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The Cognitive Chicken: Visual and Spatial Cognition in a Nonmammalian Brain

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A GENERAL AND PERSONAL INTRODUCTION

Since the 1960s, research on animal cognition has gained increased visibility and importance within psychology, partly as a result of the so-called cognitive revolution (Gardner, 1987) and partly because of some events that have occurred within the tradition of the psychology of animal learning (e.g., the emergence of evidence for constraints on learning) and of other events that occurred outside of, and sometimes in opposition to, such a tradition (e.g., the rise and development of classical ethology in Europe). Although all of these developments favored a more “liberal” interpretation of animal behavior, most of the research on animal cognition has been (and still is) quite mammal centered. It is true that an enormous amount of work has been carried out using the pigeon; but this species is typically regarded as a sort of laboratory companion of the rat in experimental psychology, rather than a representative of a different class. Truly comparative research has been usually carried out within different, more ethologically oriented traditions, looking at specific (and sometimes highly developed) abilities of nonmammals, such as hoarding in food-storing birds (e.g., Clayton, 1998; Shettleworth, 1990) or homing in pigeons (e.g., Bingman, Gagliardo, Hough, Ioalé, Kahn, & Siegel, in press).

Q1

I believe, however, that the cognitive abilities of species outside of mammalian classes may prove useful and insightful to the study of animal intelligence. In Europe, particularly within the tradition of Gestalt psychology (see, e.g., Herz, 1926, 1928, 1935) or in the work of zoologists somewhat influenced by the Gestalt tradition (e.g., Koehler, 1950), studies of the intelligence of birds and fish (and even nonvertebrate species such as insects) have been quite common. Interestingly, the kinds of cognitive problems that have been investigated within this tradition have been quite different from those typically studied in the psychology of learning and have included, for instance, detour behavior, perceptual organization, problem solving, and number concepts.

After World War II, the Gestalt research tradition largely disappeared and the remaining followers of Gestalt psychology (concentrated in a few universities in Germany, the northeast of Italy, and Japan) concerned themselves mainly with studies of human visual perception. I was fortunate to be trained in this tradition and to have turned (or re-turned) to animal research from human perceptual psychology. In this chapter, I describe some of the work that I have carried out with my collaborators in the past 15 years using nonmammalian species (mainly the domestic chicken) and address issues that were largely inspired by the European Gestalt tradition, rather than by the psychology of animal learning,



Q18 Figure 3.1. The halos of the Apostles depicted from the back seem to be localized in front of them, rather than behind them, an example of the strength of “amodal” completion. (By Giotto, “Cappella degli Scrovegni,” Padua, Italy.)

which has provided the typical background of most contemporary comparative psychology.

RECOGNIZING PARTLY OCCLUDED OBJECTS

Let us begin with a basic problem in vision. Visually guided behavior must constantly deal with the problem of “incompleteness,” because our visual environment is mostly composed of opaque objects that may well overlap and partly hide each other. In our visual experience, when an object is partially concealed by an obstacle, we do not perceive only the pieces or fragments of that object: the parts that are directly visible usually suffice for recognition of the whole object. Although previous knowledge and memory may sometimes play a part in this recognition, it has convincingly been shown that they are secondary to a more fundamental perceptual process of “amodal” completion (Michotte, 1963; Michotte, Thines, & Crabbe, 1964), which depends on detecting certain configurational relationships in visual scenes, such as the alignment of visible parts and similarities in their colors and textures (Grossberg & Mingolla, 1985).

Partial occlusion sometimes poses a serious representational problem to visual artists. Figure 3.1 shows part of the famous fresco in the “Cappella degli Scrovegni” in Padua, painted by Giotto. The halo of Jesus and the Apostles produces the impression of a complete disc behind the head when the subjects are seen in front view. The problem arises with the Apostles who are observed from the back: if you represent a complete halo, then you have to cover the head of the Saints, which is somewhat blasphemous. But, even the solution adopted by Giotto is imperfect: the Apostles seem to be dazzled by a complete Sun, placed just a few centimeters from their faces. (Alternatively, some people experience a loss of the circular shape of the halo, which becomes a sort of U-shaped ring around the Apostles’ heads.)

Do other animals perceive the completion of visual objects in the way that we do? The problem with studying nonhuman species is that we cannot ask them directly whether they perceive completion of partly occluded objects; some sort of nonverbal trick is needed to reveal this information. Most studies with birds have used conditioning procedures and the pigeon as a model. For example, after training pigeons to respond to a triangle,

Cerella (1980) found that responses to an amputated triangle (i.e., lacking a piece) exceeded those to a partially occluded triangle. He also reported that after learning to discriminate figures of Charlie Brown from other Peanuts characters, although pigeons responded to pictures representing only parts of Charlie Brown's figure, they also emitted many responses to random mixtures of these parts. These results seem to suggest that pigeons perceive complex stimuli as an assembly of local features and that responses to partly occluded objects depend only on the visual information remaining after fragmentation of the stimulus.

Q2

Mammals, like mice, seem to behave quite differently from pigeons in similar tests. Kanizsa, Renzi, Conte, Compostela, and Guerani (1993) trained mice to discriminate between complete and amputated disks. After reaching criterion, the mice performed test trials in which outlined rectangles were either exactly juxtaposed or only placed close to the missing sectors of the disks in order to produce or not produce the impression (to a human observer) of an occlusion of the missing sectors by the rectangles. Mice responded in these tests as if they were experiencing completion of the partly occluded disks; pigeons, in contrast, responded on the basis of local, visible features and failed to complete (Sekuler, Lee, & Shettleworth, 1996) or even perceive continuation of the figure behind the occluder (Fujita, 2001).

