as few times as possible to avoid trial-and-error learning or conditioned responses. On the other hand we aimed at testing each subject at least every 3 or 4 days as not to miss the exact onset of capability of passing certain task or stage.

At the beginning of each testing session the birds were called (vocally and offering treats) into the experimental complex through the door. Usually more than one subject entered initially, as some birds were especially keen on participating. The door was then closed. The birds that entered were allowed to stay in the first compartment and only one subject at a time was allowed to enter the actual compartment where the testing took place. Testing for a particular subject was terminated for the day if it performed an incorrect response. On making a wrong choice, the subject was immediately shoed out, and was never allowed to continue searching, so it could never observe where the item had actually been hidden. In order to pass a Task the subject had to respond correctly on 3 consecutive trials in one session without errors. From task 5 onwards we considered a Task passed if the bird had made 3 correct responses and no errors. This change was made as the tasks became increasingly complicated and we wished to accurately pinpoint the onset of a certain stage as well as aiming to avoid training (learning, habituation) due to overexposure to a task.

When testing was finished for the day for a subject, it was let out into the central part of the experimental complex until all subjects had completed their testing, then the whole flock was allowed back to the main aviary. Calling the subjects in from the main aviary was repeated when all the birds in the first compartment had completed testing and transferred into the central part, until eventually all the birds had their testing session. The birds were physically, but not visually separated from their flock mates at the time of testing, but neither the birds in the first compartment, nor the birds already in the central part had a direct view of the table and the manipulations taking place there. The voluntary nature of testing and the lack of total visual separation from the others resulted in the birds being relaxed and motivated in the testing situation, which is very important when trying to assess cognitive abilities, as stress may impair performance in such experiments (e.g., De Kloet et al. 1999; Weir & Kacelnik 2006).

The experimenter was seated while she manipulated the objects, and the birds were sitting on a perch level with the height of the table and about 15 cm away from the edge of the

table and altogether approximately 50 cm away from the setup. The manipulations took place when the bird was paying attention and was seated on the perch. When the manipulations were complete, the experimenter lowered both of her hands to her lap and looked up, away from the setup and directly at the bird. If the bird initiated search before this position was taken by the experimenter, it was not allowed to make the choice. Bearing in mind the dangers of experimenter cueing in this face-to-face testing situation, the outmost care was taken as not to influence the choice of the bird in any way. When the experimenter had taken up this neutral position, the bird was allowed to jump onto the table and search freely.

### *Data analysis*

We used Kolmogorov-Smirnov tests to check normality of our data for each group and each test (data were grouped by task and by group). As we found that some of our datasets were not normally distributed, we proceeded to use non-parametric analyses. To compare the performance of three groups we used Kruskal-Wallis tests with a Dunn's Multiple Comparisons test where necessary, while when comparing only two of our groups, we used Mann-Whitney U tests. To assess possible correlations between the numbers of sessions when birds have committed errors and their performance in object permanence tasks we used Spearman's Rank Correlation test. To determine the mean age of passing a task, data from all three groups were pooled.

## **Results**

### *Mean age of the subjects at passing Scale 1 tasks*

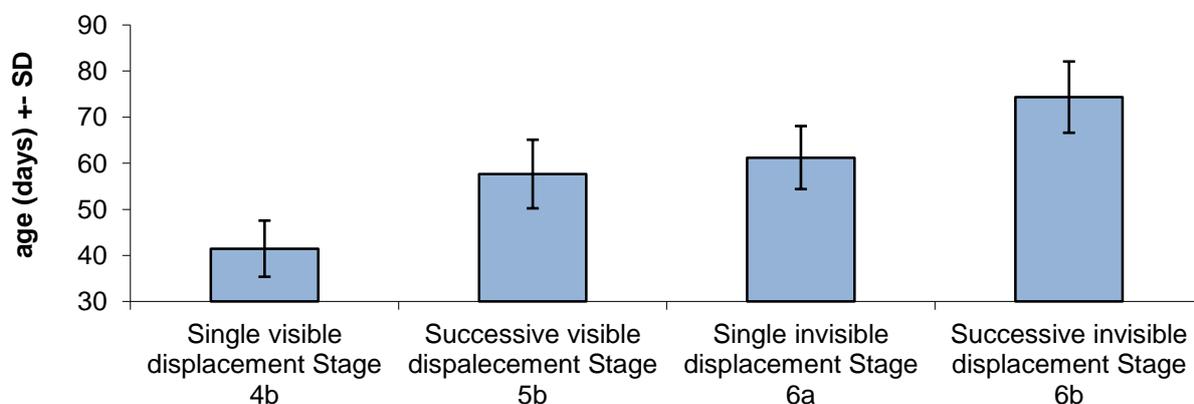
For detailed results on the mean age of passing each Task please see Table 1. The subjects were generally able to master all the tasks of Scale 1 administered to them. An exception from this is the heterogeneous performance showed in task 15, as will be explained later in this section. The onset of competence in a certain task occurred roughly at the same age in all subjects, although there was considerable age difference in the flock.

Task	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>N</i> =	20	20	8	14	8	14	8	19	13	19	13	19	14
Age(days)	36.6	41	43.5	47	48.4	57.6	61	61.2	68.4	69.1	74.3	74.3	80.7
<i>SD</i>	4	6.1	5	4	4.2	7.4	9.1	6.8	7.6	7.2	6.3	7.7	7.9

**Table 1. The mean age ( $\pm$ SD) of the birds in days when passing each task and the number of subjects taking part in the tasks.**

In summary, we found that our birds were capable of following single visible displacements (task 4, stage 4b) by the mean age of  $41.45 \pm 6.09$  (*SD*) days, successive visible displacements (task 8, stage 5b) by the mean age of  $57.64 \pm 7.44$  (*SD*) days, single invisible displacements (task 10, stage 6a) by the mean age of  $61.21 \pm 6.84$  (*SD*) days and successive invisible displacements (task 14 stage 6b) by the mean age of  $74.3 \pm 7.72$  (*SD*) days. See Figure 3.

### Mean age of passing Piagetian Stages 4b, 5b, 6a and 6b



**Figure 7. Mean maximum age of passing single visible, successive visible, single invisible, successive invisible displacements (Piagetian Stages 4b, 5b, 6a and 6b)**

Describing the results in more detail, we can say that all of the subjects ( $N=20$ ) were able to master task 1 (tracking movement of an object through an  $180^\circ$  arc) and task 2 (looking at the point of disappearance when object disappears behind a screen) when testing began (at age 25-32 days old, in nest-boxes, prior to fledging).

Task 3 (partly hidden object) was mastered at the mean age of 36.6 days ( $\pm 4$  *SD*) post hatch, while task 4 (completely hidden object) was mastered at the mean age of 41 days ( $\pm 6.1$  *SD*); in the case of both these tasks the number of subjects was 20. Passing task 3 mainly occurred on the second session, so on the first possible occasion according to our criterion.

As mentioned before, after passing task 4 we randomly assigned our subjects into 3 groups. All birds, except the one that was excluded, were tested on task 15. Table 1 shows the number of subjects participating in certain tasks and the mean age at which tasks 5 to 15 were mastered by the birds. Regarding task 5 it is important to note that some of our subjects (2 birds out of the 8 subjected to this particular task), made characteristic A-not-B errors, meaning that they kept searching under the first cover even when they witnessed the bait being hidden under the second cover. We feel that it is important to state this fact, keeping in mind that the issue of A-not-B errors is a key question of object permanence related studies, however we find that our data are not sufficient to draw any conclusions as to the possible causes of this phenomenon.

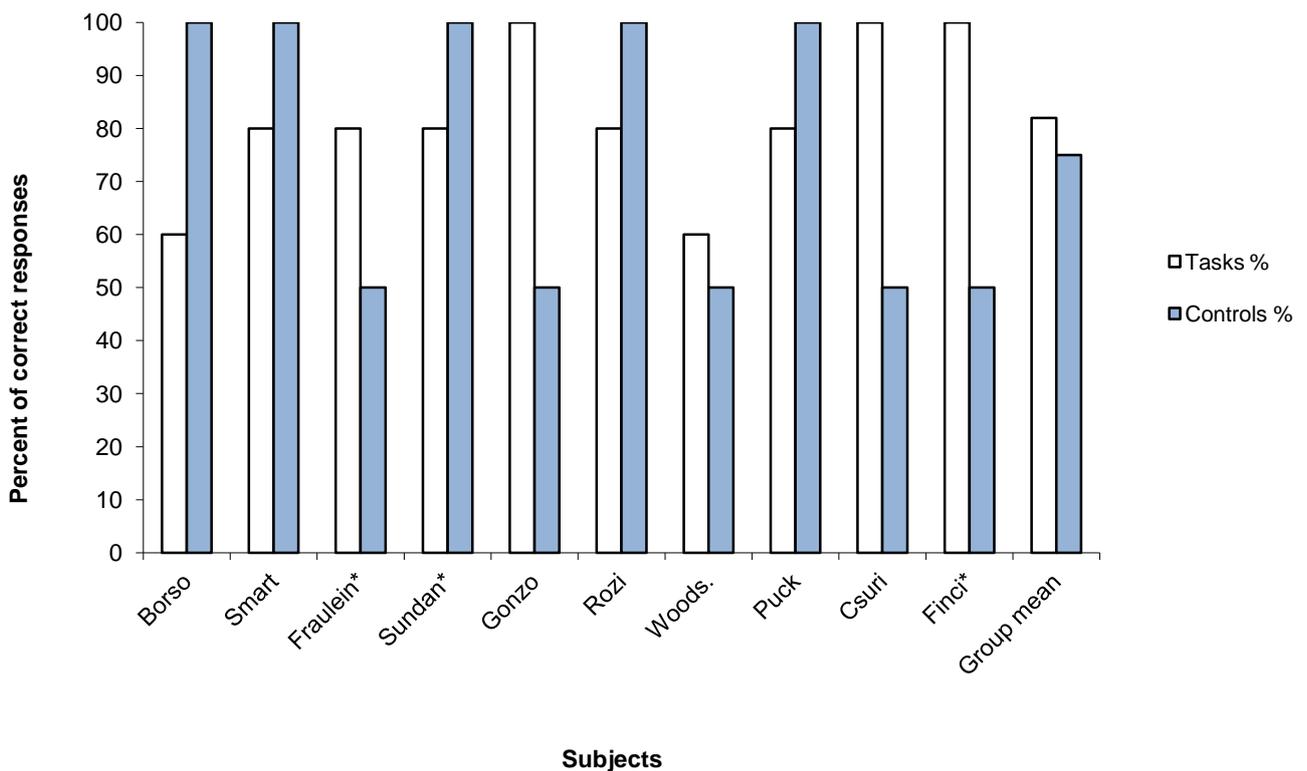
As we have mentioned before, and similarly to the findings of Pollok et al. (Pollok et al. 2000) in the case of magpies, our subjects showed inhomogeneity in their performance in task 15. Out of our total 19 birds subjected to this task, 14 birds eventually passed this task according to our original criterion, searching the screens in reverse order. However 5 individuals did the same in this task, as they had done in the previous one, attempting to follow the route of the hand concealing the desired item, and thus they found the item straight away under the first screen. This is exactly the same as Pollok et al. (Pollok et al. 2000) found in case of caching magpies. As this trick task only makes logical sense if performed following task 14, we attempted to retest these subjects after administering task 14 again, but they did not change their original strategy even after the third such session. As this response is just as logical as the criterion response from another point of view, we abandoned their testing. However, due to the uncertainty concerning task 15 we proceeded to perform task S, to further assess stage 6 competence.

### ***Task S (“Shell game”)***

As described before in the Procedures section, this extra task was designed to test for attention, spatial cognition and different memory types, as well as for stage 6 object permanence abilities. As mentioned in the Subjects section, 10 subjects ( $N=10$ ) participated in this task, five from the original Group 1, one subject from Group 2, and four from Group 3.

Three of these 10 were the birds showing particular difficulties with Task 15 (as mentioned above), so these birds were not (by no means!) excluded from further investigations into Stage 6 competence. As the five trial types are identical in their logic, and so are the two stimulus/local enhancement controls, the performance of each bird was calculated as a percentage of correct responses per the total amount of trials in both test and control trials.

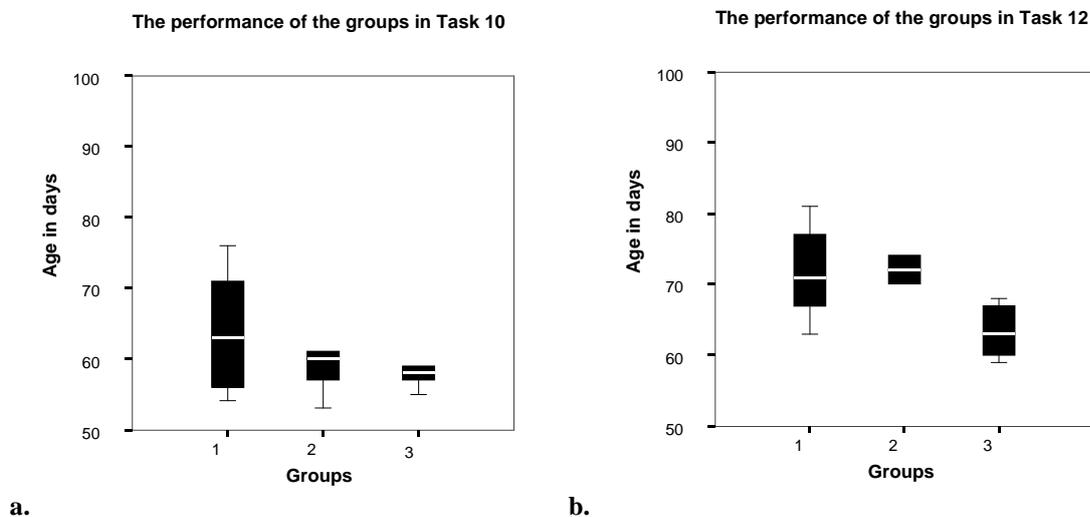
Their performance was then compared to a 33% chance level, using Wilcoxon's signed rank test (Thas et al. 2005), as there were three possible boxes to choose from in this task. We found that the performance of the birds in the Shell game was significantly better than chance ( $T+=55.00$ ,  $P=0.002$ ). Their performance in the stimulus/local enhancement control trials was also significantly above chance ( $T+=55.00$ ,  $P=0.002$ ). See Figure 4. These data suggest that jackdaws are capable of following complex invisible displacements, as well as being able to track and remember (at least for a short duration) spatial information about hidden objects, so this result may be considered as further evidence of stage 6 competence.

