

Role of Mental Representations in Quantity Judgments by Jackdaws (*Corvus monedula*)

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The representation of quantity by the preverbal or nonverbal mind is a question of considerable interest in the study of cognition, as it should be generally adaptive to most animals to be able to distinguish quantity. We already know that some primate species and human infants represent and enumerate objects in similar ways. Considerable data also exist concerning such abilities in birds. Our aim in this study has been to find out whether jackdaws (*Corvus monedula*) are capable of performing relative quantity judgments based on mental representations, and if so, what are the limiting factors to their abilities. In our setting the birds were required to make a choice between two visibly and sequentially placed set of food items which, at the moment of choice were not visible to the subjects. We investigated all the number combinations between 1 and 5. Our results show that jackdaws are able to perform relative quantity judgments successfully, even when temporal cues are controlled for, whereas their performance declines in the direction of larger set size (numerical size effect), and when the difference between the two arrays decreases (numerical distance and ratio effect). These signatures are usually interpreted as evidence for the “accumulator” model of mental representation of quantity. Our control 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).

Keywords: relative quantity judgments, mental representation, jackdaw, models

Humans’ symbolic representations of exact number, like other aspects of human knowledge, may 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 develop-

ment, maybe even at birth (Hauser & Spelke, 2004). 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.

Some researchers recently suggested the existence of *two core number systems* in both humans and nonhuman animals (Feigenson, Dehaene, & Spelke, 2004; Uller, Jaeger, Guidry, & Martin, 2003; Xu & Spelke, 2000). 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 behavioral 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, Treisman, & Gibbs,

This article was published Online First September 23, 2013.

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We thank the Jackdaws for their kind and willing cooperation, the Aktion Österreich - Ungarn for financial support of this project, Bruna Bonechi, Christine Pribersky-Schwab, Julian Hoskowitz and all the KLF staff for their invaluable support, Gabriella Lakatos and Zsuzsánna Horváth for their help with statistical analysis and valuable criticism of the manuscript. The jackdaw project at KLF was funded by FWF-Project P16939-B03. This research was also supported by ESF Research Networking Programme “CompCog” (www.compCog.org) (06-RNP-020). All experiments were conducted in accordance with animal welfare regulations of both Austria and Hungary.

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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 (Cantlon, Safford, & Brannon, 2010; Jordan & Brannon, 2006). 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 nonhuman 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 (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 nonhumans 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 (Boysen & Berntson, 1995; Boysen, Mukobi & Berntson, 1999; 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, whether 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 Pirahã, an Amazonian tribe, who have been shown (Gordon, 2004) to have a very limited number vocabulary. Frank et al. (2008) found that the lack of number words does 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 (Cantlon et al., 2010; Cordes & Brannon, 2009; Feigenson, Carey, & Hauser, 2002; Feigenson, Carey, & Spelke, 2002; Xu & Spelke, 2000). 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 (, e.g., 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

(Abramson et al., 2011), pigeons (Emmerton & Renner, 2009), meadow voles (Ferkin et al., 2005), bottlenose dolphins (Kilian et al., 2003), salamanders (Krusche, Uller, & Dicke, 2010; Uller et al., 2003), elephants (Perdue et al., 2012), and black bears (Vonk & Beran, 2012). Most, if not all, animal species have been subjected to selective pressures toward the emergence of some level of quantity representation and discrimination, as such cognitive capacities could prove to be advantageous in not only foraging contexts, but also in judgment of group size, clutch size, and so forth.

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 multispecies) 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 to provide the basis for further comparative investigations.

These birds were considered promising subjects as recent research showed that various bird species possess quantity discrimination abilities (e.g., Aïn et al., 2009; Fontanari et al., 2011; Garland, Low, & Burns, 2012; Hunt, Low, & Burns, 2008; Pepperberg & Carey, 2012; Rugani et al., 2009; Rugani, Regolin, & Vallortigara, 2011; Rugani et al., 2010; Rugani, Regolin, et al., 2010; Scarf et al., 2011; Vallortigara et al., 2010) 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 & 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 (Bogale, Kamata, Mioko, & Sugita, 2011; Smirnova, Lazareva, & Zorina, 2000; Zorina & Smirnova, 1996); moreover, Köhler previously conducted some “matching-to-sample” type numerical experiments with jackdaws (Köhler, 1941, 1950) some of which yielded positive, promising results. One of his subjects 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. This result has only been reported in the case of one subject and after substantial training, 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, Carey, and Hauser (2002) for infants, by Beran (2001) for chimpanzees, by Hauser et al. (2000) for rhesus macaques, 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, Miklósi, & Bugnyar, 2012), 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 covaries with continuous variables such as mass, volume, contour length, surface area, and so forth, thus the discrimination may not require the recognition of item number. Nonetheless, judgment has to be based on representation that is updated with the placement of each item, thus such a judgment requires interactions between an enumerative or summative process and working memory.

