



## Review

## From natural geometry to spatial cognition

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## ARTICLE INFO

## Article history:

Received 6 May 2011

Received in revised form 7 December 2011

Accepted 13 December 2011

## Keywords:

Spatial memory

Comparative cognition

Spatial cognition

Geometry

Landmarks

Reorientation

## ABSTRACT

A review of selected works on spatial memory in animals and humans is presented, and some ideas about the encoding of geometry and its role in evolution are presented, based on recently accumulated evidence from psychology, ethology and the neurosciences. It is argued that comparative analyses at the level of both spatial navigation behaviors and their underlying neural mechanisms may provide a solid foundation for the biological origins of organisms' spontaneous ability in dealing with geometric concepts. To this aim, the representations of space underlying memory tasks involving discrete (i.e., landmark arrays) or continuous elements (i.e., enclosed environments) are evaluated and compared as regards the impact of their geometric arrangement.

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## Contents

1. Introduction .....	799
2. The building blocks of phenomenal space .....	802
3. Landmarks and spatial relationships .....	802
3.1. Encoding distance and direction from single objects .....	802
3.2. Encoding geometric information in simple arrays .....	803
3.3. Encoding geometric information in complex arrays .....	806
3.4. Discriminating objects by geometry in an array .....	808
4. Geometry of enclosed spaces .....	809
4.1. The hypothesis of modularity in the spatial domain .....	809
4.2. Reorienting in large and small spaces .....	815
4.3. Middle, center and other singularities .....	816
5. Natural geometry: the role of experience and innate factors .....	818
6. Neural mechanisms underlying the encoding of geometry in enclosed spaces .....	818
References .....	820

## 1. Introduction

Since the early days of empirical research on comparative psychology, a vibrant interest for the phenomena of animal orientation, and for the mental processes (and the underlying neural

functions) that allow animals to store, process and retrieve spatial information, was soon established (Darwin, 1873; Viguier, 1883). This proved particularly true in the domain of research on spatial navigation, namely “the process of determining and maintaining a course or trajectory from one place to another” (Gallistel, 1990). Although comparative cognition is a relatively young field in the scenario of science, the number of researchers devoting their interest and efforts to this topic over the last century has increased exponentially. Just to give an example, international conferences in ethology, psychology and the neurosciences nowadays always include at least one session on spatial memory or spatial

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**Table 1**

A list of fundamental terms, basic concepts and mechanisms dealt with in the article.

Building blocks	Basic concepts	Basic mechanisms
<p>Left–right</p> <p>Directional sense</p> <p>The direction or position on a certain side in relation to a specific point of reference as assumed by an agent</p>	<p>Point</p> <p>A point is that which has no part</p>	<p>Dead reckoning</p> <p>Process of estimating one's current location based on movements made since the last known position or a fix one by integrating speeds over elapsed time, and course. Also known as path integration. New values are always calculated from previous values, hence any errors are cumulative; any external uncontrolled displacement disrupt the estimated calibration with the external world (Collett and Collett, 2000; Etienne and Jeffery, 2004)</p>
<p>Above–below</p> <p>The point or area in or to a higher position or place in space – the point or area at or to a lower position or place in space</p>	<p>Line</p> <p>A line is breadthless length</p>	<p>View-based navigation</p> <p>A process for navigation which involves a quantitative reduction of mismatch between a remembered local view of the environment (snapshot) as seen from a certain point and orientation, without information about distances or specific spatial relations but retinal sizes and separations (Cartwright and Collett, 1983). With the increase of locations there is an overload of stored images</p>
	<p>Surface</p> <p>In Euclid terms a surface is that which has length and breadth only; a surface does not have to be a plane; a face of a solid is a surface</p> <p>Animals seem to use the surface layout geometry to be successful in spatial reorientation when they represent a target location by the metric (long/short) and sense (left–right) disposition of the surfaces</p>	<p>Guidance</p> <p>Association between a conspicuous feature perceptible at a certain distance and destination. A change in the beacon may only lead to failure in reaching the destination (O'Keefe and Nadel, 1978)</p>
<p>Front-Back</p> <p>The point or area that lies ahead to a specific point of reference as assumed by an agent – the point or area that lies at the back</p>	<p>Volume</p> <p>A volume is that which has length, breadth, and depth</p>	<p>Piloting</p> <p>Identification of a spatial position and orientation with respect to a configuration of familiar landmarks, or reference points, with directions and distances (and related features such as size and appearance of a visual landmark) to those reference points (Gallistel, 1990)</p>
<p>Inside–outside</p> <p>The space closest to a specific point of reference and in between it and a certain boundary or limit – the space beyond a boundary or limit</p>	<p>Boundary</p> <p>In Euclid terms a boundary is that which is an extremity of anything</p>	<p>Compass</p> <p>A biological compass is a mechanism that allows an animal to determine and to maintain a direction in space during navigation. The local inclination of the geomagnetic field (Wiltschko and Merkel, 1966), the pattern of polarized light (von Frisch, 1949) and the apparent movement of celestial bodies (sun: Schmidt-Koenig, 1958; stars: Emlen, 1970) can all provide the sensory basis for the biological compasses. Directional information obtained from stationary visual landmarks in an environment are considered apart</p>
<p>Local-global</p> <p>Phenomenal domain of the visual field that determines a definite region or portion of space, a restriction to one place or region – the infinite space surrounding an individual but that goes well beyond the restriction of the visual field</p>	<p>Angle</p> <p>From the Latin word <i>angulus</i>, meaning “a corner”. In Euclid terms, a plane angle is the inclination to one another of two lines in a plane which meet one another and do not lie in a straight line</p>	<p>Navigation</p> <p>Navigation is the process of determining and maintaining a course or trajectory from one place to another (Gallistel, 1990)</p>
<p>Proximal-distal</p> <p>Information gathered by direct exploration in the immediate action range of an individual–information inferred at a distance</p>	<p>Axis</p> <p>Comprises a variety of parameters describing a shape, or a local portion of a shape, in terms of its global geometric properties (Cheng, 2005a,b)</p>	
<p>Idiothetic-allothetic</p> <p>Endogenous information (proprioception of an actuator and vestibular information) – information gathered from the external world (vision, audition, touch, smell). These two sources are supposed to be merged for an effective representation during navigation</p>	<p>Shape</p> <p>In Euclid terms a shape is a set of points; a part of the space occupied by the set as determined by its external boundary invariant to location and orientation, translations and size and other featural properties. The concept has been applied also to describe the arrangement of discrete objects in arrays of small numerosity, assuming elements as point in space and boundaries as a closed polygonal line connecting each element in a sequence</p> <p>Position</p> <p>Spatial location identified by the relations of objects in a certain frame of reference</p> <p>Distance</p> <p>In Euclid terms a distance is a metric measure of length separating two points in a plane</p>	

Table 1 (Continued)

