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AT THE ROOT OF NUMBER COMPETENCE

META-ANALYSIS OF THE LITERATURE ON DIFFERENT ANIMAL SPECIES AND AN EXPERIMENTAL CONTRIBUTION TO THE UNDERSTANDING OF RUDIMENTAL NUMERICAL ABILITIES IN AN ANIMAL MODEL, THE YOUNG DOMESTIC CHICK (*Gallus gallus*)

Direttore della Scuola: Ch.mo Prof. Luciano Stegagno

Supervisore: Ch.ma Prof.ssa Lucia Regolin

Dottorando: Rosa Rugani

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1. INTRODUCTION

It is virtually impossible to escape number in everyday life. Adult humans use number to measure and quantify every aspect of their environment – be it shoe size, spatial coordinates, the price of bread, an address, car speed, weights or heights. Doubtless then, number is a fundamental parameter with which we make sense of the world around us, but it is also clear that human mathematical abilities are composed of many heterogeneous skills. Whereas certain numerical concepts, such as real numbers, algebra and calculus, are only performed by a subset of human adults, other numerical abilities are widespread and comparatively easy. It is, for example, possible to discriminate the relative numerosity of two sets of objects without the help of numerals, in order to decide that a group of 9 cherries is larger than a group of 5 apples. This ability includes selecting the numerically larger or smaller of the two sets of items and does not require a symbolic representation. This, as others abilities, has been demonstrated in non-human animal species (Dehaene, Dehaene-Lambertz, and Cohen, 1998; Boysen and Capaldi, 1993; Davis and Pérusse, 1988). Those observations have led some psychologists to hypothesize that human numerical abilities evolved from numerical abilities that can be observed in animals (Gallistel and Gelman, 1992; 2000). The “Number Sense” - the ability to easily and spontaneously use number - is qualified as a biologically determined category of knowledge that includes the early emergence of numerical competence in infants, independently of language and evolutionary precursors of arithmetic in animals (Dehaene, 1997, 2001). This question has a long history: a Darwinian perspective predicts that even the most complicated human abilities should have precursors in animals. Darwin (1871/1820 p. 128) also wrote, ”*the difference in mind between man and higher animals, great as it is, certainly is one of degree and not of kind*”. This point of view leads to the prediction of intellectual continuity between animal and human abilities.

1.1. AN OVERVIEW OF ANIMALS' NUMERICAL COMPETENCE

A scientific interest in animal numerical competence has been documented for almost 100 years (Rilling 1993). One of the very first attempts to demonstrate numerical abilities in animals is the famous story of Clever Hans. Clever Hans had been trained by its owner, Von Osten, to perform a variety of arithmetic calculations, long divisions, and to answer by tapping its hoof on the ground the correct number of times. It seemed that Hans was capable of grasping mathematical concepts and its behaviour initially convinced a lot of scientists that it could really solve very difficult arithmetic operations. Only some years later was it demonstrated that the horse's abilities were due to an artifact: the horse answered correctly only when its owner or, for that matter, any other person who was interviewing him, knew the answer and when it could see them while it responded. Hans had no mathematical ability but was able to detect minute changes in the experimenter's behaviour that was made when the horse reached the correct count with its hoof tapping (Pfungst, 1907). From this unfortunate finding and for a long time thereafter, the scientific community was very sceptical about animal number abilities and performed rigorous controls in order to eliminate all potential non-numerical cues. Other early studies by Otto Koehler (1941) looked at the ability to "act on number" in a quasi-naturalistic setting in a variety of avian species (a raven, an African Gray parrot, pigeons, jackdaws and budgerigars). Pigeons (*Columba livia*) were tested in numerical discrimination tasks where they were required to select a set containing a particular number of items (e.g., 4 grains). On every trial birds were presented with two sets of grains that differed in number: one being of the correct number the other incorrect. Only the correct responses were reinforced by allowing the birds to eat the grains. A jackdaw (*Corvus monedula*) took part in a matching-to-sample task. After looking at an array of blobs on a "sample" card, the bird was presented with two lids. On one of the lids was the "sample" numerosity of different elements and on the other was a different (with respect to the sample) numerosity of elements. The bird was required to select the same ("sample") numerosity for food reward. In another experiment, pigeons and budgerigars (*Melopsittacus undulatus*) were trained to emit only a given number of

actions, for example to take just 4 seeds in an array of 10. From these and other studies Koehler concluded that birds have at least a simple ability to discriminate objects and events on the basis of their numerosity. He also noted that different species showed remarkable similarity in the limits of their ability. Indeed, mostly their performance broke down with numerosities larger that 5 or 6 elements (Koehler, 1943). In all these experiments, numerical discrimination was tested by making every effort to avoid any cueing that Hans had possibly utilized. The experimenter was hidden behind a screen, out of the sight of the bird. Punishments and rewards were obtained by a mechanical device and, also, animals were filmed for the duration of the experiment in order to provide an objective record of their behaviour. Despite his efforts to eliminate extraneous cues, Koehler's work has still been criticized for lack of control of olfactory cues and in rewarding procedures (Wesley, 1961).

Later, Davis and Pérusse (1988) argued that although animals can be trained to make numerical discriminations, they do so only as a last-resort strategy, when extensive training has been provided and when all other cues have been eliminated. In spite of this remaining criticism, various types of numerical competences have been demonstrated in non-human species (Robersts, 199). In foraging decisions, many animals behave as if they calculate the rate of return in a given food patch in order to decide whether to stay or to go (Krebs and Davies, 1993). Further evidence is provided by Hauser and colleagues, who tested Rhesus monkeys (*Macaca mulatta*) in a modified version of Wynn's violation of expectation paradigm (Wynn, 1992). The aim of these studies was to ascertain what spontaneous numerical skills Rhesus monkeys possess without laboratory training. Each animal was tested for a single trial in such a way that they had no opportunity to learn. Animals were shown two aubergines successively placed behind an opaque screen and then watched the screen being raised to reveal one or two eggplants. As suggested by Wynn's paradigm, monkeys looked longer at the impossible outcome of 1 (e.g., 1+1=1) as compared with the possible outcome of 2 (e.g., 1+1=2). This result shows that Rhesus monkeys master simple addition (Hauser MacNeilage and Ware, 1996; Hauser and Carey, 1998; Hauser et al., 2000). Subsequent experiments showed that Rhesus monkeys were not basing

their responses on cumulative surface area (Hauser and Carey, 2003) and that they were able to spontaneously compute subtraction operations (Sulkowski and Hauser, 2001).

Field studies demonstrated that American coots (*Fulica americana*) appear to base decisions about whether to develop an additional egg follicle according to the number of their own eggs present in the nest. This is particularly remarkable because coots seem to discount the number of parasitic eggs in the nest, suggesting that they are able to enumerate a subset of elements in a group and they base their responses on this relative evaluation (Lyon, 2003). American coots are also able to use tactical information in order to distinguish their own eggs from eggs layed by other female coots in their nest (Anderson, 2003).

In summary, although it has been argued that animals represent number as a last resource strategy and only following an extensive training, the data above suggest that different animal species can resolve different kinds of numerical problems spontaneously.

1.2. CLASSIFICATION AND MAIN ASPECTS OF NUMBER COMPETENCES

Fully-fledged numerical concepts are multifaceted and complex. In the last two decades various types of numerical competence have been demonstrated in non-human species (for review see Davis and Pérusse, 1988; Gallistel and Gelman, 1992; Roberts, 1997; Dehaene, 1997; Hauser and Spelke, 2004; Feigenson, 2007).

The main aspects that have been investigated are the following:

The simplest aspect of number is protonumerostity. This requires the ability to make judgements of size differences between two sets, i.e. “more than…”, “less than…”, and is considered the first and elementary level of numerical knowledge.

Another central aspect of number is the ability to represent ordinal relations between numbers, that is, both the ability to identify an object on the basis of its position in a series of identical objects and the inherent “greater than” or “less than” relationship between distinct numerosities.

No less important is the ability to manipulate numerical representations of number in arithmetic operations such as additions and subtractions.

Although, such abilities are very different from one another, they share some main aspects that have been found in different species and in different tasks: the size effect and the distance effect. The size effect indicates that for equal numerical distance, performance decreases with increasing number size. The distance effect is a systematic decrease in numerosity discrimination performance as the numerical distance between the numbers decreases. Both effects indicate that the discrimination of numerosity, like that of many physical parameters, obeys Weber's law. Weber's law describes discriminability between two numbers in the same way that it describes discriminability between values on perceptual continua such as a line length, brightness, and weight (Welford, 1960). A consequence of Weber's law is that the ability to discriminate two values depends on their ratio rather than on their absolute values.

Various results (Meck and Church, 1983; Boysen et al., 1996; Barth, Kanwisher and Spelke, 2003; Piazza et al., 2004; Pica et al., 2004; Cantlon and Brannon, 2006) support the idea that Weber's law applies to numerical abilities.

Recently two systems have been proposed to underlie many non-linguistic-numerical abilities. A first system is functional for small numberosities, with a size limit of up to 3 or 4 elements, (Hauser and Carey, 2003; Hauser and Spelke, 2004). The second is a system for larger numerosities, named the analougue magnitude system. The signature properties of such a system includes that it obeys Weber's law: discrimination between two quantities depends on their ratio.

Although these two are the most recent and are supported by the latest data some other models were been proposed during the last years.

1.3. MODELS OF NON-VERBAL NUMBER REPRESENTION

The section above described what non-human animals and human infants are capable of in the numerical domain. Separate questions include; how are numbers

represented, what is the process by which they form numerical representations, and how we can best describe the format of their numerical representations.

Has been proposed that the Arbitrary Numeron Hypotesis. In the original formulation of this model, numerons were described as indirect symbols with an arbitrary relationship to the numerosities they represent (Gelman and Gallistel 1978; Gallistel and Gelman, 1992; 2000). Like words or Arabic numbers, numerons do not, in any way, resemble the numerosities they serve to represent. Numerons help non-verbal children to form a numerical representation via non-verbal counting processes that follow the same principle as verbal counting. Although the verbal counting system uses spoken words as symbols, pre-verbal children could use the same system but apply arbitrary neuronal symbols. Numerons are applied to the set of objects or events through a process conforming to Gelman and Gallistel's five counting principles (Gelman and Gallistel, 1978).

First, counting must involve a one-to-one assignment. In other words, each element in the to-be-counted set must be mapped onto one, and only one, symbol. So the count word "three" can be applied to one and only one element.

Second, the symbols must be taken in a stable order list across counting episodes. So, we cannot count a four-element sequence as "1-2-3-4" on one occasion and "2-1-4-3" on the next.

Third, the last symbols represent the cardinality of the set.

Fourth, the abstraction principle states that anything can be counted (e.g., orange, sounds, pens, etc).

Fifth, objects can be counted in every order (e.g., from left to right, from right to left, circular pattern, and so on). Of these five principles, only the first three are essential for the counting process, while the last two serve to describe counting in its most abstract sense.

Other types of mechanism have been proposed to explain how animals make judgments about the numerosity of items in arrays. One of the earliest proposals was that animals assess small numbers by a process of Subitizing. Subitizing is defined as a fast, effortless, parallel perceptual process that is limited to the apprehension of the small value. When represented as an array of randomly

arranged small dots, presented for a fraction of a second, small numerosities can be estimated more quickly than large ones. The subjects' confidence in their estimates also falls off precipitously after six (Kaufman, Reese and Volkmann, 1949).

More recently, the subitizing hypothesis has been further specified in the Object File Model, which declares that an object-file is opened for each element in a visual array (Carey, 1998; Hauser and Carey, 1998; Leslie et al., 1998; Simon, 1997; Uller et al., 1999; Spelke and Kinzler, 2007). In this model there are no symbols that represent the numerosity of a set, but each element is represented in the visual system by a file containing the object's features such as colour, shape and size. The visual system contains a limited number of object-files that can be assigned to an object, so that a given set can be represented only when the number of objects in a set does not outnumber with the number of files available (Pylyshyn and Storm, 1988). By using this system, organisms can represent only small sets of objects.

Another model is the Mode-Control Model (Meck and Church, 1983) or Accumulator Model (Gallistel and Gelman, 1992) that shares with the Arbitrary Numeron Hypothesis the idea that animals use a serial process that conforms to the counting definition proposed by Gelman and Gallistel (1978). Meck and Church pointed out that the mental accumulator model that Gibbon (1977) proposed to explain the representation of timing can be also applied to counting. Gibbon had proposed that duration was being timed as a stream of impulses of an accumulator. In this way the accumulation grows in proportion to the duration of the stream. When the stream ends, the resulting accumulation is read into the memory, where the duration of the interval is represented. In such a system, each discrete object or event results in the closing of a switch for a constant duration, allowing pulses from a pacemaker to enter an accumulator. Meck and Church extended this system to non-verbal counting processes: at each count, the brain increments the quantity, so that for each count there is a discrete increment in the contents of the accumulator, an operation formally equivalent to pouring a cup into a container. At the end of a count, the final magnitude (represented as the contents of the container at the conclusion of the count) is read into memory,

where it represents the numerosity. Because memory is noisy (like a wave in the container) the same value could be read differently on different occasions.

In this way, number is represented as a continuous magnitude that directly reflects the magnitude of the discrete quantities it serves to represent. In the model proposed by Meck and Church, the same, or similar, mechanisms are used for timing and counting. The basic mechanisms in this model are: a pacemaker, an accumulator, a working memory buffer, a reference memory and a comparator. The pacemaker produces pulses at a constant rate that can be gated into an accumulator. From here, the accumulator value is transferred from working memory and stored in the reference memory. A comparative process allows the organism to compare the current working memory content to its reference memory content.

A fourth proposal is the Connectionist Timing Model (Church and Broadbent, 1990, 1991). In this model, a set of oscillators, with a wide range of periodicities from milliseconds to hundreds of seconds, serves as the basis of timing. The oscillators start to work at the onset of the stimulus and at the end the duration of interval is represented by a status indicator. A vector combines the results of multiple oscillators. This temporal information is represented by vectors in matrices, resulting in parallel distributions in time. The result is given by the comparison between working and reference memory. Number is computed from the relationship between durations: dividing the cumulative duration of a sequence of events by the duration of one interval.

The fifth model is the Neural Network Model (Dehaene and Changeux, 1993). In this model, number is represented by a neural network that consists of three steps: an input (the retina), with a map of objects locations and an array of numerosity detectors. The map of the object's location converts stimuli from the retina to a representation of each stimulus irrespective of the object's size. The location map sends its output to numerosity detectors, which consist of summation units and numerosity units. When the total activity of the location map exceeds the summation unit's threshold, it will be activated. Only in this case the location map sends its output to numerosity detectors that sum the outputs from the location maps and provide a representation of numbers from 1 to 5. In this model, the

activity produced by each item in the array is reduced to a unit amount of activity, so that it is no longer proportional to the contour, disposition, size, and so on, of the item. The units of activity corresponding to the entities in the array are summed across the visual field to yield a mental magnitude representing the numerosity of the array.

1.4. NUMBER DISCRIMINATION IN NON-VERBAL CREATURES

Discrimination of relative numerosities (protonumerosity; Davis and Pérusse, 1988) requires the ability to make judgements of size differences between two sets, i.e., “more than…”, “less than…”. Protonumerosity is considered as the first and most elementary level of numerical knowledge.

Discrimination of visual numerosity was first demonstrated in 6-7 month-old infants using the classic method of habituation-recovery of looking time (Starkey and Cooper, 1980). Infants were presented with slides representing a certain number of dots until their looking time started to decrease, indicating habituation. At that point, slides representing new numerosities were presented. The increment in looking time, indicating dishabituation, showed that infants could discriminate between numerosities. In subsequent studies, numerosity discrimination was demonstrated in pre-verbal infants with a variety of displays, positions, motions, sequences of actions and spoken sounds (Strauss and Curtis, 1981; Antell and Keating, 1983; Treiber and Wilcox, 1984; Starkley, Spelke and Gelman, 1990; van Loosbroek and Smitsman, 1990; Wynn, 1996).

Numerical discrimination is often found also in ecological situations whenever an animal chooses the larger or smaller between two alternative sets of food items. Such an ability would be at the base of efficient foraging strategies (Krebs, 1974). Several species prefer the larger amount of food in a spontaneous forced-choice discrimination task (Dooley and Gill, 1977; Rumbaugh, Savage-Rumbaugh, and and Hegel, 1987; Rumbaugh, Savage-Rumbaugh, and Pate, 1988; Boysen and Bertson, 1995; Anderson, 2000; Call, 2000; Boysen, Bertson and Mukobi, 2001). For example, rhesus monkeys (*Macaca mulatta*) (Hauser et al., 2000) can

discriminate between 1 vs. 2; 2 vs. 3; 3 vs. 4 and 3 vs. 5 but not between 4 vs. 5; 4 vs. 6; 4 vs. 8 and 3 vs. 8. In this task, each animal received only one trial in which it watched different quantities of apples being placed into one of two boxes. Thus, for example, a subject watched an experimenter sequentially place two pieces of apple into one box, followed by four pieces of apple into a second box. Subjects were then allowed to approach one box and eat its contents. Because the pieces of apples were placed into the box, and thus out of sight of the animals, subjects must keep the information in their working memory in order to compute which box had more food. Monkeys mastered the task even in a control experiment when both apple slices and stones were used. In this case, they saw, for example, four pieces of apple being placed into one box and three pieces of apple and a stone being placed into the other. The monkeys showed that they can operate a relative discrimination on the basis of the features of the objects placed by selecting the larger quantity of pieces of food. When presented with portions of carrot pieces poured from a cup into opaque boxes, Rhesus monkeys picked the box with the greatest number of portions for comparisons of 1 vs. 2, 2 vs. 3, and 3 vs. 4, but not for comparisons of 4 vs. 5 and 3 vs. 6. Additional experiments indicated that the monkeys based their decisions on both the number of portions and the total amount of food (Wood et al., 2008).

Infants are able to discriminate between 1 vs. 2 and 2 vs. 3, but not between 3 vs. 4 and 3 vs. 6 (Feigenson, Carey and Spelke, 2002). In this experiment, 10-month-old and 12-month-old infant were placed in front (100 cm away) of two buckets. The experimenter showed the infants the cookies being placed inside each of the buckets. The baby was then allowed to make its choice. Each baby was tested only for one trial in such a way that they had no opportunity to learn. Nevertheless, infants selected the larger quantity, showing that they can keep track of the two quantities and their relationship by choosing the buckets that yielded more. Salamanders (*Plethodon cinereus*) always chose the set that maximised their net energy gain when required to choose between 1 vs. 2, 2 vs. 3 (Uller et al., 2003). Salamanders were presented with two different quantities of live fruit flies (*Drosophila virilis*) placed in two identical plastic transparent tubes, positioned 20 cm apart. They were allowed to approach one or the other tube in order to make

their choice. Again, only a single trial was administered but instead of having the pieces of food hidden, here the flies remained visible for the duration of the experiment. Thus, the salamanders were not required to memorize the two different quantities of food available in each container but just make a decision on the basis of what they saw during the test.

In such experiments, however, changes in number are correlated with changes in a variety of quantitative variables, including total filled area, brightness, contour length in two-dimensional stimuli, and volume and surface area in three-dimensional stimuli. All these variables that co-vary with numerosity are called Continuous Variables. In more recent studies, when testing infants' small-number discrimination, in which a stricter control for continuous variables, such as contour length and volume, was used, it was found that infants respond to the latter variables rather than to number (Clearfield and Mix, 1999: Feigenson et al., 2002).

In all these studies, with the exception of the monkeys, the performance of non-verbal subjects broke down with numbers 3 vs. 4 or larger, which seems to constitute a limit for the discrimination of continuous numerosities. Therefore, after more than two decades of study, no consensus has been reached as to whether non-verbal subjects discriminate between small numerosities of elements on the basis of numerosity (Xu et al., 2005).

Representation of small numerosities is usually accounted for in terms of an object file hypothesis, in which each object in a set is represented by a unique symbol. The symbol for each individual has been called the "object file"; the number of files open would implicitly represent the number of objects in a set since there could be only one object file open for each object in the set (Hauser and Carey, 2003). The object file system could explain the results of these experiments but not the ability to discriminate between large sets of elements. Contrary to the view that non-verbal creatures can only discriminate small values with a limit of 3 or 4 elements, human infants were found to be able to discriminate between large numerosities. Using the preferential looking method, relying on infants' tendency to look longer to a novel stimulus, 6-month-old infants were found to be capable of discriminating an array of 8 from an array of 16 elements when continuous variables were controlled for (Xu and Spelke, 2000; Brannon, Abbott and Lutz, 2004). They were

also able to discriminate 4 vs. 8 elements when either surface area or contour lengths were controlled for (Xu, 2003). Employing the head-turn preference method, 6-month-old infants were shown capable of discriminating sets of 8 vs. 16 sounds when continuous variables such as sequence length, total amount of sound and element length, sequence rate of sound were controlled for (Lipton and Spelke, 2003). In contrast, 6-month-old infants were not able to discriminate between 8 vs. 12 dots (Xu and Spelke, 2000) or between 8 vs. 12 sounds (Lipton and Spelke, 2003). Six-month-old infants successfully discriminated between arrays of 16 vs. 32 discs, but not 16 vs. 24 (Xu et al., 2005). On the contrary, 9-month-old infants succeeded in discriminating between 8 vs. 12 sounds (ratio = 2.0), but their performance broke down with 8 vs. 10 (ratio = 1.5; Lipton and Spelke, 2003). Similarly 10-month-old infants could discriminate 8 vs. 12 discs but not 8 vs. 10 (Xu and Arriaga, 2007). These findings provide evidence that infants have robust abilities to represent large numerosities, suggesting that discrimination of large number of elements could have a ratio limit and that sensitivity to numerical differences increases during development.

Two systems seem to be at the basis of small and large number discrimination in non-verbal creatures as they are in human adults, which distinguish according to two systems of numerical representation. An exact system that serves to track individual objects up to 3 or 4 objects and an approximate system that serves to represent approximate numerosities in animals, infants and adult humans (Gallistel, 1990; Dehaene, 1997). The signature property of the small exact system is the size limit (up to 3 or 4 elements), while the characteristic of the large approximate system is the ratio limit (as low as 1.15 for adults and 2.0 for 6-month-old infants).

1.5. ORDINALITY

A substantial body of data suggests that pre-linguistic humans and animals can order numerosities. One of the earliest protocols to assess counting and numerical memory was developed by Mecher (1958) and later adapted by Platt and Johnson

(1971). Rats had to press a lever a certain number of times (the target number) and to signal when they had completed the task by poking their nose into a hole equipped with a photoelectric sensor. Results of this experiment show that the number of responses the rats made before head poking was roughly normally distributed around the required number. Furthermore, the standard deviation of the distribution of the obtained number of responses increased linearly with the required number of responses. Such results suggest that rats do not represent number as a precise value, but instead as a mental magnitude that is more likely to be confused with a neighboring quantity as the absolute magnitude increases. In the same year, Moyer and Landaeuer (1967) showed that when adults were required to choose the larger of two Arabic numerals, accuracy increased and latency to respond decreased with increasing numerical disparity. The same effect was also found in adult humans using a modified version of Platt and Johnson design (Whalen et al., 1999) and using a different paradigm (Cordes, Gelman and Gallistel, 2001) in 6-month-old infants (McCrink and Wynn, 2007), in chimpanzees (*Pan troglodytes*) (Tomonaga, 2007), and in Rhesus macaques (*Macaca mulatta*) (Jordan and Brannon, 2006). Few studies have directly compared the performance of children with that of non-human animals. However, Cantlon and colleagues (Cantlon and Brannon, 2006a; Cantlon et al., 2006a) demonstrated that the ordinal numerical judgments made by rhesus monkeys and pre-school children were similarly affected by the heterogeneity (in colour, shape, and size) of items within the to-be-compared sets. Specifically, performance on ordering pairs of numerosities between 1 and 9 was not affected by degree of stimulus heterogeneity in either species. A second pair of studies demonstrated that children and monkeys spontaneously match arrays based on number rather than on surface area (Cantlon et al., 2006b; Cantlon and Brannon, 2006b).

The main finding from these various studies was that humans and animals share two striking characteristics in number computation: the distance and the size effect. Both effects indicate that the discrimination of numerosity, like that of many physical parameters, obeys Weber's law. These profound homologies between human and animal abilities suggest a phylogenetic continuity in number capacity.