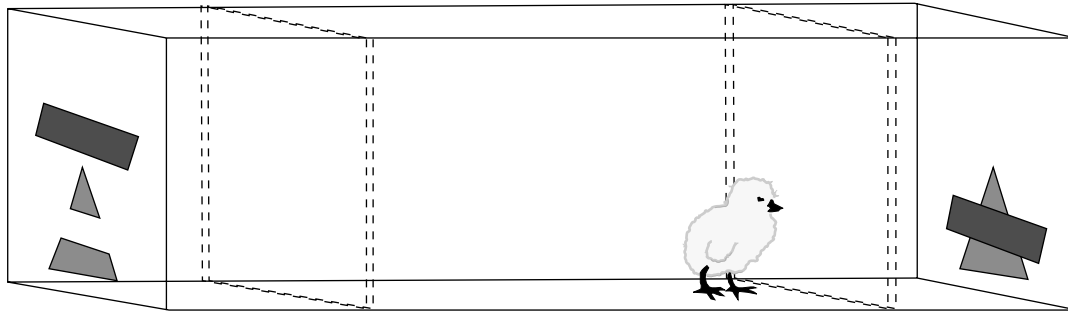
Apparently, the visual world of pigeons consists only of fragments, single unstructured pieces of actual retinal stimulation. A very strange visual world, no? However, things may not be so clear-cut, because evidence has been obtained in other studies with pigeons that global relations among component parts can be critical in discriminative control. For example, using naturalistic stimuli rather than figures of Charlie Brown, it has been shown that pigeons do not respond only to local features. Watanabe and Ito (1991) trained pigeons to discriminate color slides of different individuals and then tested them with the full face, separate parts, and randomly connected parts of the original stimuli. In this case, pigeons emitted very few responses to scrambled figures. Similarly, Wasserman, Kirkpatrick-Steger, Van Hamme, and Biederman (1993) found that scrambling the component parts of complex objects reduced pigeons' discrimination, indicative of at least partial control by the spatial configuration of the component parts (see also Kirkpatrick, 2001; Towe, 1954). These somewhat

contrasting results suggest that pigeons can perceive and discriminate complex stimuli based on either the local parts or the global configuration, much like humans—a point to which I shall return.

Some years ago, we tried to develop a different method to investigate the recognition of partly occluded objects in birds. We reasoned that filial imprinting—the learning process through which the young of some animals (usually of precocial species) come to recognize an object by simply being exposed to it for a certain time—might be an ecologically more valid context than conditioning to study the problem. In the natural environment, the mother hen and the chicks' companions are often likely to be partially concealed by vegetation; it is important for the chick not to lose contact with them even when only parts of its mother and social fellows are directly visible.

We took advantage of the fact that imprinting can occur even with artificial objects. Soon after hatching, chicks were reared with a red triangle, which thus became their "mother." At test, chicks were presented with different versions of their mother (figure 3.2) located at the opposite ends of a test cage, and we measured the chicks' time spent near and their choice of the two versions of the mother. The two versions look quite different to people. Although, overall, there is the same amount of black and red areas, in one case, we perceive a complete triangle that is, by accident, partly covered by a bar. In the other case, we perceive a completely different figure: an amputated triangle or two pieces with a small triangle and a small trapezoidal shape. We found that chicks indeed behaved as humans might do so in the same situation—they chose the partly occluded triangle.

Obviously, several control experiments were needed to demonstrate that this observation provides evidence that chicks do complete partly occluded objects (see Regolin & Vallortigara, 1995, for more details). For example, in one experiment (see figure 3.3), we reared chicks with a partly occluded triangle. At test, they preferred a complete triangle to an amputated one and they did so despite the fact that the partly occluded triangle was more similar, physically, to the amputated triangle than to the complete one. Furthermore, it is not that the chicks' choices depended on a preference for the stimulus with the more extended red area; in the reverse condition, chicks reared with an amputated triangle preferred the amputated triangle over the complete triangle at test.



Q19 Figure 3.2. Chicks imprinted on a complete triangle were later tested for choice between a partly occluded and an amputated triangle. The chicks preferred the partly occluded triangle, thus suggesting that they complete partly occluded objects. (From Regolin & Vallortigara, 1995.)

It is interesting to compare chicks' abilities with those of newborn human infants. Human newborns provide scientists with the same type of challenge offered by nonhuman species: We cannot simply ask them what they are perceiving; we must use some tricks to obtain such an answer. A technique used by developmental scientists is a procedure called habituation/dishabituation (Kellman & Spelke, 1983).

For instance, infants are habituated to a rod that moves back and forth behind a central occluder, so that only the top and bottom of the rod are visible. After habituation has occurred, babies

are shown either of two stimuli without the occluder: one is a complete rod and the other consists of the top and bottom parts of the rod, with a gap where the occluder had been. Surprise (as measured by longer looking times) when viewing the complete rod would indicate that this display is novel and that the infants did not see a complete rod during the habituation trials, whereas surprise when viewing the rod pieces is taken to indicate that the infants had perceived object unity. It takes about 4 to 7 months, depending on details of procedure, for human infants to show evidence of completion of partly occluded objects (Kellman &

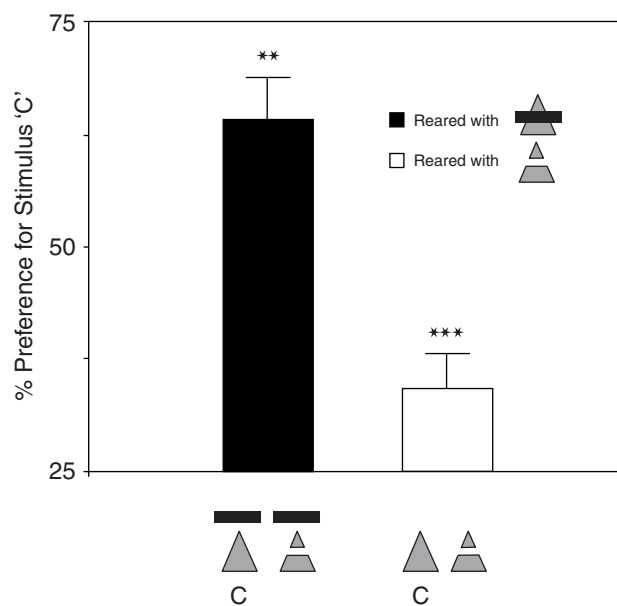


Figure 3.3. Chicks reared with a partly occluded triangle, at test, preferred a complete triangle to an amputated one. Chicks reared with an amputated triangle, at test, preferred an amputated triangle to a complete triangle. This pattern of results provides further evidence that chicks complete partly occluded objects. (Redrawn from Regolin & Vallortigara, 1995.)