Representations	
<p>Topological</p> <p>In Greek terms: <math>\Sigma</math> place, and <math>\Psi</math> definition, <i>topology</i> expresses the possibility of defining a place devoid of all metric attributes but comprising the concepts of order, enclosure, and adjacency. In some very specific and human-made environments, such as underground railway systems, distances and directions are completely ignored and only the important information for travelers – order, enclosure, and adjacency – is preserved</p>	<p>Geometrical (from the Greek terms <math>\Psi\epsilon\omega</math> Eearth, and <math>\mu\epsilon\tau\rho\iota\alpha</math> measurement)</p> <p>Defining a place including metric concepts like distances, directions, and elevations. Spatial processing proceeds along metrically expressed distances and directions: this is apparent in every simple estimation of distances in humans (e.g., before placing an object in a certain position; before deciding whether to reach a specific place by walking; before planning a certain route; and so on) and in other animal species (e.g., before jumping from one branch to the next; before deciding the shortest path to escape the predator or to reach the food before a conspecific; and so forth)</p> <p>Organisms may encode places in the continuous spatial layout and their Euclidean geometric relations: several species have been shown to be capable of determining the center of an environment, or identifying a position on the basis of its relative location to other salient points</p>

cognition among others. In trying to convey the most useful information to a general audience interested in the scientific study of natural spatial cognition, we shall first present a sketch of the type of experimental evidence provided by research in comparative spatial cognition, to then focus on some aspects of the encoding of geometry that stemmed from recent empirical investigations in a number of species and could be useful to identify some points of interest toward an “evolutionary history of geometry”.

Let us consider the classic research work by Nikolaas Tinbergen on the homing behavior of digger wasps of the species *Philantus triangulum* (Tinbergen, 1932; Tinbergen and Kruyt, 1938). These wasps lay their eggs in burrows dug in the soil, and refurbish the innermost section of the nest chambers with dead bees in order for their progeny to feed as soon as they hatch. Searching for food often brings a wasp far from the nest, and the first phase of this behavior consists, as Tinbergen observed, in a circuitous flight over the nest. The very small entrance to the underground nest is barely discernible even from a short distance, and Tinbergen showed that wasps learn the spatial arrangement of landmarks around it during this flight, in order to rely on its visual appearance to localize the entrance when homing back. He placed a number of pine cones in a circular array centered on the entrance of the nest and let the wasp to get accustomed to the array for a number of flights. Then, during one of the wasp’s outward journeys, the array was quickly moved some distance from its original position. When the wasp returned, it oriented toward the center of the shifted array, thus demonstrating that the last part of the homing flight is under control of visual cues, namely the array of pine cones. This experiment is a good example of how a navigating organism relies upon the spatial organization of visually perceived objects, in order to localize a goal. The original research by Tinbergen was then followed by a number of further studies by himself (Tinbergen, 1951) and van Beusekom (1948). They attempted to understand how the spatial organization of visual landmarks could influence the wasps’ recognition of the nest surroundings, by investigating the effects of overall changes in the size and shape of these arrays, or in the local identity of their elements (pine cones, stones, etc.) on the choice behavior of wasps that were first habituated to a specific array during some time, and were then faced with the presence of a second neighboring array at the moment of their return to the nest. Apparently, wasps pay more attention to the overall shape of the array rather than the local elements: for instance, when wasps were habituated to a circular array of pine cones they preferred a circular array of stones more than a triangular array of pine cones.

Those pioneering experiments illustrate how researchers still investigate the mechanisms that allow animals to orient in space. Broadly speaking, these methods involve transformations of the spatial arrangement in the animal’s environment and the observation of some selected behavior before and after the change is brought about (see Cheng and Gallistel, 1984; Cheng and Spetch, 1998). It is assumed that the behavior observed after these transformations reflects in some way the encoding in memory of the

spatial elements in the situation under study. Choice of an array rather than a different one adjoining it, in the experiments by Tinbergen and van Beusekom, for example, would imply that the wasps recognized its spatial arrangement as more resembling the one they were habituated to. The conclusions that can or cannot be drawn from these observations depend largely on the ability of the experimenter in devising the spatial transformations, in order that the observed behavior may actually tell something meaningful about the way spatial information is encoded and computed by the animal.

The questions posed in this experimental perspective can be simplified as such: first, it is asked whether and how animals have a sense of their position in space (“Where am I?”). Another problem consists in understanding how places that may not be directly accessible to the senses are represented (“Where is that place?”). A further question stems from the relational nature of space: assuming that an organism occupies a given (and recognized) place and that other places are represented in memory as well, the problem arises of how this system of relationships is encoded (“Where is place A relative to place B?”). In the present article, a review of selected studies addressing the contribution of visuo-spatial information to these questions is presented.

These can appear trivial questions, but their study makes sense if we just think about the spatial problems that have to be managed by organisms dealing with the most diverse situations related to their survival and everyday activities (finding food over a territory and the way back home, migrating to other regions for overwintering or breeding, avoiding risks associated to certain places such as predators, patrolling the territory in search of potential mates, and so on). In the following paragraphs we will summarize some basic notions about the core elements of spatial cognition in animals, to then focus on recent research that provided insights on the representation of places based on geometry. A significant amount of the extant literature on navigation, spatial memory, and reorientation will be carefully analyzed, based on a subdivision into two main aspects: (I) localization with reference to discrete spatial elements (landmarks) and (II) localization with reference to continuous surfaces (enclosed environments). This review will be centered around the use of relational rules, the nature of the configurational information provided by discrete elements, and the primacy of geometric over non-geometric information (the debate on the so-called ‘geometric module’), but some space will also be devoted to the aspects of early experience in the encoding of geometry and the neural underpinnings of natural geometry. For reasons of space, the review is far from being comprehensive, especially on the neuroscientific side, on which very good and recent reviews have been published (e.g. Derdikman and Moser, 2010; Postma et al., 2008; Wolbers and Hegarty, 2010). Table 1 contains a taxonomy of elements, concepts, mechanisms, and representations, that are taken from geometry, common language, and behavioral sciences and that will be crucial and often referred to in the following paragraphs.

## 2. The building blocks of phenomenal space

A first distinction that should be brought about concerns the phenomenology of experienced space: a rough division between local space and global space fits the purpose. This applies especially to organisms that move about in space under visual control (Gibson, 1979). The visual field (although differing in extension between animal species) is a window on a restricted portion of the surrounding world. Species that evolved visual systems differ in the degree of lateral placement of their eyes, but a general stance will be taken here, without further analyzing the lateralization issue. The phenomenal domain of the visual field is that of objects (including inanimate and animate objects, and their parts) and may be labelled local space. On the other hand, the environment, conceived as the space surrounding an organism, is the “container” that comprises the objects that can be perceived inside the boundaries of the visual field, and those that fall out of the boundaries, and may thus be termed global space. Despite consisting of the same basic elements as local space (objects and parts), global space, at least according to our shared human experience, is perceived as something more than just a multiplicity of objects, its extension and identity being present and continuous despite the unavoidable “piecemeal” nature of the sensory input. An important idea in the psychology of perception that is of much value in this respect is that of amodal perception or, more specifically, amodal completion (Kanizsa, 1979). Briefly, amodal completion is the perceptual phenomenon that gives rise to the compelling impression of ‘wholeness’ evoked by objects that are partly concealed by other objects or by their own parts and appendages. The fact that fragments of an object are not visible because they are covered by other interposed objects do not prevent us to perceive the partly occluded object in its entirety, and the missing parts are said to be perceived “amodally”, that is, they are present and complete without being actually perceived in the sensory modality. On a larger scale this also applies to the impression of continuity and extension that the space around our body elicits: the boundaries imposed by the visual field do not prevent us to experience the surrounding environment as a whole. Experimental evidence of amodal completion in object vision also in non-human animals (Kanizsa et al., 1993; Regolin and Vallortigara, 1995; Deruelle et al., 2000; Sovrano and Bisazza, 2008; Tvardíková and Fuchs, 2010), suggests that other animal species as well, might experience space as extending beyond the visual field in a unified and continuous fashion.