Other studies have investigated if animals can appreciate the ordinal relationship between numerosities. Thomas and colleagues (1980) tested this idea in an experiment in which Squirrel monkeys (*Saimiri sciureus*) were trained to respond to the lesser numerosities. The monkeys were trained until they reached a performance criterion on successive numerical pairs beginning with 1 vs. 2. Although some monkeys could discriminate sets containing 10 and 11 elements, it was unclear if they used an ordinal rule to solve each pair, or whether they had learned a series of pair-wise discriminations. Since each numerical pair was trained successively, it was possible that they could have learned a series of absolute discriminations and not the more abstract ordering operation.

Washburn and Rumbaugh (1991) used a different paradigm in order to investigate the numerical abilities of rhesus monkeys. Subjects were trained to select one of two Arabic numbers (ranging from 1 to 9) presented on a monitor. Whichever numeral the monkey selected resulted in the immediate delivery of the corresponding number of sugar pellets. The monkeys learned to choose the larger numeral and even responded correctly when novel combinations of Arabic numbers were presented. In addition, the monkeys' accuracy depended upon the numerical distance between the quantities the symbols represented. Although the monkeys learned to choose the larger numeral when they were presented with a novel pairs, it is impossible to rule out the possibility that they based their choice on the hedonic value associated with each of the numerals, rather than an abstract numerical symbolic rule.

This problem has been addressed in a series of studies by Brannon and Terrace (1998; 1999; 2000; 2002), that examined the ability of rhesus macaques to appreciate the ordinal relationship between numerosities. Monkeys were presented with stimuli on a touch-sensitive screen and required to respond in an ascending or descending numerical order. Non-numerical confounds were controlled for by varying relative element size over a large number of stimuli. The elements were either simple geometric shapes or more complex clipart shapes, and the stimuli contained a homogeneous or heterogeneous collection of elements. After extensive training, the monkeys learned the response rule and they were tested with both the same and novel numerical values that were outside

the range of training values. The size of the test elements varied in such a way that the smaller numerosities had the larger surface of area on 50% of trials. These data demonstrate that monkeys can discriminate the training numerosities without using non-numerical cues such as shape, color, size, or cumulative surface area. Even when, on the critical test, monkeys were presented with novel numerosities, they mastered the task demonstrating they had an ordinal numerical knowledge. Socially housed hamadryas baboons (*Papio hamadryas*), socially housed squirrel monkeys (*Saimiri sciureus*; Smith, Piel and Cantlon, 2003) and brown capuchin monkeys (*Cebus paella*; Judge, Evans and Vyas, 2005) trained to discriminate between numbers from 1 to 4, in ascending order, could then generalize this discrimination to new numbers from 5 to 9. Monkeys trained to respond (in ascending or descending order) to pairs of numerosities (1-9) spontaneously ordered in the same direction new pairs of larger value (e.g. 10, 15, 20, 30; Cantlon and Brannon, 2006b). Rhesus macaques trained to order values (6-5-4) in descending order were able to apply the descending rule to novel values (1-2-3; Cantlon and Brannon, 2006). Squirrel monkeys learned ordinal relationships between six Arabic number symbols: they chose the larger number when given a choice between combinations of any of the two learned symbols and even when a known symbol was confronted with a novel one. They also preferred the stimulus containing the largest sum when choosing between sets of 2 vs. 2, 1 vs. 2 and 3 vs. 3 symbols (Olthof, Iden, and Roberts, 1997). Chimpanzees (*Pan troglodytes*) could select the larger of two sequentially presented sweets. Two quantities of candies (M&M's chocolates) were presented sequentially (e.g. presented in two sets: 2 + 2 vs. 4 + 1, or in three sets: 2 + 2 + 3 vs. 3 + 4 + 1), each chocolate being visible only before placement in 1 of 2 cups. Therefore, chimpanzees mentally represent quantity and successfully combine and compare non-visible, sequentially presented sets of items. (Beran, 2001).

Also rats (Davis and Bradford, 1986; Suzuki and Kobayashi, 2000) and pigeons (Emmerton et al., 1997) seem to posses some serial ordering abilities. In addition one study focussed on a very different animal species: Honey bees (*Apis mellifera*) were trained to find food in a specific position along a series of four identical, equally spaced landmarks: the food was placed between the third and

the fourth landmark. At test, the number of landmarks was altered and although many bees continued to search for food at the correct distance, other bees did actually appear to rely on the number and position of landmarks: when encountering fewer landmarks, they flew further; when they encountered more landmarks, they landed at a shorter distance (Chittka and Geiger, 1995). It is reasonable to assume that spatial navigation and learning benefits from the understanding of serial ordering.

Eleven month-old infants are sensitive to the ordinal relation between numerical values (Brannon, 2002). Infants were first habituated to sequence of dot arrays that increased or decreased in numerical magnitude (e.g., 16-8-4 or 4-8-16). Infants were then tested with new numerical values that increased and decreased in value in alternation. Infants looked longer at the reversed ordinal direction. Younger infants (e.g., 9-month-old) failed in the same test (Brannon, 2002).

1.6. ARITHMETIC IN ANIMALS AND INFANTS

A handful of studies have addressed the question as to whether animals and human infants are capable of some form of addition or subtraction (for reviews see: Gallistel 1990; Dehaene, 1997; Spelke and Dehaene, 1999; Brannon and Roitman, 2003).

Summation has been demonstrated in tasks where primates were required to choose the larger of two quantities (Rumbaugh, Savage-Rumbaugh and Hegel, 1987; Rumbaugh, Savage-Rumbaugh and Pate, 1988). Chimpanzees (*Pan troglodytes*) were presented with two sets of two food wells, each of which contained a number of chocolates. To choose the sets with the larger quantity, the chimpanzee had to sum the chocolates in each of two sets and then compare the two summed values. On the critical trial the largest set of wells did not contain the larger single value. Even in this case, they preferred the larger quantity.

In 1989, Boysen and Bertson provided a very impressive demonstration of arithmetic animal ability. An adult chimpanzee (named Sheba) was led around a room to three different hiding places that could contain 1, 2, 3, or 4 pieces of

orange. Subsequently, Sheba was required to choose the Arabic number that corresponded to the number of items she had met before. She chose the correct number on 75% of times without any explicit training. Her performance was still good when pieces of orange were replaced with Arabic numerals. In another approach, Washburn, and Rumbugh, (1991) trained two rhesus monkeys (*Macaca mulatta*) to choose between two Arabic numbers on a touch-sensitive-screen. The animals had the corresponding number of pellets as a reward. Monkeys always chose the larger number even when they were presented with new combinations of numbers. A similar paradigm was used to test squirrel monkeys on problems where they were required to choose between pairs or triplets of Arabic numerals. Monkeys chose the larger sum and their performance could neither be attributed to choosing the largest single value nor to avoiding the single smallest value (Olthof, Iden and Roberts, 1997).

Using the methodology of the violation of the expectancy, Wynn (1992) showed that 5-month-old infants can solve some simple arithmetic operations. The idea was that if infants keep track of the numbers of toys they see being placed behind a screen they should look longer the screen that, when lowered, reveals an outcome that violates their expectations. For example, in the 1+1 = 1 or 2 task, one object was placed on a stage, covered with a screen, and than another object was introduced behind the screen. When the screen was removed, infants looked longer at the impossible outcomes of either one object or three objects, suggesting that infants expected two objects. In the original studies, continuous variables such as volume or surface area were not controlled for, so that infants might have attended to the number of dolls behind a screen or the amount (volume, area) of the dolls. Wynn's data were replicated by other studies where continuous variables were partially controlled for. Simon et al. (1995) replicated Wynn's paradigm but used 'Elmo' dolls in the initial phase of the trials and then surreptitiously replaced 'Elmo' dolls with 'Ernie' dolls. The infants' expectations were not violated by this identity switch. They looked longer only the numerically unexpected outcome and not the identity of the unexpected outcome. This indicates that in some sense infants represent the number of objects stripped of their non-numerical features. Controversial data obtained using Wynn's paradigm were obtained by Wakely et

al. (2000). When 5-month-old infants were presented with the 1+1 = 1 or 2 and 2-1 = 1 or 2 problems, they behaved as if they could not master them. In another test of Wynn's paradigm, Feigenson, Carey and Spelke, (2002) tested 7-month-old infants and pitted violation in surface and area against violations in number. Infants saw two small objects being placed sequentially behind a screen. The screen was then lowered to reveal one or two large objects. The outcome of large objects was expected in area and unexpected in number, while the outcome of two large objects was expected in number and unexpected in area. Infants looked longer at the unexpected area outcome than at the unexpected number outcome. These results suggest that information about area is more important than the numerical one. Wynn (2000) suggested that the failure to replicate her work might be due to subtle details in the procedure that did not optimize infants' attention to the task. Wynn's paradigm was also adapted to test Arithmetic reasoning in monkeys. Subjects viewed food items, a screen was then raised to obscure the items on the stage. Some items were then added or removed from behind the screen. Finally, the screen was lowered to reveal the expected or unexpected number of objects and looking time was measured. Monkeys looked longer when the unexpected outcome was revealed for 1+1=1 or 2 and 2-1=1 or 2 operations (Hauser et al., 1996; Sulkowski and Hauser, 2001). Cotton-top tamarins (*Saguinus oedipus)*, if presented with the 1+1 operation, looked longer at the unexpected outcome of 3 or 1 compared to the expected of 2 (Uller et al., 1999).

In summary, non-verbal-creatures are not only able to represent number, but they are also adept at adding and subtracting their numerical representations.

2. SPONTANEUS DISCRIMINATION OF SMALL SETS OF OBJECTS

Spontaneous number discrimination was investigated by taking advantage of the chick's well known sensitivity towards fine visual characteristics of their own imprinting object. Chicks of separate experimental groups were reared singly for 3 days whilst exposed to artificial stimuli of different numerosity. Chicks then underwent a 6-min free choice test between the familiar stimulus and a novel stimulus which differed in the number of items presented. Four experiments were performed on different groups of chicks, comparing sets of different numerosity of identical objects 1 vs. 3 (Experiment 2.1) and 2 vs. 3 (Experiment 2.2). A control of overall volume or surface area was carried out in Experiment 2.3 by using comparisons of 1 vs. 4 and 1 vs. 6 items. Finally, in Experiment 2.4, the simultaneous control for both surface and volume was manipulated within the comparison 2 vs. 3. Chicks would preferentially approach either of the two stimuli only if capable of discriminating between the two numerosities. In all the situations where there was partial control for the continuous variables (i.e. Experiments 2.1 and 2.2) chicks always preferred the stimulus with the larger numerosity at test. The same result was obtained when chicks were required to discriminate between two groups of identical overall numerosity, but differing in the amount of familiar and unfamiliar elements constituting each set (Experiment 2.1). When a separate control for surface or volume was used, chicks always preferred the larger stimulus. It was quite clear that birds were not computing the number but rather the amount (that is, volume, overall area, etc.). However, when the objects used for the test differed in colour, shape and size from the imprinting object, and the overall surface of the two test stimuli was controlled for, chicks chose the familiar number, even when this was the smaller amount, showing in such cases the ability to take purely numerical cues into account.

2.1. INTRODUCTION

Davis and Pérusse (1988) argued that although animals can be trained to make numerical discriminations, they do so only as a last-resort strategy, when extensive training is provided and all other cues are eliminated. In spite of this criticism, various types of numerical competences have been demonstrated in mammals (Boysen and Berntson, 1989; 1990; Mc Comb, Packer and Pusey, 1994; Murofushi, 1997; Olthof, Iden and Roberts, 1997; Brannon and Terrace, 1998; 2000; Kawai and Matsuzawa, 2000; Biro and Matsuzawa 2001; Sulkowski and Hauser, 2001; Shumaker et al., 2001; Beran and Rumbaugh, 2001; Hauser, et al., 2002; Nieder, Freedman and Miller, 2002; Kilian, et al., 2003; Hauser, et al., 2003; Smith, Piel and Candland, 2003; Beran, 2001; 2004; Feigenson, Dehaene and Spelke, 2004; Judge, Evans and Vyas, 2005; Cantlon and Brannon 2005; Cantlon and Brannon, 2006a; 2006b; Beran, et al., 2006; Cantlon and Brannon, 2007) and birds (Thompson, 1968; Pepperberg and Brezinsky, 1991; Pepperberg, 1994; Emmerton, Lohmann and Niemann, 1997; Smirnova, Lazareva and Zorina, 2000; Olthof and Roberts, 2000; Xia, Siemann and Delius, 2000; Xia, Emmerton, Siemann and Delius, 2001; Brannon, et al., 2001; Lyon, 2003; Pepperberg and Gordon, 2005; Pepperberg, 2006). Even preverbal infants are able to solve numerical problems (Starkey and Cooper, 1980; Strauss and Curtis, 1981; Antell and Keating, 1983; Starkley, Spelke and Gelman, 1990; Xu and Spelke, 2000; Lipton and Spelke, 2003; Brannon, Abbott and Lutz, 2004; Feigenson and Carey, 2005; Cantlon, et al., 2006). All these data suggest that numerical competences are possible even in the absence of language. Two different systems seem to be at the basis of these non-linguistic-numerical competences: An object-file system that serves to track exactly individual objects up to 3 or 4, and an analogue magnitude system that serves to represent approximately larger numerosities (Gallistel, 1990; Dehaene, 1997; Spelke, 2004; Spelke and Kinzler, 2007).

Some doubts have been cast recently as to whether infants and non-human animals compute the numerosity of small object arrays. Discrimination of visual numerosity was first demonstrated in 6-7 month-old infants using the classic method of habituation-recovery of looking time (Starkey and Cooper, 1980).

Infants were presented with slides representing a certain number of dots until their looking time started to decrease, indicating habituation. At that point, slides representing new numerosities were presented. The increment in looking time, indicating dishabituation, showed that infants could discriminate between numerosities. In subsequent studies, numerosity discrimination was demonstrated in pre-verbal infants with a variety of displays, positions, motions, sequences of actions and speech sounds (Strauss and Curtis, 1981; Antell and Keating, 1983; Treiber and Wilcox, 1984; Starkley, Spelke and Gelman, 1990; van Loosbroek and Smitsman, 1990; Wynn, 1996).

Moreover, some data suggest that different animal species can resolve different kinds of numerical problems spontaneously, without training. The nesting and brooding strategies of some birds demonstrate the ability of spontaneous number discrimination. American coots (*Fulica americana*) appear to base decisions about whether to develop an addictional egg follicle on the number of their own eggs in the nest (Lyon, 2003). This is particularly remarkable because coots seem to discount the number of parasitic eggs in the nest, suggesting that they are able to enumerate a subset of elements in a group, and they base their responses on this relative evaluation.

Numerical discrimination is often found also in ecological situations whenever an animal chooses the larger/smaller of two alternative sets of food items. Such an ability would be at the basis of efficient foraging strategies (Krebs, 1974). Several species prefer the larger amount of food in a spontaneous forced-choice discrimination task (Dooley and Gill, 1977; Rumbaugh, Savage- Rumbaugh and Hegel, 1987; Rumbaugh, Savage-Rumbaugh and Pate, 1988; Boysen and Bertson, 1995; Anderson, 2000; Call, 2000; Boysen, Bertson and Mukobi, 2001). Monkeys (Hauser et al., 2000) can discriminate between 1 vs. 2; 2 vs. 3; 3 vs. 4 and 3 vs. 5 but not 4 vs. 5; 4 vs. 6; 4 vs. 8 and 3 vs. 8. Infants (Feigenson, Carey, and Spelke, 2002) are able to discriminate between 1 vs. 2 and 2 vs. 3, but not between 3 vs. 4 and 3 vs. 6. Salamanders (*Plethodon cinereus*) always choose the set that maximizes their net energy gain when required to choose between 1 vs. 2, 2 vs. 3 (Uller et al., 2003). When presented with portions of carrot pieces dropped from a cup into opaque boxes, rhesus monkeys (*Macaca mulatta*) pick

the box with the greatest number of portions for comparisons of 1 vs. 2, 2 vs. 3, and 3 vs. 4, but not for comparisons of 4 vs. 5 and 3 vs. 6. Additional experiments indicate that monkeys base their decisions on both the number of portions and the total amount of food (Wood et al., 2008).

In such experiments, however, changes in number are correlated with changes in a variety of continuous quantities, including total filled area, brightness, contour length in two-dimensional stimuli, and volume and surface in three-dimensional stimuli. All these variables that co-vary with numerosity are called Continuous Variables. In more recent studies, when a stricter control for continuous variables such as contour length and volume was used, it was found that infants respond to the latter variables and not to number during small number discrimination (Clearfield and Mix, 1999: Feigenson, Carey and Spelke, 2002; Xu, 2003; Xu, Spelke and Goddard, 2005).

Therefore, after more than two decades of study, there is still no consensus as to whether non-verbal subjects discriminate between small numerosities of elements on the basis of numerosity (Xu et al., 2005).

Little work has been carried out on numerical representation in young animals. There are, however, hints for possible age effects (see Hauser and Spelke, 2004).

Here we turned our attention to spontaneous discrimination of small numerosities, introducing a novel experimental procedure: spontaneous preference after imprinting. We reared chicks with different numerosities of imprinting objects and at test they were required to discriminate between a familiar numerosity and a novel one. Chicks preferred the larger amount of quantities, when continuous variables are partially or not controlled for. Only when all continuous variables are controlled for, is chicks' choice based on number.

2.2. EXPERIMENT 2.1 Comparison 1 vs. 3

In this experiment we aimed at investigating the ability of chicks to discriminate 1 vs. 3 objects. We used a filial imprinting procedure, during which chicks were exposed to either one of the two numerosities, followed by a spontaneous choice test between both numerosities present at once. Chicks were imprinted either onto three identical objects or onto one single object, and were then tested for free choice between one and three. Moreover, half of the chicks, during testing, had to choose from exactly three objects vs. one (we called this procedure “absolute” discrimination). The other half had to choose between two identical sets comprising 4 items, of which either three or one were of the familiar colour (we called this procedure “relative” discrimination).

2.2.1. Materials and methods

Subjects

Subjects were 160 (80 males and 80 females) Hybro (a local variety derived from the white Leghorn breed) domestic chicks, obtained weekly from a local commercial hatchery (Agricola Berica, Montegalda, Vicenza – Italy) when they were only a few hours old. From arrival they were singly caged in standard metal home-cages (28 cm x 32 cm large, x 40 cm high) constantly (24h/day) lit by 36 W fluorescent lamps placed 15 cm above each cage, at a controlled temperature (about 28-31°C) and humidity (68%), with food and water available *ad libitum*.

Of the 160 subjects, 80 (40 males and 40 females) were reared with a single small yellow plastic oval object (a ‘Kinder Surprise’ capsule, Ferrero S.P.A. Alba, Italy, measuring 4 cm x 3 cm x 3 cm, which we hereafter refer to as a ‘ball’) and the remaining 80 (40 males and 40 females) were reared with three small yellow balls. The balls were suspended by a fine thread (at about the chick’s head height), and served as an artificial imprinting object (previous studies have shown that this kind of stimulus is very effective in producing social attachment in this strain of chicks; see Vallortigara and Andrew 1991).

Chicks were reared in these conditions from the morning (11 a.m.) of the first day (Monday) to Wednesday of the same week, the day on which all chicks underwent testing. Immediately after testing the last chick, all chicks were housed in groups of 3-4 birds, with plenty of food and water available, and a few hours later they were donated to local farmers.

Apparatus and procedure

Testing took part in a room located nearby the rearing room, in which temperature and humidity were controlled (25°C and 70%, respectively). The test room was kept dark, except for the light coming from two lamps (40 W), both placed 25 cm above each end of the apparatus. The apparatus consisted of a runway (45 cm long, 20 cm wide and 30 cm high) divided by two fine lines drawn on the floor into three virtual compartments (length: 15 cm each). On top of the apparatus a removable unidirectional screen made it possible for the experimenter to observe the subject's behaviour from above without being seen. One or the other stimulus was placed at each end of the runway. The reciprocal position of the two test stimuli in the apparatus and the starting position of each chick at test were fully balanced across individuals. In this way, testing consisted of a choice between one familiar ball vs. three familiar balls for all chicks.

Each chick was in turn placed in the central position of the corridor and its behaviour was recorded for six minutes by using a computer-driven event recorder. The amount of time (seconds) spent by each chick in one of the three above described compartments was recorded. The computer-driven event recorder was operated every time the chick exited from the central compartment and stepped into one compartment or moved from one compartment to another. For each chick, the number of seconds spent in each of the two side compartments was computed in the following way:

$$\frac{\text{seconds spent by the imprinting object}}{\text{seconds spent by the two test stimuli}} \times 100$$

By using this formula, values near 50% indicated no preference for either stimulus; values > 50% indicated a preference for the imprinting object and values < 50% indicated a preference for the novel object.

We tested all of the chicks (both imprinted on one or on three imprinting objects) for choice between three vs. one imprinting objects, using either an absolute or a relative discrimination. Half of the chicks (40 males, 40 females) took part in an Absolute Discrimination Test. They were presented with two stimuli: the first made of one imprinting object and the other made of three imprinting objects (balls identical to those used during imprinting). The remaining chicks (40 males, 40 females) took part in a Relative Discrimination Test in which they were required to discriminate between two stimuli of the same overall numerosities. One stimulus was made of three familiar yellow balls (identical in colour, dimension, and shape to the ball used as imprinting object) and a single unfamiliar pink ball (identical in dimension and shape to the familiar ones, but differing in colour). The other stimulus was made of three unfamiliar pink balls and a single familiar yellow ball.

2.2.2. Results and Discussion

An Analysis of variance (ANOVA) was run with the following independent variables: Sex, Testing Condition (Absolute vs. Relative) and the Number of Imprinting Objects (Chicks Imprinted on One vs. Chicks Imprinted on Three). The dependent variable was the Choice of the Familiar stimulus, as computed with the formula previously described. There were no main effects of Sex ($F(1,152)=0.768$, $p=0.382$), nor of the Testing Condition (Absolute vs. Relative, $F(1,156)=3.011$, $p=0.847$). Instead, the ANOVA revealed an effect of the Number of Imprinting Objects ($F(1,156)=9.854$, $p=0.0020$). A one-sample t-test was used to compare the overall means with chance level: Chicks Imprinted on One (N=80, Mean=43.6, SEM=3.3); Chicks Imprinted on Three (N=80, Mean=57.7, SEM=3.1). Chicks Imprinted on Three were able to discriminate between the two stimuli, selectively choosing the larger one above chance ($t(79)=2.4839$, $p=0.0151$), whereas choice

for Chicks Imprinted on One was marginally not significant, although still in the same direction ($t(79)=1.939$, $p=0.0560$).

Overall chicks seemed to prefer the set comprising the larger number of familiar elements, i.e. three. There being no difference between the two test conditions, it appears that, when faced with identical overall numerosities, chicks could base their choice on the relative amount of familiar objects – which were identifiable through a difference in colour.

2.3. EXPERIMENT 2.2 Comparison 2 vs. 3

Experiment 2.1 showed chicks can spontaneously discriminate 1 vs. 3. In Experiment 2.2 a similar procedure was employed with a new group of chicks to check whether they could also deal with what we expected to be a more difficult discrimination, i.e. 2 vs. 3. We reared the chicks with either two or three identical imprinting objects. They were then tested for spontaneous choice between two vs. three objects similar to the ones previously used during imprinting. In this way, the continuous variables co-varied with the numerosity of the stimuli at test.

2.3.1. Materials and methods

A new group of chicks (N= 80) took part in this experiment. 40 subjects were reared with two imprinting balls and the remaining 40 with three balls. All the balls utilized to build the stimuli were identical in colour, shape and size, in such a way that the surface, the volume and all the other continuous variables changed with the number of elements.

The rearing conditions, the apparatus and the experimental procedures were exactly the same as those described in the previous experiment.

The test again consisted of a 6-min free choice between the familiar and a novel stimulus, differing only in the number of items present in each stimulus. Only stimuli made of two or three identical balls were used at test.

Two different control groups were employed, one reared with one imprinting object (N=80; 40 male and 40 female chicks) and the other without any imprinting object (N=77; 36 males and 41 females).
Even these subjects took part in the same, previously described, test of numerical discrimination between 2 vs. 3 elements.