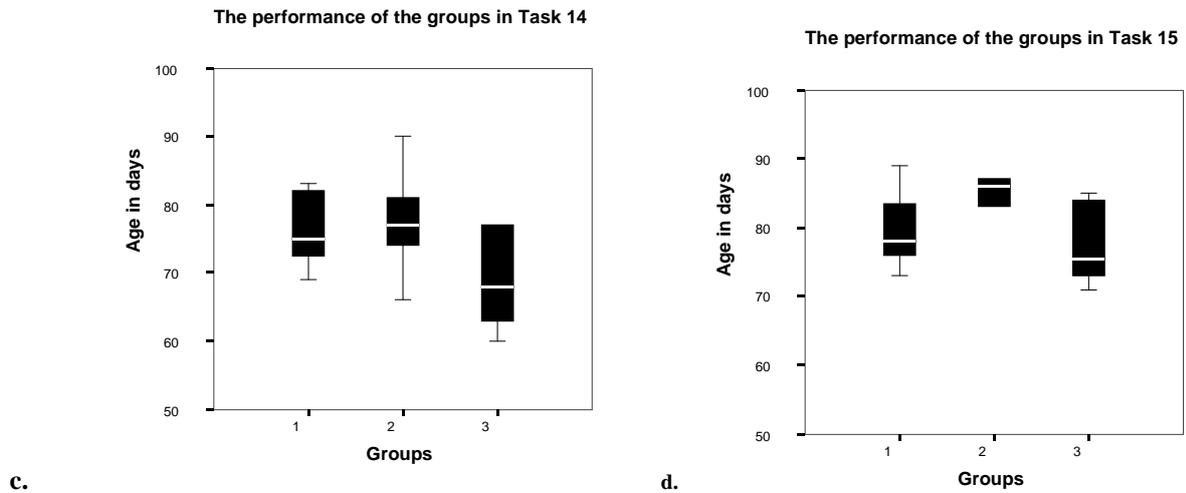


**Figure 8. Performance of jackdaws (N=10) in the Shell Game (task S) and Controls for local/stimulus enhancement. Figure shows percent of correct responses per individual and the group mean. Chance level is at 33%. (\* signals birds showing anomaly in Task 15)**

### *Comparing the performance of the three groups*

Our hypothesis was that if there is a training effect altering the age at which a certain task is passed, than we should be able to find a difference in the performance of our groups, due to the different amounts of testing. We compared performance of the groups in all tasks performed after their division following task 4. In the case of tasks which all three groups participated in, such as tasks 10, 12, 14 and 15, we used a Kruskal-Wallis test. In case of task 10, 14, and 15 we did not find a significant difference in the performance of our groups, while in task 12 there was a significant difference ( $\chi^2=6.287$ ,  $P=0.043$ ), but this result was not affirmed by the Dunn's Multiple Comparisons test. See also Figures 5 a-d. In the case of those tasks where only two groups participated, such as tasks 6, 8, 11, and 13, we used a Mann-Whitney U test, but failed to find a significant difference between the performances of our groups. This lack of difference shows that the uneven amount of experience in testing situations had no effect on the age of passing a task. Becoming capable of such performance follows the birds' ontogenic development, rather than being an effect of training.





**Figures 9 a, b, c, d. Age at which birds in the three Groups (Group 1-all tasks given, Group 2-tasks 5-9 skipped and Group 3-every second task given between 4 and 14) reached criterion on Tasks 10,13, 14, 15. Box plots show medians and interquartile ranges. We found no significant differences.**

***Testing for possible correlations between the number of sessions when an error was made and age of passing a task***

The number of sessions with errors before passing a certain task can be found in Table 2 for each individual. This confounding variable may potentially influence the age at which an individual passed a task, or reached a stage. To more precisely assess the possibility of learning and habituation during the testing procedures we calculated the cumulative number of sessions when at least one manipulation was made and thus, one search was initiated by the bird, but an error was made and session the was terminated. Theoretically each of these sessions would give an opportunity for the subject to gather information about the testing situation and so could alter the age of passing a certain task. To assess potential correlations we used Spearman’s Rank Correlation for non-parametric data. As no significant difference between the groups had been found, data from all groups were pooled.

We found no significant negative correlations between the number of sessions with errors and age in days at passing a task, meaning that birds with more experience did not reach a stage sooner. On the contrary, significant positive correlations were found in case of Task 3 ( $r_s=0.638$ ,  $P=0.002$ ,  $N=20$ ), Task 5 ( $r_s=0.783$ ,  $P=0.022$ ,  $N=8$ ), Task 7 ( $r_s=0.925$ ,  $P=0.001$ ,  $N=8$ ), Task 8 ( $r_s=0.859$ ,  $P<0.001$ ,  $N=14$ ), Task 9 ( $r_s=0.988$ ,  $P<0.001$ ,  $N=8$ ), which

means that in some cases the more prior experience birds had, at the later age were they able to master a certain task. This phenomenon may be caused by the fact that the birds were developing considerable neophobia (see also Zucca et al. 2007), which affected some individuals more/sooner than others. For example 5 birds out of the 14 needed as many as 5 or 6 sessions before being able to pass Task 8. This task is the first task in Scale 1 with successive displacement, thus by nature is considerably more complicated than those preceding it. Therefore this task is also a sub step of the Piagetian stage 5. Given our testing procedure (testing subjects every 2-3 days), we may have started testing for this ability at too early an age, aiming not to miss out on the onset of this capacity. However the rest of the birds (9 individuals) needed two or less sessions. This heterogeneity in the performance leads us to think that perhaps this is again an issue of some our birds being affected by increasing neophobia.

Group	Name	Task 3	Task 4	Task 5	Task 6	Task 7	Task 8	Task 9	Task 10	Task 11	Task 12	Task 13	Task 14	Task 15
1	Woody	0	0	0	0	0	5	0	0	0	1	2	0	0
1	Clever	0	1	1	0	0	5	0	0	0	0	0	0	0
1	Rozi	0	1	0	0	0	6	0	0	0	0	0	0	2
1	Borso	0	0	2	0	0	0	0	2	0	0	1	1	2
1	Süni	0	1	1	0	0	1	0	0	1	2	0	0	0
1	Csuri	0	1	3	0	0	1	0	1	2	0	0	0	0
1	Novak	0	1	1	0	2	5	0	0	2	0	0	0	3
1	Gonzo	0	1	1	0	0	2	0	1	0	0	2	1	4
2	Phoebe	0	1	xxx	xxx	xxx	xxx	xxx	0	5	0	1	0	1
2	Libero	0	0	xxx	xxx	xxx	xxx	xxx	0	0	1	2	0	np
2	Ortiga	0	0	xxx	xxx	xxx	xxx	xxx	0	2	0	0	0	np
2	Domin.	1	1	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx
2	Fraulein	2	0	xxx	xxx	xxx	xxx	xxx	0	0	0	0	2	np
2	Jacques	0	0	xxx	xxx	xxx	xxx	xxx	0	2	0	1	0	0
3	Smart	0	2	xxx	0	xxx	1	xxx	1	xxx	1	xxx	0	1
3	Puck	2	0	xxx	1	xxx	6	xxx	0	xxx	2	xxx	2	0
3	Finci	1	1	xxx	0	xxx	2	xxx	0	xxx	0	xxx	0	np
3	Berci	1	0	xxx	2	xxx	1	xxx	0	xxx	4	xxx	4	2
3	Marci	1	1	xxx	1	xxx	0	xxx	0	xxx	1	xxx	3	1
3	Sundan.	2	0	xxx	0	xxx	0	xxx	0	xxx	0	xxx	0	np

**Table 2. The number of sessions ending with errors for each bird before passing each task. All attempts where at least one manipulation was executed by the experimenter while the bird was present in the experimental compartment are considered a session. After making an error, the session was terminated. XXX = bird has not been subjected to the task; np=did not fulfil criterion in task even after 5 sessions.**

## Discussion

We found that, interpreted at a group level, jackdaws achieve stage 6 object permanence abilities relatively quickly, i.e. by the age of 60 days post hatch. In order to test the hypothesis that the birds' development follows the Piagetian stages we would have had to have subjected our birds to all the tasks at all ages, which was naturally not practicable. Our data suggest that the birds passed most tasks roughly as soon as they were faced with them. An exception from this is Task 8, where it may well be possible, that we had to wait for the birds' cognitive maturation to catch up with our testing schedule. Because of the above, our data provide no sufficient evidence that jackdaws progress through the stages in a fixed sequence, as using the sequential tasks of Scale 1 had given us no opportunity to explore this question. Thus our findings neither corroborate, nor refute the hypothesis that jackdaws acquire object permanence abilities in a fixed sequence, following the Piagetian stages.

However, we have shown the maximum ages by which jackdaws become capable of passing Scale 1 tasks. We suggest that our results reflect a process of maturation rather than training and experience during trials, as our subjects in the three groups had different amounts of experience, yet still they developed object permanence abilities at roughly the same ages. We attempted to assess the possibility that the number of sessions with errors prior to the certain tasks may have affected the age of passing them, however have found no evidence that more "practice" had any effect on the performance. This confirms our results from comparing the performance of the three groups, namely that the performance in the tasks of Scale 1 reflects a maturation process, and is indeed not an effect of some kind of training, habituation or other type of learning.

Jackdaws acquired object permanence abilities similar to those found in children (Piaget 1954) and some other animal species (Etienne 1984; Gagnon & Doré 1994; Dumas & Wilkie 1995; Funk 1996; Gómez 2005).

Unlike parrots (Funk 1996; Pepperberg et al. 1997) but similarly to other corvids (Pollok et al. 2000; Bugnyar et al. 2007), jackdaws reach stage 4 and 5 relatively quickly. Our subjects ( $N=19$ ) have developed stage 5 competence (the ability to follow successive visible displacements) at an average age of 61 days post hatch and showed evidence of stage 6 competence (the ability to follow advanced invisible displacements) at 81 days post hatch and thereafter. Only Eurasian Jays have been reported to acquire stages quicker than jackdaws (Zucca et al. 2007). The relatively early development of object related competence is in

accordance with the generally faster maturation and overall development of jackdaws compared to parrots and some food storing corvid species, such as ravens (Bugnyar et al. 2007).

Like great apes (Call 2001), karakiris (Funk 1996), grey parrots (Pepperberg et al. 1997), and dogs in a communicative situation (Topál et al. 2009) but unlike cats (Doré et al. 1996), and most interestingly magpies (Pollok et al. 2000) and Eurasian jays (Zucca et al. 2007), two out of eight of our jackdaws subjected to task 5 committed characteristic A-not-B errors. The differences in this matter might possibly be due to slight methodological differences in the numbers of times (in our case 3) the object was hidden under a certain cover before moving the hiding to the other cover. The A-not-B errors observed might have been caused by a local enhancement effect rather than object permanence related issues, however we feel that based on our data it would not be possible to draw any conclusions regarding this question. It is well possible that the error phase is very transient in case of corvids and this phase might have been entirely missed by the jay and magpie studies due to the differences in the testing schedule. However highly speculative, it might still be worth to note here that the A-not-B errors are now generally thought of as the mistaken interpretation of the situation, where subjects tend to generalize information as a ‘rule’. This in humans has to do with ostensive/referential signals used, which can be misinterpreted as a ‘teaching’ situation (Topál et al. 2008) (please refer to the Introduction). Of course ‘teaching’ behaviour can hardly be assumed in case of jackdaws, as in its strict sense this has only been documented in case of humans (Csibra 2007), birds may non-the-less be sensitive to ostensive cues on the receptive side.

Some of our subjects had a continuing problem with passing task 15 according to our original criterion, which is particularly interesting as magpies (Pollok et al. 2000) had very similar difficulties. Out of the 19 subjects 5 individuals did not pass task 15 according to our original criterion, however their response was not illogical when seen from another point of view, so their actions did not reveal any implications of behaviour inconsistent with stage 6 six competence. However, to further assess this issue we proceeded to test the subjects on the Shell Game, and based on these results we argue that jackdaws do actually acquire stage 6 competence.

As the method we chose has sometimes been criticised (criticisms and strong points reviewed in Pepperberg 2002) on the issue of possible training during the administration of the sequentially more and more difficult tasks, we divided our birds into three groups which each received different amounts of testing, but we could not find any significant differences in

their development, nor in their competence at the final stage. For this reason we feel that the results we acquired by using Scale 1 were not in any way artificial. By using the same method, we were able to compare our results with data on food-storing ravens and magpies. Finally we administered an extra task, task S, or the “Shell game” to assess not only object permanence abilities, but also some other cognitive capacities, such as attention and spatial memory. Our birds performed significantly better than chance in these trials. All these data suggests that jackdaws develop ability in object permanence corresponding to the Piagetian stage 6 competences.

A further criticism of the Scale 1 method lies in the face-to-face nature of testing (Collier-Baker et al. 2004; Fiset & Leblanc 2007)(Fiset & Leblanc 2007) so we took the utmost care not to bias or cue our animals in any way (the birds were not allowed to choose or search until the experimenter had taken up the neutral position mentioned in the procedures). Of course, the possibility of cueing could not be completely eliminated given our face-to-face testing procedure. On the other hand we feel that when testing animal cognition it is also of very high importance that the subject is in no way stressed when subjected to a cognitive task, as stress may impair their performance considerably (e.g., Weir & Kacelnik 2006). To have the person who had raised the birds by hand as experimenter had very favourable effects on the apparent stress level and willingness to participate.

A question of considerable interest is whether the lack of caching behaviour in jackdaws is an ancient trait, inherited from a non-caching common ancestor, or represents the loss of a skill as a secondary specialization to a less demanding ecological environment, with the common ancestor of corvids being a food-storer. In this latter case we should expect to find no differences in the performance of food-storing and non-storing corvids on non-spatial tasks (de Kort & Clayton 2006). Our findings are not contradictory to this hypothesis, but as object permanence has evident values in various respects other than food-storing, it is difficult to draw any conclusions regarding this issue.

Based on the above data we suggest that the lack of food-storing behaviour in jackdaws is not associated with inferior object permanence abilities. This is not surprising as sophisticated object permanence skills have a very wide ecological significance and are a prerequisite of various other behaviours, more fundamental than caching. Having a considerably smaller hippocampus relative to their brain size (Healy & Krebs 1992) seems to be connected with poorer spatial memory (Scheid & Bugnyar 2008), but this did not impair performance in our task S.

We know that jackdaws hardly ever make food caches in the wild, however we argue that advanced object permanence abilities may be of several other advantages in the ecological context, as these birds are known to raid caches made by other species, and also to carry objects in their throat pouches, where those are temporarily invisible to others, but the ability to track them is undeniably favourable for conspecifics who are observing. Object permanence abilities have a wider ecological significance for example in prey-predator interactions and in connection with nest-hole reproduction, which may underlie the unimpaired capacity.

## ***Experiment 2:***

### ***Role of mental representations in relative quantity judgements based on mental representations by jackdaws (Ujfalussy et al. 2014)***

#### ***What is number? – Numerical concepts***

Apart from the general introduction at the beginning of this Thesis, I felt there is a need to set the basic conceptual framework of numerical competence studies. If for no other reason, then just for the sake of being clear on nomenclature used, I would like to mention here some basic concepts.

The concepts of number may be classified into three categories (Wiese 2003; Nieder 2005). These three categories are cardinal number, ordinal number and nominal number. *Nominal number* is used as a name, identifies objects within a set (numerical labels), and thus is exclusively verbal, only found in linguistic humans, can only be represented through language, so will not be further considered here. *Cardinal number* refers to quantitative number assignment (numerical quantity), answering the question of ‘How many/much?’ For example to tell how many apples are in a bowl, we may say: ‘Five apples’, five here being a cardinal number. *Ordinal number* refers to the rank (serial order) of a certain item in a sequence, answering the question ‘Which one?’ For example to tell which apple in a row of apples is yellow, we may say: ‘The fifth apple is yellow’, fifth being an ordinal number.