Q20

Arterberry, 1998). Chicks do that soon after hatching; Lea, Slater, and Ryan (1996) duplicated our imprinting results using the same type of stimuli used with newborn infants. As expected, they found that, at test, chicks imprinted on a complete rod preferred the complete rod to the fragmented rod, whereas chicks imprinted on the fragmented rod preferred the fragmented to the complete rod. In the crucial condition, however, chicks imprinted on a partly occluded rod preferred the complete rod to the fragmented rod.

The difference between the species in developmental time-course is not surprising. Recognition of a partly occluded mother would be useful when you can move by yourself to rejoin her in order to reinstate social contact; this is the case for the highly precocial young chick but not for highly altricial species like the human newborn. The emergence of recognition of partly occluded objects can be delayed in our species, allowing the nervous system extra time for neural development.

What about other avian species? Standardized tests of object permanence include, for the initial stages of its development (specifically, stage 3), tasks in which the animal has to respond to partly occluded objects. Psittacine birds, such as parrots and parakeets (Funk, 1996; Pepperberg & Funk, 1990), mynahs (Plowright, Reid, & Kilian, 1998), and magpies (Pollok, Prior, & Güntürkün, 2000), pass these tests easily (as well as much more advanced stages of object permanence). Interestingly, pigeons, in contrast, lose interest in food when it becomes invisible behind a screen (Plowright et al., 1998).

Could it be that the difference between chicks and pigeons resides in the use of a more ecologically valid procedure (filial imprinting) and/or age differences? This conclusion is unlikely because evidence has been obtained for completion in adult hens using conditioning procedures (Forkman, 1998). As well, recent work by DiPietro, Wasserman, and Young (2002) shows that pigeons can recognize partly occluded objects but only if special training is provided that may help pigeons to distinguish the object from the occluder. This result suggests that pigeons probably can perceive amodal completion but that this may not be their "natural" way to analyze visual scenes. My point becomes clearer when we consider a phenomenon that is strictly related to amodal completion—the perception of subjective contours.

In figure 3.4, the perception of the subjective triangle is associated with the impression that the

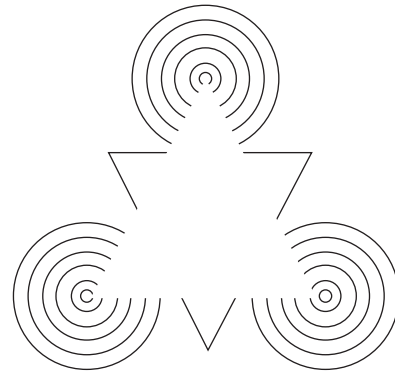


Figure 3.4. An example of subjective contours: the Kanizsa triangle (Kanizsa, 1979). Some species of birds, including the domestic chick, have been shown to perceive subjective contours (see text).

interrupted circles continue and are completed behind the illusory triangle. It has been suggested that a single unit-formation process underlies the formation of "subjective" contours and "amodal" completion (Shipley & Kellman, 1992). If so, then we can predict that those species that perceive subjective contours should also manifest completion of partly occluded objects and vice versa.

Evidence indicates that a number of mammalian species do perceive subjective contours (e.g., cats: Bravo, Blake, & Morrison, 1988; and monkeys: Peterhans & von der Heydt, 1989). In birds, young chickens (about 2 weeks old) have been shown to perceive subjective contours (Zanforlin, 1981), which would agree with evidence for completion of partly occluded objects in this species. Barn owls have also been shown to perceive subjective contours (Nieder & Wagner, 1999).

But what about pigeons? In a study on subjective contours with Kanizsa's triangles and squares, Prior and Güntürkün (1999) were able to demonstrate that 4 of 14 pigeons that they tested reacted to the test stimuli as if they were seeing subjective contours. Control tests suggested that the pigeons responding to subjective contours were attending to the "global" pattern of the stimuli, whereas the pigeons not responding to subjective contours were attending to extracted elements of the stimuli.

Perception of subjective contours is closely linked to amodal completion. In natural situations, in which objects occlude one another, boundaries may vanish and interpolation mechanisms are sometimes

needed to reconstruct contours that are absent from the retinal images. The fact that only pigeons attending to the more global aspects of the stimulation responded to subjective contours suggests that such individual variability in attending globally or locally to visual scenes can explain why pigeons fail in amodal completion tests that are effective in other species (see Sekuler et al., 1996). It is as if, for pigeons, a “featural” style of analysis is more natural than a global one, although pigeons can apparently switch to such a global style of analysis with some effort. Thus, pigeons appear to be able to respond to amodal completion but only if they are strongly encouraged to do so (e.g., DiPietro et al., 2002).

Q3

It is important to stress that the possibility of such a switch is inherent to our own visual perception. We can, with some effort, turn to a featural, mosaic-like perception of a visual scene, in which we look at fragments of partly occluded objects without completing them (visual artists, because of training and perhaps natural inclination, do this routinely). There is also evidence that such a mosaic stage normally occurs during very early phases of visual processing (see Sekuler & Palmer, 1992) and in human infants before 4 to 7 months of age.