2.3.2. Results and Discussion

An ANOVA was run with Sex and Testing Condition (Experimental Group, Reared with One, No Imprinting Object) as independent variables. The dependent variable was the Choice of the Larger Stimulus. There was a significant main effects of Sex ($F(1,231)=9.276$, $p=0.003$): Females (Mean=58.1, SEM=2.5; $t(120)=3.240$, $p=0.002$) chose the larger quantity, while Males (Mean=46.4, SEM=3.1; $t(115)=1.1613$, $p=0.248$) did not show any preference. The effect of the Testing Condition was also significant ($F(1,231)=4.427$, $p=0.013$): Chicks of the Experimental Group chose the larger quantity (Mean=59.9, SEM=3.6; $t(79)=2.750$, $p=0.007$), while chicks of both groups Reared with One and No Imprinting Object did not show any preference: Reared with One, (Mean=51.0, SEM=3.1; $t(79)=0.250$, $p=0.803$), No Imprinting Object (Mean=46.0, SEM=2.6; $t(76)=1.539$, $p=0.128$). The interaction Sex x Testing Condition was not significant ($F(1,231)=0.827$, $p=0.439$).
Only for what concerns the chicks of the Experimental Group, a separate analysis was run, in which we compared the data of the group of chicks Reared with Two or Reared with Three elements. An unpaired t-test, run on the percentage of choice for the familiar stimulus by the two different groups of chicks, revealed a statistical difference between the two groups ($t(78)=5.829$, $p<0.001$). Chicks Reared with Two, Mean=38.8, SEM=2.5; chicks Reared with Three, Mean=59, SEM=2.4. Nevertheless, when considered separately, each group was capable to discriminate between the two stimuli, selectively choosing the larger one above chance (chicks Reared with Two, ($t(39)= 4.480$, $p<0.001$); chicks Reared on Three ($t(39)= 3.750$, $p<0.001$).

The main effect of Sex is probably due to the fact that females show stronger affiliative tendencies, i.e. they are usually more attracted to social stimuli than males. This could explain females' preference for the larger stimulus and the lack of choice expressed by males. Only chicks of the Experimental Group were able to discriminate, while both No Imprinting Object and Reared with One groups preferred neither one nor the other stimulus. Moreover, results showed that chicks could discriminate 2 vs. 3, preferring the larger stimulus, even when, for chicks Reared with Two, this is not the familiar one.

2.4. EXPERIMENT 2.3 Surface vs. Volume Control

The previous experiments showed that chicks can discriminate between different numerosities of elements identical in dimension, when continuous variables of the stimuli were either not controlled for or only partially so. The aim of this experiment was to check whether chicks could also discriminate elements when the volume or the surface of the stimuli was controlled for. In this experiment we checked for the possible use of either surface or volume in the chicks' discrimination, by using balls of different size.

2.4.1. Materials and methods

A new group of 132 chicks (66 males and 66 females) took part in this experiment. 60 subjects took part in the Volume Control Test: 30 subjects were reared with a single red ball and the remaining 30 subjects were reared with four identical red balls. The size of the balls used to make the stimuli was chosen in such a way that the overall volume of the four balls was identical to the volume of the single ball. 72 chicks took part in the Surface Control Test, of these, 36 were reared with a single ball and 36 were reared with six identical red imprinting balls. Again the size of all the balls used to build the stimuli was selected in such a way that the surface of the single ball was identical to the overall surface of the six smaller balls.

The rearing conditions, the apparatus and the experimental procedures were exactly the same as those described for the previous experiment.
The test again consisted of a 6-min free choice between the familiar and a novel stimulus, differing only in the number of items present in each stimulus: 1 vs. 4 for the Volume Control Test and 1 vs. 6 for the Surface Control Test.

2.4.2. Results and Discussion

No preference emerged between the Volume Control Test and the Surface Control Test, so data of the two groups were merged together. The ANOVA revealed an effect of the Number of Imprinting Objects ($F(1,124)=27,041, p<0.001$). A one sample t-test was used to compare each mean with chance level. The independent variable was the number of imprinting objects: One big red ball (N=66), four red balls (Volume Control, N=33) or six red balls (Surface Control, N=33). The dependent variable was the percentage of choice for the familiar stimulus shown by each chick. Chicks imprinted on the one-element stimulus Mean=67.073, SEM=3.603; chicks imprinted on the four (or six) element stimulus Mean=41.528, SEM=3.859. Each group was capable of discriminating between the two stimuli, selectively choosing the bigger one above chance (chicks imprinted on the one-element: $t(65)= 38.4962$, $p<0.001$); chicks imprinted on the four (or six) element-elements $t(65)= 17.8354$, $p<0.001$).
Thus, all chicks preferred the bigger stimulus. There was no statistical difference between the two test conditions, Volume Control and Surface Control. In these situations the increased size of one of the stimuli is possibly more relevant, and for sure more attractive, even when it was compared with a larger number of smaller objects. It seems that neither Surface nor Volume were relevant in this case. They preferred only the single bigger stimulus, maybe because it is perceived as a super-stimulus.
Again, it is quite clear that at the basis of choice there is no preference for the imprinting numerosity, but for the bigger stimulus.

2.5. EXPERIMENT 2.4 Comparison 2 vs. 3

The previous experiments showed that chicks can discriminate between different numerosities. Nevertheless, they seemed to prefer the larger amount of elements when they were presented with elements of the same size, even if they were capable of discriminating between familiar and unfamiliar objects. On the contrary, when an element was significantly bigger with respect to the others, they preferred the oversized stimulus in every case: either when it was the familiar or the unfamiliar object. In all these cases the imprinting object and the testing object were similar to each other.

In the present experiment we used sets of two or three elements different from each other in shape, colour and area at training. At test, stimuli were again novel: they differed from the imprinting object in colour, shape and size, with surface area and volume controlled for. In this way, imprinting features were not present in the testing objects except for numerosity.

2.5.1. Materials and methods

A new group of 62 female chicks (31 imprinted on two-element stimulus and 31 imprinted on three-element stimulus) took part in this experiment. Three or two imprinting objects differing from each other in colour, dimension and shape were used. Chicks were tested with completely different, novel objects. These testing objects differed in colour, shape and dimension from the imprinting object, but with both volume and surface area of the two testing stimuli identical.

The rearing conditions, the apparatus and the experimental procedures were exactly the same as those described for the previous experiment.

The test again consisted of a 6-min free choice between the familiar and a novel stimulus, differing only in the number of items present in each stimulus.

2.5.2. Results and Discussion

An unpaired t-test, run on the percentage of choice for the familiar numerosities by the two different groups of chicks did not reveal any statistically significant difference between the two groups of chicks, ($t(60)=0.5554$, $p<0.5807$). Chicks imprinted on the two-element stimulus Mean=61.000, SEM=4.000; chicks imprinted on the three-element stimulus Mean=57.400, SEM=5.100. Data of the two groups were therefore merged together and the resulting mean value was compared with chance level using a one sample t-test (Mean=59.200, SEM=4.550; $t(61)=59.200$, $p=0.0476$). Chicks reared both with the two or three element stimuli were able to discriminate between them, selectively choosing the familiar number of objects: if reared with three, they chose three; reared with two, they chose two. Thus, we can say that on this occasion they really are using absolute number.

2.6. CONCLUSIONS

It had been argued that animals can make numerical discriminations but only as a last-resort strategy, when all other cues are unavailable (Davis and Pérusse, 1988). In spite of this criticism, the presence of various degrees of number competence has been largely demonstrated in animals (Gallistel and Gelman, 1992; Dehaene, 1997; Hauser and Spelke, 2004) and it is also found in absence of training. For example, in ecological situations, several species, as suggested by optimal foraging theory (Krebs, 1974), spontaneously prefer the larger amount of food. Salamanders (*Plethodon cinereus*, Uller et al., 2003) and human infants (Wynn, 1992; Feigenson et al., 2002) always chose the set that maximised their net energy gain when required to choose between 1 vs. 2 or 2 vs. 3. Even nesting and brooding behaviours unveiled some counting abilities. American coots (*Fulica americana*) can regulate the number of eggs on the basis of tactile and visual information the number of eggs that they are actually brooding (Lyon, 2003; Andersson, 2003). However, in all these studies, changes in number often correlate with changes in other continuous variables (such as brightness, contour length, filled area, dimension or volume). The use of other variables could not possibly be ruled out. When continuous variables were experimentally controlled for, neonates failed to discriminate between sets of one, two or three (Clearfield and Mix, 1999; Feigenson et al., 2002) or more elements (Wynn, 2002).

In the present study, spontaneous number discrimination was investigated by using a filial imprinting procedure.

In Experiment 2.1, chicks, imprinted either onto three identical objects or onto one single object, were able to discriminate between 1 vs. 3, even when a relative discrimination between familiar and unfamiliar objects was required, always preferring the larger amount of familiar elements.

In Experiment 2.2 only chicks reared with either two or three objects were able to discriminate between such numerosities at test, each group preferring the larger stimulus, whereas chicks of the control groups (exposed to either none or one imprinting object) did not show any preference for either of the two stimuli. These

data suggest imprinting is a necessary procedure to investigate spontaneous number discrimination abilities in chicks.

In Experiment 2.3, a partial control of either overall volume or surface area was carried out. In both cases chicks preferred the bigger stimulus, maybe because it acted as a super-stimulus and was therefore more attractive.

In Experiment 2.4, when continuous variable were controlled for, chicks showed able to discriminate between 2 vs. 3 elements. In this case, the test objects differed in color, shape and size from the imprinting object. Moreover, at test, surface area and volume were simultaneously controlled for. Only in this case did the chicks choose the familiar number, even when this was the smaller amount, therefore showing the ability to take into account purely numerical cues in such cases.

These data showed, for the first time, that spontaneous number discrimination can be based on numerical cues only, supporting the existence of a spontaneous “number sense”, considered as a biologically based knowledge system, which might have originated from adapting to the external world, under specific evolutionary pressures (Dehaene, 1997).

Filial imprinting is an ideal procedure to investigate spontaneous numerical abilities, although it cannot be used to probe the limits of such abilities. Firstly, because when a preference in the spontaneous choice test is not detected, we cannot exclude that chicks can nevertheless discriminate between the two stimuli. In fact, it may be that all groups of social elements are perceived as equally good if they comprise a minimum of elements, and therefore are treated as equally attractive by the chicks. For that reason, a different paradigm will be introduced, i.e. associative learning through conditioning procedures.

3. ACQUIRED DISCRIMINATION OF SMALL SETS OF OBJECTS

Chicks were trained to discriminate small sets of identical elements. They were then tested for choices (unrewarded) between sets of similar numerosities, when continuous physical variables such as spatial distribution, contour length and overall surface were equalized. In all conditions chicks discriminated 1 vs. 2 and 2 vs. 3 stimulus sets. Similar results were obtained when elements were presented under conditions of partial occlusion. In contrast, with sets of 4 vs. 5, 4 vs. 6 and 3 vs. 4 elements chicks seemed unable to discriminate on the basis of number, although non-numerical discrimination based on perceptual cues was observed. This adds to increasing evidence for discrimination of small numerosities of up to 3 elements in human infants and non-human animals.

3.1. INTRODUCTION

The ability to represent number and to perform exact arithmetic is likely to be a uniquely human capacity, only shown by enculturated human beings who had received specific arithmetic instruction (Gallistel and Gelman, 1992; Dehaene, 1997; Hauser and Spelke, 2004; Carey, 2004). Nonetheless, animals (and preverbal children as well, see review in Feigenson, Dehaene and Spelke, 2004) seem to possess some forms of numerical representation. This has been shown both in mammals (Boysen and Berntson, 1989; 1990; Mc Comb, Packer and Pusey, 1994; Murofushi, 1997; Olthof, Iden and Roberts, 1997; Brannon and Terrace, 1998; Kawai and Matsuzawa, 2000; Beran, 2001; 2004; Beran and Rumbaugh, 2001; Biro and Matsuzawa, 2001; Sulkowski and Hauser, 2001; Shumaker, et al.,2001; Hauser, et al., 2002; Nieder, Freedman and Miller, 2002; Kilian, et al., 2003; Judge, Evans and Vyas, 2005; Hauser, et al., 2003; Smith, Piel and Candland, 2003; Cantlon and Brannon 2005; Beran, et al., 2006) and birds (Thompson, 1968; Pepperberg and Brezinsky, 1991; Pepperberg, 1994; Emmerton, Lohmann and Niemann, 1997; Smirnova, Lazareva and Zorina, 2000; Olthof and Roberts, 2000; Xia, Siemann and Delius, 2000; Xia, et al., 2001; Brannon, et al., 2001; Lyon, 2003; Pepperberg and Gordon, 2005; Pepperberg, 2006).

One of these forms of numeracy consists in the ability to represent the precise number of objects in a visual scene up to a set size limit of three or four (Feigenson et al., 2004). For instance, when infants are allowed to choose between two quantities of crackers hidden in buckets, with choices of 1 vs. 2 and 2 vs. 3 they picked the larger quantity, but with 3 vs. 4, 2 vs. 4 and 1 vs. 4 they chose at chance (Feigenson and Carey, 2005). In a similar vein, rhesus monkeys presented with apple slices sequentially hidden in two locations and required to choose between them, preferred the larger quantity with 1 vs. 2, 2 vs. 3 and 3 vs. 4, but with 3 vs. 8 and 4 vs. 8 chose at chance (Hauser et al., 2000). Representation of small numerosities is usually accounted for in terms of an object file hypothesis, according to which each object in a set is represented by a unique symbol (the symbol for each individual has been dubbed an “object file”; it would

implicitly represent the number of objects in a set as there could be only one object file open for each object in the set; see Hauser and Carey, 2003).

However, some doubt has been cast recently as to whether infants and non-human animals compute the numerosity of small object arrays, because when number is pitted against continuous dimensions that correlate with number in the stimuli (e.g. area and contour length), infants seem to respond to continuous physical dimensions (Feigenson, Carey and Spelke, 2002) and when area is controlled for, infants fail to respond to number (Feigenson, Carey and Hauser, 2002). This is not to say that preverbal infants cannot respond to number, for they sometimes do. For instance, when objects to be discriminated are from a domain in which the continuous extent, the overall amount, is especially relevant, such as food, they indeed tend to respond to extent rather than to number (Feigenson, Carey and Hauser, 2002). But, when the task requires reaching for individual objects, then number encoding prevails over physical extent (Feigenson, 2005).

Research with animals using conditioning procedures has shown, however, that under certain conditions animals can be trained with numerosities that exceed 3-4 elements (e.g. Emmerton and Delius, 1993). However, in this case training comprises use of stimuli of different spatial extent (and different shapes, brightness and so on). It would be therefore interesting to check whether animals trained with a specific set of stimuli on the basis of number maintain the discrimination when changes in the continuous physical dimensions of the stimuli are introduced. This is the main aim of this study which has been carried out using young domestic chicks as subjects.

Little work has been carried out on numerical representation in young animals. There are, however, hints for possible age effects (see Hauser and Spelke, 2004).

Here we turned our attention to cardinal aspects in the domain of small numerosities. We trained chicks with arrays of 1 vs. 2, 2 vs. 3, 4 vs. 6, 4 vs. 5, and 3 vs. 4 elements. After training we tested chicks for generalization, under extinction conditions, when continuous variables (area and contour length) were controlled for. We also introduced a novel condition which, as far as we know, has never been investigated before, i.e. animals were faced with partly occluded

elements that could be discriminated solely on the basis of number, and were identical for what concerns continuous physical variables.

3.2. EXPERIMENT 3.1 : Comparison 1 vs. 2

Chicks' ability to discriminate one versus two elements was assessed by testing week-old birds that had been previously trained to selectively peck at stimuli picturing either one or two identical elements for a food reward.

3.2.1. Materials and methods

Subjects

The subjects were 6 male Hybro (a local commercial hybrid variety derived from the White Leghorn breed) domestic chicks (*Gallus gallus*) obtained from a local commercial hatchery (Agricola Berica, Montegalda, Vicenza, Italy) when they were only a few hours old. On arrival, chicks were immediately housed singly in standard metal cages (28 cm wide x 32 cm long x 40 cm high) at controlled temperature (28-31° C) and humidity (68%), with food and water available *ad libitum* in transparent glass jars (5 cm in diameter, 5 cm high) placed at each corner of the home cage. The cages were constantly (24hr/day) lit by fluorescent lamps (36W), sited 15 cm above each cage.

Chicks were reared in these conditions from the morning (11 a.m.) of the first day (i.e., Monday, the day of their arrival, which was considered as Day 1) to the eighth day (Tuesday of the following week). In the morning (8 a.m.) of Day 8 chicks were food deprived, while water was left available, and after about 4-5 hours (1 p.m.) they underwent a shaping procedure. At the end of the shaping, each chick was caged with food and water available *ad libitum*. On Day 9, in the early morning (7 a.m.) chicks were food deprived for about 3 hours, and then underwent a training phase (10 a.m.). For every chick, testing took place one hour after the end of such training. Immediately after having tested the last chick, all

chicks were collectively caged in groups of 3-4 birds, with plenty of food and water available, and then they were donated to local farmers.

Apparatus

Shaping, training and testing took place in a separate room (experimental room) located near to the rearing room. In the experimental room temperature and humidity were controlled (respectively at 25° C and 70%) and the lighting was provided by four 58W lamps (placed on the ceiling, 194 cm above of the floor of the experimental apparatus).

The experimental apparatus (Fig. 3.1a) consisted of a rectangular arena (31.5 cm wide x 60.0 cm long x 39.3 cm high) made of uniformly white-painted wood panels; the floor consisted of a metal grid. A moveable cardboard partition (28.5 cm wide x 46.6 cm high, visible within the arena in Fig. 3.1a), lifted from above by the experimenter, was used to gently push back the chicks to the starting point at the end of each trial. At the bottom of one of the short walls of the arena there was a slit through which (depending on the experimental phase), either one or two small plastic boxes (5.5 cm wide x 12.0 cm long x 4.0 cm high) (Fig. 3.1b,c) could be introduced. Each box contained a drawer, that could be pushed open by the experimenter. The drawer contained chick crumbs used as food reinforcement during the experiment. On top of each box one white rectangular plastic paperboard (9.5 cm x 6.0 cm) was positioned on a special support fixed onto the upper part of the box, at an angle of 60° (Fig. 3.1c).

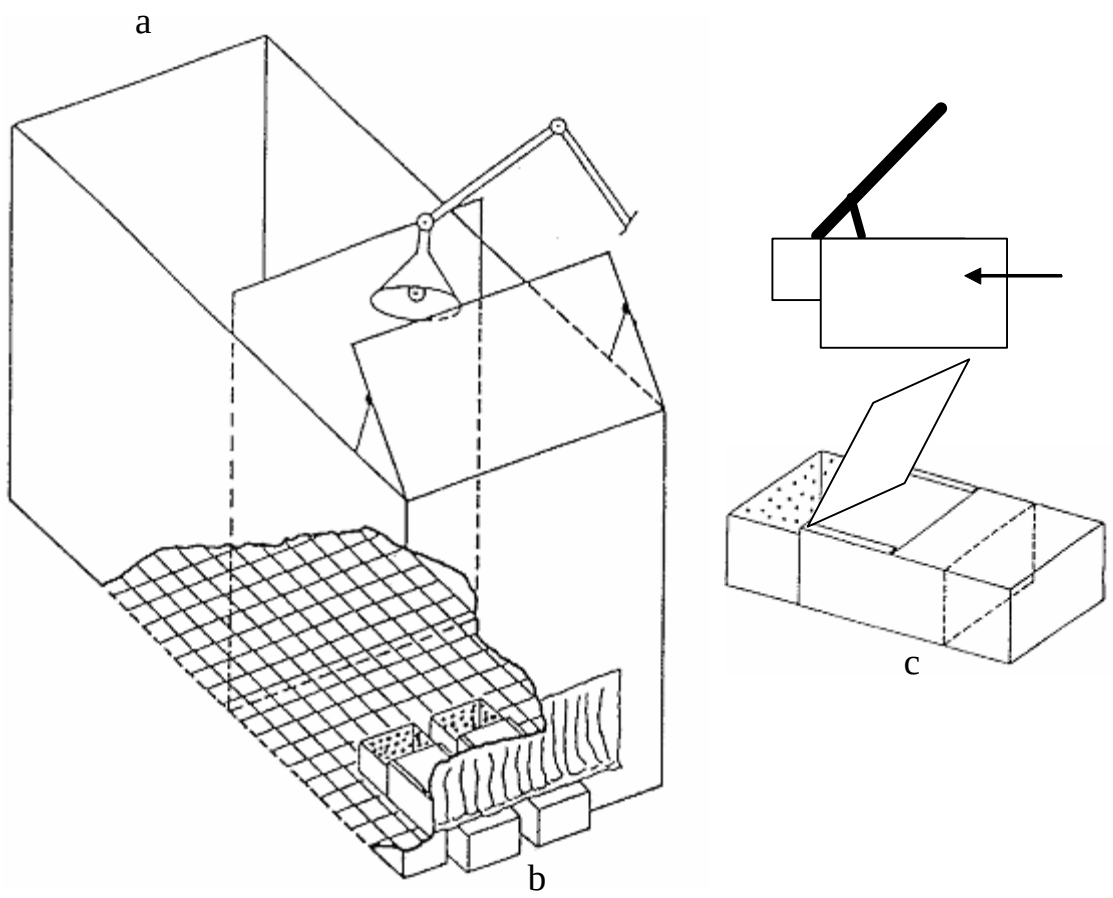

Figure 3.1. Schematic representation of the experimental apparatus (a) illustrating the position of the two food boxes used during training and testing (b), and the features of each single box (c, the inner drawer containing the food is pushed open). Stimuli were positioned on the special support located on top of each food box.

The stimuli consisted in various sets made of identical elements (small black circles), each set was painted on the top of one plastic paperboard (i.e., different paperboards were used to present different stimuli).

The stimuli used at training differed only in number. For Experiment 3.1 two stimuli were used (Fig. 3.2a): one depicting one black circle and a second stimulus depicting two black circles.

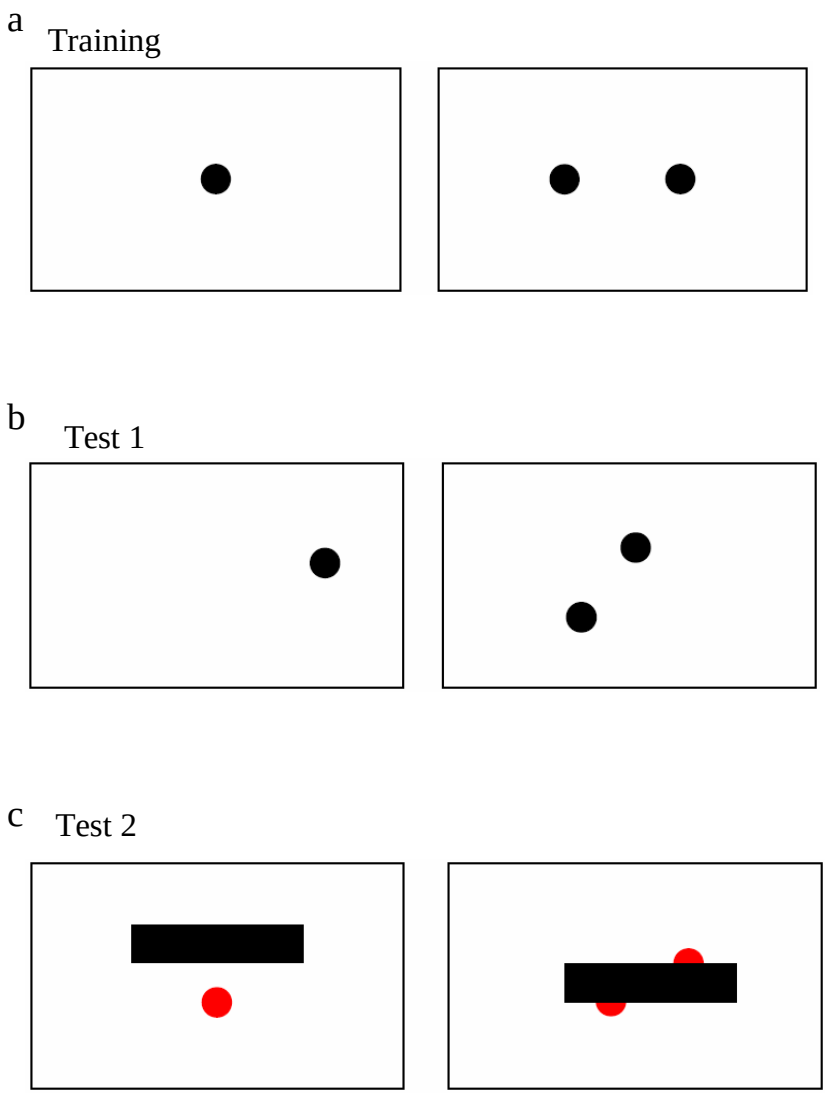

Figure 3.2. Stimuli employed in Experiment 3.1 (1 vs. 2): a) training stimuli; b) example of a pair of stimuli used in Test 1; c) example of a pair of stimuli used in Test 2.