I find it important to state that human language is required to develop a true systematic number concept, as verbal representations are the link between relations of numbers with relations of objects or events (Wiese 2003). For that reason the terms ‘counting’ and ‘number’ shall not be used when referring to non-verbal subjects, such as small human infants or animals. However, non-verbal representation of ordinality and cardinality is found in both animals and non-verbal humans, as the data in this thesis will also show.

When discussing non-verbal systems of quantity assessments (described earlier, and further referred to a bit later), especially in connection with the analogue magnitude system we often state that analogue representations obey Weber’s Law. Let me now describe this in more detail, and how this works on a neural level based on the review article of Andreas Nieder (Nieder 2005). Ernst Heinrich Weber (1795-1878) was one of the founders of experimental psychology. He discovered that two relatively heavy weights must differ by a

larger amount than two relatively lighter ones, for the difference to be detectable. He introduced the term ‘Just Noticeable Difference’ (JND or  $\Delta I$ ), which is the minimal stimulus magnitude change to produce a noticeable variation in sensory experience, and is a constant fraction ( $c$ ) of the level of stimulus intensity ( $I$ ). *Weber’s law*,  $\Delta I/I=c$ , has a wide generality across sensory magnitudes and modalities. Gustav Theodor Fechner (1801-1887), also German, also experimental psychologist, proposed an extension to Weber’s Law. He proposed that the perceived magnitude ( $S$ ) is a logarithmic function of stimulus intensity ( $I$ ) multiplied by a modality or dimension specific constant ( $k$ ), thus *Fechner’s Law* reads:  $S=k \log (I)$ . These two laws are general and fundamental in sensory discrimination and can account for some several properties of sensory neurons, as the action potential of slowly adapting neurons is a function of the logarithm of stimulus intensity. Thus, it seems that the response characteristics of receptors can explain Fechner’s Law. However it is less clear, why cognitive magnitudes, such as numerical quantity obey the same law (Nieder 2005).

A recent study involving single-cell recordings in monkeys (*Macaca mulatta*) showed that single neurons have the capacity to encode numerical quantity (Nieder et al. 2002). Nieder and colleagues have identified numerosity selective neurons in the prefrontal cortex and intraparietal sulcus which were tuned to a ‘preferred numerosity’ (i.e. preferred by the cell in question), showing maximum activity in response to this preferred quantity. Also, all numerosity-selective neurons together formed a bank of overlapping numerosity filters. Further they have found that the tuning curves of these neurons were sequentially arranged and overlapping, presenting an inherent order of cardinalities, which is important as numerosities exist in relation to one-another, and need to be sequentially ordered for meaningful assignments of quantity.

It has also been suggested that the response properties of numerosity-selective cortical cells may explain the numerical distance and size effect, the two general effects seen in analogue magnitude representations. By numerical distance effect we mean that the larger the numerical distance between two cardinalities, the easier they are to discriminate, while by numerical size effect we refer to the phenomenon that two cardinalities of a given numerical distance become more difficult to discriminate when their absolute values are higher. Supposedly, the *numerical distance effect* results from the fact that the neural filter functions of adjacent numerosities overlap heavily, thus the signal to noise ratio is low and errors occur more often, while the filter functions of remote numerosities barely overlap, thus the signal to noise ratio is high and errors occur very seldom. The *numerical size effect* is suggested to be caused by the fact that the width of the tuning curves increase linearly with the preferred

numerosity, meaning that neurons become less precisely tuned as the preferred quantity increases. So, in case of the discrimination of two small numbers, two relatively narrow tuning curves do not overlap considerably, so discrimination is relatively easy, while in case of two larger numerosities, the tuning curves are wider, thus overlap more considerably, thus discrimination becomes relatively difficult (Nieder 2005).

It has been shown that both the performance and the single-unit data for numerosity judgements are better described by a logarithmic scale (Fechner's Law), indicating that the non-verbal number line is non-linearly compressed. This way, smaller cardinalities can be represented more precisely.

### ***Ecological significance of numerical assessments***

Assessment of numerical information may be crucial to any animal's fitness and survival in several ways. The importance of cardinal judgements, perhaps, is most evident in the context of flight or fight decisions in contests, foraging and parenting (e.g. brood parasitism), while ordinal judgements are apparently essential in establishing hierarchical order and dominance rank.

Evidence of cardinal judgements from the field have been reported for example in the case where female lions (*Panthera leo*) are supposed to decide to attack or to retreat from another pride based on the number of different roars they hear compared to the number of individuals in their own group (McComb et al. 1994), or when chimpanzees (*Pan troglodytes*) enter into contest with a neighbouring clan only if they outnumber the opponents by at least a factor of 1.5 (Wilson et al. 2001).

Foraging (i.e. optimizing energy intake) is a constantly pressing problem to any organism. Field studies have addressed this context also and found for example that untrained, free-ranging rhesus monkeys (*Macaca mulatta*) are able to choose the container with the larger amount of apple slices in the comparisons 1 to 2, 2 to 3 and 3 to 4 (Hauser & Carey 2000). Since this initial study of Hauser and Carey many have adapted a similar method and found that, among many others, New Zealand robins (*Petroica longipes*) (Hunt et al. 2008), sea lions (*Otaria flavescens*) (Abramson et al. 2011), African grey parrots (*Psittacus erithacus*) (Aïñ et al. 2009) as well as wolves (*Canis lupus*) (Utrata et al. 2012) are able to distinguish between small numerosities of food pieces.

A most interesting study (Lyon 2003) has reported that American coots (*Fulica Americana*) seem to assess the set size of their own eggs, and ignore the conspecific parasitic eggs (based on visual cues) when optimizing clutch size. This study presents evidence that female birds combine egg recognition and counting to regulate clutch sizes.

The above mentioned results are just a few examples of the considerable ecological significance that numerical assessment may bear on survival and reproduction. In order to be able to ask a valid question regarding quantity related abilities, it is crucial to put the question in the context of the ecology of the given species. As in the case of physical features, cognition is also subject to selective evolutionary pressures, and produces highly sophisticated capacities if these pressures are present.

### ***Introduction to our quantity discrimination study***

Let me start here with a compact summary of some theoretical background, mostly mentioned in more detail in the general introduction. As described before, humans' symbolic representations of exact number, like other aspects of human knowledge, is suggested to have its roots in a basic knowledge system (Core knowledge, Carey, 2009; Spelke & Kinzler, 2007). A small set of distinct systems is proposed to underlie the representation of such significant aspects of the environment as objects, actions of agents, space, social partners, as well as number. These so called "core systems" may have evolved well before the time of modern humans, and thus may be shared across species (Vallortigara 2012) as well as being accessible early in development, maybe even at birth (Hauser & Spelke 2004). In order to investigate the two distinctive properties of core systems (i.e., presence early in development and presence across species), research needs to draw on developmental as well as comparative approaches.

As described earlier in more detail, some researchers recently suggested the existence of *two core number systems* in both humans and nonhuman animals (Xu & Spelke 2000; Uller et al. 2003; Feigenson et al. 2004).

In brief summary, one system is supposed to serve the approximate representation of numerical magnitude, where representation is not very precise, but does not depend on set size (Jordan & Brannon 2006). Symbols of this system are supposed to be mental magnitudes (linear or logarithmic functions of cardinal values in a set), which only approximate the number of items in a set. The behavioural signatures of this analogue system are the "numerical distance effect" and the "numerical magnitude effect", these two effects are more

generally known as the ratio effect, which follows Weber's Law in that success of relative judgment declines as the ratio of the smaller set to the larger set increases. The second system is suggested to serve more precise representation of small numbers (Xu & Spelke, 2000; Xu, 2003). In this system mental models are supposed to be created in working memory using one symbol for each item in a set. The signature of this system is the upper limit to the number of objects which may be represented, which is generally considered to be 3 or 4 (Pepperberg & Carey 2012). These two core systems seem to correspond with the two major representational models concerning mental representations of numerical information, which are the „Number analogue magnitude hypothesis” or „Accumulator model” (Meck, & Church, 1983) and the „Object file hypothesis” (Kahneman et al. 1992). However, at present there is a substantial debate over the question whether these two systems are both present, or there is only one, the “analogue magnitude” system (Jordan & Brannon 2006; Cantlon et al. 2010).

Moreover, there is a considerable debate on the relative salience of numerical attributes as opposed to continuous properties in quantity judgments in young infants (e.g., Clearfield & Mix, 1999; Cordes & Brannon, 2009; Feigenson, Carey, & Hauser, 2002; Feigenson, Carey, & Spelke, 2002), as well as non-human animals (Agrillo, Piffer, & Bisazza, 2011; Cantlon & Brannon, 2007; Stancher et al., 2013). Some researchers have argued that numerical representations are only used as basis of quantity discrimination as a “last-resort” (e.g., Davis & Pérusse, 1988; Seron & Pesenti, 2001). More recent research, however, suggested that numerical attributes are not less salient in choice decisions by young infants (Cordes & Brannon 2009), Great Apes (Hanus & Call 2007; Tomonaga 2008), monkeys (*Macaca mulatta*) (Cantlon & Brannon 2007), and other animal species (Agrillo et al., 2011; Rugani et al., 2009; Rugani, Regolin, & Vallortigara, 2007, 2008, 2010; Scarf, Hayne, & Colombo, 2011) than continuous properties.

A further interesting question regarding numerical skills of non-humans is how dependent these skills are on previous experience (as addressed in (Hanus & Call, 2007; Haun et al., 2010)) or the availability of a trained symbolic system (e.g., numerical symbols, spoken or graphic language). Chimpanzees trained in communication using lexigrams (Beran, 2004), in the use of Arabic numerals (Matsuzawa 2009) or with extensive experience in number related tasks (Beran & Beran 2004) as well as Alex, an African Grey parrot (*Psittacus erithacus*) trained to use English vocal labels and Arabic numerals (Pepperberg & Carey 2012) showed outstanding performance in number and quantity related tasks. It remains a question, however, if the processes on which these impressive results are based are commonly available to all members of the species in question. How symbolic representation effects

number or quantity related cognition has also been studied in humans, for example in case of the Piranha, an Amazonian tribe, which have been shown (Gordon 2004) to have a very limited number vocabulary. Frank et al. (2008) found that the lack of number words do not alter underlying representations; however, vocal symbols are useful for keeping track of large numerosities across time, space and modality.

Through all discussions and debates on above mentioned points, by taking the developmental approach and focusing on quantity and number related representations in human infants, various studies have shown that even young infants exhibit numerical knowledge (Xu & Spelke 2000; Feigenson et al. 2002a, 2002b; Cordes & Brannon 2009; Cantlon et al. 2010). At the same time comparative research has established that some level of quantity representation is spontaneously and naturally present in various species (e.g., Aïn et al. 2009; Pepperberg & Gordon, 2005; Pepperberg, 2006; Scarf et al., 2011; Utrata, Virányi, & Range, 2012; Ward & Smuts, 2007), and in some cases even very early in ontogeny (for example in newly hatched chicks; Rugani et al., 2009; Rugani, Regolin, et al., 2010). Numerous recent publications report the success of several animal species in various forms of Relative Quantity Judgments, other than monkeys (e.g., Beran, 2008; Evans et al. 2009) and apes (e.g., Beran, 2001; Call, 2000; Hanus & Call, 2007), such as sea lions (*Otaria flavescens*) (Abramson, et al., 2011), pigeons (*Columba livia*) (Emmerton & Renner 2009), meadow voles (*Microtus pennsylvanicus*) (Ferkin et al., 2005), bottlenose dolphins (*Tursiops truncatus*) (Kilian et al., 2003), salamanders (*Plethodon cinereus*) (Uller et al. 2003; Krusche et al. 2010), elephants (*Loxodonta africana*) (Perdue et al., 2012) and black bears (*Ursus americanus*) (Vonk & Beran 2012).

In this present study we choose to investigate the cognitive abilities of jackdaws (*Corvus monedula*) in relative quantity judgments based on mental representation of the sets. Jackdaws are colony breeders, forming monogamous pairs (Henderson, Hart & Burke, 2000), nesting in (both natural and artificial) holes, crevices and ledges. They live and forage in fission-fusion (sometimes multi-species) groups. They are omnivorous, feeding on insects, as well as seeds, fruits and other seasonally available foodstuffs. However, unlike many other corvids, they do not cache. Given these data, an investigation into their quantity-related cognition would seem of interest. Our subjects were not trained in quantity related tasks and had no previous training in any special communication skill. We aimed to determine cognitive skills that might be naturally available to the members of this species in order to provide the basis for further comparative investigations.

Jackdaws belong to the family *Corvidae*, a group of birds especially known for their exceptional abilities in social and object related cognition (Balda, 2002; Balda, R. P., & Kamil, 1992; Bugnyar & Heinrich, 2005; Bugnyar & Kotrschal, 2002; Clayton & Emery, 2005; Emery & Clayton, 2004; Scheid & Bugnyar, 2008).

Corvids tested so far also produced some positive result in quantity discrimination experiments. Gray crows (Zorina & Smirnova 1996) have been found to be able to form a general concept of “larger set” and to use this concept in novel choices. Four subjects have been trained to choose the larger of two sets of stimulus elements in the range of 1-12. The colour, form, size and pattern of stimulus elements have been varied. When birds learned to successfully choose the larger set in this range, they have been tested on a novel range of 10-20 elements. All four crows demonstrated transfer of developed reaction to the novel range.

Hooded crows (Smirnova et al. 2000) were reported to be successful in numerical matching and oddity tasks. In this experiment six subjects were trained in two-alternative simultaneous matching and oddity tasks on colour, shape and number of elements. These birds have been successful in applying the matching or oddity concept (also) to numerical stimuli.

Jungle crows (Bogale et al. 2011) have been found to have a natural tendency to select larger quantities and their decisions were reported to be affected by numerical ratio and stimulus magnitude, suggesting an analogue magnitude mechanism to be present. Bogale and co-workers trained eight jungle crows on a choice between two sets of discrete homogenous quantities (2 vs. 5) on five pattern sets of symbolic elements, and then control trials on non-numerical cues were given. Results from these control trials indicated that crows were relying on numerical, rather than continuous cues. When presented with novel choices crows tended to opt for larger numerosities.

Moreover, one jackdaw (Köhler 1941, 1950) also succeeded in matching the number of dots on a sample card to a comparison lid, even when configuration of dots and their sizes differed, so only number of items could be basis of correct choice.

However, all the above mentioned studies used extensive training on number related tasks, as well as symbolic stimuli, thus we aimed to find out whether a cognitive mechanism in assessing quantity is spontaneously available and present in jackdaws and if so, how their performance can be explained by current models of quantity representation.