The goal of our experiment was to investigate whether jackdaws are spontaneously (without any quantity related or communicational training) capable of making quantity judgments 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, although if success should decline as the ratio of the smaller set to the larger set increases, that could be interpreted as a characteristics behavioral 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. Ontogeny of object permanence abilities of our subjects has been studied using the Uzgiris and Hunt (1975) Scale 1 set of tasks before the numerical experiments (Ujfalussy et al., 2012). Hand-raising and testing took place at the Konrad Lorenz Research Station in Grünau, Austria. Jackdaws were captured from nests in Stralsund and in Baden-Württemberg, Germany, with appropriate licenses, between 13 and 20 days post hatch. After capture they were kept in cardboard boxes lined with hay and towelling, two to four birds together, until fledging between Days 26–31. A few days after fledging they were moved to a spacious outdoor aviary, approximately 12 m by 10 m and about 4–5 m 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 five 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. The floor of the experimental complex was covered with fine grained gravel. During most of the day, when no testing was

Table 1

Subjects Participating in the Certain Experiments of Our Study

Name of subject	Baseline	Numerical competence	Control
1. Csuri	[check]	[check]	[check]
2. Gonzo	[check]	[check]	[check]
3. Sundance	[check]	[check]	[check]
4. Novak	[check]	[check]	[check]
5. Fraulein	[check]	[check]	[check]
6. Finci	[check]	[check]	[check]
7. Rozi	[check]	[check]	[check]
8. Suni	[check]	[check]	X
9. Borso	[check]	[check]	[check]
10. Berci	[check]	[check]	[check]
11. Marci	[check]	[check]	[check]
12. Puck	[check]	[check]	[check]
13. Phoebe	X	[check]	X
14. Woodstock	[check]	[check]	X
	<i>n</i> = 13	<i>n</i> = 14	<i>n</i> = 11

in progress, the birds were free to roam in the entire main aviary and the experimental complex as well.

While still in the nest, the birds were fed with a wet mix consisting of ground beef, hard boiled egg yolk, cottage cheese, and a commercially available dry insect mix. Bird vitamins and ground sepia shells 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.

Because all testing was done on a 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 1.

Procedures

Apparatus. The study was performed during summer and autumn of 2005. 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 70 × 100 cm and a perch, at the level of the tabletop, but about 15 cm 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 1). A similar device was used by 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 cm tall and approx. 4 cm in diameter, with a 10 × 10 cm 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 cm wide and 8 cm long, with a 2-mm rim.

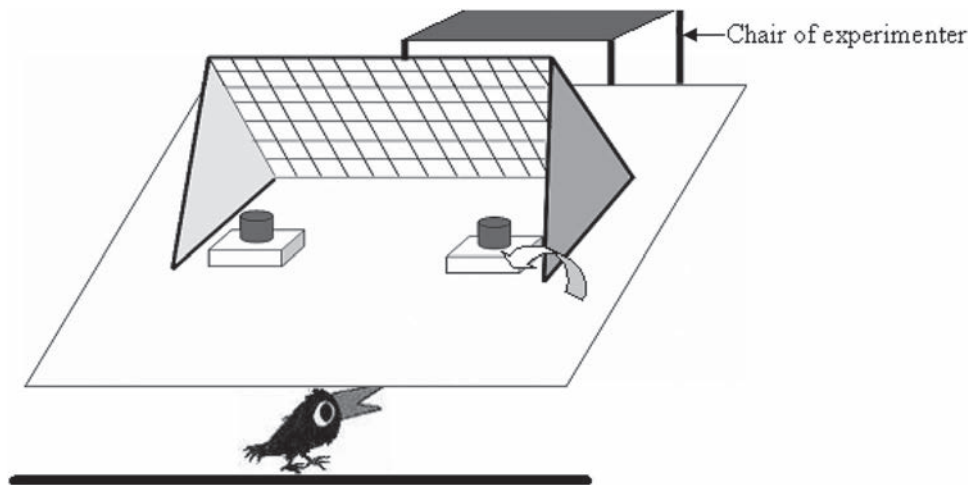


Figure 1. The experimental setup with the transparent flipping obstacle, the opaque container, the perch, and seat of the experimenter.