Procedure

Shaping. On Day 8, each chick took part in a shaping phase for which only one box was used, and the plastic paperboard was uniformly white (i.e., there were no circles painted on it) and was located horizontally on top of the box. Each chick was in turn placed within the apparatus: in front of and 20 cm away from the box, free to move around and get acquainted to the novel environment. At first, the drawer in the box was kept open and the chick was allowed a few pecks at the crumbs. The drawer was then slowly pushed closed and a few grains were placed on top of the box. When the chick had eaten all the grains on top of the drawer,

and this was closed, chicks could have the drawer pushed open by the experimenter and access the food only whenever they pecked the top of the box. Chicks had no difficulties start pecking the clear top of the box even after no grains were present on it, and in this way they easily leaned to associate pecking response with the opening of the drawer. After each correct response the chick could eat a few grains of food, and was then gently pushed back to the starting point (i.e., the farthest side of the arena, about 35 cm from the box) using the cardboard partition and kept there for 5 seconds. The cardboard partition was then lifted from above and the chick was then free to move into the apparatus and approach the food box (which had been meanwhile closed and cleared from any food leftover on its top). Only chicks' pecking responses on the centre of the top of the box were reinforced by opening the drawer and allowing the bird to access to the food, while pecks at other parts of the box or the apparatus were never reinforced. The shaping was concluded after the chick had performed 10 responses from the starting point. On average about 10 minutes were required to complete the shaping for each chick.

Training. Training started 2 hours after the end of the shaping process and lasted about 10-15 minutes. At training, two identical boxes were presented simultaneously to the chick (placed side by side, at about 3 cm from each other, see Fig. 3.1b). One box was used to present a stimulus with one single black circle (0.8 cm in diameter) positioned in the middle of the white rectangular plastic paperboard on top of the box. On the second box was the other stimulus, which had two aligned black circles (0.8 cm in diameter, 2.8 cm apart) positioned in the middle of the white rectangular paperboard (see Fig. 3.2a). Three subjects were reinforced for pecking at the first (S+=1), and the remaining three for pecking the second stimulus (S+=2). In each trial, each chick was placed in the starting position and than left free to walk towards the two boxes and peck at one of them. Only pecks at the correct stimulus were reinforced by opening the drawer and allowing the chick to eat some crumbs. Whenever the chick pecked at the incorrect stimulus or it pecked at the box and not at the stimulus itself, its response was not reinforced and the chick was immediately, but gently pushed back to the starting point. If no response was assigned by the chick within a time limit of 60

seconds, the trial was considered null and void and the chick was placed back at the starting position and it was administered another trial. At the end of each trial, the chick was placed again at the starting position, by using the cardboard partition, and was kept there for 5 seconds, after which it was given another training trial. The left-right position of the positive stimulus with respect to the negative one was changed from trial to trial according to a semi-random sequence (i.e.: L-R-L-R-L-L-R-R-L-R- L-R-L-R-L-L-R-R-L-R; Fellows, 1967). To enter the tests each chick had to reach the training criterion within a maximum of 20 blocks made of 20 trials each. The criterion being pecking the correct stimulus at least 17 times within 20 valid trials in a same block. Whenever a chick made four mistaken trials within a same block of trials that block was considered over (this could happen before reaching 20 trials) and a new block of trials was started. At the end of training, each chick was placed back in its home cage until Test 1.

Test 1: One hour after training each chick was placed in the apparatus in the starting position and underwent the test. Ten different pairs of stimuli, all drawn on identical white rectangular plastic paperboards (9.5 cm x 6 cm) were used. In each pair one stimulus consisted of one circle and the other of two circles. Dimension (0.8 cm in diameter) and colour (black) of each circle were identical to those used in the training phase, the only difference being the spatial position of the circles over the paperboard, which was randomly determined for each stimulus within a window of 7 cm x 4 cm in the centre of the plastic paperboard. In the case of the stimulus with two circles, their reciprocal distance could range from 0.2 cm to 0.32 cm (see Fig. 3.2b).

Each chick was first of all administered a re-training (criterion of 3 consecutive correct trials, which was obtained in about 10 trials). Immediately thereafter, each chick was administered the test, comprising 20 test trials (4 sections of 5 trials each). In each trial the chick, released at the starting point, was free to peck at either stimulus. Neither correct (i.e., directed at training stimulus S+) nor mistaken (directed at S- training stimulus) responses were reinforced at test. The left-right position of the positive stimulus with respect to the negative one was changed from trial to trial according to a semi-random sequence (i.e.: L-R-L-R-L-L-R-R-L-R-L-R-L-R-L-L-R-R-L-R; Fellows, 1967). At the end of each of the four test blocks (of

5 trials each) a brief re-training was administered to the chick (hence 3 such re-training periods were administered during Test 1) using the same stimuli of the previous training. The criterion to be reached in order to pass to the following testing section was of 3 correct consecutive trials, this was obtained, consistently throughout the 3 re-training sessions, in about 10 re-training trials. Sessions of testing and then retraining alternated until 20 test trials were completed. At the end of this test section each chick was placed back in its own home cage until Test 2.

Test 2: Test 2 took place one hour after the end of Test 1. Nine different pairs of stimuli, drawn on identical white rectangular plastic paperboards (9.5 cm x 6 cm), were used (Fig. 3.2c). Each pair comprised a stimulus made of one red circle and a second stimulus made of two red circles. One black bar (4.7 cm x 1 cm) was present in both types of stimuli. The size of the circles was the same as for those used in the previous training and testing. Their spatial position varied randomly from stimulus to stimulus (hence from trial to trial) within a window of 7 cm x 4 cm on the centre of the rectangular paperboard area. For the stimuli with two circles the black bar overlapped the circles so that it occluded exactly one half of each circle. In the stimuli with one single circle the bar was positioned at about 0.42 to 0.64 cm above the circle itself, so that this was not occluded by the bar. In this way the total area exposed by each stimulus was identical. Nevertheless, due to the perceptual process of amodal completion (which is known to occur in young chicks, see Regolin and Vallortigara, 1995; Lea, Slater and Ryan, 1996; Regolin, Marconato and Vallortigara, 2004) two occluded elements were perceived in one stimulus, whereas in the other stimulus a single, unoccluded, element was perceived.

Testing procedure was identical to the one described for the Test 1.

3.2.2. Results and Discussion

Data were analysed, separately for each testing session, comparing the number of correct trials (i.e, number of trials in which the chick pecked at S+) in the 20 testing trials that were administered to each chick with chance level (i.e., 10 trials).

Data were separately computed for the group reinforced for pecking at the one-element stimulus and the group reinforced for pecking at the two-element stimulus.

Test 1: We compared the data of the group of chicks previously reinforced for pecking at the one element (Mean=13.000, SEM=0.999) and that of the group previously reinforced for pecking at two elements (Mean=13.667, SEM=0.333) using a two-sample t-test. No difference was present between the two groups in their proportion of choice for S+ (t(4)=0.632, p=0.561). Data were therefore merged and the resulting mean was compared (with a one-sample t-test) with the score that would be obtained if chicks pecked at both stimuli at random during the 20 testing trials (i.e. 10). Overall, chicks preferentially pecked at S+ (N=6; Mean=13.333, SEM=0.494; t(5)=6.741, p=0.001).

The results showed that, following training, chicks could identify the correct stimulus even when the spatial disposition of the circles was modified at test as compared to training.

Test 2: Again, no statistical difference was present between the proportion of pecks assigned by the two groups of chicks at S+ (two-sample t-test, t(4)=1.336, p=0.252; chicks trained on one-element stimulus Mean=12.667, SEM=0.333; chicks trained on the two-element stimulus Mean=14.333, SEM=1.201). The overall mean was significantly different from chance level (i.e., 10; one-sample t-test, Mean=13.500, SEM=0.670; t(5)=5.218, p=0.003). Results confirmed that chicks discriminated 1 vs. 2 elements even when the overall visible area of each stimulus was identical.

3.3. EXPERIMENT 3.2 : Comparison 2 vs. 3

Experiment 3.1 shows that chicks can be trained to discriminate 1 vs. 2 elements, and that they retain such discrimination even when the overall surface of the stimuli has been controlled for. In Experiment 3.2 a similar procedure was employed with a new group of chicks to check whether they could also learn what we expected to be a more difficult discrimination, i.e. 2 vs. 3. Our hypothesis would be that chicks should be able to learn such discrimination, since it would be still

possible with a system dealing with small numerosities (Hauser and Spelke, 2004).

Moreover, in this experiment we checked for a possible use of contour length in chicks' discrimination, both with complete and with amodally-completed stimuli. We also introduced another, novel condition based on occlusion perceived with chromatically homogeneous stimuli, that allows a further control on the role of contour length. Occlusion with chromatically homogeneous patterns is shown in Fig. 3.3f, in which a black bar seems to occlude some black squares (rather than perceiving the black squares as in front of the black bar). Petter (1956), who first described the phenomenon, argued that it occurs because shorter modal (occluding) contours are needed to account for the occlusive effect of the bar on the squares, whereas larger modal contours are needed to account for the occlusive effect of the squares on the bar. This 'Petter's rule', according to which the visual system tends to minimize the formation of interpolated modal contours, has been largely confirmed in studies of human visual perception (Rock, 1993; Shipley and Kellman, 1992; Tommasi, Bressan and Vallortigara, 1995; Thornber and Williams, 1996; Singh, Hoffman and Albert, 1999) and has been shown to be at work even in the chicken's visual system (Forkman and Vallortigara, 1999).

3.3.1. Materials and methods

Subjects

Subjects were 13 male Hybro chicks obtained from the same commercial hatchery and kept in standard rearing conditions identical to those described for Experiment 3.1. Seven chicks were trained to choose the two elements while the other 6 were reinforced for pecking at the three elements. Moreover, 6 of these chicks (of which 3 trained on two elements and 3 on three elements) were tested with stimuli allowing for the control of the overall surface, and the remaining 7 chicks (4 trained on two elements and 3 on three elements) were tested with stimuli allowing for the control of the overall outline.

Procedure

The apparatus and the general testing procedure were identical to those described for Experiment 3.1.

Stimuli used in this experiment were also printed on white rectangular plastic paperboards (9.5 cm x 6 cm) placed on top of each food box. Stimuli at test could differ in dimension and spatial disposition of their elements.

Shaping: The stimulus used for shaping (a clear paperboard) was identical to that previously described.

Training: Stimuli (Fig. 3.3a) consisted of two identical paperboards over which either two or three black elements had been printed. All chicks were trained on such sets of 2 vs. 3 elements, however, for some of the chicks (N=6) the elements were black filled circles (0.8 cm in diameter) aligned along the midline of the support. In the two-element stimulus the circles were spaced 2.8 cm apart, whereas in the three-elements stimulus the circles were 1.8 cm apart. For the remaining chicks (N=7) the elements were black filled squares (0.8 cm side) aligned along the midline of the support. In the two-elements stimulus the squares were spaced 2.8 cm apart, whereas in the three-elements stimulus the squares were 1.8 cm apart. The reason for using squares for some of the chicks was to facilitate the construction of modified stimuli that were used for the control of the overall outline of these stimuli.

Test 1: For all chicks ten different pairs of stimuli were used (Fig. 3.3b). Each pair comprised one stimulus with two black circles (or squares) and one stimulus with three black circles (or squares). All elements were identical in colour and dimension to those used for the training but now their spatial position within the rectangular paperboard changed randomly from trial to trial within a 7 cm x 4 cm window (with a distance between the items ranging from 0.3 cm to 3.5 cm).

Test 2: The group of chicks trained with the filled circles underwent a test with stimuli of controlled area. These consisted of ten pairs of stimuli (one of which is shown in Fig. 3.3c, left) each pair being made of either two (0.66 cm in diameter) or three (0.54 cm in diameter) black circles. The different size was used in order to equate the area of the two stimuli (0.687 cm^2). The perimeter, though, differed by 0.94 cm (it was of 5.09 cm overall for the three elements stimulus, and

4.15 cm for the two elements stimulus). As in the first experiment, the spatial disposition of the circles of each stimulus changed from trial to trial within a 7 cm x 4 cm window.

The group of chicks trained with the filled squares underwent a test with stimuli of controlled perimeter. These consisted of ten pairs of stimuli (one of which is shown in Fig. 3.3c, right) each pair comprising one stimulus with two (0.70 cm per side) black squares and one stimulus with three (0.467 cm per side) black squares, in such a way that the perimeter length of the two stimuli was exactly the same (5.60 cm). The spatial position of the squares within the rectangular paperboard changed randomly from trial to trial within a 7 cm x 4 cm window.

Selectively the group of chicks trained with the filled squares underwent two further testing sessions in which the perimeter of the occluded elements was again controlled for, although with a different procedure. Stimuli used were similar to the occluded ones used for the Test 2 of Experiment 3.1. Two testing sessions were needed for the side shared between the element and the occluder could or could not be considered as part of the perimeter of each element.

Test 3: Ten different pairs of stimuli were used (Fig. 3.3d). Each pair comprised a stimulus made of two red squares and a second stimulus made of three red squares. One black bar (4.7 cm x 1 cm) was present in both types of stimuli. The size of the squares prior of occlusion was the same as for those used at training. All stimuli were placed in the middle of the paperboard (the position of the single squares changed from stimulus to stimulus of about 1 cm horizontally and 0.5 cm vertically). For both the stimuli with two and with three squares the black bar overlapped the squares so that it occluded a part of them (variable from square to square and from trial to trial). In this way the total perimeter (considering 3 sides) of the visible parts of the squares in each stimulus was identical.

For computing the outline of the occluded elements we considered only three sides because, during the perceptual process of figure-background segregation, margins shared by two configurations are perceived as belonging to only one of them, a phenomenon that has been described as “unilateral function of the contour” (Rubin, 1921). The same process occurs during amodal completion, in this case the contour is attributed to the configuration perceived as in front. This

means that in our stimuli the side shared between the bar and any of the elements should be perceived as part of the occluder (the bar itself).

Test 4: Ten different pairs of stimuli were used (Fig. 3.3e). Each pair comprised a stimulus made of two red squares and a second stimulus made of three red squares; one black bar was present in both types of stimuli. As for the previous testing the positions of the single squares could change from stimulus to stimulus. For both stimuli the black bar overlapped the squares so that it occluded a part of them (variable from square to square and from trial to trial). Position, dimension and colour of each square were identical to those used in the Test 3, the only difference being the perimeter control was determined in such way that the total perimeter of the occluded squares (considering 4 sides) of each stimulus was identical.

Test 5: Ten different pairs of stimuli were used (Fig. 3.3f). Each pair comprised a stimulus made of two black squares and a second stimulus made of three black squares. One black bar was present in both types of stimuli. For both the stimuli with two and with three squares the black bar overlapped the squares so that it occluded a part of them (the occluded surface was variable from square to square and from trial to trial, but it was within the same range of visible surface present in the stimuli of Test 3).

The size of the squares prior to occlusion was the same as for those used at training. The size of the bar was computed in such way that the overall outline of the whole shape (squares plus bar) was identical in the two-elements stimuli (where the bar was 4.26 cm long x 1 cm high) and in the three-elements stimuli (where the bar was 4.66 cm long x 1 cm high). Again, the position of each square could change (by about 1 cm horizontally and 0.5 cm vertically) in the different pairs of stimuli.

In these stimuli no objection can be made concerning the identity of that part of the perimeter in which the bar overlaps the squares, as this is simply not physically existent when both squares and bar are of identical colour. In this kind of stimuli, the perceptual rule stated by Petter (1956) holds. The Petter's rule claims that the surface with the shorter contours in the region where the surfaces look

superimposed has a greater probability of appearing in front of the other surface (see also Singh et al., 1999).

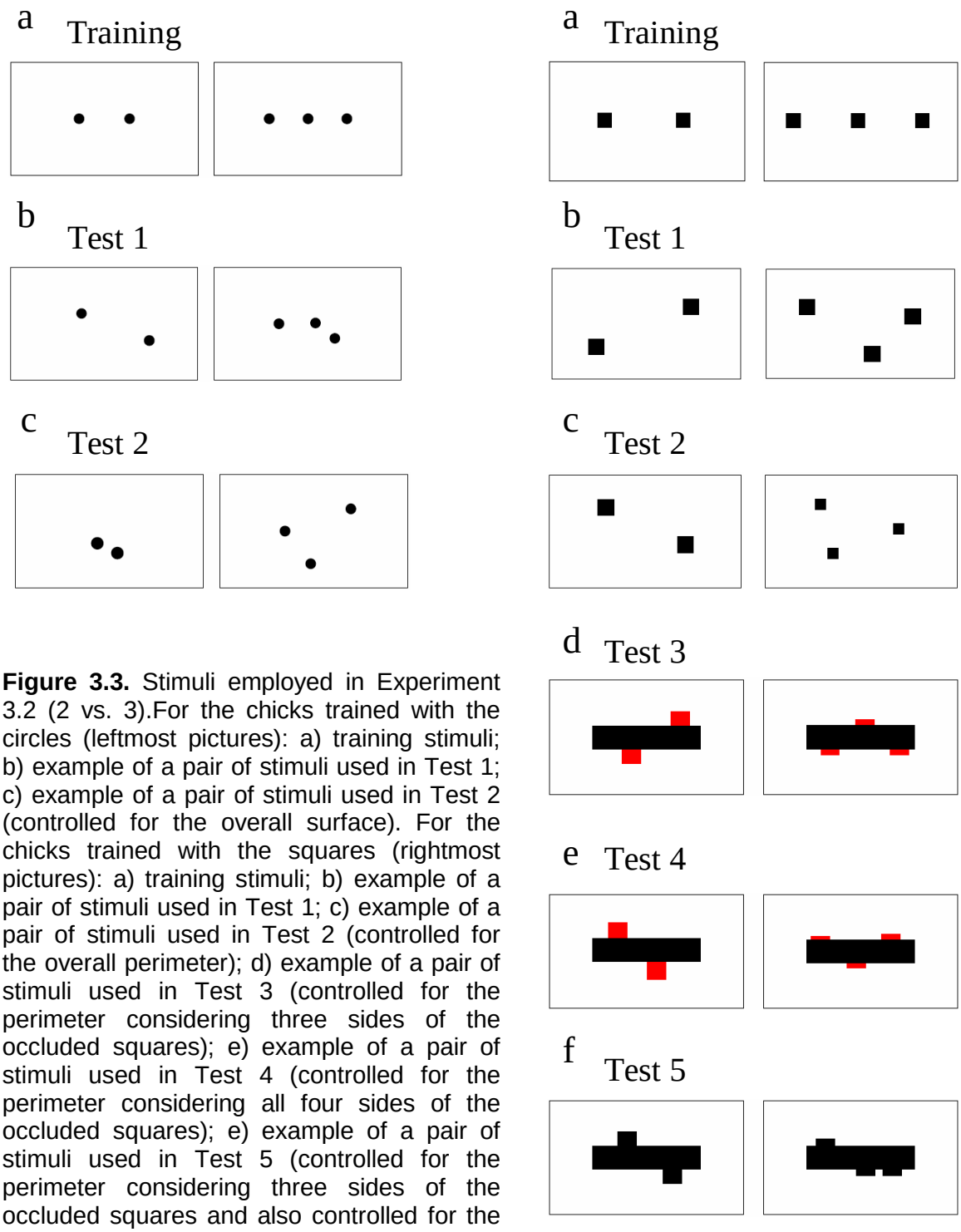

Figure 3.3. Stimuli employed in Experiment 3.2 (2 vs. 3).For the chicks trained with the circles (leftmost pictures): a) training stimuli; b) example of a pair of stimuli used in Test 1; c) example of a pair of stimuli used in Test 2 (controlled for the overall surface). For the chicks trained with the squares (rightmost pictures): a) training stimuli; b) example of a pair of stimuli used in Test 1; c) example of a pair of stimuli used in Test 2 (controlled for the overall perimeter); d) example of a pair of stimuli used in Test 3 (controlled for the perimeter considering three sides of the occluded squares); e) example of a pair of stimuli used in Test 4 (controlled for the perimeter considering all four sides of the occluded squares); e) example of a pair of stimuli used in Test 5 (controlled for the perimeter considering three sides of the occluded squares and also controlled for the overall perimeter of bar plus squares).

3.3.2. Results and Discussion

Data were analysed with a two-sample t-test to compare the means of the two groups and with a one sample t-test to compare the mean with chance level. The independent variable was the number of elements of the positive stimulus: Two for half of the chicks and three for the other half. The dependent variable was the number of correct responses emitted by each chick, computed as the average number of times the chick pecked at the correct stimulus.

Test 1: With the black circles, an unpaired t-test, run on the number of pecks by the two different groups of chicks (trained on two or on three-element stimulus), did not reveal any statistically significant difference between the two groups of chicks ($t(4)=0.315$, $p=0.767$: chicks trained on the two-element stimulus Mean=12.667, SEM=0.333; chicks trained on the three-element stimulus Mean=13.000, SEM=0.999). Data of the two groups were therefore merged together and the resulting mean value was compared with chance level with a one sample t-test (Mean=12.833, SEM=0.477; $t(5)=5.936$, $p=0.002$). The results showed that, following training, chicks could accurately identify the correct number of elements even when the disposition of the circles was randomly determined.

For chicks trained with the filled squares, an unpaired t-test revealed a statistical difference between the two groups of chicks ($t(5)=3.487$, $p=0.018$, chicks trained on the two-element stimulus Mean=13.250, SEM=0.250; chicks trained on the three-element stimulus Mean=14.667, SEM=0.333). It seems that the group of chicks trained on the three-elements performed better. Nevertheless, when considered separately, each group was capable to discriminate between the two stimuli, selectively choosing the correct one above chance (chicks trained on the two-elements: $t(3)=13.000$, $p=0.0059$); chicks trained on the three-elements $t(2)=14.015$, $p< 0.001$).

When data from the two groups were analysed all together with an analysis of variance (ANOVA) considering the stimulus shape (circles vs. squares) as well as the number of elements (two vs. three) as independent variables, the main effect of shape was not significant ($F(1,9)=4.509$, $p=0.063$), nor was the effect of number ($F(1,9)=2.728$, $p=0.133$) or the interaction ($F(1,9)=1.045$, $p=0.333$).

Test 2: With surface controlled stimuli (filled circles), a two-sample t-test did not reveal any statistical difference between the two groups of chicks ($t(4)=2.211$, $p=0.091$, chicks trained on the two-elements Mean=14.333, SEM=0.881; chicks trained on the three-elements Mean=12.000, SEM=0.557). Since there was no difference between the two groups we compared the mean of the whole group with chance level with a one sample t-test (Mean=13.167, SEM=0.703; $t(5)=4.505$, $p=0.006$). Overall, the results showed that chicks could still accurately identify the correct stimulus even when the total area of the stimuli was controlled for.

With perimeter controlled stimuli (filled squares), an unpaired t-test did reveal a statistical difference between the two groups of chicks ($t(5)=2.991$, $p=0.030$). Both groups could identify the correct stimulus above chance even when the total perimeter of each kind of stimulus was controlled, even though the group of chicks trained on the two-elements performed better. Chicks trained on the two-element stimulus (Mean=14.000, SEM=0.408; $t(3)=9.804$; $p=0.002$); chicks trained on the three-element stimulus (Mean=12.333, SEM=0.333; $t(2)=7.001$; $p=0.020$).

Test 3: When the total perimeter of the squares (considering 3 sides) was controlled, an unpaired t-test did not reveal any statistical difference between the two groups of chicks ($t(5)=1.026$, $p=0.352$, chicks trained on the two-element stimulus Mean=13.750, SEM=0.250; chicks trained on the three-element stimulus Mean=13.333, SEM=0.333). Since there was no difference between the two groups we compared the mean of the whole group with chance level with a one sample t-test (Mean=14.000, SEM=0.167; $t(6)=23.676$, $p<0.001$). Overall, chicks could generalise their response to accurately identify the correct stimulus even when the total perimeter (considering 3 sides) of each kind of stimulus was controlled for.