This distinction being established, it must be said that much of the knowledge about spatial cognition in animals and humans can be divided into two main subfields: the processing of information peculiar to local space, and that peculiar to global space. Strictly speaking, a division can be traced between the empirical work carried out to understand the spatial representations and operations that take place on the local space of visual stimulation, often limited to a restricted portion of the field for technical convenience (i.e., the frontoparallel space of a computer display) and the research that deals with the spatial representations and operations that concern the global space that an organism travels by. Both domains can be described mathematically as spaces where the meaningful information is metric in nature and thus includes both distance and direction as the two main building blocks. It must be underlined, however, that the debate is still lively concerning whether and how the actual perception of local space departs from Euclidean metrics (Shepard, 1964; Suppes, 1977; Krantz et al., 1989), and some alternative metrics have been proposed to provide a more plausible account, such as Minkowskian (Attneave, 1950), Riemannian (Luneberg, 1947) and affine metrics (Todd et al., 2001). Furthermore, the rules governing global space and local space might prove to be the same, as some empirical studies have shown (compare for instance Cheng, 1989 and Spetch et al., 1992), but much research

has still to be carried out to provide a unified account bridging them. Hereafter the discussion will concern spatial cognition at the global level, assuming a substrate (such as terrain or seafloor) as a two-dimensional plane over which behavior, and thus spatial orientation, takes place by means of vision.

The parsing of the surrounding environment into meaningful elements brings us to another distinction between two relevant concepts, this time of a more operational nature, the distinction between landmarks and surfaces. In a given environment these are the major classes of external, or *allothetic*, spatial cues usually available for orientation (and opposed to orientation dependent on internal or *idiothetic* information, such as vestibular or kinesthetic signals due to the animal's own displacement). The notion of landmark is that of any object or part of object, conspicuous enough to be associated with its spatial location. Landmarks are ubiquitous in natural and artificial (architectural) environments and their exploitation in spatial navigation has been studied extensively in animals and humans. Ideally, a landmark can be imagined as a point in space, so that its cartesian co-ordinates relative to an established frame of reference can be thought of as the relevant spatial content, whereas perceptual features (color, shape, texture, and all other sensory aspects) are of some value in terms of spatial analysis only to the extent that they help in the recognition of its identity and the discrimination between other landmarks (and thus between the spatial positions associated with them; more will be said on this issue in the following sections). On the other hand, surfaces are present in natural environments in a much less ubiquitous way than they are in the artificial, man-made space of architecture and urbanism, at least when we think of a surface as a flat, level and continuous two-dimensional plane such as a wall, ceiling or floor. However, parts of the natural environment, except for some actual cases of surfaces *strictu sensu* (the surface of a lake, a snow field, a smooth vertical cliff), can be often perceived as surface-like at least in a loose way, as in the case of the visual appearance of a mountain, or even that of an inhomogeneous collection of discrete objects such as the trees of a forest seen from a distance. The study of spatial cognition has deliberately focussed on processes peculiar to the analysis of these two main classes of orienting elements, and on their interaction.

Another fundamental distinction could be traced between the proximal and the distal space. The former refers to a portion in space in the immediate action range of an individual. Spatial information in the proximal space could be gathered by direct exploration. By contrast, information in the distal space could be inferred at a distance. The contribution of visual cues in this context has been extensively examined, particularly in small scale laboratory settings, even though information sources other than vision can, at least in principle, provide useful information as well.

## 3. Landmarks and spatial relationships

### 3.1. Encoding distance and direction from single objects

The simplest form of spatial orientation is that involving a goal directly associated with a visual object. When the spatial location of a landmark coincides with the goal, the orientation behavior (‘aiming’ or ‘target approaching’) simply requires that the navigating organism recognizes the landmark in its local space and moves toward it. A slightly more complex mechanism involves orientation toward a hidden goal located at a short distance from a landmark or a set of landmarks, as in the case of the digger wasp searching for the entrance of its burrow. Orientation toward a goal nearby a landmark (also called a “beacon”) implies that the animal, besides being able to identify the beacon as such and to recognize it among other potential landmarks, is also able to determine the distance and direction of the goal relative to it. This mechanism may involve

a single landmark, provided that it is visually distinctive and/or radially asymmetrical, otherwise only distance information can be obtained efficiently. A white cylinder located over a featureless space, for instance, can in principle be used by a navigating organism only to determine the distance  $d$  from a hidden goal, namely the locus of all points on the plane that are equidistant from the goal (a circle having the cylinder in its center and a radius of length  $d$ ). A cylinder with a visual marking on its surface, instead, would make both distance and direction to a goal potentially available, pinpointing unambiguously to a single location.

Orientation with reference to a single landmark has been studied, among others, in the honeybee, *Apis mellifera* (Cartwright and Collett, 1983) and in the Mongolian gerbil, *Meriones unguiculatus* (Collett et al., 1986) using the same method. The animals were first trained to find a food reward (a sucrose cup in the case of bees and a buried sunflower seed in the case of gerbils) located at a given distance and direction from a cylindrical object in a featureless room. After training, control trials were carried out in which the reward was absent and the spatial distribution of the animal's searching behavior was measured. Bees and gerbils searched in the spatial region where food was found during the training trials, showing that they remembered its position. Among trials carried out in the absence of food, some test trials were interspersed during which the cylinder was either removed or replaced with a differently sized replica (halved or doubled). When the cylinder was absent, animals searched randomly, thus showing that they were actually using it as a landmark. Both bees and gerbils responded to reductions in cylinder size searching proportionally closer to it, whereas a magnification of the cylinder resulted in searching proportionally further away in bees but not in gerbils, that searched at the same distance as in the control trials. These results show that in the case of bees, distance from a single landmark is likely evaluated as a function of the retinal projection of the landmark size, an important monocular cue. By contrast, the apparent size of the landmark was not the only cue used by the gerbils to locate the reward. A relevant question remains, however, as to whether gerbils relied on a view-matching strategy to solve the task at all. In apparent contrast with the prediction of view-based matching, the gerbils did not search farther from the landmark, toward the perimeter wall of the arena, in the landmarks expansion test. Nevertheless, differences in visual acuity as well as differences between the size of the arena, particularly in relation to the subjects' size, might have favored a stronger reliance on extra-landmark visual cues, particularly those providing distance information from the perimeter wall of the arena, in rodents, but not in bees.