Why should there be such a striking species difference in the relative importance of the two strategies of perceptual analysis, and what mechanisms could underlie the major reliance on one or another strategy? As to the first issue, Fujita (2001) observed that pigeons are grain eaters; grain is a type of food that is usually abundant and does not require the animal to search behind obstacles. Fowl, in contrast, engage in finding and eating worms and insects that often hide under leaves or soil and may be only partly visible. Thus, there could be ecological differences favoring perception based on response to parts or on reconstruction of the whole objects, on the basis of their parts. I would add here that finding food that moves (prey) or that does not move (grain) can also be crucial in this respect (although looking for grains in grass may also require the recognition of occluded objects and it is unknown whether birds in these cases tend to respond only to parts).

As to the issue of mechanisms, it is interesting to observe in experiments using conditioning procedures, such as those performed with pigeons, that the stimuli fall into the frontal binocular visual field of the animals, a portion of the visual field that is mainly represented within the tectofugal pathway in pigeons (Güntürkün & Hahmann,

1999; Hellmann & Güntürkün, 1999). The frontal visual field seems to be specialized for (myopic) foraging for food on the ground, whereas the lateral visual field seems to be specialized for predator detection and flight control. Near-sighted acuity would favor examination of fine stimulus details and may be responsible for the local advantages observed in most experiments that used frontal presentations of visual stimuli; the lateral visual fields, in contrast, may be more concerned with the larger-scale integration of scene and flight control information (Martinoya, Rivaud, & Bloch, 1984), thus showing more sensitivity to global information (see also Cook, 2001).

Unlike the case of pigeons (Hodos, Macko, & Bessette, 1984), lesions to the thalamofugal visual system markedly affect chicks' performance on tasks that rely on frontal viewing (Deng & Rogers, 1997; 1998a, 1998b). This observation suggests that, unlike in pigeons, the frontal field is represented within the thalamofugal system in chicks.

We recently hypothesized that these differences could be also associated with brain asymmetry. Research using temporary occlusion of one eye, which takes advantage of complete decussation of optic nerve fibers and of large segregation of function between the hemispheres in the avian brain (see Andrew, 1991; Rogers, 1995; Vallortigara, 2000; Vallortigara, Zanforlin, & Pasti, 1999; Vallortigara, Cozzutti, Tommasi, & Rogers, 2001), has revealed that the right eye (which sends input mainly to the left hemisphere) is dominant in pigeons' visual discrimination learning (Güntürkün, 1997) and presumably favors a featural strategy of analysis of visual scenes. Chicks, in contrast, have shown a more balanced and complementary use of the two eyes, with the left eye (and right hemisphere) being dominant when more global strategies of analysis are needed (such as in spatial analyses; see Vallortigara [2000] for a review).

We recently put these ideas to a test (Regolin, Marconato, Tommasi, & Vallortigara, 2001; Regolin, Marconato, & Vallortigara, 2004). In the first experiment, three separate groups of newly hatched chicks were imprinted (in a binocular condition): (1) on a red cardboard square partly occluded by a superimposed black bar, (2) on the complete red square, or (3) on an amputated version of the red square (consisting of the two visible parts of the occluded square with a missing central part). At test, each chick was presented with a pair of stimuli located at opposite ends of a test cage: a

complete square and an amputated one. Chicks could freely approach either stimulus.

When tested with only their left eye uncovered, chicks behaved very much like binocular chicks would do, choosing the complete stimulus (the square). In contrast, when tested with only their right eye uncovered, chicks tended to choose the amputated square. These findings suggest that, in the chick, the neural structures fed by the left eye (mainly located in the right hemisphere) are more inclined to perform a “global” analysis of visual scenes, whereas those fed by the right eye (mainly located in the left hemisphere) seem to be more inclined to perform a “featural” analysis of visual scenes. Interestingly, even in humans, the right hemisphere seems to play a more important role in amodal completion (Corballis, Fendrich, Shapley, & Gazzaniga, 1999).

Q4

ESTABLISHING THE DIRECTION OF VISUAL OCCLUSION

Another basic computational problem in perceiving occlusion deals with establishing the direction of depth stratification (i.e., determining which surface is in front and which is behind). Usually, when two objects differ in color, brightness, or texture, humans solve occlusion indeterminacy by determining, on the basis of contour collinearity, what boundaries belong with each other and thereby allowing the formation of modal (occluding) and amodal (occluded) contours (Michotte, 1963). However, humans can perceive unconnected and depth-stratified surfaces even in chromatically homogeneous patterns.

Consider figure 3.5. Although it would be possible, in principle, to perceive a peculiar, but unitary object, the hen appears as being *behind* the fence when the region of the legs is inspected (because of the differences in color that specify the direction of occlusion), whereas it appears to be in *front* of the fence when the region of the upper part of the body is inspected.

The reason that larger surfaces (such as the trunk of the hen) tend to be seen modally as being in front of, rather than behind, might depend on the geometrical property that overlapping objects in which larger surfaces are closer present shorter occluding boundaries than when smaller surfaces are closer. Shorter modal (occluding) contours are needed to account for the occlusive effect of the

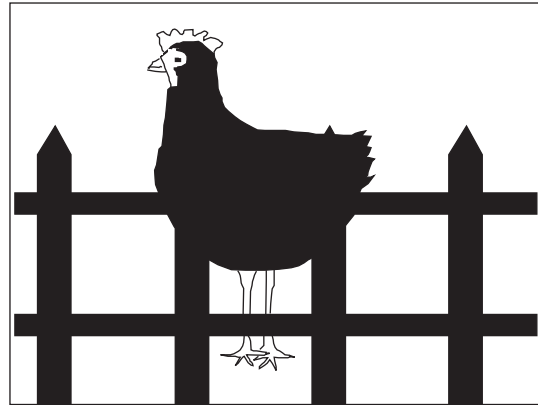


Figure 3.5. The hen appears to be standing in front of the fence in the region of the trunk, but if one inspects the region of the legs, then it appears as though standing behind the fence. Domestic hens seem to be susceptible to this sort of illusion (see text).

hen on the fence, whereas larger modal contours would be needed to account for the occlusive effect of the fence on the upper body of the hen.