Test 4: For the stimuli with the control of total perimeter of the squares (considering 4 sides) an unpaired t-test did not reveal any statistical difference between the two groups of chicks ($t(5)=0.661$, $p=0.538$, chicks trained on the two-element stimulus Mean=9.750, SEM=0.479; chicks trained on the three-element stimulus Mean=9.333, SEM=0.333). The mean of the whole group was therefore compared with chance level with a one sample t-test (Mean=9.571, SEM=0.297; $t(6)=1.442$, $p=0.199$). The results show that chicks were unable to generalise the

acquired response to discriminate between these stimuli when the total perimeter (considering 4 sides) of each kind of stimulus was controlled.

A reasonable explanation for this difficulty arises from consideration of the amount of overlapping when contour length is equalised for three or four sides. In the former case the percentage of visible stimulus with the three-square stimulus is of 44%, whereas in the latter it is only of 16%. Given that there is evidence in humans that amodal completion is progressively diminished when smaller and smaller portions of the occluded stimulus are visible (Sekuler and Murray, 2001; Shipley and Kellman, 1992) it is perhaps not surprising that a similar outcome is observed in our chicks. To circumvent this problem Test 5 was devised.

Test 5: For the stimuli in which both the squares and the bar were black and for which the overall total external perimeter (squares plus bar) was controlled, an unpaired t-test did not reveal any statistical difference between the two groups of chicks ($t(2)=1.414$, $p=0.293$, chicks trained on the two-element stimulus Mean=12.500, SEM=0.500; chicks trained on the three-element stimulus Mean=13.500, SEM=0.500). Since there was no difference between the two groups, the mean of the whole group was compared to chance level with a one sample t-test (N=4, Mean=13.000, SEM=0.408; $t(3)=7.353$, $p=0.005$). The results show once again (although surprisingly given the difference between these patterns and the original ones used during training) that, with stimuli for which the overall perimeter was controlled, chicks successfully generalised the acquired discrimination (2 vs. 3).

3.4. EXPERIMENT 3.3 : Comparison 4 vs. 5

From the previous experiments it seems that young chicks can discriminate sets of 1 vs. 2 and 2 vs. 3 elements. Experiment 3.3 tested chicks' ability to discriminate 4 vs. 5 elements. If the chicks succeeded discriminating 1 vs. 2 and 2 vs. 3 due to the fact that they utilize a system that deals with small numbers, then we expect chicks to fail in this task since the numerosities of 4 and 5 would be too large for

such system (Hauser and Spelke, 2004). In order to facilitate the learning some of the chicks were trained with stimuli allowing the subjects to rely on some non numerical (i.e., spatial) cues as well as on numerical cues. The remaining chicks could rely on numerical cues alone (training condition which we expected to be a true test of number discrimination abilities, but which of course should also be the most difficult to learn).

3.4.1. Materials and methods

Subjects

Subjects were 11 male Hybro chicks. Of these 6 were trained to choose four elements and the remaining 5 were trained to choose five elements. Rearing conditions were exactly the same as described for the previous experiments.

Procedure

The apparatus and the testing procedure were identical to those described for the previous experiments.

Stimuli were printed on white rectangular plastic paperboards (9.5 cm x 6 cm) placed on top of the food boxes.

Shaping: The stimulus used for the shaping (a clear paperboard) was identical to that previously described.

Training: Some of the chicks (N=6; called “number plus space” group) were trained on stimuli (Fig. 3.4a, left) consisting of sets of either 4 or 5 identical black circles (0.6 cm in diameter) positioned at the vertices of a regular polygon. In the four-element stimulus the circles were spaced 0.4 cm apart and placed on the vertices of a virtual square, whereas in the five elements stimulus the circles were 0.3 cm apart and placed at the vertices of a virtual pentagon. Both virtual polygons (square and pentagon) had been constructed by inscribing them within a 1.5 cm diameter circle.

The remaining chicks (N=5; “number only” group) were trained on stimuli made of sets of either 4 or 5 identical aligned black circles (0.5 cm in diameter), all circles

were placed along a same, horizontal, line placed in the midline of the plastic paperboard support. Each chick was trained on three different pairs of stimuli (Fig. 3.4a, right). This was achieved by presenting the three stimulus pairs in semi-random order throughout the training. Each pair comprised one stimulus with four elements and one stimulus with five elements. In the first pair, the four circles were spaced 0.4 cm apart, whereas the five circles were spaced 0.2 cm so that the total length of the two segments was identical (Fig. 3.4a, right, upper picture). In the second pair all circles were 0.2 cm apart, both in the four and in the five element stimulus, whereas in the third pair they were all 0.4 cm apart from each other (Fig. 3.4a, right, mid and lower picture, respectively).

Chicks underwent a maximum of 20 blocks of 20 training trials. The learning criterion needed in order to be admitted to the test was set at 17 correct out of 20 trials within the same block. Chicks not reaching learning criterion within the 20 blocks were discarded from the study.

Test 1: The same stimuli used for the training were also used for the Test 1 session (Fig. 3.4b).

The “number plus space” group of chicks underwent some further testing:

Test 2: Ten different pairs of stimuli were used (Fig. 3.4c). Each pair comprised either four or five identical black circles (0.6 cm in diameter) the spatial position of which was made to change (i.e., their reciprocal distance ranged from 0.1 cm to 0.75 cm) from trial to trial within the outline of the circle within which the polygon had been inscribed.

Test 3: Each chick was tested with the same two stimuli used at training, but from each stimulus one of the circles had been removed (for each chick one same circle was missing throughout Test 3). Overall four different pairs of stimuli were produced by removing one different circle for each pair (Fig. 3.4d), and each chick was tested with only one of the four pairs.

Test 4: One single pair of stimuli was used for testing all chicks (Fig. 3.4e), this pair comprised a stimulus representing the outline of a square and a second stimulus representing the outline of a pentagon both drawn by connecting together the circles present in the training stimuli with a 0.2 cm thick black line (the circles were removed).

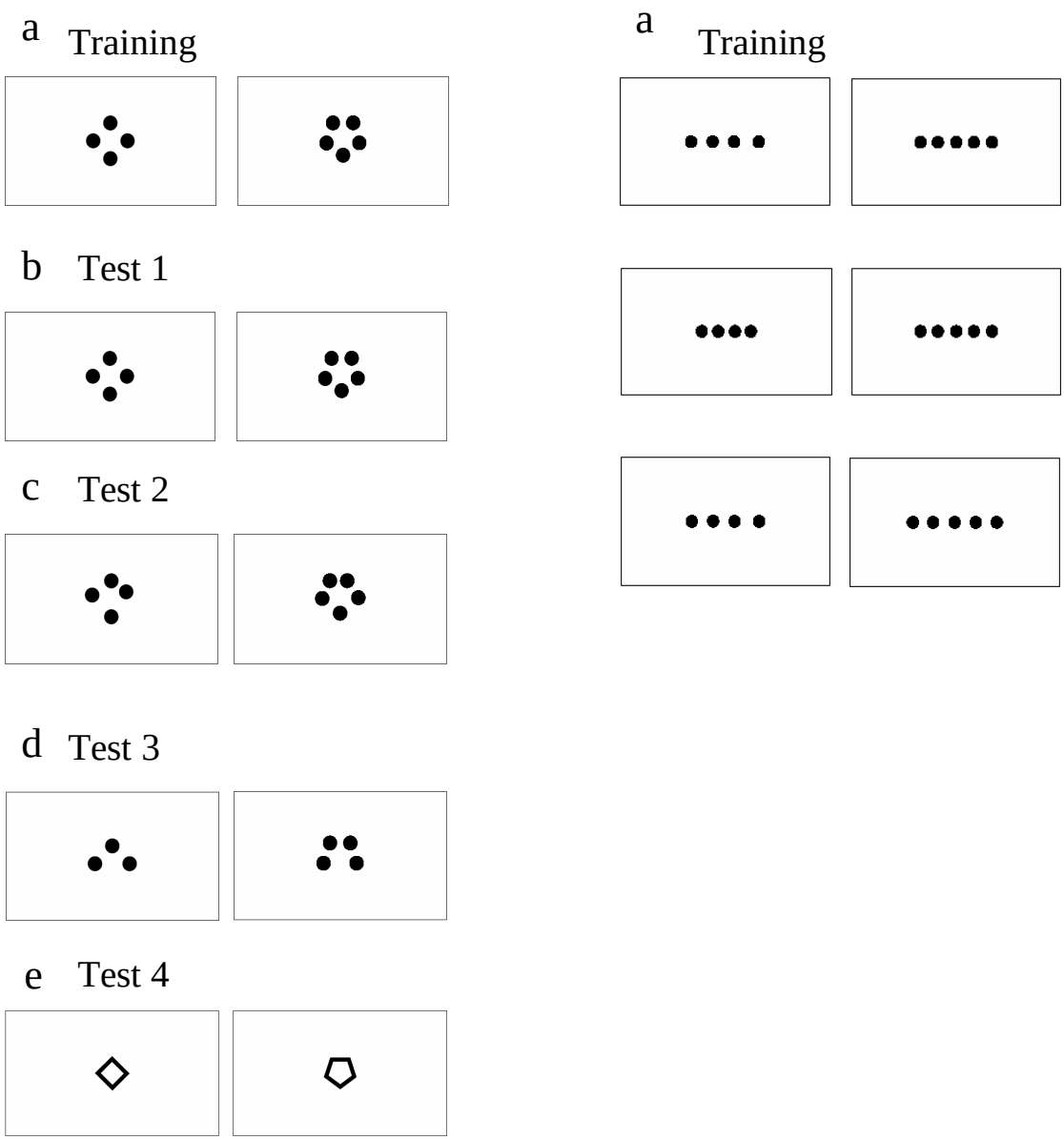

Figure 3.4. Stimuli employed in Experiment 3.4 (4 vs. 5).
For the chicks of the “number plus space” condition (leftmost pictures): a) training stimuli; b) the pair of stimuli used in Test 1; c) example of a pair of stimuli used in Test 2 (the spacings between the circles were changed); d) example of a pair of stimuli used in Test 3 (one circle was removed from each pattern); e) example of a pair of stimuli used in Test 4 (shapes were used instead of sets of circles).
For the chicks of the “number only” condition (rightmost pictures): a) the three types of training stimuli employed (upper: same length; middle: small spacing; lower: large spacing).

3.4.2. Results and Discussion

Data were analysed, separately for each testing session, considering the number of correct trials (i.e, number of trials in which the chick pecked at S+) in the 20 testing trials administered to each chick.

Such data were also separately computed for the group reinforced for pecking at the four-element stimulus vs. the group reinforced for pecking at the five-element stimulus.

Test 1: For the chicks of the “space plus number” group there was no difference (two-sample t-test $t(4)=0.893$, $p=0.422$) between those reinforced for pecking at the four elements (Mean=12.667, SEM=0.667) and those previously reinforced for pecking at five elements (Mean=13.333, SEM=0.333). Data were therefore merged and the resulting mean was compared (using a one-sample t-test) with the score that would be obtained if chicks pecked at both stimuli at random during the 20 testing trials (i.e. 10). Overall, chicks preferentially pecked at S+ (Mean=14.000, SEM=0.447; $t(5)=8.948$, $p<0.001$). Chicks of this group hence showed the ability to discriminate 4 vs. 5 elements and were admitted to subsequent testing sessions.

None of the chicks in the “number only group” reached the training criterion within the 20 blocks of 20 trials each; hence no chick could be admitted to the testing session.

Test 2: There was no difference (two-sample t-test $t(4)=1.678$; $p= 0.164$) between chicks previously reinforced for pecking at four elements (Mean=9.000, SEM=1.999) and those previously reinforced for pecking at five elements (Mean=12.667, SEM=0.882). Data were therefore merged and the resulting mean was compared (using a one-sample t-test) with the score that would be obtained if chicks pecked at both stimuli at random (i.e. 10). Overall, chicks behaved at random with the new configurations in which the distances of the circles constituting the polygons was modified (Mean=10.833, SEM=1.393, $t(5)=0.598$, $p=0.576$).

Test 3: There was no difference (two-sample t-test $t(4)=1.474$, $p=0.214$) between chicks previously reinforced for pecking at four elements (Mean=9.667,

SEM=2.028) and those previously reinforced for pecking at five elements (Mean=13.000, SEM=0.999). Data were therefore merged and the resulting mean was compared (using a one-sample t-test) with chance level (i.e. 10). Overall, chicks behaved at random with new configurations in which one of the circles was removed (Mean=11.333, SEM=1.256, t(5)=1.061, p=0.337).

Test 4: There was no difference (two-sample t-test t(4)=0.555, p=0.609) between chicks previously reinforced for pecking at four elements (Mean=11.667, SEM=2.333) and those previously reinforced for pecking at five elements (Mean=13.000, SEM=0.578). Data were therefore merged and the resulting mean was compared (using a one-sample t-test) with chance level (i.e. 10). Overall, chicks preferentially pecked at S+ during Test 4 (Mean=13.250, SEM=1.116, t(5)=2.913, p=0.033). Chicks therefore seemed to respond on the base of the spatial configuration of the overall array of circles rather than on the base of number, although it is quite unexpected that they showed able to generalise the discrimination from sets of circles to outlines of the corresponding polygons in which no circles could be found.

It seems that with sets of 4 vs. 5 chicks are able to acquire and retain the correct discrimination only if some non numerical (i.e., spatial) cues are also provided, but are nevertheless unable to generalise such discrimination to modified versions of the stimuli, with the exception of Test 4, in which chicks were capable of generalising from patterns of circles to the corresponding shape (square vs. pentagon). Chicks' successful performance in Test 1 and, in particular, in Test 4 sessions could reasonably be attributed to the use of shape cues. Discrimination in Test 2 and 3, on the other hand seemed to depend much less, if at all, from the overall shape of the stimuli (though stimuli in this case also differed for their total surface). When considering together data from these two testing sessions, the overall performance of the two groups of chicks is suggestive of some difference, although not statistically significant (F(1,4)=5.512, p=0.079). Chicks trained on the 4 elements perform worse, and actually their performance does not differ from chance level (Mean=9.333, SEM=1.282; one-sample t-test: t(2)=0.655, p=0.205) while chicks trained on the 5 elements seem to select the correct target, and do so

above chance (Mean=12.833, SEM=0.601; one-sample t-test: t(2)=4.714, p=0.042).

Successful chicks (those trained on the five elements) are indeed choosing on the basis of continuous variables, such as amount of surface, maybe because they benefit from a stronger association between larger amount and positive reinforcement, while the chicks trained on the four elements went through a training to select the less preferred stimulus, i.e., smaller amount (differences in preference for large vs. small amounts and corresponding differences in amount of training required to reach criterion using a larger quantity as S+ as compared to a smaller quantity have been reported in the literature, Koehler, 1941).

3.5. EXPERIMENT 3.4 : Comparison 4 vs. 6

Successful discrimination of 1 vs. 2 and 2 vs. 3 elements, and failure of discrimination of 4 vs. 5 elements, supports the hypothesis that chicks possess a small numerosity representation system. Such system would implicitly encode cardinal properties, up to a limit of about 3-4 elements, by using, presumably, an object file system (Hauser and Carey, 2003). Alternatively, the failure in discrimination of 4 vs. 5 elements could have been due to the disparity ratio becoming too small, rather than to the absolute numerosities exceeding the capacity of the underlying small numerosities representation system. In order to understand whether chick's discrimination was based on the exact number of items in each set or rather on the disparity ratio, in Experiment 3.4 we employed sets of 4 vs. 6 elements. With such sets the ratio is identical to that of stimuli employed in Experiment 3.2 (e.g., 2 vs. 3), but the actual number of elements presents in each set is increased.

Each chick underwent two subsequent training phases: Training 1 and Training 2. In Training 1 sets of aligned elements were employed. In Training 2, the spatial disposition of the elements in each set changed randomly, from trial to trial, within the rectangular paperboard.

3.5.1. Materials and methods

Subjects

Subjects were 8 male Hybro chicks. Of these, 4 were trained to choose four elements and the remaining 4 were trained to choose six elements. Rearing conditions were exactly the same as described for the previous experiments.

Procedure

The apparatus and the testing procedure were identical to those described for the previous experiments.

Stimuli were printed on white rectangular plastic paperboards (9.5 cm x 6 cm) placed on top of the food boxes.

Shaping: The stimulus used for the shaping (a clear paperboard) was identical to that previously described.

Training 1: Stimuli consisted of two identical paperboards over which either 4 or 6 black elements had been printed. The elements were, for both stimuli, black filled circles (0.5 cm in diameter) aligned along the midline of the support. Each chick was trained on two different pairs of stimuli. Each pair comprised one stimulus with four elements and one stimulus with six elements. In the first pair all circles, both in the four and in the six element stimulus, were 0.5 cm apart, whereas in the second pair they were all 1 cm apart from each other.

Training 2: Ten different pairs of stimuli were used. The elements were, for both stimuli in each pair, black filled circles (0.5 cm in diameter) whose spatial position changed from trial to trial within a 7 cm x 4 cm window in the middle of the 9.5 cm x 6.0 cm rectangular paperboard. The distance between the single elements ranged from 0.3 cm to 3.0 cm.

Both Training 1 and Training 2 comprised a maximum of 20 blocks of 20 training trials. The learning criterion needed in order to be admitted to the test was set at 17 correct out of 20 training trials within one same block. With four mistaken trials within a same block a new block of trials was started.

3.5.2. Results and Discussion

None of the chicks that entered this experiment reached the learning criterion within the 20 blocks administered in Training phase 1 and 2, and could not, therefore, be admitted to the test. In the final (i.e. 20th) block, the average percentage of correct responses for Training 1 was (Mean $\pm$ SEM) 54.123 $\pm$ 4.730 for the group of chicks reinforced on 4 elements (range 63.636% to 42.857%), and of 41.268 $\pm$ 5.264 for the group of chicks reinforced on 6 elements (range 55.555% to 33.333%). In Training 2, the average percentage of correct responses in the final block was of 45.907 $\pm$ 9.214 for the group of chicks reinforced on 4 elements (range 63.636% to 20.000%), and 41.665 $\pm$ 8.335 for the group of chicks reinforced on 6 elements (range 55.000% to 33.333%). A reasonable explanation for this difficulty is that, in this experiment and for these particular conditions of training, chicks could not use the object file system which creates a file for each object of the stimulus set. Maybe the set size of the stimuli exceeded the processing limits of such system. Neither could the analogue magnitude system support the task, likely because a 2:3 ratio exceeds the limits (associated with Weber's Law) of the analogue magnitude system. Further experiments with large numerosities and higher ratios (e.g. 1:2 ratio such as in 4 vs. 8 elements) would appear necessary.

3.6. EXPERIMENT 3.5 : Comparison 3 vs. 4

Previous experiments showed that chicks can correctly discriminate between sets of 1 vs. 2 and 2 vs. 3 elements. When required to discriminate 4 vs. 5 elements chicks' performance drop to chance level. In Experiment 3.4 (4 vs. 6), with sets ratio identical to that of sets employed in Experiment 3.2 (2 vs. 3), but with larger number of elements, chicks again could not discriminate between the stimuli. This seems to rule out the possibility that the failure to learn the 4 vs. 5 discrimination was due to the smaller disparity ratio between the stimuli. Maybe an object file

system is engaged in the resolution of this task. The aim of this experiment is to probe the exact limit of this system by using sets of 3 vs. 4 elements.

3.6.1. Materials and methods

Subjects

Subjects were 10 male Hybro chicks. Of these, 5 were trained to choose three elements and the remaining 5 were trained to choose four elements. Rearing conditions were exactly the same as described for the previous experiments.

Procedure

The apparatus and the testing procedure were identical to those described for the previous experiments.

Stimuli were printed on white rectangular plastic paperboards (9.5 cm x 6 cm) placed on top of the food boxes.

Shaping: The stimulus used for the shaping (a clear paperboard) was identical to that previously described.

Training: Stimuli consisted of two identical paperboards over which either 3 or 4 black elements (filled circles, 0.5 cm in diameter) had been printed, aligned along the midline of the support. Three different pairs of stimuli were used. In the first, the circles, both in the three and in the four element stimulus, were spaced 0.4 cm apart. In the second and in the third pairs, the elements in both stimuli were spaced, respectively, 1.2 cm and 1.5 cm apart.

At training, chicks underwent a maximum of 20 blocks of 20 training trials. The learning criterion needed in order to be admitted to the test was set at 17 correct out of 20 trials within one same block. Chicks not reaching learning criterion within the 20 blocks were discarded from the study.

Test 1: Ten different pairs of stimuli were used. Each pair comprised one stimulus with three black circles and one stimulus with four black circles. All elements were identical in colour and dimension to those used for the training but now their spatial position within the rectangular paperboard changed randomly

from trial to trial within a 7 cm x 4 cm window (with a distance between the items ranging from 1 cm a 3.5 cm).

Test 2: In the second test a control for the overall area was performed. Ten pairs of stimuli were used, each pair being made of either three (0.5 cm in diameter) or four (0.43 cm in diameter) black circles. Different sizes were used in order to equate the area of the two stimuli (0.58 cm^2). The perimeter, though, differed by 0.71 cm (it was of 4.71 cm overall for the three elements stimulus, and of 5.42 cm for the four elements stimulus). As in the first experiment, the spatial disposition of the elements of each stimulus on the paperboard changed from trial to trial within a 7 x 4 cm window.

Test 3: Ten pairs of stimuli were used, each pair being made of either three (0.5 cm in diameter) or four (0.375 cm in diameter) black circles. Different sizes were used in order to equate the perimeter of the two stimuli (4.71 cm). The area, though, differed by 0.148 cm^2 (it was of 0.590 cm^2 overall for the three elements stimulus, and 0.442 cm^2 for the four elements stimulus). As in the previous experiments, the spatial disposition of the circles of each stimulus changed from trial to trial within a 7 x 4 cm window.

3.6.2. Results and Discussion

Only a single subject out of the 10 that entered this experiment reached the learning criterion by pecking 19 times the correct stimulus in a block of 20 trials (this occurred in the 19th block of trials). Only this subject underwent the three testing phases but it performed at random in all tests. It scored 10 correct responses out of 20 in Test 1; 9 correct responses in Test 2 and, finally, 10 correct responses in Test 3.

For the remaining 9 chicks in the final (i.e. 20th) block, the average percentage of correct responses was of (Mean $\pm$ SEM) 42.886 $\pm$ 7.023 for the chicks reinforced on 3 elements (range 55.555% to 20.000%), and of 47.860 $\pm$ 8.841 for the reinforced on 4 elements (range 69.231% to 33.333%).

Data from this experiment seem to confirm that the upper limit is around the three vs. two elements discrimination. For the chicks discrimination between sets of three vs. four elements would seem impossible, with these stimuli.

3.7. CONCLUSIONS

The results of Experiment 3.1 and 2 show that young chicks are capable of discriminating sets of 1 vs. 2 and 2 vs. 3 elements. This is not particularly surprising in itself and merely confirms evidence collected in a variety of species (see the Introduction for a list of references concerning this). What is interesting is that although training was done with only one specific set of stimuli, in which number co-varied with several continuous physical variables, such as density of the elements, surface area and contour length, chicks seem to encode number rather than physical variables. When tested with changes in the positions of the elements (Test 1 of experiments 1 and 2) or with equalized overall surface area (Test 2 with circles in Experiment 3.2) and contour length (Experiment 3.2, Test 2 to 5 with squares) of the stimuli to be discriminated, chicks did not go back to random choice, they consistently maintained the discrimination on the basis of number. Considering that during training continuous physical variables co-varied with number as cues for successful visual discrimination, the finding that following equalization of continuous variables chicks use number strongly suggests that number provides a natural and important cue for discrimination in these animals, a cue which is spontaneously encoded even when continuous variables suffice for successful discrimination (see also Cantlon and Brannon, 2007).