Another monocular cue that has been shown to control estimation of distance from a landmark when searching for a hidden goal is parallax, namely the relative motion of the retinal projection of an object as a function of the subject–object distance (see Gallistel, 1990). Animals with frontally placed eyes are of course able to obtain more accurate (short) distance estimations by exploiting binocular depth perception (stereopsis).

It has been hypothesized that bees store in their memory the appearance of landmarks as seen from the position of the goal, and can then return to the goal by moving in the environment until the image on their retina matches the stored image. In other words, bees' spatial memory would be reduced to an operation of pattern matching between the stored view and the current view, and in an operation of discrepancy reduction by means of displacement, a mechanism that has been termed "snapshot memory" (see Collett and Collett, 2002, for a review on memory-based navigation in other insects). However, in both experiments described above it is implicit that the animals had estimated the direction to the goal by reference to some visual cues other than the landmark (whose intrinsic radial symmetry would have allowed animals to evaluate accurately distance alone), and it must be concluded that these

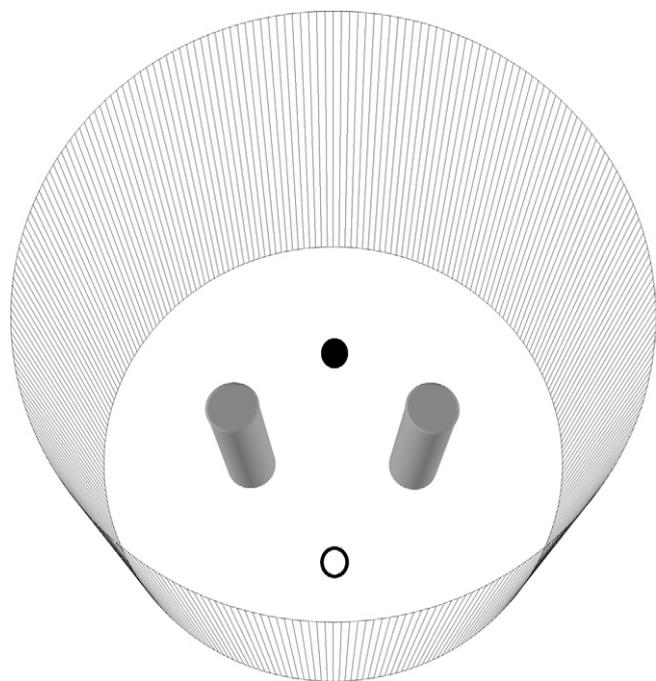
cues were obtained from uncontrolled features over the walls, floor, or ceiling of the experimental room. Another demonstration that distance and direction to the goal can be actually evaluated with reference to a single landmark, was provided by Collett et al. (1986), carrying out a modified version of the same experiment. Gerbils were trained to find the sunflower seed at a constant distance and direction from a landmark, but a second landmark was present throughout training and its position changed from trial to trial, thus providing irrelevant information. During control trials, gerbils searched at the correct location, showing that they had learnt to rely upon the stable landmark and to ignore the unstable one (see Biegler and Morris, 1993, for similar results on rats).

Of course, studying orientation based on a single landmark in an absolutely featureless environment is a hard challenge to researchers, since the presence of barely visible edges, discontinuities or illumination inhomogeneities can never be totally excluded, and can thus be exploited by the navigating organism. The description of those experiments was nonetheless relevant, because their results suggested with a certain confidence that, whatever the mechanism at work, animals can estimate distance and direction with reference to a single landmark. As it has already been assumed, these parameters can be thought of as the main elements of spatial analysis. Other experiments carried out on bees and pigeons (*Columba livia*) showed that goal localization with reference to a single landmark is likely the outcome of two separate processes deriving distance and direction independently (Cheng, 1994, 1998), a result that has been interpreted against the assumption of a memory mechanism based on snapshot matching, rather supporting a mechanism based (I) on internal representations of the vectors connecting the landmarks to the goal and (II) on the computation of the trajectory to the goal as a vector sum (Cheng, 1988, 1989, 1990; but see Cheng and Sherry, 1992; Gould-Beierle and Kamil, 1996).

### 3.2. Encoding geometric information in simple arrays

We shall now focus on the ability of animals at orienting toward a goal with reference to more than one landmark, bringing us closer to the main topic of this article, the encoding of geometry. A landmark array offers a better frame of reference to derive directional information, limiting the number of potential ambiguous alternatives to the actual goal and making less likely that unwanted cues (not belonging to the geometric structure of the landmark array) take control over the determination of direction. Indeed, in order to oblige animals to rely only upon landmarks when searching for a goal, the position and overall orientation of the landmark-goal constellation is usually changed in the experimental environment from one trial to the next, thus reducing the likelihood that animals use other spatial cues. It is worth considering here that these procedures systematically set into conflict separate geometric information sources, especially in the case the macroscopic surface layout of the arena presents an asymmetrical structure.

As already alluded in the description of the homing behavior of digger wasps, even hymenopterans can rely upon the overall appearance of a landmark array during navigation, in other words they can attend to the global visual shape arising from separate elements. This is an ability that depends on another very general law of perceptual organization, namely the fact that a number of discrete elements are perceived as a unitary form according to simple principles, such as proximity and similarity (Koffka, 1935; Kanizsa, 1979). It is not surprising that digger wasps, pigeons or gerbils share these perceptual laws with humans, since they provide a common ground for experiencing the visual world in a meaningful fashion, a world that is occupied by objects. Early in the last century, the psychologist Mathilde Hertz had already shown that honeybees and jays (*Garrulus glandarius*) perceive complex forms composed of many separate and identical elements, by demonstrating that



**Fig. 1.** When in a circular enclosure and in the presence of a pair of identical landmarks, the goal (marked by the filled dot) has a geometrically equivalent “twin” position defined by the same geometric relationships (open dot) with respect to the landmarks.

they can learn to choose one element in the structure, an ability possible only if one assumes that the animals perceive the shape and orientation of the overall pattern (Hertz, 1928, 1935). Those by Hertz were somehow the first accounts of spatial memory tasks accomplished by animals that made use of geometry as an orienting cue.

The minimally conceivable instance of a landmark array, however, consists of only two landmarks. Ideally, a goal located at a given position with reference to a pair of landmarks, if these are identical in appearance and the surrounding environment is featureless, has a geometrically equivalent “twin” position, that is a position sharing the same geometric relationships (distance and direction) with respect to the array (see Fig. 1). This ambiguity is immediately resolved, at least in principle, if the appearance of the landmarks is made to differ or, again, if the surrounding environment contains other spatial features that can provide directional information. Moreover, the classes of transformations that can be carried out when using multiple landmarks are (1) the removal of one or more landmarks; (2) the displacement of one or more landmarks; (3) the addition of one or more landmarks; (4) changes in the identity (size, color, shape, or any combination of these) of one or more landmarks; and selected combinations of these classes of transformations.