This “rule,” according to which the visual system tends to minimize the formation of interpolated modal contours, was first described by Petter (1956) and has been confirmed in several studies of human visual perception (Shipley & Kellman, 1992; Singh, Hoffman, & Albert, 1999; Tommasi, Bressan, & Vallortigara, 1995). It should be noted that Petter’s rule is independent of the empirical depth cue of relative size (Tommasi et al., 1995) and can be made to play against information based on other depth cues, thereby generating intriguing visual paradoxes such as the hen/fence illusion (see Kanizsa, 1979, for further examples).

Recently, we wondered whether Petter’s rule reflected a geometrical regularity that is incorporated into the design of all vertebrate brains or whether it is limited to the human visual system (see Forkman & Vallortigara, 1999). We presented domestic hens with two chromatically identical patterns, a diamond and a ladder, shown on a computer touchscreen (see figure 3.6). Hens were reinforced for pecking at the pattern that was higher up on a grid that provided pictorial depth information (i.e., on the pattern that to a human appears as being farther away). Every 10th trial was a nonrewarded probe trial with the two patterns partially overlapping. In the absence of other cues, depth stratification can

REPRESENTING COMPLETELY OCCLUDED OBJECTS

Under certain conditions, objects are not simply partly occluded by other objects but rather are entirely covered by other objects; thus, they are completely unavailable to direct sensory experience. In this case, an internal representation of the unseen objects is needed to guide behavior.

This problem has been traditionally investigated within the Piagetian framework of “object permanence.” According to Piaget (1953), human object permanence develops in stages. In stage 1, children do not search for an object that they have seen disappear. In stage 2, they track the object’s movement. In stage 3, children recover a partly occluded object. In stage 4, they recover a fully occluded object. In stage 5, children can retrieve an object that has been hidden successively in several locations (i.e., hidden, exposed, and rehidden several times). Finally, in stage 6, they can master invisible displacements (e.g., an object is hidden in a container, the container is moved behind an occluding device, the object is transferred to this second device, the children are shown that the first container is empty, and the children successfully infer where the object now resides).

Several comparative studies have been conducted within the Piagetian framework. However, extreme caution in interpreting their results is needed. For instance, some early studies (Etienne, 1973) reported that young domestic chicks apparently did not recover a fully occluded object (stage 4). More recently, however, we have shown that simple modifications of the behavioral procedure can dramatically improve animals’ performance (see Regolin, Vallortigara, & Zanforlin, 1995a).

As in Etienne’s (1973) experiments, we presented chicks with a goal-object that was made to disappear behind one of two screens opposite each other. Chicks searched at random behind either screen when the goal-object was a palatable prey (i.e., a mealworm), as originally found by Etienne (1973). However, chicks were also able to choose the correct screen when the goal-object was a “social” partner (i.e., a red ball on which they had been imprinted). Moreover, chicks also appeared to make use of the directional cue provided by the movement of the prey when they were tested in the presence of a cagemate. These results suggest that the previous failure to obtain detour behavior with the double screen, using the prey as a target, was not due to a

Figure 3.6. Schematic representation of Forkman and Vallortigara’s (1999) experiments to investigate how hens disambiguate relative depth in chromatically homogeneous patterns. During rewarded trials, the two stimuli, the ladder and the diamond, never overlapped (*top*); during the probe trials (*bottom*), they partially overlapped (see text). During the probe trials, the touch-sensitive area was defined as that part of the touch-sensitive area of each symbol that did not overlap with that of the other symbol.

occur on the basis of a minimization of interpolated occluding contours. In humans, the diamond is usually perceived to be in front of the ladder because shorter interpolated contours are needed to account for the occlusive effect of the diamond on the ladder. The hens pecked more often at the ladder during the probe trial. These findings suggest that there may be quite general visual constraints that are related to the geometrical and physical properties of the world and that must be incorporated in the design of any efficient biological visual system (see also Vallortigara & Tommasi, 2002).

Figure 3.7. Schematic representation of the experimental apparatus used to study the representation of hidden objects in chicks. The imprinting stimulus is visible behind the small window-grid barrier. Two symmetrical apertures, placed at the midline of the corridor, allowed the chick to pass around the barrier. After entering the apertures, the chick is faced with a choice between a correct and an incorrect compartment (A, B are incorrect compartments; C, D are correct compartments). (After Regolin et al., 1994.)

cognitive limitation but rather to the evocation of fear responses to the novel environment that interfered with the correct execution of the spatial task.

Further work into detour behavior has shown that 2-day-old chicks master some, but not all, aspects of stage 4 of object permanence (see Regolin, Vallortigara, & Zanforlin, 1994, 1995b; Vallortigara & Regolin, 2002; and see also Campbell, 1988, for similar evidence in adult hens). For instance, although chicks do have an object concept that maintains a representation of the object in the absence of direct sensory cues, it seems that they are not able to predict the resting position of an imprinted ball from its direction of movement prior to occlusion (Freire & Nicol, 1997, 1999). It is not yet clear whether this finding reflects a basic cognitive limitation or an adaptation to ecological demands (for instance, when prey or other interesting objects hide themselves behind an occluder, it is more likely that they will reappear, after some time, in the same location where they were seen to disappear rather than at the other side of the occluder; see Haskell & Forkman, 1997).