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 color. This treat is generally desired by the birds, but it is not their most desired food. In the control experiments small pieces of gray 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 odor cues.

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). 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, however we need to point out

how important it is in the study of animal cognition that the subject is in no way stressed, as stress may considerably impair performance (Weir & Kacelnik, 2006). Our subjects at the time of these experiments were becoming increasingly neophobic (as reported also in Zucca et al. [2007] in case of jays), thus we felt 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., 2012), 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. To show this, 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 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, whereas the remaining 5 made only a single error. Thus no bird erred more than once in the 8 possible trials.

Quantity Discrimination Experiment

After the baseline experiment, we began our main study. 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 nontransparent containers, thus were invisible at the moment of choice. 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 noncorrective 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 because 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 before 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 2nd or 3rd 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 the size of the food pieces. Thus the sole difference between the sets 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 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. 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 SPSS 13.0 software. We have used Shapiro-Wilk 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 with the 50% chance level by Wilcoxon signed-ranks 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 ($1-5 p = .0002$, $2-5 p = .0005$, $1-4 p = .0002$, $2-4 p = .002$, $2-3 p = .002$, $1-3 p = .001$, $1-2 p = .002$), but failed to do so in the case of the combinations 3–5, 4–5, and 3–4 (see Figure 2). 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. The linear regression showed that the ratio of the sets is a good predictor of the mean percentage of the correct choices, $r = -0.907$, $F(1, 8) = 37, 29$, $p < .001$, and 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 3.

Individual performance could not be analyzed 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 ($p < .05$). 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 ($p = .91$, Wilcoxon’s 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 ($p = .0039$, Wil-

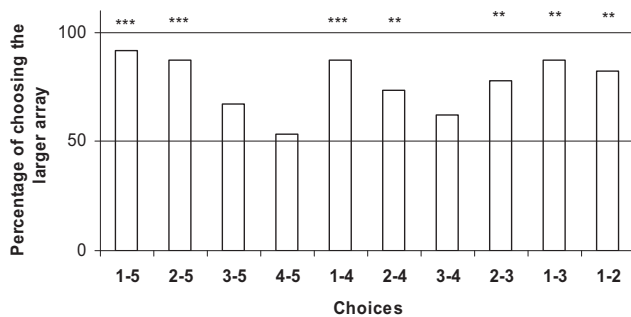


Figure 2. Group performance ($n = 14$, total of 28 trials/per choice) of choosing the larger quantity in all possible choices between 1 and 5. ** $p < .01$, *** $p < .001$. Chance level is at 50%.

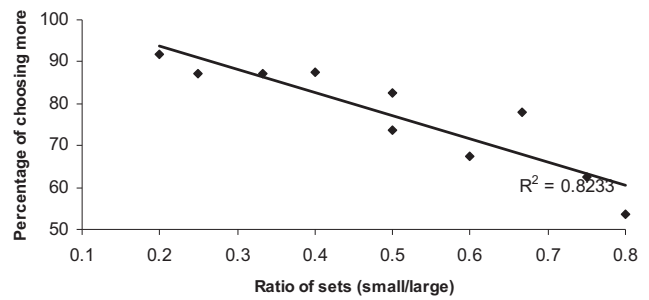


Figure 3. Group performance ($n = 14$) of choosing the larger quantity presented as a function of the ratio (small/large) of the two quantities. \blacklozenge signify the observed performance, and the straight line signifies the linear trend between the two variables, $r = -0.907$, $F(1, 8) = 37, 29$, $p < .001$; $R^2 = 0.8233$.

coxon matched-pairs signed ranks test), but showing that second trials were slightly 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 ($\bullet\bullet\bullet 1-4 p = .004$, $\bullet 1-2 p = .008$). 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 ($\bullet 3-2 p = .004$). In this case they still chose the side with more food pieces and did not avoid the side with the stone (see Figure 4). 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.