Collett et al. (1986) trained gerbils to localize a sunflower seed buried at a fixed distance and direction with respect to an array of two landmarks. In this case the array retained a stable position and orientation in the experimental room throughout the training phase. As expected, gerbils searched in the correct position during control trials. This confirmed the use of directional cues emanating from some room features, as in the experiment with the single landmark, otherwise the gerbils should have searched also at the equivalent twin location (as in Fig. 1). During test trials, when one landmark was removed from the array, gerbils searched consistently at two locations: apparently they were using the residual landmark as if it were, in turns, one or the other of the two landmarks which were present during training. In another test the array

was expanded, shifting one of the landmarks apart in one direction: gerbils searched mainly in two distinct regions, each located at the exact distance and direction from a single landmark. These experiments show that gerbils encoded the distance and direction from each landmark, and used this information with reference to individual landmarks independently, without any evidence of averaging or extrapolation. However, although the spatial search strategy appeared to be based on individual vectors, the array must have been encoded also as such, since the gerbils could determine “which landmark was which” in the expansion test, as shown by the fact that they searched inside the region comprised between the two landmarks and not externally to it. The array might have acted as a reference system, providing the information about the boundaries of the spatial region where the goal had to be searched. In order to use this reference system, it can be deduced that the gerbils had encoded it as a unified structure.

Other gerbils were trained with an array of two visually distinctive landmarks, which was shifted about in the experimental room from one trial to the next, while the landmark-goal constellation was kept stable. During control trials, gerbils searched at the correct location, showing that they had learned the position of the goal relative to the array, since a single landmark would not be sufficient to determine direction, and extra-array cues would be uninformative. This also proved that gerbils correctly distinguished between the visual identities of the landmarks (and associated the correct distance and direction to the goal from each of them), otherwise two major regions of searching would have been obtained instead of one. In another condition the orientation of the array was kept constant from trial to trial, the gerbils were released always on one side of the experimental room, and tests were carried out in which the gerbils were released on the opposite side: gerbils searched again at the correct location, disregarding of the release point, a further evidence that gerbils were treating the whole landmark array as a reference system.

In a recent study, Rodrigo et al. (2006) trained rats (*Rattus norvegicus*) to reach a goal signaled by a beacon in the presence of a second landmark located at a short distance; subsequently the rats were tested after placing the beacon progressively farther away from the other landmark. During these tests the rats’ search pattern shifted in the direction of the second landmark (a phenomenon known as spatial peak shift or spatial generalization), suggesting that, even when they are not the most informative, all objects in an array are taken into account during spatial learning (for similar results in pigeons, humans and bees, see respectively Cheng et al., 1997; Cheng and Spetch, 2002; Cheng, 2000).

Avian species have been largely used in spatial memory tests involving arrays of two landmarks. In a series of experiments comparing pigeons and humans, Spetch et al. (1997) trained pigeons to find a food reward buried under wood chips at a distance from two identical landmarks. The landmark-goal constellation formed an isosceles triangle whose base  $b$ , was defined by the landmarks and whose height  $h$  (the virtual segment from the midpoint between the landmarks to the goal), was half of  $b$  in length. Control trials carried out in the absence of food showed that pigeons searched at the correct location. During test trials the distance between landmarks was either increased (expansion tests) or decreased (contraction tests). In both cases pigeons searched in an unsystematic fashion between the landmarks but at the correct perpendicular distance  $h$  from  $b$ , and no evidence of averaging was found. The test trials, moreover, did not show any preservation of the landmarks-goal constellation shape, in that pigeons did not search in the position that maintained the spatial relationships to the landmarks as it could be obtained through a similarity transformation of the training arrangement. However, it is interesting to notice that pigeons must have used the whole array as a reference system rather than individual landmarks (as in the case of Collett et al.’s gerbils discussed above),

since they were able to search at a rather constant distance  $h$  from  $b$ , where  $b$  is the imaginary line connecting the landmarks. Humans instructed to localize the goal in a table-top version of the same task, in contrast, searched systematically along the symmetry axis in both types of test trials. They proportionally scaled the perpendicular distance of their spatial search in the expansion test, according to the amount of expansion of  $b$ . In the contraction test, however, this 'shape preservation' was not observed, and subjects concentrated their searching behavior at the learned distance  $h$  from the contracted array. Apparently, human subjects were using configurational information and were able to scale their spatial search according to an increase (but not to a decrease) in size.

Kamil and Jones (1997) trained birds of a corvid species, Clark's nutcrackers (*Nucifraga columbiana*) in a task involving two landmarks and the use of a geometric rule. These birds are very well-known for their outstanding spatial memory abilities, being able at remembering the position of tens of thousands of food caches stored in hiding sites scattered over their territory (Vander Wall, 1990), and their abilities have been shown to depend on spatial memory (Vander Wall, 1982). In the experiment by Kamil and Jones (1997), Clark's nutcrackers had to localize a food reward hidden halfway between two visually distinctive landmarks on the floor of a laboratory room. The methodology involved a multiple-exemplar training schedule, in that the inter-landmark distance during each trial of the training phase was set at a particular value chosen in a fixed set (20–120 cm, with 20 cm increments). During control and test trials the nutcrackers' spatial searching was measured in the absence of the reward, respectively using the same set of inter-landmark distances and a novel set (30–110 cm, with 20 cm increments). Precise searching behavior and generalization were observed: birds searched consistently halfway during the control trials and also with novel inter-landmark distances during test trials. Kamil and Jones concluded that nutcrackers had learned a general rule based on the encoding of geometric relationships existing between landmarks, rather than individual landmark–goal relationships. This conclusion might perhaps sound a bit too confident about the spatial abilities of these birds, because it makes a claim about a learned 'general rule'. However, it does not suppose that birds were able to find a position halfway between landmarks by means of an explicit representation of a concept, as it may seem at first sight. It simply assumes that birds had encoded spatial relationships between landmarks, and that these relationships had a role in a searching behavior that reflected the observable properties of that concept – a closer look at the data and further experiments were necessary to understand more precisely which role they had. When error data (the amount of displacement from the physical midpoint) were separately analyzed in the dimensions parallel and normal to the landmark array, Kamil and Jones found that only the error component parallel to the array was directly proportional to inter-landmark distance. This seems to suggest that two processes were at work during the birds' spatial orientation, one for identifying the virtual segment connecting the landmarks and one for determining the exact position along that segment. The latter could have involved either a configural process (based for instance on the comparison of the distance from each landmark) or the evaluation of the distance from one landmark only. To tackle this problem, Kamil and Jones attempted to distinguish whether the halfway position was encoded independently of the array orientation in the experimental room. Throughout training, the array had retained the same North–South absolute orientation (and the landmarks had never been swapped). In additional test trials the orientation of the array was thus modified, with rotations of 15, 45 or 90°. Apparently, these changes influenced the searching pattern depending on the extent of rotation, since the smaller rotations (15 and 45°) induced searching behavior based more on the array-centered axis, whereas the 90° rotation dramatically induced the animals to search mostly

along the room-centered axis, implying that a single landmark was used to pinpoint the goal.