To assess the jackdaws’ ability to represent and discriminate quantity we gave our subjects a two-choice relative quantity task, in which items of both sets were presented sequentially. A similar method has been used by Wynn (1992), Feigenson et al. (2002) for

infants, by Beran (2001) for chimpanzees, by Hauser et al. (2000) for rhesus monkeys, by Evans and colleagues (2009) for capuchin monkeys, as well as Hanus and Call (2007) for the four Great Apes. Also this method has been adapted by Hunt et al. (2008) for the New Zealand robin and by Utrata et al. (2012) for wolves. In a previous study we have found that jackdaws develop advanced object permanence abilities relatively fast (Ujfalussy et al. 2013), so we assumed that keeping track of hidden objects would not be an issue. Because in our test, two sets of items were presented one-by-one, and the whole set was at no point visible to the subject, success in this task suggests that subjects form mental representations of the sets. In their 2009 article Evans et al. argue that such a test has implications for our understanding of the evolution of the enumerative process, as sequentially presented items evoke such a process, or at least something similar to summation. However, Evans and colleagues (2009) also discuss and we agree that such tests are not to be interpreted as numerical discriminations as the number of items in a set co-varies with continuous variables such as mass, volume, contour length, surface area, etc., thus the discrimination may not require the recognition of item number. Nonetheless, judgement has to be based on representation that is updated with the placement of each item, thus such a judgement requires interactions between an enumerative or summative process and working memory.

As to our knowledge no such experiment has been performed on corvids, the goal of our experiment was to investigate whether jackdaws are spontaneously (without any quantity related or communicational training) capable of making quantity judgements based on mental representations and to find out how the control of presentation rate and duration affects performance. Performance in the various relative quantity judgment tasks may be informative about the potential underlying mechanisms. A set size limitation at 3 or 4 may indicate that a precise small number representation system (i.e., “object file” system) is present, while if success should decline as the ratio of the smaller set to the larger set increases, that could be interpreted as a characteristics behavioural signature of an analogue magnitude system (i.e., “accumulator” system).

## Method

### *Subjects*

We hand-raised young jackdaws (*Corvus monedula*) to participate in this and some other experiments in spring, 2005 (see Table 3). The study was performed during summer and autumn of 2005. Ontogeny of object permanence abilities of our subjects has been studied using the Uzgiris and Hunt (1975) Scale 1 set of tasks prior to the quantity related experiments (Ujfalussy et al. 2013). Hand-raising and testing took place at the Konrad Lorenz Research Station in Grünau, Austria. Detailed description of the subjects and their circumstances were given previously in the *Method/Subjects* section of the previous experiment.

Average age of subjects at the start of the quantity related experiments was  $148.7 \pm 6.1$  days post hatch. As all testing was done on the voluntary basis on behalf of the birds, not all individuals participated in all steps of the experiments. For exact information on the subjects participating, please see Table 3.

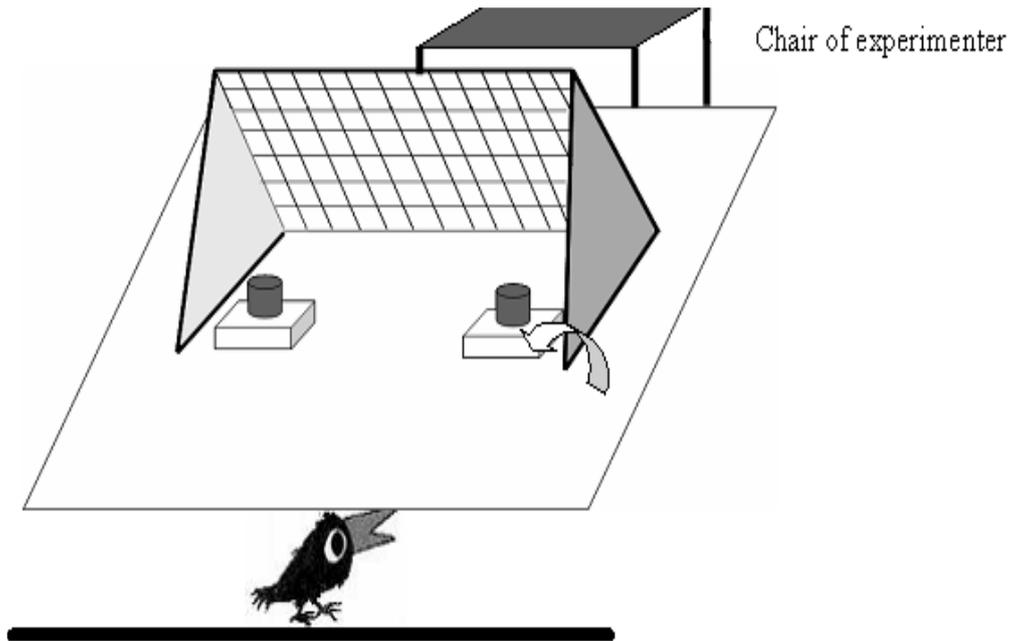
	<b>Name of subject</b>	<b>Baseline</b>	<b>Numerical Competence</b>	<b>Control</b>
<b>1</b>	Csuri	✓	✓	✓
<b>2</b>	Gonzo	✓	✓	✓
<b>3</b>	Sundance	✓	✓	✓
<b>4</b>	Novak	✓	✓	✓
<b>5</b>	Fraulein	✓	✓	✓
<b>6</b>	Finci	✓	✓	✓
<b>7</b>	Rozi	✓	✓	✓
<b>8</b>	Suni	✓	✓	x
<b>9</b>	Borso	✓	✓	✓
<b>10</b>	Berci	✓	✓	✓
<b>11</b>	Marci	✓	✓	✓
<b>12</b>	Puck	✓	✓	✓
<b>13</b>	Phoebe	x	✓	x
<b>14</b>	Woodstock	✓	✓	x
		<b>N=13</b>	<b>N=14</b>	<b>N=11</b>

**Table 3. Subjects participating in the certain test phases of our experiment.**

## **Procedures**

### *Apparatus*

All testing took place in a side compartment of the experimental complex by the main aviary the aviary. This compartment was furnished with a table, approximately 70x100 centimetres and a perch, at the level of the tabletop, but about 15 centimetres from the edge of the table. The table was equipped with a transparent flipping obstacle, made of wire mesh and supported by two wooden triangles on the sides. It was fastened to the table by two hinges and had two possible positions, as it could be either open to the side of the experimenter or it could be flipped to be open to the birds (see Figure 10). A similar device was used by Zucca et al. (Zucca et al. 2007) when testing Eurasian jays. The use of this obstacle became necessary as initially the participating subjects found it difficult to wait until all manipulations were executed, so some means of restraining them from intervention was required. The sets of items were placed in two identical opaque containers, 5 centimetres tall and approx. 4 centimetres in diameter, with a 10x10 centimetre wooden base. The containers were designed to allow the birds to reach for the hidden items, but so that their content was not visible to the observer. In case of the Baseline experiment two small, white, oval plastic trays were used, approx. 5 centimetres wide and 8 centimetres long, with a 2 millimetre rim. The experimenter was seated on a small chair during testing, which was carried into the compartment in the beginning of each testing session. The items to be hidden were small pieces of cat food, identical in size and colour, and were held in the hands of the experimenter before placement. This treat is generally desired by the birds, but it is not their most desired food. In the control experiments small pieces of grey stone were used, very similar size (volume, shape, surface area, contour length) as the food pieces. These stones were kept in the cat food container in order for them to acquire the smell of the reward. The opaque containers were also stored filled with cat food to control for odour cues.



**Figure 10. The experimental setup with the transparent flipping obstacle, the opaque container, the perch and seat of the experimenter.**

### ***Procedure of testing***

Testing sessions took place every day when the weather allowed, but the certain individuals were tested only every second or third day on average, depending on their willingness to participate.

At the beginning of each testing session the birds were called (by calling words and offering treats) into the experimental complex through the door. Usually more than one subject entered at the first time, as some birds were especially keen on participating. The door was then closed. The entering birds could stay in the first compartment and only one subject at a time was allowed to enter the actual compartment where the testing took place. The experimenter was seated while she manipulated the objects, and the birds were sitting on a perch level with the height of the table and about 15 cm away from the edge of the table and altogether approximately 50 cm away from the setup. The manipulations took place when the

bird was paying attention and was seated on the perch. When the manipulations were made, the experimenter flipped the obstacle and then lowered both of her hands to her lap and looked down, away from the setup and directly at her hands. In the rare case when the bird has initiated search (i.e., jumped onto the table from the perch) before this position was taken by the experimenter, it was not allowed to make the choice (subject was shooed back to perch and trial was terminated). These unsuccessful trials were repeated during another session. Bearing in mind the risks of experimenter cueing in this face-to-face situation, the utmost care was taken not to influence the bird in any way. Of course, with this procedure the possibility of cueing could not be completely eliminated. As any kind of anxiety was contra productive to testing (Weir & Kacelnik 2006) and our subjects at the time of these experiments were becoming increasingly neophobic (as reported also in Zucca et al. (2007) in case of jays), we decided that the advantages of having their hand-raiser as sole experimenter were far outweighing the remaining risks of possible cueing. When the experimenter has taken up the above described, totally neutral position, the bird was allowed to jump onto the table and choose freely. The noise of jumping onto table and pecking into the container was audible to the experimenter, so the outcome of the choice was viewed and noted by the experimenter only when the bird was already handling the chosen array (picking out the pieces and consuming the treats). When testing of a subject was finished, the door to the central compartment was opened and the bird was shooed out the door. Then the door was closed again and another subject was called in from the main aviary or the first compartment. Calling the subjects in from the main aviary was repeated when all the birds in the first compartment were done testing and transferred into the central part, until eventually all the birds willing to enter had their testing session. When testing was finished for the day, the whole flock was allowed back into the main aviary.

During the sessions (while in the testing compartment) the birds were physically, but not visually separated from their flock mates, but neither the birds in the first compartment, nor the birds already in the central part had a view of the table and the manipulations taking place there. View of the table was occluded by black rubber blinds from both compartments, thus subjects not participating could not see the perch or the table, but if the participant jumped from the table and perch to the wire mesh, it could see its flock mates. The voluntary nature of testing and the lack of total visual separation from the others resulted in the birds being usually relaxed and motivated in the testing situation, which is very important when trying to assess cognitive abilities, as stress may impair performance in such experiments (e.g. De Kloet, Oitzl, & Joëls, 1999; Weir & Kacelnik, 2006).

### ***Baseline experiment***

As we have already assessed that all subjects in this experiment were capable of following invisible displacements (Ujfalussy et al. 2013) we could safely assume they could follow the placement of items into an opaque container.

Nonetheless we still had to ascertain that our birds show a general strong preference for a larger amount of food over a smaller amount in a two-way choice task. In order to show this, just before the initiation of the quantity discrimination experiment, our subjects were given a single session of 8 trials where they had to choose between two, simultaneously placed, visible sets, one of which contained 1, while the other contained 2 pieces of dry cat food. In this experiment the transparent flipping obstacle was not yet installed, as the trays had been prepared by the experimenter behind a cardboard screen, and then simultaneously pushed out to the sides. The birds were allowed to make their choice (i.e. jump to and consume one of the sets) once the experimenter has lowered her hands onto her lap and has looked down. In case the bird initiated search before this position has been taken by the experimenter, the bird was not allowed to choose.

Birds (N=13) demonstrated a clear preference for the larger amount. Eight subjects made no errors in 8 consecutive trials, while the remaining 5 made only a single error. Thus no bird erred more than once in the 8 possible trials.

### ***Quantity discrimination experiment***

Following the baseline experiment, we began our main study over the course of the next possible testing session (approx. in 2-3 days). Here our subjects were required to make a relative quantity judgment in a two-way choice situation. The birds had a choice of two sets containing different amounts of food pieces which were visibly and sequentially placed into two non-transparent containers, thus were invisible at the moment of choice. In all trials the set was placed first on the left side then the right side regardless of the item numbers. Making a correct choice for the more pieces in this situation would require some kind of mental representation of both sets.

The birds were given choices in between all the possible 10 combinations of item numbers between 1 and 5, namely 1-5, 2-5, 3-5, 4-5, 1-4, 2-4, 3-4, 1-3, 2-3 and 1-2. The experimenter sat opposite the bird, drew its attention to the food item between her fingers and

first placed one or more items one-by-one into the opaque container to her left, and then she placed one or more items one-by-one into the container on her right. When the experimenter placed all items required for a certain choice, she flipped the transparent obstacle, lowered her hands to her lap and looked down. When this posture was taken up, the bird was allowed to choose freely. Each subject was presented with a certain combination two times, as the choices were balanced for the two sides, so for example 2-4 and 4-2 were both given once. In this way all the birds were given 20 choice trials overall, a certain combination only two times to minimize the possibility of learning from being tested. Note that the method used is a non-corrective one, meaning that the subject was allowed to consume the amount of food chosen in all cases. This way making a choice was always rewarded, which is also a well-established way to counteract few-trial learning.

At the beginning of each session the birds were given 10 'warm-up' trials, to establish their state of attention and how well they could concentrate. This was necessary, as our subjects were kept in an outdoor aviary and so their daily routine could only be controlled to some extent, for example when they had been startled by some unknown stimuli prior to the experiments, they might be still stressed and not able to focus their attention. The 'warm-up' trials consisted of the experimenter placing one tiny piece of dry cat food into one of the containers (5 times on one side, 5 times on the other in a semi-random order, starting side randomized session to session), while birds had to attend to her actions and retrieve the hidden item going to the correct location straight away. If the birds made 2 or fewer mistakes in the 10 'warm-up' trials, they were further tested in the quantity discrimination tasks. If they made more than 2 mistakes, the testing session was postponed until the next day. Testing a certain individual came about every 2<sup>nd</sup> or 3<sup>rd</sup> day on average, while 4-6 trials were given during a single session, depending on the bird's state of attention and willingness (i.e., when the bird became reluctant to sit on the perch and pay attention to the experimenter's actions, the session was terminated).

### *Control experiment*

However, positive results from the above described *Quantity discrimination experiment* may be explained by the fact that the placing of a larger set takes more time and more movements than placing of a smaller set, thus the choice might have been based on temporal stimuli, rather than quantity, even maybe stimulus enhancement.

To control for the above mentioned possibility we have conducted a second experiment in which certain sets were balanced in placement time and movement by the placing of small stones, similar in size and shape, but different in colour to the food pieces. Thus the sole difference between the sets and their placement was the quantity of food pieces on the two sides. Before the experimenter started to place the items, one-by-one into the container, the array was mixed up, so stones and food pieces were randomly placed. Before this experiment the birds were trained to be able to differentiate between stones and food pieces very precisely, by non-numerical training sessions where they had to choose between a stone and a food piece placed into the opaque containers. The subjects needed 3-4 such training sessions before learning to choose food over stone reliably. The birds started on the control trials only after they had reached an 80% (8/10) criterion on the training trials on two consecutive sessions.

For the control experiment we chose two choices from the first experiment in which the birds were successful (••1-4, •1-2, black dots signifying the small stones, numbers meaning number of food pieces) to see if their performance will be impaired by the balancing of non-numerical factors. We also choose one in which they did not show significant preference for the more pieces (•3-4), because if the performance would get better in this case, we could argue that the birds simply avoid the side with the stone. To further rule out this possibility we also included a “trick” trial in which the stone was placed on the side with the more pieces (•3-2).