The chicks' successful discrimination of 1 vs. 2 and 2 vs. 3 items could have been based on the relative numerosity differences in these stimuli (rather than on the cardinal or exact number of items in each set). Conversely, their failure to discriminate 4 vs. 5 items (Experiment 3.3) could have been due to the disparity ratio becoming too small, rather than to the absolute numerosities exceeding the capacity of the underlying processing system. In order to counter the latter possibility, we performed an additional experiment in which the stimuli were paired in the ratios that the chicks could discriminate with small numerosities (e.g. 2 vs. 3), but with set-sizes that exceed 3, and therefore the set-size limit of the small numerosity representation system, i.e. stimuli consisting of 4 vs. 6 elements (Experiment 3.4). Results showed that chicks were unable to discriminate in this

case. Further research with larger ratio (e.g., 1:2) will be necessary to explore the exact limits of the large numerosities representation system of young chicks.

We also provided the first evidence of numerical discrimination of partly occluded objects. Chicks maintained the discrimination when the overall area of the visible parts of the stimuli were equalized (Experiment 3.1, Test 2) and also when contour length (on three boundaries) was equalized. Chance-level choice when contour length was equalized on four boundaries was likely to be due to the small visible area that remained available in this condition. This hypothesis is sustained by two sources of evidence. First, when contour length was equalized in non-occluded squares (Experiment 3.2, Test 2 with squares) chicks discriminated on the basis of the number. Second, when tested with chromatically-homogeneous stimuli which were equalized for contour length (Experiment 3.2, Test 5) chicks did choose correctly on the basis of number. These findings provides further support to the evidence that non-human species can complete partly occluded objects (reviews in Vallortigara, 2004, 2006).

The results of the Experiment 3.3, Experiment 3.4 and Experiment 3.5 suggest, however, that the ability of chicks to use numerical representations to discriminate between the two sets of stimuli undergoes an abrupt breakdown when facing a discrimination between 4 vs. 5, 4 vs. 6 and 3 vs. 4 or elements. This is consistent with the overall evidence available for human infants (Feigenson et al., 2004); whereas non-human primates demonstrated a slightly higher capacity with a set-size limit for discrimination of small numerosities at around 4 rather than at around 3 elements. It could be that this difference is related to age. Further research with adult birds would be needed to confirm this hypothesis.

Interestingly, the capacity to discriminate between the two sets of stimuli was not completely abolished in the condition number plus space. Chicks retained a discriminative ability using, however, the perceptual characteristics of the two stimuli: shape and surface. When shape was a viable cue, all chicks successfully generalised the acquired discrimination to the novel stimuli. In the case of surface there was a peculiar limitation: discrimination was successful when chicks were trained with the five-elements set as positive, but not when trained with the four-elements set as positive. The most reasonable explanation for this finding is that

discrimination based on total extent is biased to a preference for the large amount, so that choice for the discriminative stimulus is directly linked to the amount of reward and chicks found more natural to peck at the discriminative stimulus with the larger extent in order to obtain more reward than vice versa. Similar effects have been reported previously in the literature (Koehler, 1941).

In conclusion, our results show that young chicks spontaneously encode numerical representations of small numerosities up to a set size limit of about 3 elements, whereas they turn to use of perceptual (non-numerical) cues when faced with larger numerosities. It remains to be established whether with large discrimination ratios (e.g. 1:2) young chicks would be also capable of showing another form of numerical representation, that of large approximate numerosities which has been documented in human infants and non-human primates (Feigenson et al., 2004; Hauser and Spelke, 2004).

4. UNDERSTANDING ORDINALITY

Numerical competencies were investigated for the first time in very young nonhuman animals. Chicks learned to identify the 3rd, 4th or 6th in a series of 10 identical positions (Experiment 4.1). Use of spatial information (i.e., distances) was ruled out in Experiment 4.2 (chicks generalised the reinforced response to an array of stimuli rotated by 90° as compared to training) and Experiment 4.3 (chicks generalised their response to a series where distances between the single positions had been manipulated). Chicks found the correct position even when both identity and distance of each position changed from trial to trial (Experiment 4.3). Overall, young chicks seemed to use ordinality when required to identify a target by its numerical serial position.

4.1. INTRODUCTION

In the last decade there has been an increasing interest in the study of numerical competencies in nonverbal creatures – namely pre-verbal infants and non-human species - in the attempt to better understand the role of language in such processes (reviews in Gallistel and Gelman, 1992; Dehaene, 1997; Hauser and Spelke, in press). The use of behavioural tests suitable to nonverbal subjects provides a unique opportunity to compare numerical abilities among species and to investigate their development and evolutionary origin. Unfortunately, though, apart from our own species, research concentrated on adult animals, therefore neglecting the important issues related to the ontogenesis of such processes.

Discrimination of relative numerosities (protonumerosity; Davis and Pérusse, 1988) requires the ability to make judgements of size differences between two sets, i.e. “more than…”, “less than…”. Protonumerosity is considered as a first and elementary level of numerical knowledge, and is often found in ecological situations whenever an animal chooses the larger/smaller between two alternative sets of items. Such an ability would be the basis for efficient foraging strategies (Krebs, 1974). Several species spontaneously prefer the larger amount of food, for example, salamanders (*Plethodon cinereus*, Uller et al., 2003) and human infants (Wynn, 1992; Feigenson et al., 2002) always chose the set that maximised their net energy gain when required to choose between 1 vs. 2, 2 vs. 3. This did not happen with 3 vs. 4, which seems to constitute a limit for discrimination of contiguous numerosities at least for salamanders and for 10-month old infants.

Even neonates stare longer at the array representing a novel number of dots than at a familiar one (Antell and Keating, 1983). However, changes in number correlate with changes in other continuous variables such as brightness, contour length, filled area, dimension or volume and when such variables were experimentally controlled, neonates failed to discriminate between sets of one, two or three elements (Clearfield and Mix, 1999; Feigenson et al., 2002). The performance of rhesus monkeys in ordinal comparison tasks, though, is not improved nor impaired when monkeys were tested with stimuli that were heterogeneous in colour, size or shape (Calton and Brannon, 2006).

From the experimental evidence available, it seems that at least some animal species as well as preverbal infants do discriminate between small numerosities. Better evidence for cardinal representations comes from studies in which animals (i.e., chimpanzees and pigeons) were trained to associate symbols or numerals with different absolute numbers of things (Matsuzawa, 2003; Boysen, et al., 2001; Xia et al., 2001). Overall, these results indicate the presence of a representation of cardinality (the ability to represent the number of discrete entities in a set).

Another central property of number is ordinality: the ability to identify an object on the base of its position in a series of identical objects. Eleven month-old infants are sensitive to the ordinal relations between numerical values (Brannon, 2002). Infants were first habituated to sequences of dot arrays that increased or decreased in numerical magnitude (e.g., 16-8-4, or 4-8-16). Infants were then tested with new numerical values that increased and decreased in value in alternation. Infants looked longer at the reversed ordinal direction. Younger infants (i.e., nine-month-olds) failed in the same test (Brannon, 2002).

Ordinality has been also extensively investigated in non-human species. Rhesus monkeys (Brannon and Terrace, 1998; 2000), socially housed hamadryas baboons, socially housed squirrel monkeys (Smith et al., 2003) and brown capuchin monkeys (Judge et al., 2005), trained to discriminate between numbers from one to four, in ascending order, could then generalise this discrimination to numbers from five to nine. Monkeys trained to respond (in ascending or descending order) to pairs of numerosities (1-9) spontaneously ordered in the same direction new pairs of larger values (i.e., 10, 15, 20, 30) (Calton and Brannon, 2006). Rhesus macaques when trained to order values (6-5-4) in descending order, were able to apply the descending rule to novel values (1-2-3) (Brannon and Cantlon, 2006). Squirrel monkeys learned ordinal relationships between six arabic number symbols: they chose the larger number when given a choice between combinations of any two of the learned symbols, and even when a known symbol is confronted with a novel one. They also preferred the stimulus containing the largest sum when choosing between sets of 2 vs. 2, 1 vs. 2 and 3 vs. 3 symbols (Olthof et al., 1997). Chimpanzees could select the larger of two

sequentially presented quantities even when the stimuli were never viewed in their totality (Beran, 2001).

Rats (Davis and Bradford, 1986; Suzuki and Kobayashi, 2000) and pigeons (Emmerton et al., 1997) also seem to possess some numerical ordering abilities. In particular, at the base of the work described in the present paper is the original study by Davis and Bradford (1986). The authors first demonstrated that rats are capable of learning to select and enter a target tunnel determined solely on the basis of its ordinal position in an array of six. The performance was learned relatively rapidly by rats and was maintained after alteration in size and shape of the array of tunnels. Moreover, rats retained the correct numerical discrimination throughout a 12-month period.

One study has focussed on a quite different animal species. Honey bees (*Apis mellifera*) were trained to find food in a specific position along a series of four identical, equally spaced landmarks: the food was placed between the third and the fourth landmark. At test, the number of landmarks was altered and even though many bees continued to search for food at the correct distance, other bees did rely on the number and position of landmarks. When encountering fewer landmarks, they flew further; when they encountered more landmarks, they landed at a shorter distance (Chittka and Geiger, 1995). It is reasonable to assume that spatial navigation and learning benefits from the understanding of numerical ordering.

Anecdotal data have been reported concerning adult chickens' sensitivity to ordinality: hens could learn to peck selectively at every other grain (or at every other two grains) in a series of aligned grains (see the description of the original experiments run by Geza Révész reported in Katz, 1937). Young chicks were, moreover, capable of learning to identify the central element in a series of 9 identical ones (Regolin, 2006). Nobody has checked, though, if this is also possible for the other positions in the line, as the central object may benefit from being perceptually more salient due to perceptual symmetry.

We investigated if young chicks could learn to identify and peck for food reinforcement at a certain position in a series of identical positions.

4.2. EXPERIMENT 4.1

Chicks' ability to identify a certain target-location on the basis of its position in a series of identical possible locations was assessed by training and subsequently testing the birds to peck either at the 3rd, the 4th or the 6th position in a series of ten identical ones.

4.2.1. Materials and methods

Subjects and rearing conditions

Sixty-two male domestic chicks (*Gallus gallus*) were used. The animals were obtained weekly (every Monday morning) from a local commercial hatchery (Agricola Berica, Montegalda, Vicenza - Italy) when they were only a few hours old. On arrival, chicks were caged in groups of two per cage, in standard metal home cages (28 x 32cm, 40 cm high) at controlled temperature (28°-31°C) and humidity (68%). Food and water were available *ad libitum* in transparent glass jars (5 cm in diameter, 5 cm high) placed at each corner of the home cage. The cages were constantly (24h/day) lit by fluorescent lamps (36 W), placed 15 cm above each cage.

Chicks were reared in these conditions from Monday morning (11.00 am) to Wednesday afternoon (5.00 pm), when they were isolated one per cage. On Thursday (10.00 am) the food jars were removed from the home cage (water was left available) and after a few hours (3.00 pm) chicks underwent training. At the end of training each chick was caged overnight with food and water available *ad libitum*. On Friday, in the early morning (7.00 am) chicks were food deprived and then re-trained (8.00 am). Testing took place for each chick one hour after the end of the re-training.

Immediately after the end of the behavioural observations all chicks were caged in social groups of five to seven birds, with food and water available *ad libitum*, and a

few hours later all chicks (i.e. those used in this as well as in all other experiments in this research) were donated to local farmers.

Apparatus

Training, re-training and testing took place in a separate room (experimental room) located near to the rearing room. In the experimental room temperature (25°C) and humidity (70%) were controlled, the room was lit by four 58 W lamps (placed on the ceiling, 248 cm above the experimental apparatus).

The apparatus (Fig. 4.1a) consisted in a square-shaped arena (76 x 76 cm, x 45 cm high) made of uniformly white-painted wood panels. Along the midline of the floor of the arena, were ten identical holes (2.5 cm in diameter), perfectly aligned and spaced 1 cm from one another. The overall length of the array of holes was 34 cm. The distance of the first hole in the line from the closest wall of the apparatus (i.e. from the chick's starting point) was 22.5 cm. The distance of the last hole (i.e. the 10th) from the end wall of the apparatus was 19.5 cm. The side distance, i.e. from any hole and the left or right wall of the apparatus was of 36.25 cm.

All of the holes could be blocked from underneath by a white wooden sliding bar (115 x 4.5 cm, 3 cm thick), positioned just underneath the floor of the apparatus and manoeuvred by the experimenter. On the surface of this bar, at a precise point, a small elongated niche (0.8 x 2 cm, x 2 cm deep) had been made. The niche contained some chick crumbs to be used as food-reinforcement during the experimental procedures. Normally, all holes were blocked by the sliding bar and looked identical to each other; however, by properly sliding the bar, the niche could be made to coincide with one hole (the reinforced one) so as to allow the animal access to the food.

The apparatus was thoroughly cleaned and randomly rotated from trial to trial in the experimental room.

There were three separate experimental groups. Each group was reinforced on a different ordinal position: the third (N=20 chicks), the fourth (N=20 chicks) or the sixth (N=22 chicks) in the series of 10 positions.

Procedure

Training. On Thursday, Day 4 of life, each chick underwent a training phase. The chick was placed in the apparatus, in the starting position (Fig. 4.1a), between the wall of the apparatus (within 5 cm from it) and the first hole in the series. For a couple of minutes the chick was free to move around and get acquainted with the novel environment. Then it underwent a shaping procedure: the to-be-reinforced hole was unblocked and some chick crumbs could be found in close proximity to the hole and inside it, in the niche below. Thereafter, chicks could only find the food in the hole itself, and gradually the sliding bar was operated in order to progressively prevent access to the niche. Chicks' pecking responses to the correct hole were reinforced by sliding the bar and allowing the animal access the food. Eventually the hole was completely blocked before each trial and any leftover visible crumbs were removed; chicks learned to peck directly on top of the correct position in order to have this position unblocked so that it could access the food.

The main training phase was then started. Twenty trials were administered to each chick, and, in each trial, the chick was placed in the starting position and then left free to walk towards and peck at any hole in the line. Only pecks at the correct position were reinforced by opening the corresponding hole and allowing the chick to eat some crumbs; after each trial the chick was placed again at the starting position. Chicks were allowed only one peck on each trial with the trial terminating after 180 sec with no peck (during training chicks were rather slow in responding, especially in the very first trials, whereas during re-training and testing the time-limit was set at 60 sec). A trial was considered correct whenever the chick walked directly to the correct position and pecked at it. All chicks pecked at least five times at the correct hole within the twenty training trials.

Re-training. On the morning of Day 5 (Friday) chicks underwent re-training to ascertain whether they had actually learned to peck at the correct position during the training of the previous day. Re-training lasted 5-10 min, including two minutes of familiarisation with the apparatus. All of the chicks trained on the previous day also reached the re-training criterion (7 correct responses in 10

consecutive trials). At the end of the re-training each chick was placed back in its home-cage until the test.

Test. One hour after the re-training each chick was placed in the apparatus, in the starting position, and underwent the test. The test, differently from the re-training, involved no familiarization phase, and a larger set of trials, in fact each chick was administered 20 consecutive testing trials. In each trial the chick was free to walk to and peck at any of the ten positions in the series. In each trial each chick was allowed to peck once only, so, after the first peck, no matter onto which position, that trial was considered over. Only correct responses (pecks at the position reinforced at training) were reinforced with some food. If no response occurred within the time-limit of 60 sec, the trial was considered as null (this never occurred in Experiment 4.1). At the end of each trial the chick was gently pushed back to the starting position by a cardboard partition. After about two seconds the cardboard partition was lifted and the chick was allowed a new trial.

For this as well as for all experiments in this research all test trials were scored by direct observation and were also video-recorded by an overhead digital video camera. Video-recordings were later scored by a second (blind) observer. One hundred per cent agreement between the two scorings was always reached.

4.2.2. Results and Discussion

Test results of the first experiment are represented in Fig. 4.1b. Pecks emitted by each chick to any of the 10 positions in the series were computed as percentages ([number of pecks to a given hole/20] x 100) and averaged separately for the three experimental groups.

In all cases chicks chose the correct hole well above chance (i.e. 10%): chicks trained on the 3rd position: $t(19)=2.972$, $p=0.008$; on the 4th position: $t(19)=23.619$, $p<0.001$; on the 6th position: $t(21)=13.757$, $p<0.001$.

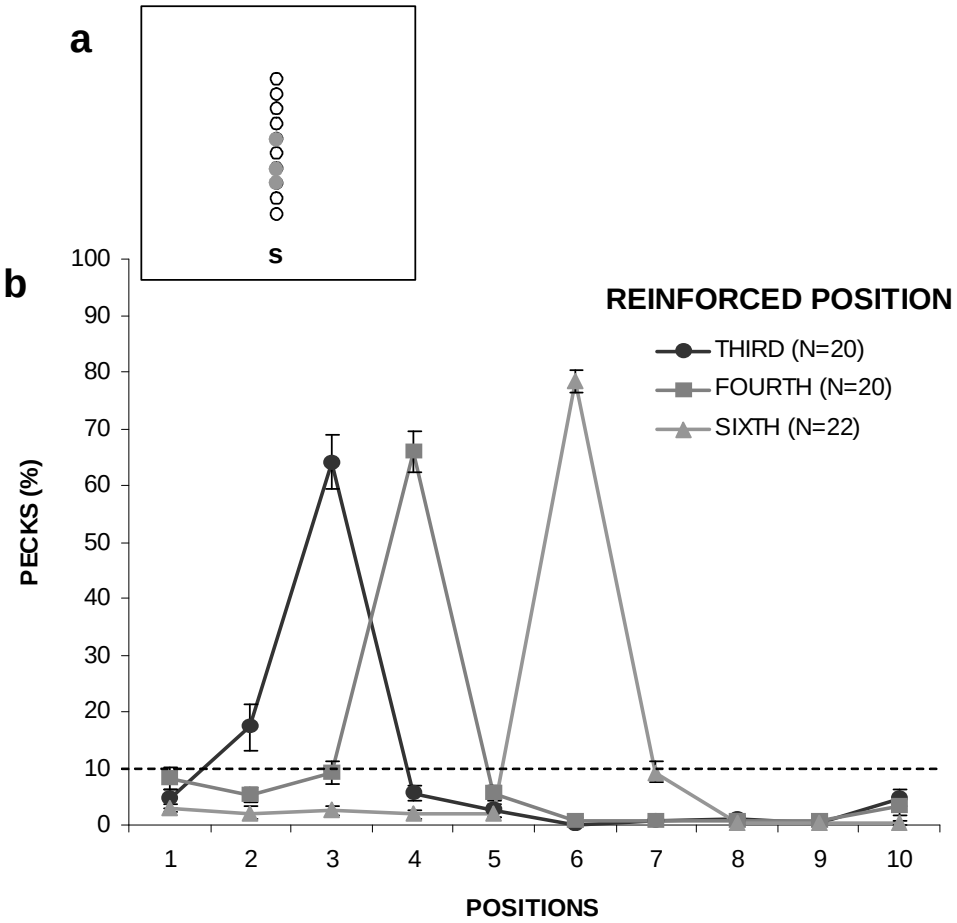

Figure 4.1. **a)** Schematic representation of the apparatus used for the training and for the test in Experiment 4.1 (S=chick's starting position, full circles indicate the positions reinforced in the three experimental conditions).
b) Results of Experiment 4.1: Mean values (± SEM) are shown of the pecks assigned on each position in the series, separately for the three experimental conditions. The dotted line (y=10) represents chance level.

As can be seen from Fig. 4.1b, chicks clearly discriminated the correct ordinal position, while all other positions were chosen at, or even below, chance level. Even the two positions immediately adjacent to the correct one (i.e. the previous and the next in the series) were pecked at chance level (including the pecks assigned at the second position in the group of chicks reinforced on the 3rd position ($t(19)=1.7631$, $p=0.094$).

As differential reinforcement was provided over test trials, we checked if chicks' performance remained stable by running, for the correct responses scored in each of the three reinforced positions, a repeated measures ANOVA over 4 blocks of 5 trials each (trials 1-5; 6-10; 11-15 and 16-20). In general, chicks' performance got

better and better during the 4 blocks of trials, although the effect of blocks was not significant in the case of chicks trained on the 4th position (for the chicks trained on the 3rd position: $F(3,19)=6.183$, $p=0.001$; on the 4th position: $F(3,19)=2.414$, $p=0.0759$; on the 6th position: $F(3,21)=5.118$, $p=0.003$). So, understandably, it seems that chicks are learning over test trials, due to differential reinforcement. Nevertheless, in all cases, their performance was already above chance level in the first block of 5 trials: for the chicks trained on the 3rd position Mean=2.350, SEM=0.357; $t(19)=5.1821$, $p<0.001$; for the chicks trained on the 4th position Mean=2.800, SEM=0.247; $t(19)=9.312$, $p<0.001$; for the chicks trained on the 6th position Mean=3.545, SEM=0.261; $t(21)=11.667$, $p<0.001$.

The raw number of pecks directed at each hole by chicks of the three experimental groups was analysed through analysis of variance with the reinforced position (either third, fourth or sixth) as the between subjects factor, and the ordinal position in the series (from first to tenth) as the repeated measures factor. The ANOVA revealed a significant effect both for the position pecked in the series ($F(9,59)=118.658$, $p=0.0001$) and for the interaction of the reinforced position x position in the series ($F(18,59)=171.491$, $p=0.0001$). This means that in all conditions chicks pecked much more only at one position: that reinforced at training. The interaction could be explained by the difference in the pecks assigned to the two positions adjacent to the correct one in the three experimental groups. In fact, when limiting the analysis to the pecks assigned at the positions adjacent to the correct ones, an effect of the interaction between the experimental group and pecks at the two adjacent positions in the sequence (previous vs. next) is found ($F(2,59)=7.283$, $p=0.002$; Fig. 4.2); but there is no main effect of the experimental group ($F(2,59)=2.391$, $p=0.100$) nor of the pecks at adjacent positions ($F(1,59)=0.853$, $p=0.359$). Chicks behaved similarly when reinforced on the 3rd or on the 4th positions: in both cases they pecked at chance level the previous side position (i.e. the 2nd position is pecked at chance level in the group reinforced on the 3rd position, while chicks reinforced on the 4th position pecked the 3rd position at chance level). However both groups pecked significantly below chance level at the other adjacent position, i.e., the 4th position for the group reinforced on the 3rd ($t(19)=3.454$, $p=0.003$), and the 5th position for the group

reinforced on the 4th (t(19)=3.708, p=0.002). The group of chicks trained to peck at the 6th position behaved differently, pecking the position after (7th) the correct one at chance, and pecking below chance level at the previous (5th) position (t(21)=13.218, p<0.001).

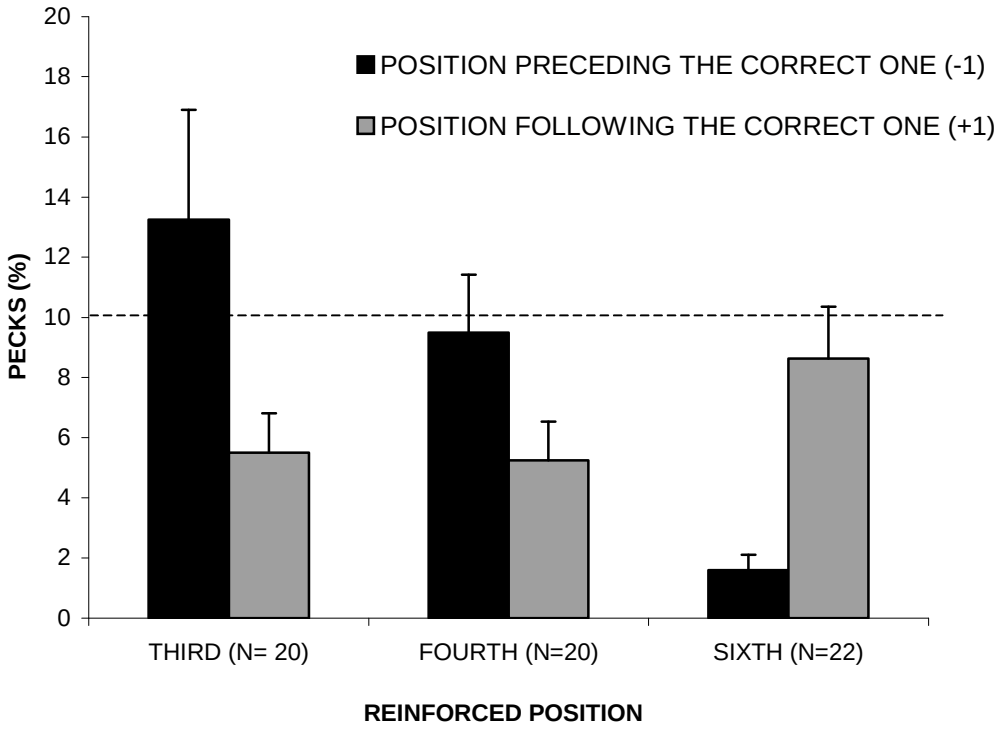

Figure 4.2. The interaction between reinforced position and pecks assigned at the two positions adjacent to the correct one is represented. Percentages of pecks (Means ± SEM) are represented separately for the three experimental groups. The dotted line (y=10) represents chance level.