In a following study (Kamil and Jones, 2000), Clark's nutcrackers were trained using the same protocol to find a hidden goal  $G$  that bore precise spatial relationships with respect to two distinctive landmarks,  $A$  and  $B$ . Four groups of birds were trained, each group using one of the following rules: the goal could be found (i) halfway between the landmarks (as in the previous experiment), (ii) at a proportional distance between the landmarks (namely one quarter from landmark  $A$  and three quarters from landmark  $B$ ), (iii) at a constant and equal distance from both landmarks outside the line connecting them, or (iv) at a constant and equal direction from both landmarks outside the line connecting them. For the first two groups, the goal  $G$  was always on the straight line  $AB$  connecting the landmarks, whereas for the two other groups the goal  $G$  was always on the perpendicular bisecting the straight line  $AB$ . In the group experiencing constant distance, hence, distance  $GA$  was the same as distance  $GB$  and their value was held constant from trial to trial, whereas angle  $ABG$  (which was the same as angle  $BAG$ ) changed, since inter-landmark distance was made to vary from trial to trial. In the group experiencing constant direction, the angle  $ABG$  was the same as angle  $BAG$  and their value was held constant from trial to trial, whereas distances  $GA$  and  $GB$  changed, since inter-landmark distance was made to vary from trial to trial. Clark's nutcrackers in each group learned to localize the goal with the various inter-landmark distances. Moreover, they transferred this ability also to novel inter-landmark distances, both inside (interpolation) and outside (extrapolation) the fixed set of training distances. However, the group trained to find the goal at a constant distance learned more slowly, and searched less precisely during both control and test trials. This group also showed no transfer during extrapolation tests, suggesting that learning and generalization were harder to achieve if based on distance rather than on direction. Swapping landmarks (equivalent to a 180° rotation) had little influence on searching behavior, suggesting that the configuration was used rather than individual landmarks in this case. When one landmark was removed, all groups showed accurate spatial searching with respect to the position (and appearance) of the residual landmark. Similarly to the previous experiment, a small rotation of the array (22°) did not prevent accurate search with respect to the array, but a larger rotation (90°) did, inducing animals to rely more on individual landmarks rather than on the overall array (see also Jones and Kamil, 2001, for similar results).

Kamil and Jones (2000) concluded that the performance of Clark's nutcrackers in these tests depended on the encoding of geometric rules, based both on local and global spatial cues (distances and directions evaluated respectively from individual landmarks and from the array as a whole), conceding that distance was estimated more easily from individual, near, landmarks (see also Bennett, 1993; Gould-Beierle and Kamil, 1999 for analogous results), whereas direction was estimated with reference to the overall array. A further conclusion that can be derived is that nutcrackers appeared to do better in all the conditions in which the shape of the landmark–goal constellation was preserved across trials. This might be a consequence of the preferential use of directional information to individual landmarks with the constraint that the goal had to be found equidistant from the landmarks, but it could also depend directly on the use of shape information, as if the birds were able to discount absolute size of the landmark array and 'see' the constant shape that the array and the goal formed throughout training.

Biegler et al. (1999) have countered this interpretation assuming that nutcrackers learned separate landmark–goal vectors associated to the various inter-landmark distances during training and generalized the center in the novel inter-landmark distances by averaging these vectors in the transformation test. The

nutcrackers' pattern of error in the extrapolated inter-landmark conditions revealed however that the birds' strategy likely reflects a genuine representation of the global spatial relationships existing between landmarks (Kamil and Jones, 1999). Nonetheless, the question concerning how the nutcrackers represented these cues largely remains unresolved. Kamil and Jones argued that the nutcrackers' searches reflected an explicit mapping of the configurational geometry (Kamil and Jones, 1997). By contrast, it has been shown that the birds' behavior could be formalized in mathematical terms without making any assumptions of explicit geometric mapping (Collett, 2000).

Jones et al. (2002) compared the performance of Clark's nutcrackers, pigeons and jackdaws (*Corvus monedula*) in the two-landmark array bisection task devised by Kamil and Jones (1997). Pigeons could learn the task almost as precisely as Clark's nutcrackers, whereas jackdaws took longer and were not precise during tests with novel inter-landmark distances. Apparently, the multiple-exemplar training schedule facilitated learning of the underlying 'halfway rule' in pigeons, since these results conflict with those of Spetch et al. (1997) described above. It is however important to say that Spetch et al. (2003) trained pigeons in the "constant direction-variable distance/constant distance-variable direction" experimental conditions used in the experiment by Kamil and Jones (2000), and they found that pigeons could be trained but showed a larger error magnitude than Clark's nutcrackers, and poorer generalization in their searching behavior when tested with novel distances. The "constant direction-variable distance" condition of Spetch et al. (2003) is comparable, in terms of task geometry, to the experimental conditions used in Spetch et al. (1997), and described above. It is not surprising that the results obtained in these two cases are similar, suggesting that, at least in pigeons, (i) finding a goal in between two landmarks according to some geometric rule is easier than finding it outside the landmarks and that (ii) multiple-exemplar training may induce a facilitation in learning the task.

Research comparing relational (i.e., relations among landmarks) and vector (i.e., distance and direction) encoding has been carried out in young children as well. Vector encoding seems to be available in children by the end of the second year (Bushnell et al., 1995; Newcombe et al., 1998). Less is known about the time in life when relational encoding emerges in children. Uttal et al. (2006) trained 4-year-old children to find a toy with either one or two landmarks present in a large open space. On subsequent trials, the number and locations of the landmarks were changed to determine how children establish the location of the toy. The results showed that with only one landmark present during training, the children encoded the location of the toy in terms of distance and direction to the single landmark. With two landmarks present during the initial training, children appeared able to code both the middle location between the two landmarks and the distance and direction from the toy to landmarks.

### 3.3. Encoding geometric information in complex arrays

Spatial memory involving arrays of three or more landmarks has been investigated more frequently, and it has the advantage of being more ecological as the number of landmarks increases. Usually, a number of landmarks are placed in an open field and the task to be completed requires the animal to find a goal hidden somewhere in the search space enclosed by the landmark array or around it. These procedures allow to address relevant theoretical issues, particularly those related to the exploitation of the computational explosion that presumably arises in naturalistic setting. Are animals able to rely on global geometric descriptors of the scene to navigate? Are landmarks in arrays equally represented by the navigator?