The last trial of the control experiment was designed to assess whether the jackdaws based their choice on number of pieces or on total volume. In order to do so, subjects were presented with a choice between 1 large piece of food (one entire cat food piece) and three small bits of cat food, the two arrays being equal in total volume. We assumed that in case our subjects' choice was made on the number of pieces placed, they should choose the side with the three small pieces. However, if they track total volume, they should choose randomly.

## *Data analysis*

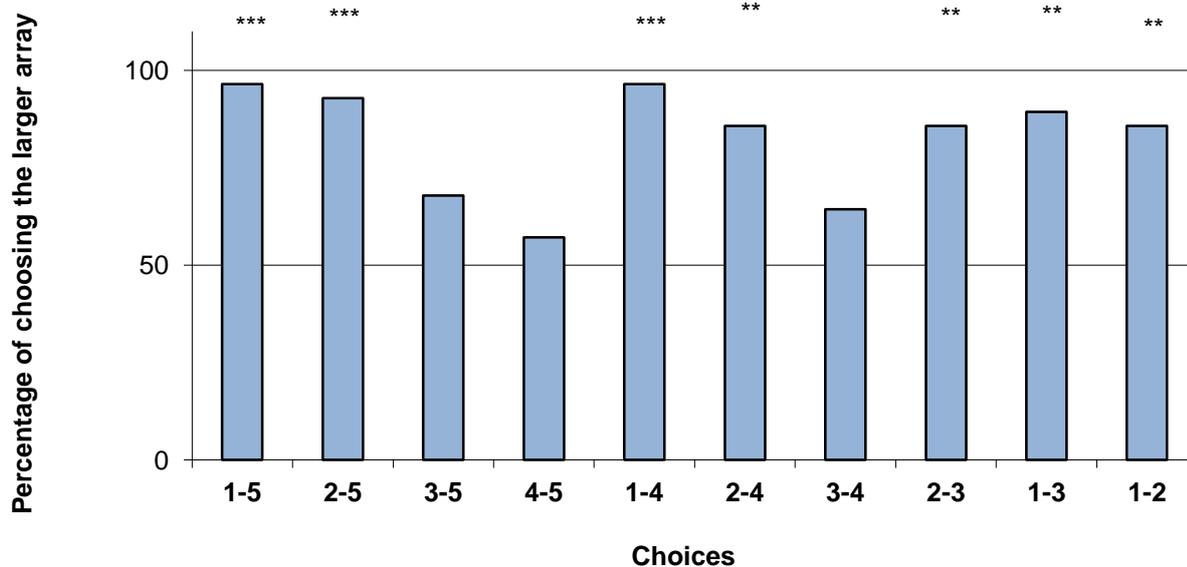
We have measured the percentage of choosing the array containing the larger amount of food pieces in each choice. Data has been analyzed using Microsoft Excel, Graphpad InStat and the SPSS 13.0 software. We have used Shapiro-Wilk's tests to check for normality of our data. As we have found that some of our datasets were not normally distributed, we have proceeded in using non-parametrical analysis and compared performance to the 50% chance level by Wilcoxon signed rank test.

We proceeded to use a linear regression to see whether there is a significant correlation of the percentage of correct choices and the ratio of the sets.

## Results

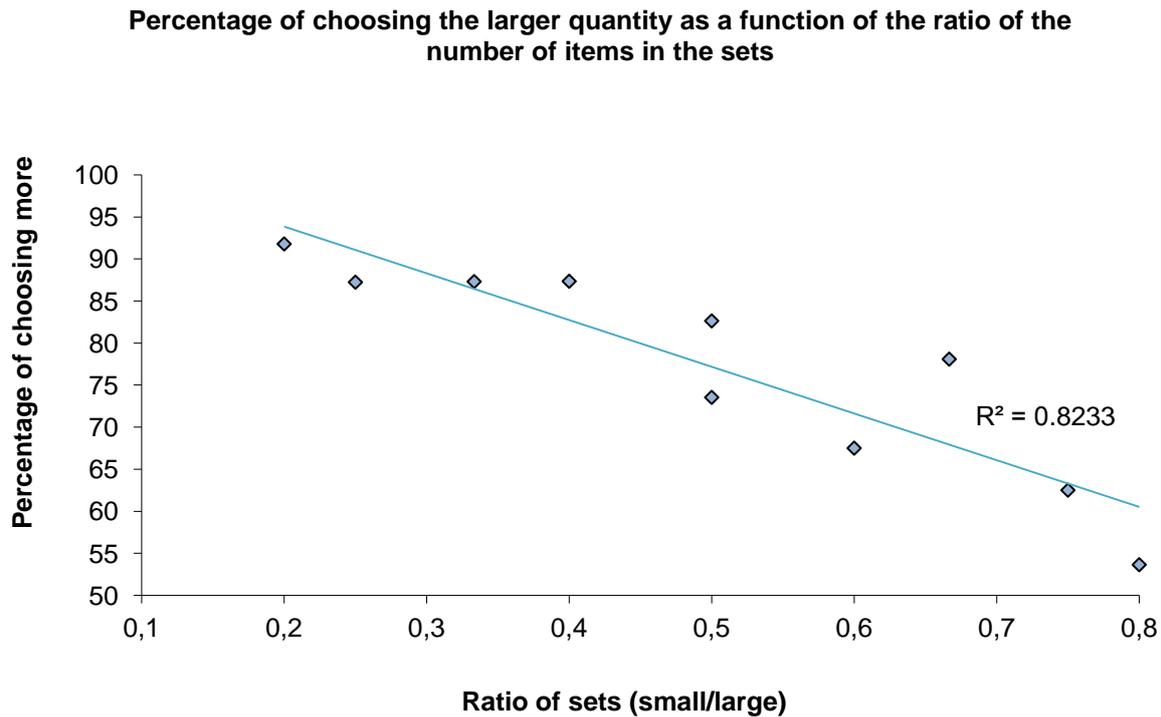
### *Quantity discrimination experiment*

The birds performed significantly better than chance in the choice combinations 1-5, 2-5, 1-4, 2-4, 1-3, 2-3, and 1-2 (1-5  $p=0.0002$ , 2-5  $p=0.0005$ , 1-4  $p=0.0002$ , 2-4  $p=0.002$ , 2-3  $p=0.002$ , 1-3  $p=0.001$ , 1-2  $p=0.002$ ), but failed to do so in the case of the combinations 3-5, 4-5, and 3-4. (See Figure 11) Note that in these choices the set sizes were relatively large and the difference between sets was relatively small. These results are in accordance with Weber's Law, meaning that successful discrimination depends on the ratio of the sets.



**Figure 11.** Group performance ( $n=14$ , total of 28 trials/per choice) of choosing the larger quantity in all possible choices between 1 and 5. \*\*= $p<0.01$ , \*\*\*= $p<0.001$  Chance level is at 50%.

The linear regression showed that the ratio of the sets is a good predictor of the mean percentage of the correct choices ( $r = -0.907$ ,  $F(1, 8) = 37.29$ ,  $p < 0.001$ ), it explains 82% of the variance in performance. For the percentage of choosing the larger set presented as a function of the ratio of the two quantities, please see Figure 12.

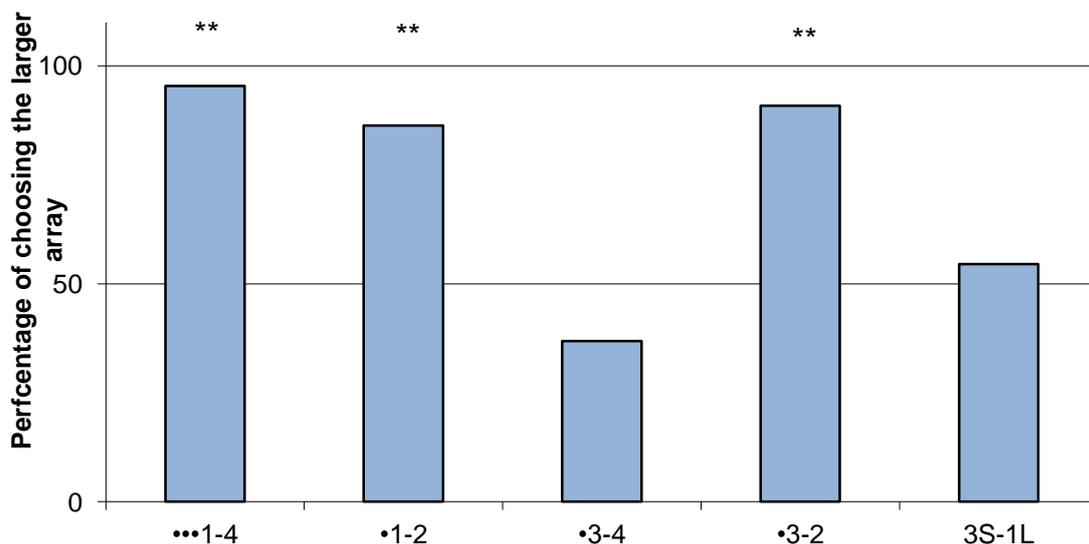


**Figure 12.** Group performance (n=14) of choosing the larger quantity presented as a function of the ratio (small/large) of the two quantities. ♦ signify the observed performance, while the straight line signifies the linear trend between the two variables ( $r = -0.907$ ,  $F(1, 8) = 37, 29$ ,  $p < 0.001$ ;  $R^2 = 0.8233$ ).

Individual performance could not be analysed separately in each choice, as subjects were given one choice type only twice (once with larger set on side A and once with larger set on side B). We analyzed performance collapsing data from all choice types on the individual level and found that all individuals performed significantly above chance ( $p < 0.05$ ). When checking for learning effects we have found no significant difference comparing performance in the first 10 and second 10 trials, regardless of trial type ( $p = 0.91$ ,  $W = -2$ , Wilcoxon matched-pairs signed ranks test). When comparing performance in all first trials with all second trials in a given choice type, a significant difference was found ( $p = 0.0039$ ,  $W = 45$ , Wilcoxon matched-pairs signed ranks test), but showing that second trials were worse, and not better, as would be expected as an effect of learning.

### *Control experiment*

The results of our control experiment showed that performance was not impaired in the case of the choices where the animals were previously successful ( $\bullet\bullet\bullet 1-4$ ,  $\bullet 1-2$ , black dots signify the small stones) by the introduction of the stones to control for temporal factors ( $\bullet\bullet\bullet 1-4$   $p=0.004$ ,  $\bullet 1-2$   $p=0.008$ ). (See detailed statistics in Table 4.) We also found that the placement of the stones did not improve performance in the choice where they were unsuccessful before ( $\bullet 3-4$ ). The birds also solved the “trick” task ( $\bullet 3-2$ ) significantly above chance, where the stone has been placed on the side with more food pieces ( $\bullet 3-2$   $p=0.004$ ). In this case they still chose the side with more food pieces and did not avoid the side with the stone (see Figure 13). Our birds chose randomly between the one large and the three small cat food pieces, indicating that they most probably discriminate quantity by tracking total volume. This control trial however differs from those in the *Quantity discrimination experiment* in that birds in these trials were able to see the total volume of one of the sets before making a choice. Taking this difference into consideration we may not rule out the possibility that our subjects were considering other (continuous or perhaps numerical) attributes when making a decision.



**Figure 13.** Group ( $n=11$ , total of 22 trials/choice) performance of choosing the larger quantity of food pieces in the control experiment. \*\*= $p<0.01$ , \*\*\*= $p<0.001$  Chance level is at 50%. Black dots signify the small stones. 3S= three small food pieces, 1L= one large food piece

<b>Choice:</b>	<b>W=</b>	<b>T (+)=</b>	<b>P:</b>
<b>1-5</b>	91.0	91.0	0.0002
<b>2-5</b>	78.0	78.0	0.0005
<b>3-5</b>	15.0	15.0	0.0625
<b>4-5</b>	7.0	14.0	0.5625
<b>1-4</b>	91.0	91.0	0.0002
<b>2-4</b>	55.0	55.0	0.002
<b>3-4</b>	10.0	10.0	0.125
<b>2-3</b>	55.0	55.0	0.002
<b>1-3</b>	66.0	66.0	0.001
<b>1-2</b>	55.0	55.0	0.002
<b>••1-4</b>	55.0	55.0	0.002
<b>•1-2</b>	36.0	36.0	0.0078
<b>•3-4</b>	9.0	12.0	0.31
<b>•3-2</b>	45.0	45.0	0.0039
<b>1N-3K</b>	3.0	9.0	0.81

**Table 4. Details of statistics – Quantity discrimination and control tests**

## **Discussion**

Our results show that the capacity to make relative quantity judgements founded on mental representations of items in the sets is present in the non-caching Corvid species, the Jackdaw. We found that their representational system is spontaneously available, as subjects do not require any training in order to successfully solve choice tasks. The subjects were successful in making choices for the larger set regardless of the fact that the items were presented one-by-one in each set, so birds never had the opportunity to view the sets as a whole. This suggests that birds could meet the high attentional demands (Hanus & Call 2007; Scheid & Bugnyar 2008) of such a task; moreover they do mentally represent the sets and are able to update this representation with each new item added. This proposes the presence of a summative process aiding the mental representations (Evans et al. 2009). It is important to state that, similarly to other natural choice situations, our test of quantity discrimination may not be considered a numerical discrimination (Hanus & Call 2007), as item number co-varies with continuous variables, such as total volume, cumulative surface area, contour length, etc.

Our subjects were able to select the larger set of items in all choices offered (all possible combination between 1 and 5), with the exception of three combinations in which the

sets were relatively large and the difference between them was relatively small (4-5, 3-4, 3-5). Thus, the birds' performances generally followed Weber's/Fechner's Law, namely performance declined in the direction of larger quantities and smaller differences between the sets. Moreover, their performance was not impaired even when the possible temporal factors have been controlled for. This is similar to the finding of Evans and his colleagues (2009) who have found that presentation timing was neither helpful nor detrimental to capuchin monkeys' performance in choosing the larger of sequentially placed sets.

We found no evidence for a set size limit (usually considered to be 3 or 4), as our birds were successful in the 1-4, 1-5, 2-5 choices, thus our results may not be explained by the "object file model". The success and failure patterns presented indicate that the possible mechanism underlying the birds' performance may best be accounted for by the analogue magnitude representation or "accumulator" model. As described before and as Figure 3 shows, the ratio between the quantities (small/large) proved to be the best predictor of performance. In case of choices where the ratio of the sets was equal (1-2 and 2-4, ratio=0.5) birds demonstrated a similar performance, so it seems that the distance component and magnitude component of Weber's law bears the same significance in discrimination.

These findings are in accordance with recent reports on infants (Xu & Spelke 2000; Cantlon et al. 2010), apes (Beran & Beran 2004; Hanus & Call 2007; Tomonaga 2008), monkeys (Evans et al. 2009) and other vertebrates (Ain et al. 2009; Agrillo et al. 2011; Scarf et al. 2011; Baker et al. 2012).

In our control experiment (similar to (Hauser & Carey 2000; Hunt et al. 2008)) we aimed to find out how much our subjects rely on the temporal cues provided by the piece-by-piece placement of items. The results show that controlling for such cues did not impair performance.