Discussion

Our results show that the capacity to make relative quantity judgments founded on mental representations of items in the sets is present in the noncaching Corvid species, the Jackdaw (*Corvus monedula*). We found that their representational system is spontaneously available, as subjects do not require any training 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 et al., 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

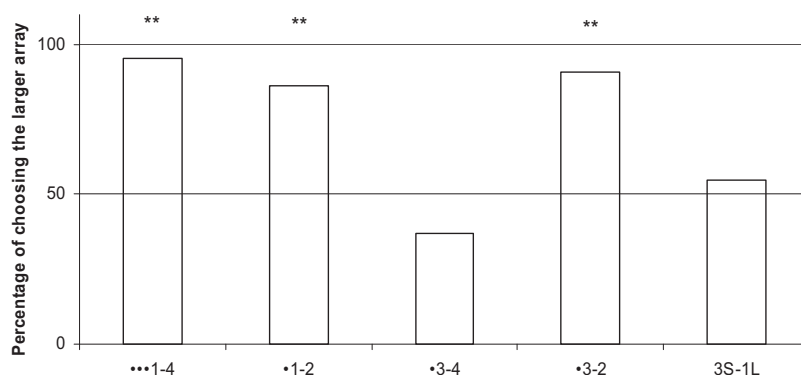


Figure 4. Group ($n = 11$, total of 22 trials/choice) performance of choosing the larger quantity of food pieces in the control experiment. $**p < .01$, $***p < .001$. Chance level is at 50%. Black dots signify the small stones. 3S = three small food pieces, 1L = one large food piece.

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 covaries with continuous variables, such as total volume, cumulative surface area, contour length, and so forth.

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 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 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 "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 (Cantlon et al., 2010; Xu & Spelke, 2000), apes (Beran & Beran, 2004; Hanus & Call, 2007; Tomonaga, 2008), monkeys (Evans et al., 2009), and other animal species (Agrillo et al., 2011; Ain et al., 2009; Baker et al., 2012; Scarf et al., 2011).

In our control experiment 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 versus 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 side with the 3 small pieces, however in this trial the birds chose randomly. This result may suggest that jackdaws base their relative judgment 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 argue that contrary to the "last-resort hypothesis" 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 (2008) 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 (RT) across unisensory and multisensory conditions (Jordan & Baker, 2010). All these findings support the hypothesis that relative quantity judgments 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 equal in volume (3 small pieces vs. 1 large) may also bring up a question of concern, 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, Evans, & Harris, 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, Evans, & Ratliff, 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 judgment tasks.

We, based on this study, naturally cannot speculate whether numerical or continuous variables are the more dominant cues in relative quantity judgments, 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 judgments 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 behavior 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 we state that our birds were able to choose the larger amount of food, even though they never saw the sets in total. Based on this we argue that jackdaws are able to mentally represent sequentially placed sets and can use this information as basis for further quantity related cognitive processes, such as relative quantity judgments. The subjects’ performance showed ratio effects, which suggest that the representational system underlying the birds’ performance is best described as analogue magnitude estimation.

Moreover, we report that jackdaws were able to make successful choices with very little previous experience or training on these specific trial types, so it seems that required abilities are spontaneously available to members of this species.

Results of our control trials indicated that the birds were not using temporal cues to discern the larger amounts of food, although they possibly were using total volume as a cue rather than number of items. Results of our last control trial type seem to also suggest that discriminations may not be purely numerical.