The same problems and opportunities described in the case of arrays composed of two landmarks apply also in the case of three or more elements. If the geometry of the array is regular (i.e., multi-axially or radially symmetrical), the landmarks are all identical, and there aren't other spatial cues providing directional information, then the spatial position of the goal can be confused with other positions in the search space. This is the case, for instance, of an equilateral triangle-shaped array, but not of an isosceles triangle-shaped array. In the equilateral situation, any non-central spatial position evaluated relative to the three identical landmarks (which are spaced apart a constant distance between each other), would have two 'twin' positions. In the isosceles case, instead, the apex landmark would provide directional information sufficient to avoid any ambiguity. Any breaking of symmetry in the geometric configuration of a regular-shaped landmark array has thus the intrinsic effect of providing directional information over the search space, and the same is true when differences exist between the perceptual identities of individual elements in the array (their color, shape, etc.), or when extra-array cues are present. The ensemble of these deviations from regularity, are given the name of 'polarizing' cues.

Interesting results on the encoding of geometric relationships between multiple landmarks come from the so-called test of reaction to change in exploratory behavior. In this paradigm, an animal is allowed to explore an environment containing an array of objects. After the animal is habituated to the array, the experimenter changes the spatial arrangement of objects and the animal is reintroduced in the environment. In hamsters (*Mesocricetus auratus*), it has been shown that changes in the geometric configuration of the array induce a renewal of exploratory activity directed either selectively to the displaced objects or to all objects. In contrast, when only the size of the configuration is modified, no such changes in exploratory activity are observed (Poucet et al., 1986; Thinus-Blanc et al., 1987). These data demonstrate that hamsters spontaneously encode the spatial relationships between objects, and it can be hypothesized that the lack of re-exploration of the configuration when it differs in size might correspond to the formation of a geometric category. Similar results have been also obtained in rats (Wilz and Bolton, 1971; Save et al., 1992), gerbils (Thinus-Blanc and Ingle, 1985) and monkeys (Gouteux et al., 2001a,b). Interestingly, data obtained in rats, showed that a spatial change consisting in the mirror reflection of an array of three distinctive landmarks, does not exert renewed exploration (Skov-Rackette and Shettleworth, 2005), suggesting that sense (the distinction of left from right) is not easily included in the encoding of spatial relationships between landmarks. Evidence from spatial reorientation experiments, however, provided contradictory results when spatial behavior in enclosures was compared to that in arrays of landmarks (see next section).

Apart from these studies on the spontaneous reaction to changes in spatial configurations, arrays of multiple landmarks are frequently used in experiments exploiting some form of training. Collett et al. (1986) used multiple landmark arrays in the paradigm involving seed-finding in gerbils. For instance, when the gerbils were trained with a scalene triangle-shaped array and the release point changed from trial to trial, the animals easily mastered the task. This also occurred when the landmark was an equilateral triangle-shaped array, the goal was in the center (thus it was uniquely determined with reference to array geometry) and the room light was extinguished while the gerbils were *en route* to the goal, suggesting that (I) the position of the goal could be computed in advance relying on the overall geometry of the array, and (II) the realization of the displacement toward the goal involved an anticipatory representation in terms of distance and direction.

Collett et al. (1986) also performed a number of transformational tests that made use of arrays of three landmarks. In a first experiment gerbils were trained to find the goal in the center of

an equilateral triangle-shaped array and on test trials one or two landmarks were removed from the array. The animals searched accurately at a single location in the test with two landmarks, showing that they could extract distance and direction information from the geometric arrangement provided by the residual landmarks. When only one landmark was left in place, gerbils' searching activity concentrated at three locations, each at the correct distance and direction as if the gerbils were relying on each of the three landmarks in the array individually. Interestingly, using the same array during training and subsequently shifting one of the landmarks farther away (thus transforming it in an isosceles triangle-shaped array), gerbils searched in a single place, at the correct distance and direction with reference to the two unchanged landmarks, confirming that subsets of landmarks in the array can be efficiently used for orientation, as it was already suggested by the experiments involving training with two landmarks.

In another experiment, the goal was at a short distance from one of the landmarks in a scalene triangle-shaped array, and any landmark differed in appearance from each other. When a deformation of the array (shifting farther away the landmark closer to the goal) was brought about, gerbils searched in the vicinity of the shifted landmark, showing that they attributed a higher priority to the landmark located nearby the goal. Following the removal of that landmark, however, gerbils searched in the goal location as dictated by the two residual landmarks, demonstrating that notwithstanding the fact that the landmark closer to the goal had taken control over the search for the goal, the relationships between *all* landmarks and the goal had been encoded. A last interesting experiment involved the localization of the goal in the center of an equilateral triangle-shaped array, and the subsequent addition of a fourth landmark, that transformed the array into a parallelogram-shaped one. In this case the gerbils searched mostly in the triangle-shaped array embedded in the parallelogram-shaped array, that preserved the same shape orientation with respect to extra-array cues (i.e. the room) as in the training phase. It appears therefore that gerbils can orient easily by relying on many aspects of multiple landmark arrays, and not only on the individual appearance of the single elements.

In the already mentioned work aimed at comparing pigeons and humans, Spetch et al. (1997) also trained pigeons to find a goal in the center of a square-shaped object array. After learning the task with a single exemplar array, pigeons were tested in two transformed versions of the array. In the "left-right expansion test", two landmarks were displaced farther apart along one dimension, thus making the array rectangle-shaped. In the "diagonal expansion test" the landmarks were displaced along two dimensions, thus giving rise to a larger square-shaped array. In both tests, pigeons searched consistently in regions of the modified search space that preserved a constant distance and direction to one or two landmarks. Human subjects tested in a table-top version and in an outdoor version of the task (in a grassy field) searched precisely in the center in both test conditions (the "left-right" and the "diagonal" expansion). These results provide thus a confirmation of the result obtained by the same authors using an array of two landmarks: pigeons can achieve a good level of place learning based on multiple landmarks, but once the array of landmarks undergoes a transformation they tend to follow individual landmarks or subsets of them rather than relying on the relationships between all elements. Again, these results are hard to reconcile with those obtained in the adaptation of the 'bisection' task for pigeons (Jones et al., 2002). However, absolute metric encoding from single landmarks has been observed also in an analogous task in Clark's nutcrackers (Kelly et al., 2008), suggesting that relational rules are not spontaneously used in avian species, but rather emerge following specific procedures with multi-exemplar training trials.

Similar results have been obtained in dogs, *Canis familiaris* (Fiset, 2004), in young children and in a New World monkey, the common marmoset *Callithrix jacchus* (MacDonald et al., 2004) whereas in another New World primate, the squirrel monkey *Saimiri sciureus*, a similar test showed absence of encoding of either configural or elemental spatial rules (Sutton et al., 2000). Interestingly, chimpanzees have been shown to be unable to solve a task involving bisection, in which they were presented with a number of large boxes in a row (three, five, seven or nine) and were required to pass through the box in the middle to obtain a reward (Yerkes, 1934). Using a sort of a table-top variant of this task, however, Rohles and Devine (1966, 1967) showed that a female chimpanzee could learn to locate the central object in a half-circular arrangement of up to seventeen objects, despite there was little evidence of transfer from smaller to larger numerosity. Moreover, the fact that the chimpanzee was successful even when the objects were asymmetrically distributed in the overall configuration, suggests that she might have exploited a counting strategy when solving the task, making the interpretation of these results in terms of authentic visual bisection less tenable. However, a very recent study on bonobos (*Pan paniscus*) and capuchin monkeys (*Cebus apella*) showed that these two species could be trained to find a location in the middle of two landmarks and could generalize to novel (larger) inter-landmark test distances, after having experienced a constant- but also a variable- inter-landmark distance training set (Poti et al., 2010). The middle-searching generalization task was hard to accomplish when the landmark array was comprised of four, rather than two, landmarks.