To assess whether jackdaws base their decisions solely on number of items, we have conducted an additional test with a "one large vs. three small pieces" choice, where the two sides were equal in total volume. Our hypothesis was that if jackdaws consider only the number, they should choose the container with the 3 small pieces, however in this trial the birds chose randomly. This result may suggest that jackdaws base their relative judgement of quantity on total volume of items in the sets, as well as perhaps numerical attributes. As described in the Introduction, there is considerable debate over the salience of numerical versus continuous attributes in quantity discriminations.

In their 2007 article Cantlon and Brannon (2007) argue, that contrary to the "last-resort hypothesis" (i.e. that subjects only use numerical information as basis of judgement as a

last resort) both number-naïve and number-experienced rhesus monkeys (*Macaca mulatta*) showed a stronger bias for basing their decision on number than on cumulative surface area. They claim that their finding support the argument that monkeys and other animals naturally represent numerical values. Cordes and Brannon (2010) claim that while 6-month-old infants are capable of representing both number and cumulative area, changes in the latter are less salient and/or more difficult to detect than number changes. Recent findings show that preschool children are significantly more accurate in a complex numerical task when provided with multisensory information about number, as well as report that there is no difference in reaction time across unisensory and multisensory conditions (Jordan & Baker 2010). All these findings support the hypothesis that relative quantity judgements may be based on both numerical and continuous attributes as redundant cues, since the presence of the combination of numerical and continuous information is most common in nature.

The use of sets equalling in volume (3 small pieces versus 1 large) may also bring up a question of concern and interest as now there is evidence that in these natural choice procedures animals may be biased to choose based on largest item in a set rather than maximizing intake (Beran et al. 2008). When different size pieces are offered in the sets the notion of wholeness and contiguity may also play a role in suboptimal responding (Beran et al. 2009).

Based on the above we may not rule out the possibility that jackdaws' choices were made based on numerical attributes, as well as continuous variables, perhaps total volume. Similar results were published by Tomonaga (2008), where chimpanzees were found to base their choice on multiple cues and were shown to be very flexible in switching between cues in relative judgement tasks.

We, based on this study, naturally cannot speculate whether numerical or continuous variables are the more dominant cues in relative quantity judgements, however Gallistel and Gelman (2000) present a model of nonverbal quantity representation, which suggests that discrete and continuous, as well as countable and uncountable quantity judgements can be made by use of the same representational system, the "accumulator". In this case making a choice based on number of items in the set should not be more sophisticated than total volume, or other nonnumeric attribute.

Considering the diverse social and physical environment of these birds, these above results are not surprising. It is easy to see the adaptive benefits of a quantitative representational system in a species in which individuals are subjected daily to such tasks as for example assessing group size and amount of available food. The lack of food-storing

behaviour does not seem to be associated with poor number related skills; however this question may only be assessed by the study of a food-storing Corvid with this method.

In summary, our birds were able to choose the larger amount of food, without quantity related training, and even though they never saw the sets in total. Thus jackdaws are able to mentally represent sequentially placed sets and use this information as basis for further quantity related cognitive processes, such as relative quantity judgements. The subjects' performance showed ratio effects, which suggest that the representational system underlying the birds' performance is best described as analogue magnitude estimation. Further results indicate that they possibly were using total volume as a cue rather than number of items, thus discrimination skills may not be purely numerical.

## General Discussion

Let me start here by a compact summary the most important findings of our experiments.

As a result of our *OP studies* we concluded that jackdaws achieve stage 6 in object permanence, that is, they become capable of following multiple invisible displacements. Their ability to do so emerges relatively quickly, at the maximum average age of 81 days post hatch. The OP abilities found in jackdaws resemble those found in children, apes, monkeys, dogs, and other (food caching) corvids. In two (/8) of our subjects we observed characteristic A-not-B errors. Further, jackdaws were capable of successfully following the displacements of the Shell game, which not only requires stage 6 competence, but advanced spatial memory and attentional capacities.

In our study of *quantity judgments* based on mental representations of the sets, we found that our birds were capable of mentally representing sets presented one-by-one into non-transparent containers, suggesting an internal/mental updating or ‘summative’ process. Further, jackdaws were capable to use this information as basis of successful relative quantity judgements. Their performance declined only in three cases, where sets were large and distance between them was small. Performance did not decline when temporal/stimulus enhancement controls were introduced. Results suggest that birds may be basing their quantity judgements on multiple (numerical and continuous) cues, as it is the most common case in nature.

Now, let me try and put these findings into a bit of context, starting with *object permanence*. First of all, I would like to address the main criticism of the Piagetian framework and the *Scale 1* set of tasks, namely that allegedly this method is a means of step-by-step training the subjects to master the tasks growing in difficulty (Doré & Dumas 1987), thus acquiring a certain concept. The main question of interest in this case is whether the animal solves the given problem by cognitive processing or by using repetitions or mistrials for trial-and error learning (Pepperberg 2002). To address this issue which we were aware of beforehand, we designed our set of experiments to minimize possibilities of such alternative interpretations. We used a strictly non-corrective training method, where the experimenter never demonstrated correct responses and minimized the number of trials from which general

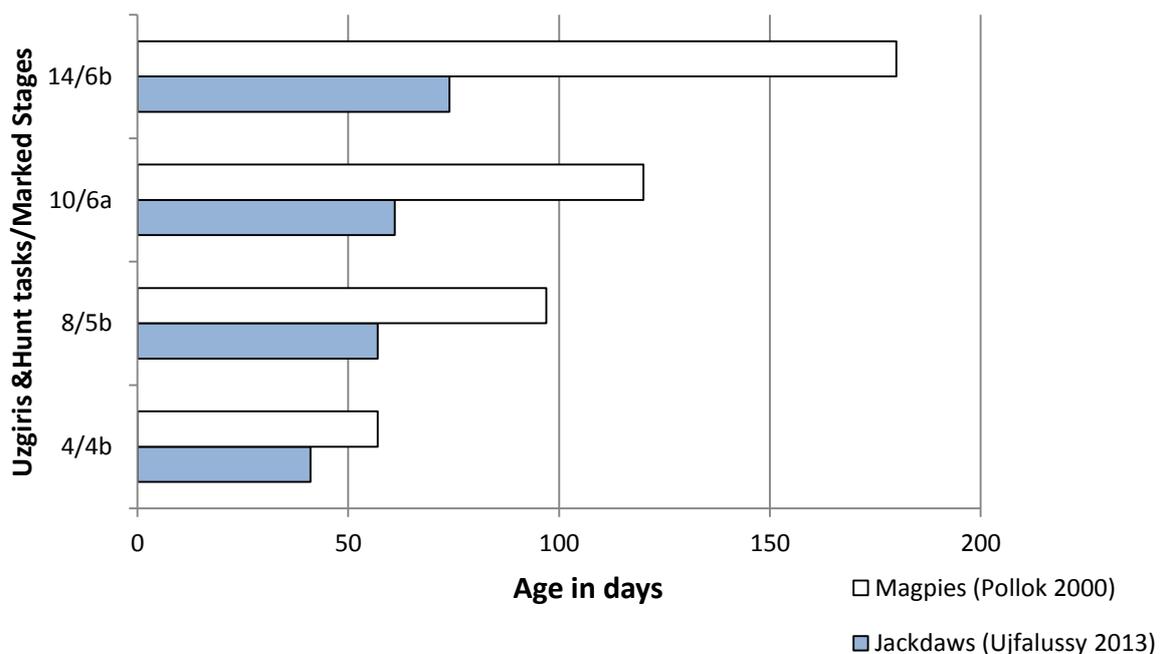
information could be gathered. One-trial learning is not probable, but even if subjects could devise rules that assist them in learning a certain concept in course of the early tasks, they could hardly transfer such specific rules to entirely new situations. However, in order to out rule these alternative explanations we have (as described earlier in more detail) divided our subjects into three groups and checked for the differences in development, but found none. We also have not found any interaction between the number of erroneous sessions and development as reported in the results section. Based on this it is safe to state that we found no evidence to corroborate the concerns of Doré and Dumas and others concerning the possibility of stepwise training.

In the discussion section of the OP studies we have stated that our results show the maximum ages by which jackdaws are capable to pass a certain task. We cannot say anything certain for the minimum ages. But what does that mean? Well, what we actually mean by this statement is that our subjects practically passed every task shortly after they were first faced with it, as shown in Table 2 at the end of the OP results section. Since the tasks of Uzgiris and Hunt (1975) are meant to be given in a sequence, we have no way of knowing the earliest age at which subjects would have passed the certain tasks. We could only have any idea of this, if we could have given all subjects all tasks at all ages, which, of course, is practically impossible to do. Perhaps an exception from this is Task 8 (see Table 2 again) where it is conceivable that we had to wait for some cognitive maturation to take place in order for the birds to solve the task (complex visible displacement with three covers). If so, than in this case we can say that the mean passing age is a minimum age.

Some years earlier Pollok and colleagues conducted a series of OP studies with the same methodology on magpies (*Pica pica*). In the discussion of their publication (Pollok et al. 2000) they make some very interesting assumptions and suggest to investigate non-caching corvids, namely jackdaws with the same method to test these assumptions. They found that magpies reached Stage 5 competence relatively early. At the time the study was done they could only contrast their findings to those of gray parrots (Pepperberg et al. 1997) and kakarikis (Funk 1996), the value of which comparison may be questionable considering the different rates of maturation in these species. It may well be possible that due to different speeds of physical development, and maturation of executive skills, a developmental mismatch between knowledge and action is detected in the case of these psittacine species (Baillargeon 1987).

As Pollok et al. found that magpies develop object permanence at a much faster rate than both gray parrots and kakarikis, they suggest that their results support the hypothesis that

food storing promotes early development, but also point out that some phylogenetic constraints may also play a role, thus a comparison with jackdaws may be of interest. I also feel that this comparison is just and may yield some interesting information, as jackdaws and magpies both reach independence at the age of approximately 10 weeks, thus their rate of maturation is comparable. Pollok et al. hypothesized that jackdaws may develop OP abilities slower than magpies as food storing is not a relevant evolutionary pressure in their case. However our findings do not corroborate their hypothesis. On the contrary, we found that jackdaws reach marked stages (all stages, in fact) of Piagetian object permanence (single visible displacements (task 4, stage 4b), successive visible displacements (task 8, stage 5b), single invisible displacements (task 10, stage 6a) and successive invisible displacements (task 14, stage 6b) considerably quicker than magpies. Please refer to Figure 14 below.



**Figure 14. Development of marked stages of object permanence in jackdaws and magpies**

Based on this finding we suggest that food storing and early development of OP is in no direct connection, and indeed the phylogenetic constraints mentioned may play a much more important role. Moreover, if we keep in mind the notion that the common corvid ancestor was most probably a food storer and the loss of this trait is a secondary specialization in jackdaws (de Kort & Clayton 2006) we should not be surprised that the development rate of cognitive abilities which have a high relevance in contexts other than food storing also is

similar. Cognitive traits related to caching behaviour, such as OP capacities and development, could have been kept intact as they probably are not in any way costly to keep and are undoubtedly useful in contexts other than caching.

However, if here we assume the (more parsimonious, see Kort et al. 2006) scenario that jackdaws secondarily lost their food storing behaviour, question still remains as to why this happened. As jackdaws often share habitat with closely related caching corvids, there is a suspicion that the reason might be found somewhere in the social ecology domain. We know that jackdaws live in large and complex social groups and form life-long monogamous partnerships within these groups. Emery and colleagues (Emery et al. 2007) presented empirical evidence that rook and jackdaw partnerships resemble the alliances of dolphins and primates. It has been documented that jackdaws regularly share food and objects other than in the context of feeding offspring or courtship behaviour (de Kort et al. 2003; von Bayern et al. 2007). This sharing behaviour among same sex, unrelated conspecifics is thought to be a means of social bonding and is suggested to play a crucial role in coalition forming. For caching behaviour to be lost, the ecological pressure (i.e. dependence on the consumption of stored food for survival and/or reproduction) had to be lifted. An interesting (yet speculative) explanation could be that it might be social interactions, such as this food sharing behaviour that had weakened the pressure of dependence of stored food.

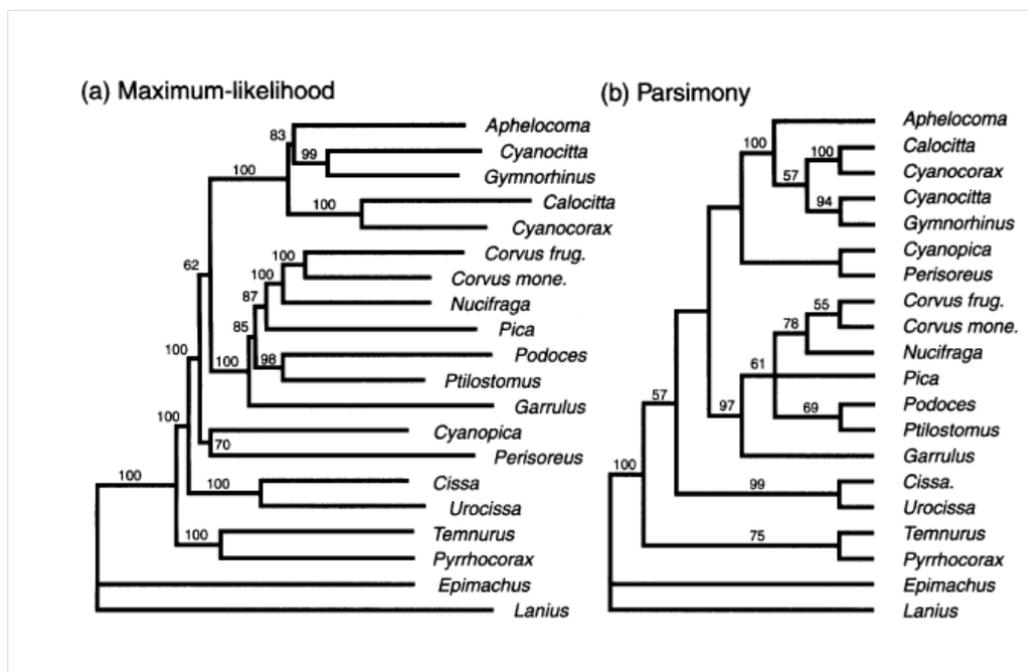


Figure 15. Phylogenetic trees of corvid species constructed by Ericson et al. (2005) based on nucleotide sequence data

Pollok et al. also suggested that maturation of the hippocampus may be a key process in the development of OP. We know little about the maturation speed of the hippocampus of jackdaws, however, the differences in final hippocampal development (Krebs et al. 1989) and similarities in OP capacities do not seem to support this notion. As already mentioned earlier the hippocampal region relative to body weight is smaller in non-caching species than in caching species, thus it is smaller in jackdaws than in magpies. The reason of this however is hardly the connection to OP capacity, but perhaps differences in spatial memory (Scheid & Bugnyar 2008).