References

- Abramson, J. Z., Hernández-Lloreda, V., Call, J., & Colmenares, F. (2011). Relative quantity judgments in South American sea lions (*Otaria flavescens*). *Animal Cognition*, *14*, 695–706. doi:10.1007/s10071-011-0404-7
- Agrillo, C., Piffer, L., & Bisazza, A. (2011). Number versus continuous quantity in numerosity judgments by fish. *Cognition*, *119*, 281–287. doi:10.1016/j.cognition.2010.10.022
- Al Ain, S., Giret, N., Grand, M., Kreutzer, M., & Bovet, D. (2009). The discrimination of discrete and continuous amounts in African grey parrots (*Psittacus erithacus*). *Animal Cognition*, *12*, 145–154. doi:10.1007/s10071-008-0178-8
- Baker, J. M., Morath, J., Rodzon, K. S., & Jordan, K. E. (2012). A shared system of representation governing quantity discrimination in canids. *Frontiers in Psychology*, *3*, 387. doi:10.3389/fpsyg.2012.00387
- Balda, R. P., & Kamil, A. C. (1992). Long-term spatial memory in Clark’s nutcracker, *Nucifraga columbiana*. *Animal Behaviour*, *44*, 761–769. doi:10.1016/S0003-3472(05)80302-1
- Balda, R., & Kamil, A. (2002). Spatial and social cognition in corvids: An evolutionary approach. In M. Bekoff and C. Allen (Eds.), *The cognitive animal*. Boston, MA: Bradford.
- Beran, M. J. (2001). Summation and numerosness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *115*, 181–191. doi:10.1037/0735-7036.115.2.181
- Beran, M. J. (2004). Chimpanzees (*Pan troglodytes*) respond to nonvisible sets after one-by-one addition and removal of items. *Journal of Comparative Psychology*, *118*, 25–36. doi:10.1037/0735-7036.118.1.25
- Beran, M. J. (2008). Monkeys (*Macaca mulatta* and *Cebus apella*) track, enumerate, and compare multiple sets of moving items. *Journal of Experimental Psychology: Animal Behavior Processes*, *34*, 63–74. doi:10.1037/0097-7403.34.1.63
- Beran, M. J., & Beran, M. M. (2004). Chimpanzees remember the results of one-by-one addition of food items to sets over extended time periods. *Psychological Science*, *15*, 94–99. doi:10.1111/j.0963-7214.2004.01502004.x
- Beran, M. J., Evans, T. A., & Harris, E. H. (2008). Perception of food amounts by chimpanzees based on the number, size, contour length and visibility of items. *Animal Behaviour*, *75*, 1793–1802. doi:10.1016/j.anbehav.2007.10.035
- Beran, M. J., Evans, T. A., & Ratliff, C. L. (2009). Perception of food amounts by chimpanzees (*Pan troglodytes*): the role of magnitude, contiguity, and wholeness. *Journal of Experimental Psychology: Animal Behavior Processes*, *35*, 516–524. doi:10.1037/a0015488
- Bogale, B. A., Kamata, N., Mioko, K., & Sugita, S. (2011). Quantity discrimination in jungle crows, *Corvus macrorhynchos*. *Animal Behaviour*, *82*, 635–641. doi:10.1016/j.anbehav.2011.05.025
- Boysen, S. T., & Berntson, G. G. (1995). Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes*, *21*, 82. doi:10.1037/0097-7403.21.1.82
- Boysen, S. T., Mukobi, K. L., & Berntson, G. G. (1999). Overcoming response bias using symbolic representations of number by chimpanzees (*Pan troglodytes*). *Animal Learning & Behavior*, *27*, 229–235. doi:10.3758/BF03199679
- Bugnyar, T., & Heinrich, B. Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proceedings. Biological Sciences / The Royal Society*, *272*(1573):1641–6, 2005. doi:10.1098/rspb.2005.3144
- Bugnyar, T., & Kotrschal, K. (2002). Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it “tactical” deception? *Animal Behaviour*, *64*, 185–195. doi:10.1006/anbe.2002.3056
- Call, J. (2000). Estimating and operating on discrete quantities in orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, *114*, 136–147. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10890585>. doi:10.1037/0735-7036.114.2.136
- Canlon, J. F., & Brannon, E. M. (2007). How much does number matter to a monkey (*Macaca mulatta*)? *Journal of Experimental Psychology: Animal Behavior Processes*, *33*, 32–41. doi:10.1037/0097-7403.33.1.32
- Canlon, J. F., Safford, K. E., & Brannon, E. M. (2010). Spontaneous analog number representations in 3-year-old children. *Developmental Science*, *13*, 289–297. doi:10.1111/j.1467-7687.2009.00887.x
- Carey, S. (2009). *The origin of concepts*. New York, NY: Oxford University Press. Retrieved from http://www.tandfonline.com/doi/abs/10.1207/S15327647JCD0101N_3
- Clayton, N. S., & Emery, N. J. (2005). Corvid cognition. *Current Biology*, *15*, 80–81. Retrieved from <http://www.yaroslavvb.com/papers/clayton-corvid.pdf> doi:10.1016/j.cub.2005.01.020
- Clearfield, M., & Mix, K. (1999). Number versus contour length in infants’ discrimination of small visual sets. *Psychological Science*, *10*, 408–411. Retrieved from <http://pss.sagepub.com/content/10/5/408.short> doi:10.1111/1467-9280.00177
- Cordes, S., & Brannon, E. M. (2009). The relative salience of discrete and continuous quantity in young infants. *Developmental Science*, *12*, 453–463. doi:10.1111/j.1467-7687.2008.00781.x