One problem with the classic Piagetian or other object-permanence tests is that they provide evidence that animals represent and maintain something in memory, but little can be deduced as to the precise nature of this. Consider the case of the detour problem. Some years ago, we tested the representational

abilities of young chicks in the task shown in figure 3.7. Chicks could observe an imprinting object (a small red plastic ball) through a window, but in order to rejoin their “mother,” they had to make a detour, using one or another of the two symmetrical apertures that allowed them to go outside of the corridor. We knew from previous work that chicks can learn to make a detour (Regolin et al., 1994), but we were interested in what happens the first time that a chick loses sight of its mother. If the chick moves randomly in the environment when the ball is no longer available to direct perception, then no straightforward conclusion can be drawn because the chick might have the ability to represent the object but lack any ability to discover its position (admittedly, a more economic and conservative tenet would be to deny possession of both capacities). On the other hand, if the chick moves nonrandomly and shows the ability to orient toward the disappeared goal, choosing the C-D rather than the A-B compartments, then some sort of mental representation of the goal can be ascribed to the animal. We found that 18 of the 20 animals tested chose the correct compartments C-D. However, does this provide any evidence that chicks do “represent” the ball in much the same way as we would do in similar circumstances? Obviously not, for the only specific aspect that needs to be represented here is the spatial location of the object. Nothing can be said about other

properties of the object, such as its color or shape. But, of course, these other aspects are open to experimental investigation.

One interesting procedure that may be used to investigate other aspects of animals' representations exploits the observation that prior feeding with one type of food selectively reduces the value of that food (see Hetherington & Rolls, 1996). In a series of experiments, we fed 5-day-old chicks in an enclosure with two food-plates, each with a different type of food (see Cozzutti & Vallortigara, 2001). The food was devalued by prefeeding with one of the food types. When tested with food that was displaced, the chicks moved to the location previously occupied by the nondevalued food. Similar results have been reported even for adult hens (Forkman, 2000; and see Clayton & Dickinson, 1999a, 1999b, for evidence in corvids). This result suggests that these birds can remember the contents of food caches apart from their positions (i.e., that they are able to conjoin "where" and "what" information to form "declarative-like" memories).

DELAYING MEMORIES

The notion that objects are separate entities that continue to exist when out of sight of the observer is relevant when considering that these "represented" objects serve to guide the course of action. When a prey has disappeared from sight, the predator can maintain a representation of its continuing presence for some time and thus actively search for it. But, how long can the representation be maintained? This issue has been investigated using the so-called delayed response problem (Hunter, 1913). However, very little is known about delayed responding in avian species. Studies on object permanence in birds (discussed earlier) did not address the issue of delay. Obviously, the so-called matching-to-sample task is derived from the delayed response problem and has been largely used with pigeons and other avian species. However, the delays used are typically very short (on the order of seconds, see Foster, Temple, MacKenzie, Demello, & Poling, 1995, for evidence in hens).

We trained 5-day-old chicks to follow an imprinted object (a small red ball with which they had been reared) that was moving slowly in a large arena, until it disappeared behind an opaque screen (see Vallortigara, Regolin, Rigoni, and Zanforlin, 1998). At test, each chick was initially confined in a

transparent cage, from which it could see and track the ball while moving toward, and then behind, one of two screens. The screens could be either identical or they could differ in color and pattern. Immediately after the disappearance of the ball (or with a certain delay), the chick was released and was allowed to search for the imprinted object behind either screen. Results showed that the chicks could take into account the directional cue provided by the ball's movement and its concealment, up to a delay period of about 180 s, regardless of the perceptual characteristics of the two screens. If an opaque partition was positioned in front of the transparent cage immediately after the ball had disappeared so that, throughout the delay, neither the goal-object nor the two screens were visible, then chicks were still capable of remembering and choosing the correct screen, although for a much shorter period (about 60 s). A 1-min delay is quite comparable to the retention intervals observed in primates under similar testing conditions (Fletcher, 1965; Wu et al., 1986).

Q5

It is possible to claim that the chicks simply learned to associate the proximity of the ball to a screen as a cue to direct approach responses toward that screen. Nevertheless, in order to solve the problem, the chicks needed to maintain some representation of the position of the correct screen and to continuously update the content of the representation from trial to trial on the basis of the directional cues provided by the movement of the ball, particularly in the condition in which the screens were not visible. In mammals, such "on-line" maintenance of information during short temporal intervals is usually described as "working memory" and is believed to be represented in the neural circuitry of the prefrontal cortex (Fuster, 1989; Goldman-Rakic, 1987). Involvement of the prefrontal cortex in Piagetian object-permanence tasks has been suggested in both humans and monkeys (Diamond & Goldman-Rakic, 1989). Interestingly, there is evidence that a region resembling the mammalian prefrontal cortex exists in the avian telencephalon—a semilunar area in the caudalmost part of the forebrain, called the neostriatum caudolaterale (NCL) (see Mogensen & Divac, 1982).

In pigeons, it has been shown that temporary receptor blocking of D₁ receptors (the dopamine receptor subtype in the mammalian prefrontal cortex) in the NCL has an important effect on working memory (Güntürkün & Dürstewitz, 1998). Moreover, neurons in the NCL have been found that respond selectively during the delay period of

Figure 3.8. Schematic representation of the test apparatus used to investigate geometrical representations. The animal could find food (or other desired targets) in the rectangular enclosure at, say, corner A. In one version of the test (*left*), all walls were white and the task for the animal was to distinguish between corners A, C and corners B, D using purely geometrical information (corner A and its rotational equivalent, corner C, are in fact indistinguishable on the basis of purely geometrical information but can be distinguished from corners B and D, which, in turn, are geometrically equivalent and cannot be distinguished from each other). In another version of the task (*middle*), one wall (indicated by the dotted line) was colored differently (with some species, panels with different features and colors were positioned in the four corners instead of using a colored wall as nongeometrical information, see rightmost figure). The animal in this case could disambiguate the two geometrically equivalent corners A and C using the nongeometrical information provided by the colored wall (or by the panels).

a working memory task, and they show activity patterns that are identical to those described for delay cells in the primate prefrontal cortex (Kalt, Diekamp, & Güntürkün, 1999).