In connection with the magpie study of Pollok et al. there is one more thing that is worth to mention, namely that some of their subjects showed exactly the same response in Task 15 as some of our subjects. Task 15 is supposed to be a trick task where the item is hidden under the first (out of 3) cover, but the experimenter continues “hiding” under the second, then the last cover. Criterion, as described in the OP method section, is searching in reverse order. The bird in this case is supposed to assume that hiding was done under the last cover and go there first. After seeing that cover empty, the subject should then move on to the second cover, and when finding that one also empty, finding the item finally under the first cover. This makes clear sense, but there is also another possibility in reasoning. It is important to note that the hiding hand is never opened to show content during the whole hiding process. This way the bird has no way to know if the item is still in the hand after leaving the first (or second) cover. Criterion is based on the subject to assume that it is still there. However, if this assumption is not taken for granted, it is “logical” behaviour from the subject to search all places where the item could possibly be. That is exactly what 5 of our subjects did, and this same behaviour was found in magpies some years earlier (Pollok et al. 2000). Human infants (4-6 years old) and dogs (adult) were also tested in a very similar paradigm (Watson et al. 2001). In this experiment dogs tended to visit the last cover first (12 out of 19 subjects), but interestingly children visited the first and the last screen with approximately equal probability (10/24 started with first cover, 13/24 started with the last cover, while only one child out of 24 checked the middle screen first).

A further interesting result is that we have found two of our eight jackdaws subjected to Task 5 committed characteristic A-not-B errors. Two individuals out of eight is naturally not considered to be significant at a group level, none the less the incidence in itself is important. This result was also a bit unexpected, as an A-not-B error phase has not been found in closely related magpies (Pollok et al. 2000) or in Eurasian jays (Zucca et al. 2007). In Task 5 the object is hidden three times under one of the covers and then, on the fourth hiding

hidden under the other cover. An A-not-B error occurs when the subject keeps searching under the cover used in the first three hidings, instead of finding the item under the other cover. As mentioned before in the discussion of the OP experiment, there could be several reasons why we found this error and the magpie and jay studies have not. We cannot rule out the possibility that there has been a slight, undocumented difference in testing routine. Perhaps jays and/or magpies also go through this phase, but it may be very transient, thus difficult to detect. This is well possible, as we could only document the characteristic error in two out of eight subjects. However, it is also possible (and may be worth further investigation) that jackdaws are unique in this respect among corvids, and more like gray parrots (Pepperberg et al. 1997) or kakarikis (Funk 1996), where an A-not-B error phase has also been detected.

Recent literature on infants (Topál et al. 2008) and dogs (Kis et al. 2012) suggests that the error is caused by the subject's sensitivity to ostensive/referential signals, as the error only arises in social hiding situations. Jackdaws are thought of as highly social among corvids, being colony breeders, living and foraging in large flocks. They have a tendency to be much more cooperative than closely related corvids, such as jays, ravens, magpies, etc., where conflict situations are much more common. Food sharing among non-related, same sex individuals has been documented and interpreted as a device of coalition forming (von Bayern et al. 2007). Moreover, jackdaws have been reported to respond to human attentional states and communicative cues (von Bayern & Emery 2009), namely the direction of the gaze in a cooperative situation. Interesting to mention that jackdaws have an analogous eye-morphology to humans, meaning that their irises are bright blue, contrasting the dark of the pupil and the surroundings of the eye, thus the direction of their gaze may be easier to detect. It may be well possible (and again, worth to investigate) that jackdaws, are especially sensitive to ostensive/referential cues, those of conspecifics and perhaps those of humans, which may be the reason why, similarly to for example to apes, infants and dogs, the A-not-B error phase is present in their development of object permanence.

Stage 6 object permanence (the ability to follow invisible displacements) has been reported in several species other than human, for example apes (e.g. Call 2001), monkeys (e.g. Neiwirth et al. 2003), and among birds, gray parrots (Pepperberg et al. 1997), as well as Eurasian jays (Zucca et al. 2007). However, as Irene Pepperberg has pointed out (Pepperberg 2002) the strict implications of this are sometimes mistaken. In the Piagetian sense Stage 6 means not only that subjects mentally represent invisible transfer of an object, but also that they encode specific attributes of that object (connecting also to General introduction/*Mental*

*representation of objects and their attributes*, as well as */Core System of Object Representation*). Success in finding hidden objects does not necessarily imply full representational capacities. The only way to demonstrate that the object is fully encoded (according to Pepperberg) is by way of a substitution, where the initial object is invisibly substituted for a less favourable item during the trial. If in this case the subject displays displeasure, surprise at the item found or keeps searching, we can deduce that the item was mentally encoded, together with its attributes.

We did not give jackdaws the substitution task. The reason for this lies in the difficulties in coding “displeasure” or “surprise” in their case, these criteria being undoubtedly very subjective. Since jackdaws were very interested in most kind of food items and some non-food items as well, ongoing search would have been also very hard to detect. These are mere practical reasons and we do agree that such a task would have yielded further valuable information. None the less, when the birds were presented with the Shell game, suggested by Doré et al. (Doré et al. 1996) to further assess Stage 6 competence, they proved to be able to meet not only the enhanced representational requirements, but also those of attention and spatial cognition and working memory. They showed evidence in task S of “insight” and “reasoning” about the possible location of the hidden item. Based on performance of our birds we have no reason to suspect that they did not mentally represent what they were searching for, however further research in this direction could also bring some new evidence.

In general we can conclude that object related cognition does not seem to be advanced only in food-storing species. Non-storing species, such as jackdaws also have some quite impressive cognitive abilities “up their sleeve”. We feel that it is very interesting to study corvids’ object related and social cognition in contexts other than food caching, as this way non-caching species may be included for further comparison.

Now let me continue with the broader interpretation of our results from the *quantity discrimination* experiments. Let us first look into the history of the particular type of the test we used, where items are sequentially presented and the sets are not visible at the time of choice, in fact never visible in their entirety. Relative quantity (previously named numerosness) judgements have a long history in the field of animal cognition, of which initially apes and monkeys were the main subjects. For example Dooley and Gill (Dooley & Gill 1977) tested chimpanzee Lana on selection of the larger array of cereal pieces. Lana was successful in choosing the larger set in comparisons 1-10, her performance declining only when the distance of the sets was only 1 or 2 cereal pieces. Many experiments followed (e.g.

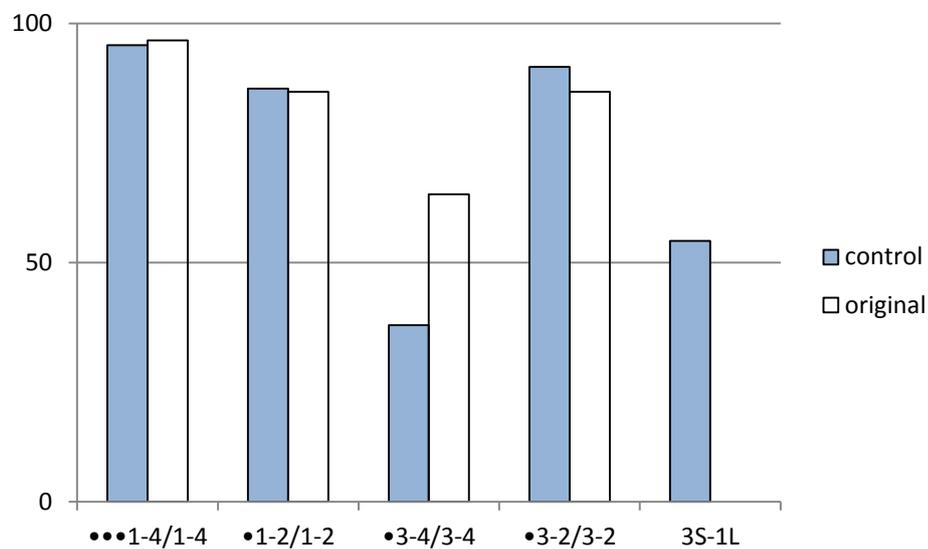
(Matsuzawa 1985; Boysen & Berntson 1989) investigating relative judgements with addition, summation, the use of symbols, Arabic numerals reporting success in apes and monkeys alike. However, with the exception of Boysen and Berntson, where the subject reported on previously observed sets, these experiments involved the subjects viewing the sets concurrently. A change to this came about in 2000 when Joseph Call (Call 2000) tested orang-utans and reported that his subjects did not have to see both quantities at once in order to select the larger one. Shortly after, following Wynn's experiment on children (Wynn 1992), Hauser and colleagues (Hauser & Carey 2000) published the results of their research with semi-free ranging rhesus monkeys, which were found to be capable of choosing the larger of two sequentially placed, non-visible arrays, in case of small numbers. This was followed by the work of Beran (e.g. Beran 2001, 2004) on chimpanzees using a similar method with larger numbers in the sets, and many others since. Success in these tasks suggests that apes and monkeys can form a mental representation of the food sets after viewing individual pieces for a brief duration.

It has been shown in case of human children that sequential presentation of individual items during a numerical equivalence task is more difficult than simultaneous presentation of the entire set (Clearfield & Mix 1999). The tests in which items are sequentially presented are important assessments of quantity discrimination because they have implications for our understanding of the enumerative process (Evans et al. 2009). One at the time presentation suggests an enumerative (at least a summative) process to be involved. This is not to say that the process of comparing two sets necessarily requires the recognition of number, as in natural choice situations volume or overall surface area of the items co-varies with number. Choice could be based on any of these, or other, continuous variables. However, comparison of the sets placed in this manner requires repeated updates of the representational system and the retention of the information for enough time to support judgement. This means that success in such tasks suggests complex interactions between an enumerative and/or summative process, working memory and decision making.

As in our previous OP experiments jackdaws proved to possess advanced abilities of object representations, we thought it would be both fair and exciting to try them at this sophisticated test type, where at that time only primates were reported to be successful. This setup may also offer yet another domain of physical cognition, where capabilities of primates and corvids could be contrasted. Our results suggest that jackdaws, similarly to monkeys and apes, are capable of such a repeated updating of their representations.

As reported, performance was not impaired in the control situations. We believe that our control situation, unlike in the case of Evans et al. (Evans et al. 2009) with capuchin monkeys and similarly to Hunt et al. (Hunt et al. 2008) with New Zealand robins, was not strictly only temporal control. By evening out the two sets by the placement of stones similar in size and shape to the food items, we did a bit more than controlling for temporal factors. Temporal patterns of the placing of each set were naturally evened out, but together with this we also assessed stimulus enhancement and referential signals. Moreover, supposing that our subjects coded continuous attributes (for the sake of simplicity let us just say volume) they had to exclude the volume of the stones from the quantity assessment of the food items. This procedure has also an enhanced attention and processing demand, as volume of food items and (similar) volume of stones had to be coded separately.

I would like to add here that instead of stating that the stone controls did not *impair* performance, perhaps it would be more precise to say that it did not *alter* performance of our birds in these relative quantity judgement situations. Reason for this being that our exact “stone control situations” were not all the same in their logic. To remind the reader, we have included a figure below, showing performance in the original and in the control setting of the certain choices.



**Figure 16. Jackdaws' performance in control choices and respective quantity discrimination tasks.**

We chose two choices (1 vs. 4 and 1 vs. 2) where the birds' performance was good in the initial quantity judgement experiment. In these cases the hypothesis was that if performance remains the same, than the role of temporal/local enhancement/referential signals

may be ruled out, however if it should fall back, than we shall suspect one of these factors, or perhaps that the differential processing of stones proved to be too difficult. We also chose a choice in which the subjects performed poorly (3 vs. 4). In this case, if performance would improve with the stone placement, we could suspect that the birds use the stone as a kind of signal or marker, for example that they just avoid the side with the stones. The trial in which the stone was placed on the side with the larger amount served similar purposes. As shown in the figure above, performance in control trials was totally comparable to those in the original choice situations, so it is safe to assume that factors controlled were not responsible for performance, rather judgment was based on quantity of food items.

Which quantity attribute(s), numerical or continuous, choices were based on, however cannot be decided, but also this question may not be as relevant, as previously thought. The debate over coding numerical (discrete) or continuous information has a long history in search of the origins of “true” numerical processing (as described in the Introduction in more detail), while according to the recent model of Gelman and Gallistel (Gallistel & Gelman 2000), there may not be a basic difference. Their model of non-verbal quantity representation suggests that discrete (countable or numerical) and continuous (uncountable) quantity judgements are based on the same mechanism, thus neither are to be considered more sophisticated than the other. Their model is based on the information gathered from both human and non-human studies of non-verbal processing. This data suggests that non-verbal representatives of number are analogue mental magnitudes (real numbers) with scalar variability (i.e. noise), and greater the encoded magnitude, the noisier the representation. In the authors’ view representing countable and uncountable property in completely different systems would be an obstacle of performing operations necessary in nature, so they state that numerical and continuous information should be represented with the same kind of symbols. Our results from jackdaws corroborate this hypothesis, as our birds also appear to use an analogue magnitude representational system, as performance is best predicted by the ratio of the sets.

The competing theory of Kahneman and colleagues (Kahneman et al. 1992), later defined by Uller and colleagues (Uller et al. 1999) suggests that animals as well as young children construct a mental model of an observed scene providing quantitative information and create one “object file” for each countable item producing one-to-one correspondence between those files and the actual objects. This system is supposed to be limited by memory space to keep the actual files active, thus this space should be a limiting factor. This limit is found to be somewhere around 3 and 4, meaning that none of the arrays may be larger than 3

or 4. Results of experiments with rhesus macaques (Hauser & Carey 2000) and a bit later with human infants in a similar setting (Feigenson et al. 2002b) seemed to confirm predictions of this model. We however found no evidence of a set size limit around 3 or 4.

We of course cannot rule out the possibility, but there is no reason to suspect that jackdaws might have a larger capacity of working memory than that of humans or primates, and so their set size limit may be somewhere higher, thus it is most parsimonious to conclude that an analogue magnitude system may be at work in this case.

We have found no evidence for a separate “small number system” being present in jackdaws dealing with small numerosities, as no breakdown in performance toward larger numbers has been observed. Ratio dependence may explain the performance in small quantity discrimination. However, it is interesting to note that the performance of our birds was robust over occlusion, which is supposed to be evidence pointing to the presence of a separate system used for small quantities (Spelke 2000). Performance with large numbers is predicted to break down over occlusion, but this is clearly not the case here, and also not the case in the primate studies, dealing with quantities up to 10. As described before in more detail, there is a hypothesis that small quantities are dealt with using the core object system, rather than the core number system (Spelke 2000). We cannot rule out the possibility that jackdaws switch systems (object system to number system) between the small and the large quantities and that their representation of small quantities is more precise, and that of large quantities is noisier. However, if there is such a shift, it is not detectable in our experiment, thus the most parsimonious hypothesis seems to be that jackdaws utilize only one core system of number representation, as we found no difference between the small number and the large number choices.

Perhaps speculative, but let me briefly mention one alternative “system” which may explain our birds’ performance in all given choices. The “object file model” implies that performance breaks down if the number of items *in any of the sets* exceeds 3 (or possibly 4). This is apparently not the case. But suppose that jackdaws can track quantity up to approx. 3 via an object system (see core system of object representation in the introduction), which is precise, and deal with all the larger quantities as one category, something like “a lot” or “more than 3”. If we suppose that jackdaws represent the ordinal position of this category, in fact they use concept that  $1 < 2 < 3 < \text{“a lot”}$ , this may explain all our success and failure patterns. Something similar to this 1-2-3-many system has been identified in an indigenous Amazonian tribe, the Pirahá, who possess a one-two-many counting system (Gordon 2004). The language of the tribe has no words for numbers other than one and two, but has a word for more than

two. Gordon has shown that the lack of a counting system clearly affects the numerical cognition of this tribe as performance with quantities greater than 3 was very poor, but also found evidence for an analogue estimation process for larger numerosities.