- Cordes, S., & Brannon, E. M. (2008). The difficulties of representing continuous extent in infancy: Using number is just easier. *Child Development, 79*, 476–489. doi:10.1111/j.1467-8624.2007.01137.x
- Davis, H., & Pérusse, R. (1988). Numerical competence in animals: Definitional issues, current evidence, and a new research agenda. *Behavioral and Brain Sciences, 11*, 561–579. doi:10.1017/S0140525X00053437
- De Kloet, E. R., Oitzl, M. S., & Joëls, M. (1999). Stress and cognition: Are corticosteroids good or bad guys? *Trends in Neurosciences, 22*, 422–426. doi:10.1016/S0166-2236(99)01438-1
- Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science, 306*(5703), 1903–7. doi:10.1126/science.1098410
- Emmerton, J., & Renner, J. C. (2009). Local rather than global processing of visual arrays in numerosity discrimination by pigeons (*Columba livia*). *Animal Cognition, 12*, 511–526. doi:10.1007/s10071-009-0212-5
- Evans, T. A., Beran, M. J., Harris, E. H., & Rice, D. F. (2009). Quantity judgments of sequentially presented food items by capuchin monkeys (*Cebus apella*). *Animal Cognition, 12*, 97–105. doi:10.1007/s10071-008-0174-z
- Feigenson, L., Carey, S., & Hauser, L. B. (2002). The representations underlying infants' choice of more: Object files versus analog magnitudes. *Psychological Science, 13*, 150–156. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/11933999>. doi:10.1111/1467-9280.00427
- Feigenson, L., Carey, S., & Spelke, E. S. (2002). Infants' discrimination of number vs. continuous extent. *Cognitive Psychology, 44*, 33–66. doi:10.1006/cogp.2001.0760
- Feigenson, L., Dehaene, S., & Spelke, E. S. (2004). Core systems of number. *Trends in Cognitive Sciences, 8*, 307–314. doi:10.1016/j.tics.2004.05.002
- Ferkin, M. H., Pierce, A. A., Sealander, R. O., & Delbarco-Trillo, J. (2005). Meadow voles, *Microtus pennsylvanicus*, can distinguish more over-marks from fewer over-marks. *Animal Cognition, 8*, 182–189. doi:10.1007/s10071-004-0244-9
- Fontanari, L., Rugani, R., Regolin, L., & Vallortigara, G. (2011). Object individuation in 3-day-old chicks: Use of property and spatiotemporal information. *Developmental Science, 14*, 1235–1244. doi:10.1111/j.1467-7687.2011.01074.x
- Frank, M. C., Everett, D. L., Fedorenko, E., & Gibson, E. (2008). Number as a cognitive technology: Evidence from Pirahã language and cognition. *Cognition, 108*, 819–824. doi:10.1016/j.cognition.2008.04.007
- Gallistel, C., & Gelman, I. (2000). Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences, 4*, 59–65. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10652523>. doi:10.1016/S1364-6613(99)01424-2
- Garland, A., Low, J., & Burns, K. C. (2012). Large quantity discrimination by North Island robins (*Petroica longipes*). *Animal Cognition, 15*, 1129–1140. doi:10.1007/s10071-012-0537-3
- Gordon, P. (2004). Numerical cognition without words: Evidence from Amazonia. *Science, 306*, 496–499. doi:10.1126/science.1094492
- Hanus, D., & Call, J. (2007). Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): the effect of presenting whole sets versus item-by-item. *Journal of Comparative Psychology, 121*, 241–249. doi:10.1037/0735-7036.121.3.241
- Haun, D. B. M., Jordan, F. M., Vallortigara, G., & Clayton, N. S. (2010). Origins of spatial, temporal and numerical cognition: Insights from comparative psychology. *Trends in Cognitive Sciences, 14*, 552–560. doi:10.1016/j.tics.2010.09.006
- Hauser, L. B., & Carey, S. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings Biological Sciences / The Royal Society, 267*(1445), 829–33. doi:10.1098/rspb.2000.1078
- Hauser, L. B., & Spelke, E. S. (2004). Evolutionary and developmental foundations of human knowledge. In M. Gazzaniga (Ed.), *The cognitive neurosciences*. Cambridge, MA: MIT Press. Retrieved from http://www.filosoficas.unam.mx/~mael/home_archivos/hauser2004b.pdf