A possible explanation for this effect could be that chicks identify the correct position on the basis of the closest end of the sequence (i.e. somewhat similarly to the *working-up strategy* described by Suzuki and Kobayashi, 2000). This means that they would start from the first hole in order to identify the third and the fourth (hence making mistakes more often on the previous position to the correct one rather than on the subsequent one), whereas chicks seem to start from the last, i.e. the 10th position in order to identify the 6th position (i.e. see the *working-down strategy* described by Davis and Bradford, 1986). Hence the 6th hole would be perceived as closer to the final end of the sequence (although its actual position is

rather central). If this is true it could be that chicks in this test were able to identify up to the 5th position in a series of ten. The 6th would actually be the 5th one when starting from the end of the sequence of ten positions.

The results of Experiment 4.1 showed that, following training, chicks could accurately identify a given position in a sequence of identical ones, and precisely identified such positions up to at least five in a series of ten. Nevertheless, chicks in this experiment could have relied on information other than numerical (ordinal), as they could have used the relational spatial (metric) information provided by the experimental apparatus (Chiandetti et al, 2007) or simply computed the absolute distance or the walking time of the correct position from the starting point (or from the beginning of the sequence).

In order to check for these possible alternative explanations we ran a series of control experiments on new groups of chicks of the same age. In Experiment 4.2 and 3 the role of geometric information and of distance were excluded as chicks were required to find the correct position in a sequence rotated by 90° as compared to the one used for the training, or in a new testing sequence where spacing between the single positions was manipulated. In Experiment 4.4 an even stricter control was performed as the identity and the relative positions of each single element in the sequence were changed from trial to trial.

4.3. EXPERIMENT 4.2

Naive chicks were trained in the apparatus described in Experiment 4.1, and then required to respond in a different apparatus, where the correct position had to be identified within a series identical to the one used at training, but rotated by 90°. The new series was horizontally positioned in front of the chick's starting point, hence the correct position could not be located on the basis of absolute distances from the starting point.

4.3.1. Materials and methods

Subjects and rearing conditions

The subjects were a new group of 21 male Hybro domestic chicks. Chicks were reared in the same standard conditions described for Experiment 4.1, from Day 1 to Day 5 of life (day of testing).

Apparatus

The apparatus used for pre-training, training and for the first test was the one described for Experiment 4.1. For the generalization test a new apparatus was used (Fig 4.3a). It was the same size as the previous one, but on its floor a line of 10 holes (all identical to those described for the standard apparatus) was made along one side (about 14 cm from it). Thus the new series was rotated by 90° as compared to the training one, and placed horizontally with respect to the chick's starting point (at about 60 cm from it). In this way the animal, once it had learned to recognize a reinforced ordinal position (i.e. the 4th position) in the standard apparatus, was then required to identify it in this novel apparatus, where no objective end of the series closer to the subject could be recognised, and a given hole could be identified both starting from the left or from the right end, providing in the two cases a markedly different behavioural response.

Procedure

All chicks were reinforced for pecking at the 4th hole with a procedure identical to that described for the first experiment. Thereafter each chick took part in a first test (on Day 5), identical to the one of the first experiment, and then (1 hour later) it underwent a generalization test in the new apparatus. For this test each chick was placed in the usual starting point within the arena in front of the horizontal line of blocked holes. As soon as any pecking response was performed, the chick was gently pushed back to the starting position. Only correct responses (i.e. approaching and pecking at the 4th hole either from the left or from the right end of the sequence) were reinforced. Each chick underwent a series of 20 consecutive trials. If no response was assigned by the chick within the time-limit of 60 sec, the

trial was considered as null (this occurred for some of the trials in a minority of the chicks of Experiment 4.2).

4.3.2. Results and Discussion

Test in the training apparatus

An Anova run on the pecks scored in the first test, in the training apparatus, revealed a significant effect of the position in the series ($F(9,21)=35.353$, $p=0.0001$). At test, chicks pecked significantly above chance (i.e., 10%) selectively at the 4th position (Means$\pm$SEM: 50.714 ± 5.190, $t(20)=7.845$, $p<0.0001$), whereas all other positions were pecked either at or below chance level. Overall, chicks' behaviour in this test was not different from that of the chicks trained to peck at the 4th position in Experiment 4.1 ($F(1,41)=0.951$, $p=0.335$, n.s.).

Generalization test in the new apparatus

An Anova was run on the average percentage of pecks assigned at each of the ten positions in the horizontal series, considered as a repeated measures factor (4.3b). A significant effect of the position in the series was found ($F(9,20)=12.476$, $p=0.0001$), indicating a heterogeneous distribution of pecking. Only the 4th position from the left was pecked much more than all of the others and in particular, this position was the only one pecked significantly above chance level, i.e. 10% (Mean=29.438, SEM=3.790; $t(20)=5.129$, $p<0.0001$). All other positions were pecked rather heterogeneously, but in all cases either at or below chance level (the third position being chosen more than the others, although not significantly above chance level, Mean=16.817, SEM=3.640; $t(20)=1.873$, $p=0.076$).

Throughout the test trials chicks' performance remained stable: when a repeated measures Anova was run comparing pecks to the 4th position in the 4 blocks of 5 trials each (trials 1-5; 6-10; 11-15 and 16-20) there was no significant difference across blocks ($F(3,20)=0.288$, $p=0.8338$). Chicks' performance was above chance already in the first block of trials (Mean=30.714, SEM=5.461; $t(32)=3.7931$, $p=0.0006$). As in this experiment some chicks scored null trials percentages had to

be used rather than raw data in order to compare chicks' performance with chance level (10%).

In conclusion, from Experiment 4.2 chicks seem able to generalise the learned response to a new sequence where the target must be identified on the basis of its position in the series without relying on the absolute distance from the starting point or on geometrical information.

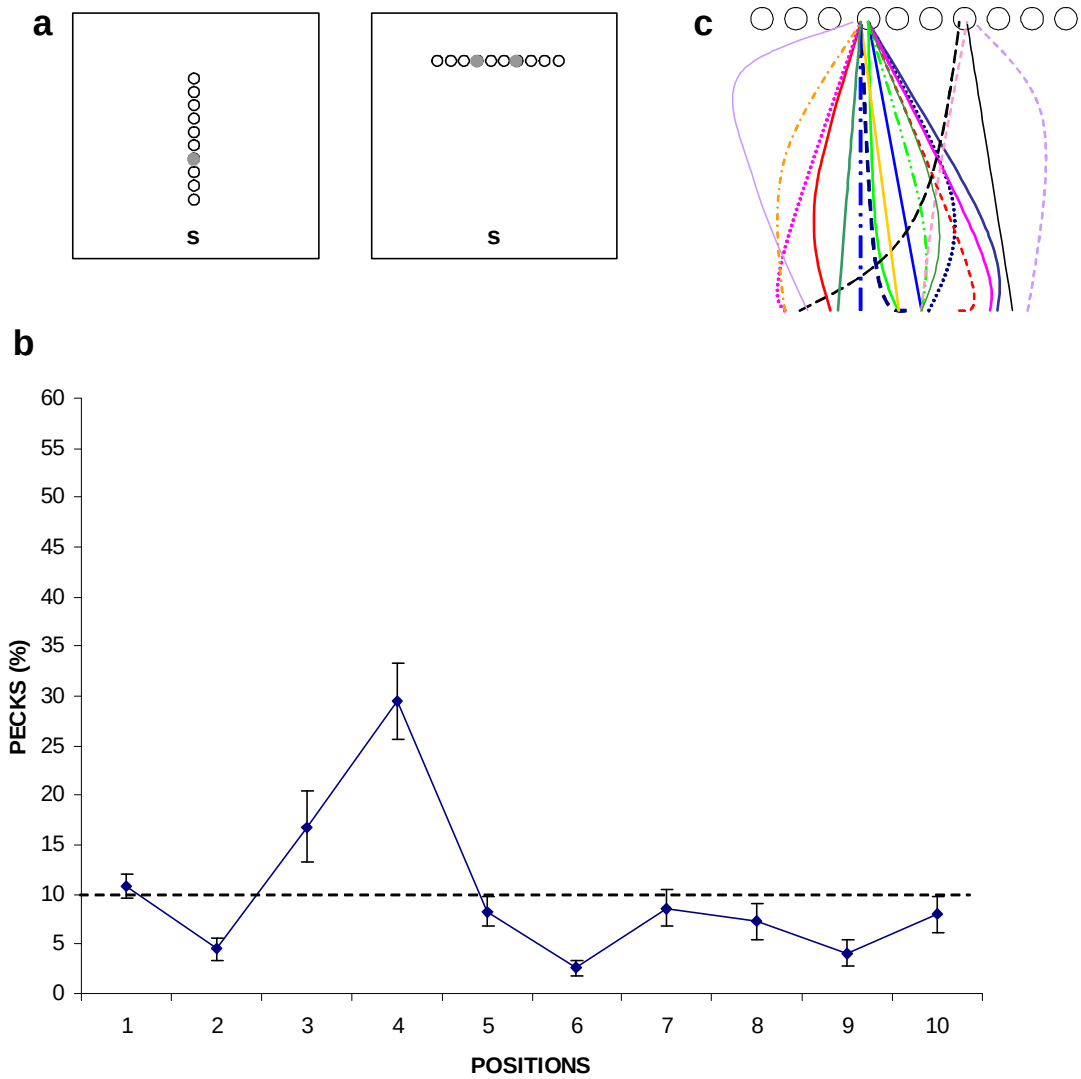

Figure 4.3. **a)** Schematic representation of the apparatus used for the training (leftmost figure, the full circle indicates the reinforced position) and for the generalization test (centre, the full circles indicate the two possible correct positions for the chick) in Experiment 4.2 (S=chick's starting position). On the right are represented the average correct trajectories followed by each chick during the test.
b) Results of Experiment 4.2: Mean values (± SEM) are shown of the pecks assigned on each position in the series used for the generalization. The dotted line (y=10) represents chance level.

A very interesting finding, however, is that chicks identified as correct only the 4th position from the left end, and not the 4th from the right end (i.e. the 7th in Fig. 4.3b) which was chosen at chance level. A preference for targets located in the left hemispace has been recently reported for two avian species, domestic chicks and pigeons, in a spontaneous food-sampling task and in a task requiring chicks to peck at the central position in a series of items (Diekamp et al., 2005; Regolin, 2006), and has been ascribed to a bias in the allocation of attention, somewhat similar to that shown by humans and dubbed as "pseudoneglect" (Jewell and McCourt, 2000; Albert, 1973).

In order to better understand chicks' behaviour in this task, from the videorecordings of the test, the trajectories of each chick when emitting a correct response (on the 4th position either from the left or from the right end) were tracked and averaged for each chick (see Fig. 4.3c). In particular, we wanted to see if chicks walked first from the starting point to the beginning of the line and then walked along it until they reached the correct position, or if, rather, they walked straight from the starting point towards the correct position. (The hypothesis of a bias in chicks' responses due to a lateral - leftward - bias in the allocation of attention would be better supported in this second instance.) By analysing the trajectories it was clear that all chicks (except, possibly, one) walked almost directly towards the correct position. Moreover, very few animals (4 out of 16: X^2 (1)=7.200, p=0.007) consistently chose the 4th position from the right end; all others went to the 4th position from the left.

4.4. EXPERIMENT 4.3

A new group of birds was trained to peck at the fourth position with the same procedure already described for Experiment 4.1, and was then required, at test, to generalise the learned response to a new sequence in which the distance from the starting point of each hole had been experimentally manipulated in such a way that, at test, ordinal position and distance from the starting point were different than in the training apparatus. The aim was to ascertain if, at test, chicks would

identify as correct the target located at the same absolute distance as in the training apparatus, or in the correct ordinal position.

4.4.1. Materials and methods

Subjects and rearing conditions

The subjects were a new group of 33 male Hybro domestic chicks. They were reared in standard conditions, as described for Experiment 4.1, from Day 1 to Day 5 (i.e. the day of testing).

Apparatus

The same apparatus already described for Experiments 4.1 and 4.2 was used for the training and for the first test, and then chicks underwent a generalization test on a novel apparatus.

The new apparatus (76 x 76 cm, x 45 cm high) presented only five aligned identical holes (2.5 cm in diameter) placed along the midline of the floor. The holes were spaced about 8 cm (±1 mm) from one another, so that the overall line length was 44.5 cm and the distance of the first hole of the line was 25 cm from the wall of the apparatus (where the starting point was). The distance between one hole and the next had been calculated so that the second hole of this new sequence was now at the same absolute distance from the starting position where the fourth hole was in the training apparatus, whereas the fourth hole in this new apparatus was at the distance where the tenth hole was in the training apparatus (Fig. 4.4a).

Procedure

The same training procedure was used as in Experiment 4.1. Testing started in the morning of Day 5. A first test (about 1 hour after the re-training) was run using the training apparatus (according to the procedure described for Experiment 4.1). About one hour after the first test, the generalisation test was run. Each chick was placed in the new apparatus, at the starting point, and underwent 20 consecutive trials. Once the chick had pecked at a certain hole, it was gently pushed back in

the starting position. Only the choice of the correct position (i.e. the 4th in the new apparatus) was reinforced with some chick's crumbs. If no response was assigned within the time-limit of 60 sec, the trial was considered as null (this never occurred in Experiment 4.3).

4.4.2. Results and Discussion

Test in the training apparatus

An Anova run on the pecks scored at the first test, on the training apparatus, revealed a significant effect of the position in the series ($F(9,32)=123.272$; $p<0.001$). As for Experiment 4.1 and for the first test of Experiment 4.2, chicks pecked significantly above chance only at the 4th position (Mean$\pm$SEM= 62.121$\pm$3.850; $t(32)=13.538$; $p<0.001$), while all other positions were pecked at or below chance level.

Generalization test in the new apparatus

Chicks' responses were scored and computed as average proportions of choices for each position (Fig. 4.4b). An Anova run on such data (considered as repeated measures) showed a significant effect of the serial position ($F(4,128)=11.621$, $p=0.0001$). The fourth position was chosen much more than all of the others. In fact an Anova limited to the responses assigned to all other positions (but the 4th) confirmed no heterogeneity was found in responses to these positions ($F(3,96)=1.512$, $p=0.216$). When comparing choices of each position with chance level (20%, using two-tailed one-sample t-tests), only choices for the 4th position were significantly above chance level (Mean=36.212, SEM=3.371; $t(32)=4.809$, $p<0.001$); choices for the other positions were all either below or not different from chance level.

As differential reinforcement was provided over test trials, we checked if chicks' performance remained stable by running a repeated measures Anova over 4 blocks of 5 trials each (trials 1-5; 6-10; 11-15 and 16-20). When choices for the 4th position were considered, there was no significant difference across blocks

($F(3,32)=1.257$, $p=0.2935$). Nevertheless, when considering results obtained in the first block of trials only (Mean=1.545, SEM=0.282) chicks did not score above chance ($t(32)=1.9326$, $p=0.0622$), whereas they scored above chance in all of the other three blocks of trials.

When choices for the 2nd position were considered, instead, there was a significant difference across blocks ($F(3,32)=2.944$, $p=0.037$), as from the first to the last block choices of such position increased, although in all cases they remained below or at chance level.

Although choice of the 4th position was not significantly above chance in block 1, it was marginally so. If birds did initially go to the 2nd position but this choice extinguished from lack of reinforcement, one would expect a decrease in choice of such position over blocks, whereas an increase was actually observed. So, results are not just a consequence of learning over testing trials.

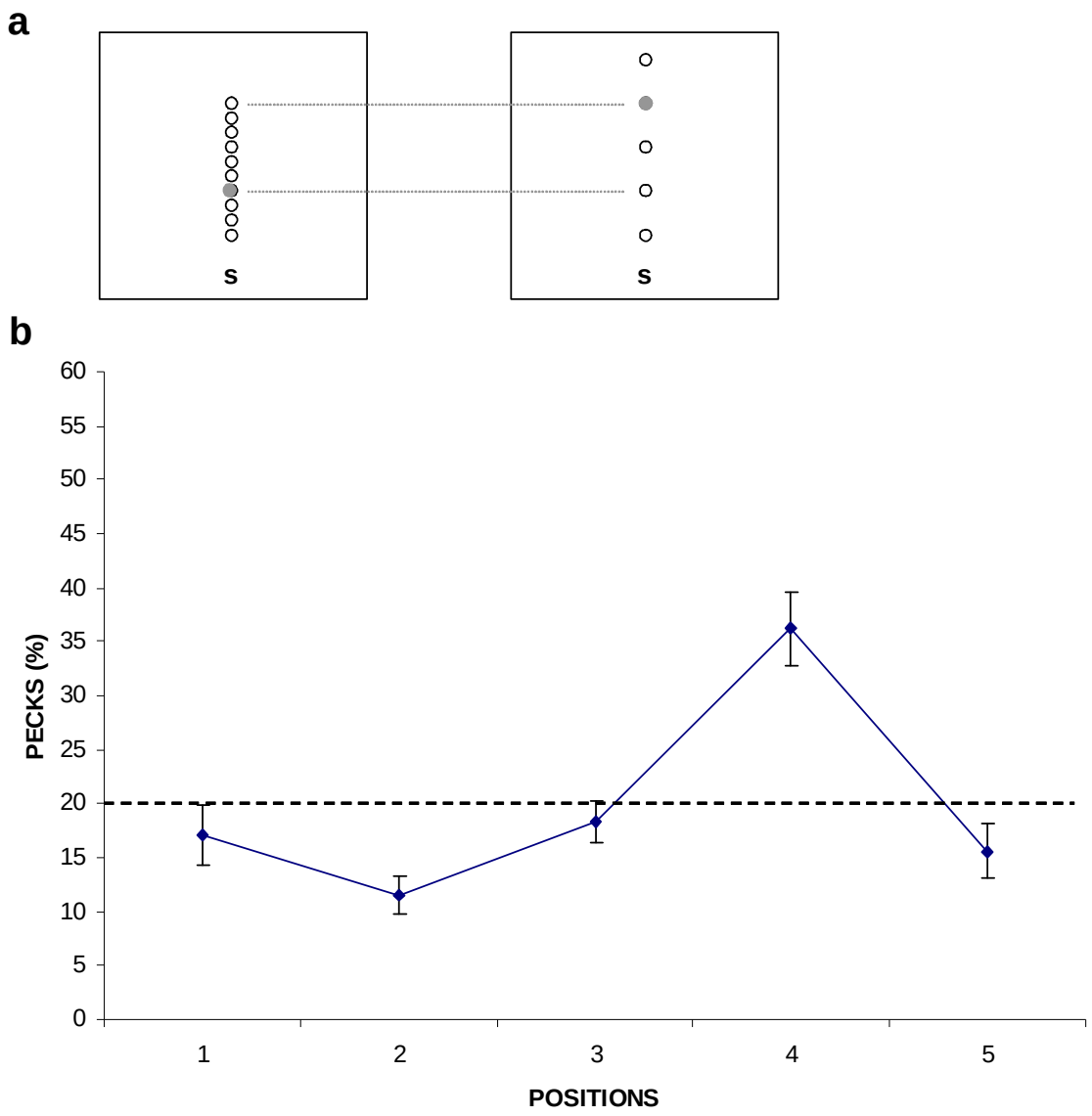

Figure 4.4. **a)** Schematic representation of the apparatus used for the training (leftmost figure, the full circle indicates the reinforced position) and for the generalization test (rightmost figure, the full circle indicates the correct position on the base of serial order) in Experiment 4.3 (S=chick's starting position).
b) Percentage of pecking responses assigned by chicks to each of the 5 positions in the generalisation apparatus (Means ± SEM). The dotted line (y=20) represents chance level.

Chicks that had been trained to peck at the 4th position, generalised their behavioural response in the new apparatus, by correctly pecking at the 4th serial position even if now such position was located much farther away (i.e. over 24 cm more distant from the starting point than it was at training). If chicks had taken into account the actual distance from the starting point, they would have pecked at the second hole in the series, this did not actually happen.

4.5. EXPERIMENT 4.4

From the previous experiments it seems that chicks' behaviour is best accounted for by assuming that chicks can learn and use ordinal information to identify the position reinforced at test. A possible issue concerning the results so far described is that in the apparatuses of Experiments 4.1, 4.2 and 4. 3, the position of each hole was rigid, as holes had been carved in the wooden floor of each apparatus. This means that the individual position of each hole could not be changed within the sequence throughout the 20 testing trials. In Experiment 4.4 we dealt with this problem by devising a new apparatus and by using an array made of detached and singly displaceable objects.

4.5.1. Materials and methods

Subjects and rearing conditions

A new group of male domestic chicks (N=23) took part in this experiment. Rearing conditions were exactly the same as those described for the previous experiments.

Apparatus

The test apparatus (Fig. 4.5a), located in the experimental room, consisted in a circular arena (95 cm in diameter) with the floor uniformly covered by a white plastic sheet. Within the arena, along the inner wall (33 cm high), were positioned 7 food containers (at 5 cm from one another).

The containers were small glass jars (5 cm in diameter and 5 cm high, identical to those used as food containers in the chicks' home cages), that had been painted in black. The upper opening of each jar was covered in transparent mash where a small opening had been made through which chicks could reach the food with their beaks. But in all jars only a small amount of chick crumbs was present, so that chicks could not actually reach the food through the opening, except for one of the jars (the reinforced one) which at training contained more food (although no difference was visible from the outside) so that the chicks could actually reach it when pecking through the upper opening.

In order to prevent the chicks from looking at the stimuli during the 10 seconds of retention, and in particular to prevent them seeing the displacement of the jars from one trial to the next (occurring during the time between two consecutive trials) each chick was visually isolated for 10 seconds within a poliplack® opaque cylinder (diameter of 14.5 cm, 18 cm high, which at the same time constituted the starting box for this test). The cylinder was positioned in the centre of the arena, the chick was inserted in the cylinder from the open top just before the beginning of the first trial, and placed back inside it thereafter, at the end of each trial. At the start of each trial the cylinder was lifted from above in order to release the chick into the arena.

Procedure

Training. On Day 4, every bird was in turn taken from its home cage and placed at the centre of the arena, facing the 7 black jars (containing food) placed along the wall. Only the third jar from the left for some of the chicks (N= 18) or from the right for the others (N=5) contained enough food to be reached by pecking (through the opening in the mesh on the top of the jar). At first, some food was placed by the third jar, outside, and the chick was allowed to peck it. The food outside was then removed and only when the chick pecked at the correct jar, could it reach the food and eat a few grains. (To facilitate training the third jar was also at first positioned a little in front of the line of other jars, towards the chick.) After each trial the chick was confined in the starting box and then immediately released to

move into arena and to peck any jar, although food could be reached only when the jar in the correct position was searched.

The training ended when a chick had directly searched for food at least eight times in twenty trials in the correct position (once all jars had been perfectly re-aligned).

Re-training. On Friday, one hour before the test, the subjects underwent re-training until each chick promptly walked to and pecked at the correct jar. The learning criterion was 10 consecutive correct trials, and the time required to complete the re-training was about 8-10 min. This phase was not video-recorded, as it was only used to assess the chicks' learning. At the end of re-training each chick was placed in its home-cage until the test.

Test. Test started 1 h after training (on Day 5). Each chick was placed in the apparatus and positioned in the starting box in order to prevent it from seeing the arena before the beginning of the first trial. Each chick underwent 20 consecutive trials, if no response was assigned within the time-limit of 60 sec, the trial was considered as null (this never occurred in Experiment 4.4). For the test enough food was placed in each jar so that the chick was always reinforced. At the end of each trial, once the chick had made a choice, it was placed back within the starting box and kept there for 15 sec (the time required to perform the manipulation of the jars). The starting box was then lifted and the chick was again free to peck at a jar for food reinforcement.

From one testing trial to the next, the position of the jars was regularly manipulated, in order to ensure that a chick identified the correct jar by its ordinal position, rather than any other cues.