If we speculate this hypothesis further we could suppose that Spelke (2000) was indeed right, it might be possible that the core object system deals with small sets, and the number system is only utilized with large quantities. In this case for example our current experiment (and in fact many others using similar methodology and gaining similar results) only probed the “object system”, whereas relative judgements of larger sets probe the analogue representations of the core number system. However, shedding more light to this problem might prove to be very difficult, as with small numbers, the ratio of the sets is naturally large, thus the ratio dependency of the analogue magnitude model is hard to distinguish from the object tracking system. So is it conceivable that jackdaws use a 1-2-3-many system for small amounts and also possess an analogue estimation system for large quantities? I believe that it would be well worth investigating performance with larger quantities, with similar ratios in the future to answer this and some other questions in more detail.

Following Hauser and Carey (2000) we have also included a control trial where subjects had to choose between 3 small pieces of food and 1 large piece, the two sets equalling in volume. In the original article Hauser and colleagues hypothesized that if numerical information is coded by the rhesus monkeys (*Macaca mulatta*), than they should be expected to choose the 3 small pieces over the one large piece, which they did, while if continuous variables are coded, than choice would be random, just like we found in the case of jackdaws. However, this may not be so simple. Why should one suppose that a subject will only consider the number of items placed and take absolutely no notice of the size of the pieces? Clearly, this makes little sense in a natural foraging situation. Rhesus monkeys in the Hauser et al. experiments were situated approx. 10 meters from the experimenters. Perhaps from this distance the difference in size of the placed pieces ( $1/6^{\text{th}}$  vs.  $1/2$  of an apple) was not clearly visible/detectable, thus monkeys had to depend on the number of items placed/number of movements/placement time. In our case, however birds sat on a perch approx. 40-50 cm from the containers and from that distance item size was clearly detectable.

Various publications have recently reported (e.g. Cantlon & Brannon 2007; Tomonaga 2008; Cordes & Brannon 2009) that natural choice of quantities is based on continuous and numerical attributes alike, as multiple, redundant cues. This also points to the idea that there isn't considerable difference in the relative salience of numerical vs. continuous variables.

This relates well to the notions of the representational model suggested by Gelman and Gallistel, described a bit earlier. Researchers claim that this also mimics the natural foraging situation. For example Tomonaga (Tomonaga 2008) found that chimpanzees use multiple cues, including numerosity, very flexibly in two-way choice situations. Contrary to the “Last Resort Hypothesis”, suggesting that animals only use numerical information as a last resort (see in more detail in the Introduction) rhesus monkeys (Cantlon & Brannon 2007) have been found to code and use number as basis of discrimination in every instance where ratio of sets was not particularly unfavourable, while young human infants (Cordes & Brannon 2009) have been shown to represent changes in number/discreet quantity. This all suggests that numerical values, parallel to continuous properties are represented naturally.

We suggest that similarly to those mentioned above, our subjects also coded both numerical (discreet) and continuous information. If we suppose that the above is true, it is indeed not so simple to speculate on what the subjects will base decision on. Especially considering that the use of sets equalling in volume brings up further concerns. It has been found by Beran et al. (2008) that chimpanzees do rely on more than one property of food items when making choices between alternative sets, but an interesting twist to that has also been documented. Surprisingly chimpanzees were biased to select the set with the biggest individual item, even when the array contained less food overall. This bias was hard to interpret in strict terms of optimal foraging, as it is difficult to understand why any animal would prefer large individual items at the expense of overall intake. The authors could only speculate the reason of this phenomenon, and proposed explanations such as perhaps the largest food item might have been used as a dominant cue, or that perhaps animals rely on a sort of shortcut in decision making where they do not evaluate each problem individually, rather heuristics may be used to allow more rapid responding. Beran and colleagues further investigated this bias and found that not only size, but magnitude, contiguity and wholeness plays a role in perception of food amounts by chimpanzees (Beran et al. 2009). Chimpanzees seemed to undervalue the total amount of food in arrays where items did not appear to be whole. This is yet another evidence of seemingly suboptimal responding in natural choice situations which prevent the subjects from maximizing food intake.

All the above points out that fabricating a simple hypothesis when interpreting a 3 small = 1 large non-visible choice is not possible. There are too many possible explanations for the certain outcomes, thus this choice is not suitable for what it was initially intended, namely to determine the type of information mentally represented and guiding choice behaviour. However, it would most certainly be very interesting to assess this testing

paradigm in more detail and gather some more detailed information on what may influence choice in situations similar to this one.

Some of the research that has shown advanced quantity related abilities in animals (mainly monkeys and apes) was based on experiments involving extensive training of a small number of subjects. There are only a few exceptions from this, such as the study of semi-free ranging rhesus monkeys (Hauser & Carey 2000) and the interesting field experiment with a food-hoarding songbird, the New Zealand robin (Hunt et al. 2008). I think that spontaneously available and trainable capacities should not be confused, especially when speculating on possible underlying mechanisms. Not only did we not use any training prior to the experiments, we also used a strictly non-corrective testing method, where correct response has never been demonstrated, while the subject was rewarded for making a choice, regardless of the choice being correct or not. Also the animals faced each choice only one time. Therefore, we claim that our results in quantity judgements and mental representation of items in jackdaws reflect abilities spontaneously available to any adult member of the jackdaw species.

Studies of numerical/quantity related cognition in birds has been largely dominated by (non-caching) non-corvids (see table below with the most important references).

<b>Birds' numerical/quantity related cognition studies</b>			
<i>Corvids</i>		<i>Non-Corvids</i>	
<i>Non-caching</i>	<i>Caching</i>	<i>Non-caching</i>	<i>Caching</i>
(Köhler 1941)	(Zorina & Smirnova 1996)	(Ain et al. 2009)	(Hunt et al. 2008)
	(Smirnova et al. 2000)	(Pepperberg & Carey 2012)	(Garland et al. 2012)
	(Bogale et al. 2011)	(Rugani et al. 2008, 2009, 2011)	
		(Fontanari et al. 2011)	
		(Scarf et al. 2011)	
		(Vallortigara 2012)	

**Table 4. Research on numerical/quantity related cognition in birds**

Apart from the pioneering study of Otto Köhler, non-caching corvids have not been tested, but quantity related testing of caching corvid species is also limited. This is a bit

surprising, considering how many other impressive cognitive abilities have been documented, especially in caching corvid species. We unfortunately cannot relate our data to those of Smirnova et al. on hooded crows (Zorina & Smirnova 1996; Smirnova et al. 2000) or Bogale et al. (Bogale et al. 2011) on jungle crows, as their aims and methods were fundamentally different from ours, thus we feel it would be very interesting to perform tests similar or perhaps identical to ours with at least one caching species from the corvid family.

As described in the Introduction, non-caching species have been shown to have a smaller hippocampus than caching species (Healy & Krebs 1992). One question inevitably arises from this fact. Is the difference in the size of the hippocampal complex only reflected in spatial memory and cache recovery, or perhaps in other object related cognitive abilities? In the course of our two experiments we have found no evidence for impairment any of the tested cognitive abilities. We tend to agree with the idea that the common ancestor of caching and non-caching corvid species was a food-storer (de Kort & Clayton 2006), where the dependence on stored food was an important selective pressure. In case of non-storing species, such as the jackdaw, this selective pressure has been apparently lifted. How and why this happened, we can only speculate, however considering the ecology of the species, it is probable that group living and connected factors may be in the background. Social mechanisms, such as food offering (de Kort et al. 2003), food and object sharing and coalition forming (von Bayern et al. 2007) may decrease the dependence on stored food and cause storing behaviour to weaken and maybe even diminish with time, but object related cognition (in most part) most probably has not been influenced.

Sadly we lack the possibility to contrast our data with those of a closely related species, however when we compare them to those of primates, we find striking similarities, as detailed above at various points. As mentioned in one section of the Introduction, recently a number of complex cognitive abilities have been reported in the family *Corvidae* which parallel those of primates. It has been suggested (Emery & Clayton 2004b; Seed et al. 2009) that intelligence in Corvids and Apes are examples of convergent evolution. The basis of this idea mainly comes from the social domain (social learning, imitation, ToM, etc.), but there are some examples of comparable performance from the physical domain as well. Corvids, as well as primates, display insight, innovation and tool use. Ravens (*Corvus corax*) have provided evidence for insight when faced with a novel problem, where a piece of meat has been attached to the end of a string, which has been tied to a perch. In order to get the food, the bird had to repeatedly pull on the string, and then step onto it to keep it from falling back. Ravens solved this problem as soon as faced with it, did not need any trial-and error learning

(Heinrich 1995). Innovation and tool use was most impressively demonstrated by New Caledonian crows (*Corvus moneduloides*), who manufacture, use and carry around two types of tools made of *Pandanus* leaves in the wild. Field observations of tool use suggested complex cognition, which was confirmed by laboratory experiments, where a New Caledonian crow, Betty proved to be capable of modifying non-functional novel material and choose correct length and diameter when constructing a tool to reach normally inaccessible food.

As described in more detail in the appropriate sections, our findings in the domain of object related and numerical cognition also parallel those of primates. Stage 6 object permanence and the ability to select the larger set based on the repeated update of mental representation even excels the performance of some primate species. In this respect we think that our findings corroborate the hypothesis that corvids may indeed be “feathered apes” (Emery 1992), and that non-caching jackdaws are no exceptions.

Corvids and primates have been shown to have been exposed to similar evolutionary pressures during their evolutionary histories (Seed et al. 2009), such as spatiotemporally dispersed food resources, omnivory and extractive foraging, and the need for cooperation and behavioural coordination. While their divergent anatomy may constrain an evolutionary response in some instances, in some other cases a similar response was obviously given. It would be tremendously interesting to me personally, and to the field I believe, to further investigate object/quantity related cognition and mental representations in corvids, further investigating the points that this Thesis was not able to cover, as well as perhaps venture into the social cognition domain with jackdaws.



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## Summary

The aim of research described in this thesis was to investigate physical cognition of a non-caching corvid species, the jackdaw (*Corvus monedula*) by utilizing comparative methods. The first experiment assessed the development of mental representations of the physical world, its objects and their interactions. The ontogeny and final stage of Piagetian object permanence (Piaget 1954) was documented by use of a paradigm (“Scale 1”, (Uzgiris & Hunt 1975b) that has been utilized with a wide variety of species, including three caching species from the corvid family, magpies, ravens and Eurasian jays. Contrary to the prediction that object permanence capacities of a non-caching species may be inferior to those reported in caching species (Pollok et al. 2000), we found that jackdaws develop object permanence abilities even quicker than magpies, where physical development of the two species follow approximately the same rate. We report that jackdaws reach stage six object permanence, i.e. are capable of following multiple invisible displacements, which finding has been corroborated by results of an additional test of stage six proposed by Pepperberg (2002), the Shell game. The second experiment assessed mental representations of object quantity and quantity discrimination based on this representation. Several corvid species have been reported to possess sophisticated cognitive abilities, some paralleling those of apes (Emery & Clayton 2004b). However, there were only a few experiments related to quantity representation in corvids, mainly in caching species, and utilizing training-based paradigms. We used a non-corrective testing procedure (Hauser & Carey 2000) where sets to be discriminated were never visible to subjects in their entirety, but objects were placed sequentially into one of two opaque containers. Thus, subjects had to rely on mental representations in discrimination of quantities. We found that jackdaws’ quantity discriminations follow Weber’s/Fechner’s law, meaning that their performance declines in the direction of larger set size (numerical size effect), and when the difference between the two arrays decreases (numerical distance). These results are usually interpreted as the signatures of an analogue magnitude representational system. We controlled for temporal/referential cues by evening out the sides with the use of non-food items. Results suggest that jackdaws do not use temporal cues, but may well use total volume as basis for discrimination, perhaps among other attributes (choice may be based on multiple cues).

## Összefoglaló

A disszertációban ismertetett kutatás a csóka (*Corvus monedula*), egy táplálékrajtó viselkedést nem mutató varjúféle, egyes, a fizikai világgal kapcsolatos kognitív képességeinek feltárására irányult, összehasonlító pszichológiai módszerekkel. Első kísérletünkben a tárgyi világról és elemeinek interakciójáról alkotott mentális reprezentációk fejlődését vizsgáltuk. A piagetianus tárgyállandóság (Piaget 1954) ontogenezisét egy olyan paradigma (Uzgoris & Hunt 1975a) segítségével dokumentáltuk, amelyet korábban már számos állatfaj, köztük három táplálékrajtó varjúféle, a szarka, a mátyásmadár és a holló esetében használtak sikerrel. Eredményeink nem támasztják alá azt a feltételezést (Pollok et al. 2000), amely szerint a táplálékrajtó viselkedést mutató varjúfélék tárgyállandósággal kapcsolatos képességei felülmúlják az ilyen viselkedést nem mutató nem mutató csókákéit. Éppen ellenkezőleg, azt találtuk, hogy a csókák még a szarkáknál is gyorsabban fejlődnek a tárgyállandóság tekintetében, pedig a két faj fizikai fejlődésének üteme közel azonos. Eredményeink szerint a csókák elérik a tárgyállandóság 6. szintjét. Ezt megerősítette egy további kísérlet, amely Pepperberg (2002) szerint alkalmas a többszörös láthatatlan áthelyezések követésének (6. szint) további vizsgálatára. Második kísérletünkben tárgyak mennyiségének mentális reprezentáción alapuló megítélését vizsgáltuk. Számos varjúféle esetében találtak bizonyítékokat kiemelkedő kognitív képességekre, amelyek akár emberszabásúak hasonló képességeivel is vetekszenek (Emery & Clayton 2004b), ennek ellenére viszonylag kevés mennyiségi reprezentációt vizsgáló kísérletről tudunk. Az ilyen irányú néhány kísérlet alanyi táplálékrajtó fajok voltak, a módszer pedig hosszas tréningezést igényelt. A mi módszerünk (Hauser & Carey 2000) spontán reprezentációs képességeket vizsgált, valamint a tárgyakat egyenként helyezzük el két átlátszatlan tartály egyikébe, így az alany soha nem láthatta egészében az elrejtett tárgyak összességét. Választásában tehát azok mentális reprezentációjára kellett hagyatkoznia. Azt találtuk, hogy a csókák teljesítménye követi a Weber/Fechner szabályt mivel a teljesítmény a magasabb számok, illetve a kisebb különbségek irányába romlik, ami egy analóg mennyiségi reprezentációs rendszerre enged következtetni. Kontrol kísérletünkben a lehelyezési időt és a referenciális jelzéseket apró kavicsok beiktatásával kiegyenlítettük. Eredményeinkből arra következtethetünk, hogy a csókák választásukat nem a lehelyezési időre/referenciális jelek mennyiségére alapozzák, ám nem kizárható, hogy a teljes térfogatot is számításban veszik döntési helyzetben.

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