- Henderson, I. G., Hart, P. J. B., & Burke, T. (2000). Strict monogamy in a semi-colonial passerine: The jackdaw *Corvus monedula*. *Journal of Avian Biology, 31*, 177–182. doi:10.1034/j.1600-048X.2000.310209.x
- Hunt, S., Low, J., & Burns, K. C. (2008). Adaptive numerical competency in a food-hoarding songbird. *Proceedings Biological Sciences / The Royal Society, 275*, 2373–2379. doi:10.1098/rspb.2008.0702
- Jordan, K. E., & Baker, J. M. (2010). Multisensory information boosts numerical matching abilities in young children. *Developmental Science, 2*, no–no. doi:10.1111/j.1467-7687.2010.00966.x
- Jordan, K. E., & Brannon, E. M. (2006). A common representational system governed by Weber's law: Nonverbal numerical similarity judgments in 6-year-olds and rhesus macaques. *Journal of Experimental Child Psychology, 95*, 215–229. doi:10.1016/j.jecp.2006.05.004
- Kahneman, D., Treisman, A., & Gibbs, B. J. (1992). The reviewing of object files: Object-specific integration of information. *Cognitive Psychology, 24*, 175–219. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/1582172>. doi:10.1016/0010-0285(92)90007-O
- Kilian, A., Yaman, S., Von Fersen, L., & Güntürkün, O. (2003). A bottlenose dolphin discriminates visual stimuli differing in numerosity. *Learning & Behavior, 31*, 133–142. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/12882372>. doi:10.3758/BF03195976
- Köhler, O. (1941). Von Erlernen unbennanter Anzahlen bei Vögeln (On the learning of unnamed numerosities by birds). *Die Naturwissenschaften, 29*, 201–218.
- Köhler, O. (1950). The ability of birds to "count". *Bulletin of Animal Behaviour, 9*, 41–45.
- Krusche, P., Uller, C., & Dicke, U. (2010). Quantity discrimination in salamanders. *The Journal of Experimental Biology, 213*, 1822–1828. doi:10.1242/jeb.039297
- Matsuzawa, T. (2009). Symbolic representation of number in chimpanzees. *Current Opinion in Neurobiology, 19*, 92–98. doi:10.1016/j.conb.2009.04.007
- Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology, Animal Beh.*
- Pepperberg, I. M. (2006). Grey Parrot (*Psittacus erithacus*) numerical abilities: Addition and further experiments on a zero-like concept. *Journal of Comparative Psychology, 120*, 1–11. doi:10.1037/0735-7036.120.1.1
- Pepperberg, I. M., & Carey, S. (2012). Grey parrot number acquisition: The inference of cardinal value from ordinal position on the numeral list. *Cognition, 125*, 219–232. doi:10.1016/j.cognition.2012.07.003
- Pepperberg, I. M., & Gordon, J. D. (2005). Number comprehension by a grey parrot (*Psittacus erithacus*), including a zero-like concept. *Journal of Comparative Psychology, 119*, 197–209. doi:10.1037/0735-7036.119.2.197
- Perdue, B. M., Talbot, C. F., Stone, A. M., & Beran, M. J. (2012). Putting the elephant back in the herd: Elephant relative quantity judgments match those of other species. *Animal Cognition, 15*, 955–961. doi:10.1007/s10071-012-0521-y
- Rugani, R., Fontanari, L., Simoni, E., Regolin, L., & Vallortigara, G. (2009). Arithmetic in newborn chicks. *Proceedings Biological Sciences / The Royal Society, 276*, 2451–2460. doi:10.1098/rspb.2009.0044
- Rugani, R., Kelly, D. M., Szelest, I., Regolin, L., & Vallortigara, G. (2010). Is it only humans that count from left to right? *Biology Letters, 6*, 290–292. doi:10.1098/rsbl.2009.0960
- Rugani, R., Regolin, L., & Vallortigara, G. (2007). Rudimentary numerical competence in 5-day-old domestic chicks (*Gallus gallus*): identification of ordinal position. *Journal of Experimental Psychology: Animal Behavior Processes, 33*, 21–31. doi:10.1037/0097-7403.33.1.21
- Rugani, R., Regolin, L., & Vallortigara, G. (2008). Discrimination of small numerosities in young chicks. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 388–399. doi:10.1037/0097-7403.34.3.388