The experimenter changed:

- The distance between the jars,
- The position of the whole sequence of jars within the arena (which was shifted at each trial by about 10-20 cm to the left or right),
- The ordinal position of each jar (all jars moved at least one position).

Moreover, on the 7th and on the 13th test trial, a novel jar was used to replace the correct one in order to ensure that chicks' choices could not depend on unique characteristics of the correct jar itself, rather than its ordinal position.

4.5.2. Results and Discussion

Results can be seen in Fig. 4.5b, represented as percentages of choices for each of the seven spatial positions. A response was considered correct only if the chick approached and tried to peck exactly at the third jar, i.e. the one reinforced at training (the third from the right end of the series for some of the chicks and the third from the left end for the remaining of the chicks). In the figure, and for the analysis, data of the two groups were mirrored so that the only one correct position was considered (represented as 3rd from the left in Fig. 4.5).

Data were analysed with Anova on the percentage of choices for each position throughout the 20 testing trials, with the seven positions as repeated measures. A significant effect of the position was found ($F(6,22)=20.734$, $p<0.001$). The third position was chosen above all others. In fact, an Anova limited to all positions except the third confirmed that no heterogeneity was present in chicks' responses ($F(5,22)=1.221$, $p=0.304$). Moreover, only the third position was chosen above chance level (i.e., 14.3%; Mean=44.783, SEM=4.875; $t(22)=6.253$, $p<0.001$). The chicks responded at or below chance level to all of the other positions.

We trained some of the animals on the 3rd position from the left end, and the others on the right end in order to control for the presence of chicks' possible preferences to rely on either end-side in order to locate the correct position (as side preferences did emerge in the previous experiment). No difference was noticed by the experimenters during training in the two groups of animals (training sessions were not videorecorded, and shaping trials were not scored), nor was there any statistical difference between the percentage of correct choices at test (left trained: N=18, Mean=47.778, SEM=6.026; right-trained: N=5, Mean=34.000, SEM=2.915; $t(21)=1.176$, $p=0.253$). Nevertheless, the imbalance in the two sample sizes, and the fact that a higher percentage of correct responses were scored by chicks trained and tested on the 3rd position from the left makes it worth investigating a possible preference for identifying the correct position from the left end side. In particular a rather high percentage of mistaken trials on the 5th position (Mean=16.000, SEM=1.871) was scored by the group of chicks trained on

the right end. However the size of this group is too small to be more than suggestive.

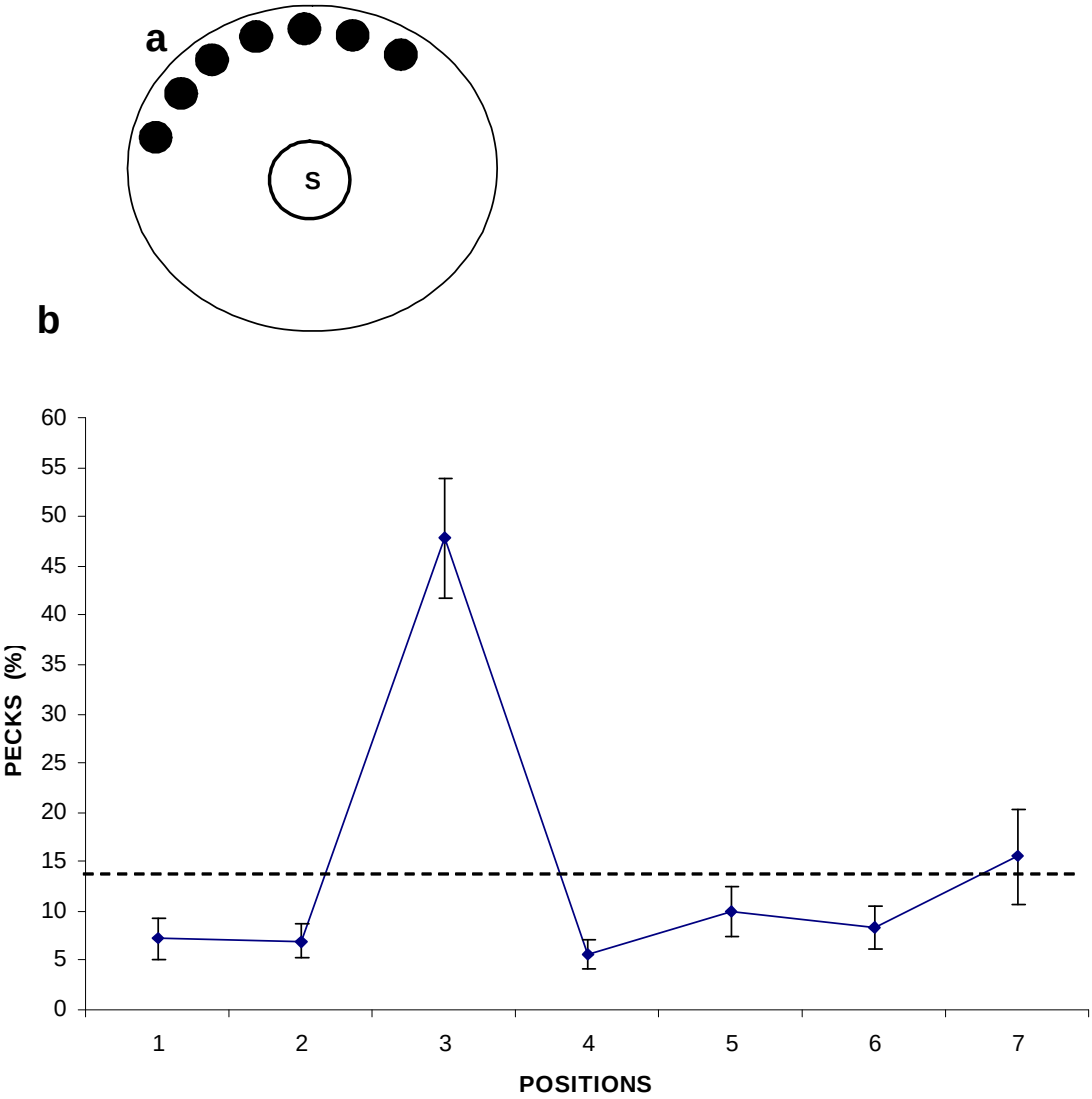

Figure 4.5. **a)** Schematic representation of the apparatus used in Experiment 4.4; the black circles represent the positions of the seven food jars (S=chick's starting position). The reinforced position was the 3rd in the series.
b) Percentages of pecking responses assigned by chicks to each of the seven positions (Means ± SEM). The dotted line (y=14.3) represents chance level.

4.6. CONCLUSIONS

Numerical competencies have recently become a much debated and investigated topic in comparative research, as the presence of rudimental numerical abilities in animals has important implications for our understanding of the phylogenetic origins as well as development of such abilities. In particular, the actual role of language in the understanding of numbers and quantities could be clarified. In this perspective another extremely interesting model of investigation is represented by pre-verbal infants (Wynn, 1992; Feigenson et al., 2002; Xu et al., 2005).

Most studies have concentrated on discrimination of different amounts of biologically relevant items, such as food or social companions. Several animal species have shown at least some degree of this kind of numerical competence: rhesus monkeys (*Macaca mulatta*), Hauser et al., 2000; tamarin monkeys (*Sanguinus oedipus*), Hauser et al., 2003; 2002; dolphins (*Tursiops truncatus*) Kilian et al., 2003; lion (*Panthera leo*), McComb et al., 1994; salamanders (*Plethodon cinereus*), Uller et al., 2003; (for a review see Hauser and Spelke, 2004).

Another property of number sets is constituted by ordinality, i.e. the ability to identify a target in a series of identical ones exclusively on the base of its serial position (in space, or, possibly, in time). Representation of ordinal positions in arbitrary sequences (i.e., not numerical ordering) has been documented in animals (i.e., monkeys; Chen et al., 1997) using the “derived list” paradigm used with human subjects, in which subjects benefit from retrieving the ordinal positions of items from previously learned lists while learning the derived lists on which the ordinal positions of the list items are maintained.

Also proper numerical ordinal competencies seem present in primates (rhesus monkeys, Brannon and Terrace, 1998); but also in rats (Davis and Bradford, 1986; Suzuki and Kobayashi, 2000) and pigeons (Emmerton et al., 1997). Even an insect species, the honey bee (Chittka and Geiger, 1995) is capable of returning to bait on the base of its position relative to a series of landmarks.

To our knowledge the understanding of numerical serial order has never been investigated before in animals at a very early stage of development. We used the

young domestic chick as a model, as chicks of this species display sophisticated visual and motor abilities soon after hatching. Moreover, there are reasons to believe that adults of this species may be sensitive to ordinality (see the Introduction).

The results of the four experiments reported show that five-day-old chicks can successfully learn to identify a target on the basis of its serial position in a series of 10.

It would be interesting to investigate the upper limits of this ability in chicks, as in our experiments chicks' performance did not seem to worsen with the higher rank positions. This would of course require sequences made of more elements, such as 12 or even 15. Differently from what happens with neonates, for which developmental changes were reported (Brannon, 2002), 5-day-old chicks' performance was as good with higher as it was with lower ordinal positions (see the results of Experiment 4.1). Because the domestic chicken is a precocial species, whose chicks are born quite mature, highly visual and mobile, it may be that basic abilities for survival in their environment are already available from birth. It may otherwise be that the positions used in our study (3- 4- and 6- in a series of 10) are quite easy to identify by young chicks, and developmental changes cannot be excluded for more difficult tasks (i.e., for higher ordinal positions).

In Experiment 4.2 and, possibly, Experiment 4.4, a peculiar finding was that whenever, at test, positions had to be identified on a left/right oriented series, chicks would more often refer the correct position starting from the left end of the series rather than from the right end. In the absence of environmental asymmetries a possible explanation would be that of a hemispheric dominance for this sort of task: the left visual hemifield (i.e. the right hemisphere) would control chicks' behaviour. Recent data showed the presence of right hemispheric dominance in bird species (chickens and pigeons) engaged in visuo-spatial tasks (Diekamp et al., 2005; Regolin, 2006). The experimental control situations of Experiments 4.3 and 4 may have also called into action similar lateralised mechanisms, possibly due to the spatial nature of the task required by the generalisation test rather than to the specific competence required (detection of numerical serial positions).

In conclusion, understanding of ordinality seems a basic skill as it can be found in species very different from humans and other primates. Moreover, our study did not involve complex training procedures, and employed animals only a few days olds. The ability to use ordinal information is therefore already available, at least in some animal species, very early during ontogeny and may have been selected due to its high adaptive value.

5. GENERAL CONCLUSIONS

Davis and Pérusse (1988) argued that, although animals can be trained to make numerical discriminations, they do so only as a last-resort strategy, when extensive training is provided and all other cues are eliminated. In spite of this criticism, in the last decade various types of numerical competences have been demonstrated in nonverbal creatures – namely pre-verbal infants and non-human species – that demonstrated the presence of number competence in the absence of language (reviews in Gallistel and Gelman, 1992; Dehaene, 1997; Hauser and Spelke, 2004). The presence of such non-linguistic-numerical-abilities drove Dehaene (1997) to suggest the existence of a spontaneous "number sense". This could be considered as a biologically based knowledge system, which might have originated from adapting to the external world, under specific evolutionary pressures. Two different systems seem to be at the basis of these numerical competences unsupported by lenguage: An object-file system that serves to track a number of individual objects exactly up to a maximum of 3 or 4, and an analogue magnitude system that serves to represent larger numerosities approximately (Gallistel, 1990; Dehaene, 1997; Spelke, 2004; Spelke and Kinzler, 2007).

Discrimination of relative numerosities (protonumerosity; Davis and Pérusse, 1988) requires the ability to make judgements of size differences between two sets, i.e. "more than…", "less than…". Protonumerosity is considered as the first and most elementary level of numerical knowledge, and is often found in ecological situations whenever an animal is allowed to choose between two different sets of food items. Several species, as suggested by optimal foraging theory (Krebs, 1974), spontaneously prefer the larger amount of food. Salamanders (*Plethodon cinereus*, Uller et al., 2003) and human infants (Wynn, 1992; Feigenson et al., 2002) always chose the set that maximised their net energy gain when required to choose between 1 vs. 2 or 2 vs. 3. This did not happen with 3 vs. 4 which seems to constitute a limit for discrimination of contiguous numerosities at least for salamanders and for 10-month old infants. Another ecological situation in which animals seem to count is tied to nesting and

brooding behaviours. American coots (*Fulica americana*) can regulate the number of eggs in their own nest by compensating experimental manipulations on the number of eggs that they are actually brooding (Lyon, 2003).
However, alternative explanations should be considered when accounting for these numerical abilities. For example, changes in number often correlate with changes in other continuous variables (such as brightness, contour length, filled area, dimension or volume). When continuous variables were experimentally controlled for, neonates failed to discriminate between sets of one, two or three (Clearfield and Mix, 1999; Feigenson et al., 2002) or more elements (Wynn, 2002).

In the present study three separate sets of experiments were carried out to investigate respectively: Spontaneous numerical discrimination following imprinting (Employing 3000 three-day-old chicks), number discrimination using a conditioning procedure (Employing 40 five-day-old chicks), and ordinal numerical competence (Employing 60 five-day-old chicks).

Spontaneous number discrimination was investigated by using a filial imprinting procedure, during which chicks were exposed to either one of the two numerosities, followed by a spontaneous choice test between both numerosities present at once. Chicks of separate experimental groups were reared singly for 3 days whilst being exposed to artificial stimuli of different numerosity. Chicks then underwent a 6-min free choice test between the familiar stimulus and a novel stimulus which differed in the number of items presented. Chicks would coherently approach either of the two stimuli only if capable of discriminating between the two numerosities. In Experiment 2.1, chicks were imprinted either onto three identical objects or onto one single object, and were then tested for free choice between one and three. Moreover, half of the chicks, during testing, had to choose between three objects vs. one (we called this procedure “absolute” discrimination). The other half had to choose between two identical sets comprising 4 items, of which either three or one were of the familiar colour (we called this procedure “relative” discrimination). Chicks imprinted on one and chicks imprinted on the three-element-stimulus, in both testing condition, preferred the set comprised of the

larger number of familiar elements, i.e. three. There being no difference between the two test conditions, it appears that, when faced with identical overall numerosities, chicks' could base their choice only on the relative amount of familiar objects – which were identifiable through a difference in colour.

In Experiment 2.2, the ability to discriminate between 2 vs. 3 identical objects, following a different rearing procedure (i.e., with none, one, two or three imprinting objects), was investigated. Only chicks reared with either two or three objects were able to discriminate between such numerosities at test, each group preferring the larger stimulus. Chicks of the control groups (none or one imprinting object) did not show preference for neither of the two stimuli. These data suggest imprinting is a necessary procedure to investigate spontaneous number discrimination abilities in chicks.

In Experiment 2.3, a partial control of overall volume or surface area was carried out by using, respectively, comparisons of 1 vs. 4 and 1 vs.6 items. In every case chicks preferred the bigger stimulus, maybe because it acted as a super-stimulus and was therefore more attractive.

In all the situations where there was partial control for the continuous variables (i.e. Experiments 2.1 and 2.2) chicks always preferred the stimulus with the larger numerosity at test. The same result was obtained when chicks were required to discriminate between two groups of identical overall numerosity, but differing in the amount of familiar and unfamiliar elements constituting each set (Experiment 2.1). When a separate control for surface or volume was used, chicks always preferred the larger stimulus. It was quite clear that birds were not computing number but rather amount (i.e. volume, overall area, etc.).

Finally, in Experiment 2.4, within the comparison 2 vs. 3, the test objects differed in color, shape and size from the imprinting object. Moreover, at test, surface area and volume were simultaneusly controlled for. Only in this case did the chicks choose the familiar number, even when this was the smaller amount, therefore showing the ability to take into account purely numerical cues in such cases.

In a second set of experiments, number discrimination was assessed by employing a conditioning procedure. Continuous variables were controlled for by

taking advantage of the chick's ability to amodally complete partly occluded objects.

Chicks were trained (for food reinforcement) to discriminate small sets of identical elements. At test, the continuous variables, as such as spatial distribution, contour length and overall surface, were controlled for. Nevertheless the chicks still mastered the task.

In Experiment 3.1, chicks were demonstrated to be able to discriminate between 1 vs. 2 elements when the spatial disposition of items was changed from trial to trial and even when elements were partially occluded, in such a way that surface area and volume of the two stimuli were equalivalent.

In Experiment 3.2, chicks discriminated between 2 vs. 3 items when the contour length and area of the elements were controlled for as well as when the objects were partly occluded.

In Experiment 3.3, when the numerosities 4 vs. 5 were employed, chicks were showen to be capable of acquiring and retaining the correct discrimination only if some non-numerical (i.e., spatial) cues were also provided.

These data show that the ability to discriminate small groups of elements is possible only on the basis of their numerosity, supporting the hypothesis that chicks possess a small numerosity representation system. Such a system would implicitly encode cardinal properties, up to a limit of about 3 vs. 4 elements, by using, presumably, an object file system (Hauser and Carey, 2003). Alternatively, the failure in discrimination of 4 vs. 5 elements could have been due to the disparity ratio becoming too small, rather than to the absolute numerosities exceeding the capacity of the underlying small numerosities representation system. In order to understand whether the chick's discrimination was based on the exact number of items in each set or on the disparity ratio, in Experiment 3.4 sets of 4 vs. 6 elements were used. With these numerosities the ratio is identical to that of stimuli employed in Experiment 3.2 (e.g., 2 vs. 3), but the actual number of elements present in each set is increased. Even though two different training sessions were administered to the chicks, no chick was found capable of learning the discrimination. These results rule out the involvement of the Analogue Magnitude System, which depends on the disparity ratio, and support the

hypotheses that the Object File System is involved in the resolution of this task. In fact, the absolute number of elements, rather than their ratio, was relevant in the problem solving. Moreover, in order to delineate the exact limit of chicks' ability, another experiment (Experiment 3.5) comparing 3 vs. 4 was run. Data from (Experiment 3.5) seem to confirm that the upper limit is set at 2 vs. 3 element discrimination. In fact, chicks failed to discriminate between sets of 3 vs. 4 elements.

These results show that young chicks spontaneously encode numerical representations of small numerosities up to a set size limit of about 3 elements. Even if chicks were trained on different numerosities of identical element, with continuous variables changing with number, they maintained the discrimination, at test, when the overall area and contour length of the visible parts of the stimuli were equal. However chicks start to use perceptual (non-numerical) cues when required to discriminate between larger numerosities. These results also provided the first evidence of numerical discrimination of partly occluded objects. Chicks maintained the discrimination when the overall area and contour length were equivalent.

In the third set of experiments another central property of number ordinality was investigated. Ordinality is the ability to identify an object on the exclusive basis of its position in a series of identical objects. Rhesus monkeys (Brannon and Terrace, 1998; 2000), rats (Davis and Bradford, 1986; Suzuki and Kobayashi, 2000) pigeons (Emmerton et al., 1997), honey bees (Chittka and Geiger, 1995) seem to posses some serial ordering abilities. In the present work, young chicks were required to peck, for a food reinforcement, at a certain position in a series of identical positions. The possibility of use some other cue, such as spatial cues, to solve the problem was ruled out in a series of control experiment.

In Experiment 4.1 chicks were trained and subsequently tested to peck either at the third, the fourth or the sixth position in a series of ten identical ones. The results showed that chicks could accurately identify a given position. Nevertheless, chicks in this experiment could have relied on information other than numerical (ordinal), since they could have used the relational spatial (metric) information

provided by the experimental apparatus or simply computed the absolute distance or the walking time to the correct position from the starting point (or from the beginning of the sequence).

In order to check for these possible alternative explanations we ran a series of control experiments on new groups of chicks of the same age.

Naive chicks were trained in the apparatus described in Experiment 4.1, and were then required to respond in a different apparatus, where the correct position had to be identified within a series identical to that used at training, but rotated at 90°. The new series was horizontally positioned in front of the chick's starting point, hence the correct position could not be located on the basis of absolute distances from the starting point.

In Experiment 4.2, a different group of chicks was trained to peck the fourth position in a line of ten identical (in the same apparatus used in Experiment 4.1). Chicks were then required to respond in a different apparatus, where the correct position had to be identified within a series identical to the one used at training, but rotated at 90°. The new series was horizontally positioned in front of the chick's starting point, hence the correct position could not be located on the basis of absolute distances from the starting point. From the results obtained in Experiment 4.2 chicks seem able to generalise the learned response to a new sequence where the target must be identified on the basis of it position in the series without relying on the absolute distance from the starting point or on geometrical information. A very interesting finding concerns the fact that chicks identified as correct only the fourth position from the left end, and not the fourth from the right end which was chosen at chance level. This preference for targets located in the left hemispace could be ascribed to a bias in the allocation of attention, somewhat similar to that shown by humans and called "pseudoneglect" (Jewell and McCourt, 2000; Albert, 1973).

The aim of Experiment 4.3 was to ascertain whether, at test, chicks would have identified as correct the target located at the same absolute distance as in the training apparatus, or in the correct ordinal position. Another group of birds was trained to peck at the fourth position with the same procedure already described for Experiment 4.1, and was then required, at test, to generalize the learned

response to a new sequence in which the distance from the starting point of each hole had been experimentally manipulated in such a way that, the ordinal position and distance from the starting point at test were different than in the training apparatus. Chicks are able to generalise their behavioural response in the new apparatus by correctly pecking at the fourth serial position, even if this position was now located much farther away. If chicks had taken into account the actual distance from the starting point, they would have pecked at the second hole in the series, this did not happen.

From these first three experiments it seems that the behaviour of chicks is best accounted for by assuming that chicks can learn and use ordinal information to identify the position reinforced at test. A possible issue concerning the results so far described is that in all apparatus the sequences were made of fixed target positions, i.e. they never changed throughout the 20 testing trials. In Experiment 4.4 we dealt with this problem by devising a new apparatus and a series consistingof detached and singly displaceable objects (i.e. jars). Some of the animals were trained on the third (in a line of 7 identical) position from the left end, and the others the third from the right end in order to control for the presence of chicks' possible preferences to rely on either end-side in order to locate the correct position (as side preferences did emerge in the previous experiment). Moreover, on some of the test trials, a novel jar was used to replace the correct one in order to prevent chicks' choice being dependent on unique characteristics of the correct jar itself, rather then by its ordinal position.

No difference was noticed by the experimenters between the two groups (trained on the third from the left or trained on the third from the right) during training, both of groups mastered the task.

In conclusions, the understanding of ordinality does not seem to require complex training or sophisticated mental skills, but can be seen in species very different from man and other primates, and is already available very early during ontogeny, having almost certainly been selected due to its high adaptive value.

In the first set of experiments, by employing a spontaneous choice paradigm, the ability to discriminate small sets of objects was confirmed in 3-day-old-chicks even when the continuous variables were controlled for. These data showed, for the first

time, that spontaneous number discrimination can be based on numerical cues only.

In the second set of experiment, chicks' ability to discriminate between small sets of object (up to 3) was confirmed by employing operant conditioning procedures. What is interesting is that although training was done with only one specific set of stimuli, in which number co-varied with several continuous physical variables, the chicks seemed to encode number rather than physical variables. These data also provided the first evidence of numerical discrimination of partly occluded objects. Furthermore, discrimination of small numerosities in young chicks seems to be carried out using an Object File System, with a set-size limit of around 4 elements. It remains to be established whether, with large discrimination ratios (e.g. 1:2), young chicks would be also capable of showing another form of numerical representation, that of large approximate numerosities which has been documented in human infants and non-human primates (Feigenson et al., 2004; Hauser and Spelke, 2004).

The results of the four experiments investigating ordinal abilities show that 5-day-old-chicks can successfully learn to identify a target on the exclusive basis of its serial position in a series of 10. A peculiar finding, in Experiment 4.3, was that whenever position had to be identified on a left/right oriented series, in the generalization test, chicks would more often find the correct position by starting from the left end of the series rather than from the right end. In the absence of environmental asymmetries a possible explanation would be that there is a right hemispheric dominance (left visual hemifield) for this sort of task. It would be interesting for future experiments to establish the limit of such ordinal ability, using a different apparatus with more positions as well as trying to understand the hemispheric asymmetry raised in this experiment.

All these data demonstrated the presence of rudimentary numerical competence even in a species so distant and so different from humans. These results support the hypothesis that numerical competences are not only a prerogative of adult humans but that such abilities should have an evolutionary precursor in animals.

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