Preliminary results obtained in my laboratory also suggest that lesioning of chicks' NCL severely impairs performance in the delayed response task at delays of 30 s or longer but not in the absence of a delay (Pagni, Gagliardo, Chiandetti, Diekamp, Güntürkün, and Vallortigara, unpublished). Thus, although the anatomical structure of the avian NCL is very different from the primate neocortical architecture of the prefrontal cortex, the neuronal mechanisms that have evolved to master analogous cognitive demands may be similar.

MAKING "NATURAL GEOMETRY"

Quite sophisticated spatial cognition can be observed in nonmammalian vertebrate brains, even in those species that do not show the amazing abilities

at retrieving large numbers of hidden items that are exhibited by food-storing birds. Direct comparisons with mammals in similar tasks, however, have rarely been performed. One interesting exception are tests on the "geometric sense of space" (Cheng, 1986; Gallistel, 1990).

When disoriented in an environment with a distinctive geometry—such as a rectangular-shaped arena (figure 3.8a), animals can (partially) reorient themselves, even in the absence of any extra-arena cues, by simply using the geometry of the environment. Suppose that a food target is located at corner A and then is made to disappear. Following passive disorientation (i.e., being turned slowly without viewing the environment) and in the presence of only proximal corner cues, the animals should choose at random among the four corners. But, in fact, partial disambiguation of the problem is possible: Corner A (the food location) appears in the same geometrical relation to the shape of the environment as corner C. Thus, geometrical information alone, which cannot unambiguously differentiate

between corners A and C and is geometrically equivalent, is sufficient to distinguish between corners A-C and corners B-D.

Several species of animals been shown to be able to reorient using this “purely geometrical” information (birds: Kelly, Spetch, & Heth, 1998; Vallortigara, Zanforlin, & Pasti, 1990; primates: Deipolyi, Santos, & Hauser, 2001; Gouteux, Thinus-Blanc, & Vauclair, 2001; fish: Sovrano, Bisazza, & Vallortigara, 2002). Interestingly, however, it has been reported that human infants (Hermer & Spelke, 1994) and adult rats (Cheng, 1986) fail to reorient using nongeometrical information, such as a distinctive differently colored wall in the rectangular cage, despite the fact this featural information would allow fully successful reorientation (see figure 3.8b).

These findings have been interpreted to suggest that spatial reorientation depends on an encapsulated, task-specific mechanism or “geometrical module” (Cheng, 1986; Cheng & Gallistel, 1984; see also Fodor, 1983). The module encodes only the geometrical properties of the arrangement of surfaces as surfaces. In the case of the spatial reorientation task in the rectangular environment, for instance, the geometrical module would use only “metric properties” (i.e., the distinction between a long and a short wall) and what is known in geometry as “sense” (i.e., the distinction between right and left). Use of geometrical information for spatial reorientation makes sense ecologically. The large-scale shape of the landscape does not change across seasons, whereas there are important seasonal changes in the nongeometrical properties of the landscape (e.g., the appearance of grass and vegetation, snowfall and melting, and so on).

Human adults, in contrast to young children and rats, easily solve the distinctive-color-wall version of the reorientation task in the rectangular environment (i.e., when both geometrical and nongeometrical information are available; see Hermer & Spelke, 1994), suggesting that the most striking limitations of the geometrical module can be overcome during human development. Hermer and Spelke (1994; 1996) thus suggested that the performance of human adults, compared with that of rats and human infants, indicates that some representational systems become more accessible and flexible over development and evolution. These authors suggested that language, and more specifically spatial language, may provide the medium for representing conjunctions of geometrical and

nongeometrical properties in the environment (Hermer-Vasquez, Spelke, & Katsnelson, 1999). Indeed, the ability to orient correctly in the distinctive blue-wall task (Hermer & Spelke, 1994) correlated with the ability of children to produce and use phrases involving “left” and “right” together with “blue” and “white” when describing the locations of hidden objects (MacWhinney, 1991).

It could be that human beings conjoin geometrical and nongeometrical information using language as a medium (Spelke, 2003), but this seems not to be the case for nonhuman animals. We found, in fact, that young chickens (Vallortigara et al., 1990; Vallortigara, Pagni, & Sovrano, 2004) can easily combine geometrical and nongeometrical information (see also Kelly et al., 1998, for similar results in pigeons). The performance of chicks in these tasks, in which they were able to identify the correct location conjoining geometrical and nongeometrical information, is therefore identical to that of human adults and clearly surpasses that of rats or human infants. We recently found that that even fish (*Xenotoca eiseni*) reorient themselves by conjoining geometrical and nongeometrical information in the rectangular arena task (Sovrano, Bisazza, & Vallortigara, 2003, in press; Vallortigara & Sovrano, 2002; Vallortigara, Feruglio, & Sovrano, in press).

Research carried out in my laboratory has further explored the capabilities of encoding geometrical information in the chick’s brain. We found that chicks can learn to localize the central position of a closed environment in the absence of any external cues (Tommasi, Vallortigara, & Zanforlin, 1997). After several days of training, during which food-deprived chicks were allowed to eat food that was progressively buried deeper under sawdust in the center of the floor of an arena, they developed a ground-scratching strategy to uncover the food and eat it. With training, the chicks became more accurate in finding food so that when they were eventually tested in the absence of any food, their pattern of ground scratching was limited to the central area. We also showed that chicks were able to generalize to arenas of different shapes. For instance, when trained to find the center in a square-shaped arena and then tested in a triangular or circular one of nearly the same size, the chicks searched in the central region of the novel arena.