- Rugani, R., Regolin, L., & Vallortigara, G. (2010). Imprinted numbers: Newborn chicks' sensitivity to number vs. continuous extent of objects they have been reared with. *Developmental Science*, *13*, 790–797. doi:10.1111/j.1467-7687.2009.00936.x
- Rugani, R., Regolin, L., & Vallortigara, G. (2011). Summation of large numerosity by newborn chicks. *Frontiers in psychology*, *2*, 179. doi:10.3389/fpsyg.2011.00179
- Scarf, D., Hayne, H., & Colombo, M. (2011). Pigeons on par with primates in numerical competence. *Science*, *334*, 1664. doi:10.1126/science.1213357
- Scheid, C., & Bugnyar, T. (2008). Short-term observational spatial memory in Jackdaws (*Corvus monedula*) and Ravens (*Corvus corax*). *Animal Cognition*, *11*.
- Seron, X., & Pesenti, M. (2001). The number sense theory needs more empirical evidence. *Mind & Language*, *16*, 76–88. doi:10.1111/1468-0017.00158
- Smirnova, A., Lazareva, O. F., & Zorina, Z. A. (2000). Use of number by crows: Investigation by matching and oddity learning. *Journal of the Experimental Analysis of Behavior*, *73*, 163–176. doi:10.1901/jeab.2000.73-163
- Spelke, E. S., & Kinzler, K. D. (2007). Core knowledge. *Developmental Science*, *10*, 89–96. doi:10.1111/j.1467-7687.2007.00569.x
- Stancher, G., Sovrano, V. A., Potrich, D., & Vallortigara, G. (2013). Discrimination of small quantities by fish (redtail splitfin, *Xenotoca eiseni*). *Animal Cognition*. doi:10.1007/s10071-012-0590-y
- Tomonaga, M. (2008). Relative numerosity discrimination by chimpanzees (*Pan troglodytes*): evidence for approximate numerical representations. *Animal Cognition*, *11*, 43–57. doi:10.1007/s10071-007-0089-0
- Ujfalussy, D. J., Miklósi, A., & Bugnyar, T. (2012). Ontogeny of object permanence in a non-storing corvid species, the jackdaw (*Corvus monedula*). *Animal Cognition*. doi:10.1007/s10071-012-0581-z
- Uller, C., Jaeger, R., Guidry, G., & Martin, C. (2003). Salamanders (*Plethodon cinereus*) go for more: Rudiments of number in an amphibian. *Animal Cognition*, *6*, 105–112. doi:10.1007/s10071-003-0167-x
- Utrata, E., Virányi, Z., & Range, F. (2012). Quantity discrimination in wolves (*Canis lupus*). *Frontiers in Psychology*, *3*, 1–9. doi:10.3389/fpsyg.2012.00505
- Uzgiris, I. C., & Hunt, J. (1975). *Assessment in infancy: Ordinal scales of psychological development*. Evanston, IL: University of Illinois Press.
- Vallortigara, G. (2012). Core knowledge of object, number, and geometry: A comparative and neural approach. *Cognitive Neuropsychology*, *29*, 213–236. doi:10.1080/02643294.2012.654772
- Vallortigara, G., Regolin, L., Chiandetti, C., & Rugani, R. (2010). Rudiments of mind: Insights through the chick model on number and space cognition in animals. *Comparative Cognition & Behavior Reviews*, *5*, 78–99. doi:10.3819/ccbr.2010.50004
- Vonk, J., & Beran, M. J. (2012). Bears “count” too: Quantity estimation and comparison in black bears (*Ursus Americanus*). *Animal Behaviour*, *84*, 231–238. doi:10.1016/j.anbehav.2012.05.001
- Ward, C., & Smuts, B. B. (2007). Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). *Animal Cognition*, *10*, 71–80. doi:10.1007/s10071-006-0042-7
- Weir, A. A. S., & Kacelnik, A. (2006). A New Caledonian crow (*Corvus moneduloides*) creatively re-designs tools by bending or unbending aluminium strips. *Animal Cognition*, *9*, 317–334. doi:10.1007/s10071-006-0052-5
- Wynn, K. (1992). Addition and subtraction by human infants. *Nature*, *358*, 749–750. doi:10.1038/358749a0
- Xu, F. (2003). Numerosity discrimination in infants: Evidence for two systems of representations. *Cognition*, *89*, B15–B25. doi:10.1016/S0010-0277(03)00050-7
- Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition*, *74*, B1–B11. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10594312>. doi:10.1016/S0010-0277(99)00066-9
- Zorina, Z. A., & Smirnova, A. A. (1996). Quantitative evaluations in gray crows: Generalization of the relative attribute “larger set”. *Neuroscience and Behavioral Physiology*, *26*, 357–364. doi:10.1007/BF02359040
- Zucca, P., Milos, N., & Vallortigara, G. (2007). Piagetian object permanence and its development in Eurasian jays (*Garrulus glandarius*). *Animal Cognition*, *10*, 243–258. doi:10.1007/s10071-006-0063-2

Received July 12, 2012

Revision received June 19, 2013

Accepted June 26, 2013 ■