We have also shown that when the environmental change involved a substantial modification in the size of the arena, as is the case for the transition from a square-shaped arena to an arena of the same

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Figure 3.9. Amount of searching behavior as a function of the distance from the center during training in the small enclosure in binocular chicks (*top*) and during test in a larger enclosure of the same shape in binocular (*bottom left*), left-eyed (*bottom middle*), and right-eyed (*bottom right*) chicks. As can be seen, during test, binocular and left-eyed chicks showed one peak located in the center of the large enclosure and another peak located at a distance from the walls corresponding to the previously learned distance from the center in the training (small) enclosure. Right-eyed chicks, in contrast, showed only one peak located at the distance from the walls corresponding to the previously learned distance from the center in the training (small) enclosure. (After Tommasi & Vallortigara, 2001.)

shape, but of a larger size, the scratching bouts of chicks in the test (larger) arena were localized in two regions: in the actual center of the test arena and also at a distance from the walls that was equal to the distance from the walls to the center in the training (smaller) arena (see figure 3.9). Apparently, two behavioral strategies seem to be available to the chicks: (a) encoding a goal location in terms of absolute distance and direction from the walls and (b) encoding a goal location in terms of the ratios of distances from the walls independent of their absolute values. As can be seen in figure 3.9, chicks showed one peak located in the center of the large enclosure and another peak located at a distance from the walls corresponding to the previously learned distance from the center in the training (small) enclosure. Tests carried out under monocular viewing (after binocular training) revealed striking asymme-

tries of brain function: encoding of absolute distance being predominantly attended to by the left hemisphere and encoding of relative distance being predominantly attended to by the right hemisphere (see figure 3.9; Tommasi & Vallortigara, 2001).

When training was performed in the presence of a conspicuous landmark (e.g., a red cylinder) located at the center of the arena, animals searched in the central location, even after the removal of the landmark. Apparently, domestic chicks seem to be able to use the geometrical relationships among the walls of the arena as well, although they were not explicitly trained to do so. Furthermore, marked changes in the height of the walls of the arena produced some displacement in the spatial location of searching behavior, suggesting that the chicks also used the angular size of the walls to estimate distances within the arena.

These results provide evidence that chicks encode information about the absolute and relative distance of the food from the walls of the arena and that they encode this large-scale spatial information even when the orientation of a single landmark alone would suffice for food localization. Encoding of large-scale information using the shape of the arena seems to be based on hippocampal function: Lesions to the hippocampus rendered chicks unable to find the center of the arena in the absence of the landmark or to follow the landmark when it was displaced from the center of the arena to another location (Tommasi, Gagliardo, Andrew, & Vallortigara, 2003).

Previously, similar studies on spatial localization in pigeons using expansion tests provided somewhat different results. Spetch and her colleagues, using both naturalistic settings (Spetch et al., 1997) and a touch-screen procedure (Spetch, Cheng, & MacDonald, 1996), compared pigeons' and humans' search for an unmarked goal located in the middle of a square array of four identical landmarks. Humans searched in the middle of expanded arrays, whereas pigeons preserved distance and direction relative to a single landmark. I believe that the difference in performance between chicks (and humans) and pigeons reflects the fact that encoding based on arrays of discrete landmarks is different from encoding the shape of a test environment based on extended surfaces (see also Pearce et al., 2001) and may have different neural substrates (see, for evidence, Vallortigara et al., 2004). Recent research carried out by Spetch, Gray, and Nguyen (2002) seems to confirm that searching based on surfaces of an enclosure is different from searching based on an array of discrete landmarks: When tested in the center localization task in a closed arena, rather than with an array of discrete landmarks, pigeons showed both relative and absolute encoding when tested in expanded arenas, exactly as did chicks in the tasks that we investigated.

CONCLUSIONS

For a long time, the domestic chick has been recognized in comparative psychology as providing ideal material for the study of early learning (Spalding, 1873). More recently, the chick has become a reference model for the investigation of the neurobiological basis of certain forms of learning such as imprinting (Horn, 1998) and passive

avoidance (Rose, 2000), and it has become the most used vertebrate species for investigation of lateralization of brain functions (Andrew, 1991; Andrew & Rogers, 2002; Rogers, 1996; Vallortigara et al., 1999). Several features of the chick model have facilitated neurobiological research, the most important being the fact that the chick's experience can be precisely controlled both in the embryo and immediately after hatching and that at an early stage of its life, the chick is capable of highly organized patterns of behavior, making very early learning accessible to investigation.

The brief survey reported here shows that chicks possess quite remarkable cognitive abilities that can be revealed using as tools those forms of early learning that have been the concern of classic ethologists and early comparative psychologists. This evidence, together with reasonable knowledge of the chick's neuroanatomy (Rogers, 1995), can allow investigators of the brain-mind relationship to proceed a step further, moving from investigation of the neural basis of simple basic learning abilities (imprinting, passive avoidance learning) to cognitive phenomena that have direct counterparts in humans, such as completion of partly occluded objects, biological motion perception (Regolin, Tommasi, & Vallortigara, 2000), and object and spatial representations (Vallortigara, 2001, 2004). Some recent work by the group headed by Toshiya Matsushima in Japan has provided remarkable evidence from single-unit recordings in the unanesthetized chick on the neural machinery that may underlie the chick's anticipation of forthcoming events, particularly the quality/quantity and temporal proximity of rewards (Matsushima, Izawa, Aoki, & Yanagihara, 2003; Aoki, Izawa, Yanagihara, & Matsushima, 2003). In the next few years, we can thus expect new recruits among both neurobiologists and comparative psychologists who are attracted to comparative cognitive research by the many possibilities offered by the humble chick. Certainly, it will be increasingly difficult to seriously consider the expression "chicken brain" as an insult.

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