When multiple landmarks are available and the goal is closer to one of them, the nearby landmark usually exerts a higher predictive control over the localization of the goal, it assumes the status of a 'beacon': after transformations of the landmark array the animals will follow that landmark (Collett et al., 1986; Bennett, 1993; Biegler and Morris, 1993; Gould-Beierle and Kamil, 1999; Kamil and Jones, 2000). This phenomenon corresponds to an instance of overshadowing (Rescorla and Wagner, 1972). Overshadowing takes place when one stimulus becomes more strongly predictive of a response than any other stimulus present from the beginning in the learning context – it literally puts the other stimuli in the shadow. Overshadowing has been documented in many spatial memory tasks involving landmarks, such as the well-known Morris water maze (Morris, 1981). In this task a rat has to swim to a platform hidden just below the surface in a large pool filled with opaque water: after training to swim toward the platform from a fixed release point, rats accomplish the task also when they are released from novel release points. Since the pool is usually circular (hence its shape cannot be predictive of the platform location), the position of the platform can be derived by reference to landmarks that can be either external to the pool (usually objects in the experimental room) or internal to it, if they are available. It has been shown that rats can rely on multiple landmarks for their orientation, and in this case geometric relationships between landmarks are crucial (Benhamou and Poucet, 1998). Similar results have been obtained using the most diverse types of methodologies in a great number of species, among them fish (Odling-Smee and Braithwaite, 2003), turtles (López et al., 2001), pigeons (Sutton, 2002), chicks (Vallortigara and Zanforlin, 1986), rats (Greene and Cook, 1997), primates (Menzel, 1973), and many others (see Thinus-Blanc et al., 2009).

Overshadowing has been reported to occur in the water maze when one landmark is closer than other landmarks to the hidden platform (Sanchez et al., 1999). This, and other effects (such as blocking and latent inhibition) that are typical of associative learning where stimuli are usually presented sequentially in time, have all been shown to take place also in spatial learning situations involving the simultaneous presence of a constellation of

landmarks (Rodrigo et al., 1997; Prados et al., 1999). Despite overshadowing seems to suggest that a selected landmark might take control over spatial learning to the expenses of other landmarks, some of the experimental conditions involving the removal of a landmark in the works by Collett et al. (1986) and by Kamil and Jones (2000) indicated that gerbils and Clark's nutcrackers could use the residual landmarks to orient to the goal, even when the removed landmark had been shown to overshadow other landmarks (see also Rodrigo et al., 2006). This raises the problem of understanding how, given a search space defined by a constellation of landmarks and a goal, the information conveyed by the landmarks is redundant for an animal that relies on them for searching the goal. In other words, it is interesting to know how many landmarks can be removed from the array without disrupting the ability of the animal to successfully exploit the residual subset of landmarks in the array. In this respect, Prados and Trobalon (1998) showed that in a water maze task, where the platform could be localized by reference to four external landmarks, rats oriented successfully after the removal of any two landmarks in the array but not after the removal of three landmarks, unless the residual landmark happened to be located very close to the goal.

Goodyear and Kamil (2004) trained Clark's nutcrackers to find a goal whose position was specified by the relationships with an array of four landmarks. Each landmark in the array was at a different distance from the goal. Moreover, the average distance of the landmarks from the goal was made to differ for three distinct groups of birds (close, medium or far), but one of the landmarks was 70 cm from the goal in each condition. Test conditions in which only a selected single landmark was present showed that birds in each group searched with an increasing spatial precision as the distance of the landmark used in testing decreased. On the other hand, the spatial precision with respect to the 70 cm landmark increased linearly in the three groups, suggesting that birds' use of absolute landmark-goal distance, efficient at short ranges, leaves the place to use of relative distance as soon as the goal is located at a large distance from the array.

Kamil and Cheng (2001) developed a model of multiple landmark memory inspired by the empirical evidence obtained with Clark's nutcrackers. Based on the assumption that direction from distant landmarks is estimated more accurately than distance, they proposed that Clark's nutcrackers exploit in particular the stored bearings from a number of landmarks to the goal, in order to locate it with the smallest possible error. In the case that absolute bearings are used (as if they were compass readings of each landmark-to-goal direction), it follows that as the number of landmarks increases, the bearings (conceding a constant 1–2% error associated to each of them) will pinpoint to a smaller and smaller intersection area where the animal should concentrate searching. Similar predictions follow from considering relative bearings (directions as evaluated from configurations of multiple landmarks). This was substantiated both by MonteCarlo computer simulations (Kamil and Cheng, 2001) and by real experiments with Clark's nutcrackers (Kamil et al., 2001). Simulating pigeon homing behavior by means of a back-propagation neural network model, however, Jones and Bingman (1996) showed that when the number of landmarks exceeds four (i.e. with six landmarks), this would be detrimental to the success and accuracy of simulated homing trials from new locations, suggesting that the ideal landmark array would include four landmarks located around the goal (the pigeon loft) in a symmetrical arrangement.

The study of multiple landmark use in human spatial navigation goes far beyond the example given in the comparative experiments by Spetch et al. (1997) described above. Indeed, it has constituted the subject of specialized research activity in experimental psychology since many decades. In this respect, much of the empirical work on adult humans was inspired by James J. Gibson's

'ecological approach' to perception (Gibson, 1979; Hancock et al., 1995), whereas much of the developmental work owes to the 'genetic epistemology' tradition established by Jean Piaget (Piaget et al., 1948; Piaget and Inhelder, 1948; Newcombe and Huttenlocher, 2000). Many recent works on humans have exploited the advantages of navigation in simulated environments using virtual reality techniques, providing results converging with those obtained in animals (see for instance Jacobs et al., 1997, 1998; Hamilton and Sutherland, 1999; Astur et al., 1998; Waller et al., 2000; Doeller et al., 2010). In fact, virtual reality made it possible to adapt well-established animal research paradigms to human subjects, without recurring to cumbersome physical replicas of the spatial settings originally developed in the animal psychology laboratory. It must be said that before the advent of virtual reality, a large tradition of research on human spatial memory made use of navigation tasks that were carried out in 'ecological' spatial settings (houses, campuses, malls, outdoor environments) and were aimed at comparing the explanatory power of an approach based on the knowledge of the global spatial layout, with an approach based on an intrinsic, first-person perspective recall of serial tokens of spatial information, which can be labelled the 'survey vs. route debate' (Taylor and Tversky, 1992). Both this ecological tradition and that interested in understanding the geometrical foundations of human spatial memory are now profiting of the possibility to have subjects navigating in complex (see Foreman et al., 2005 for an example) as well in simplified spatial environments presented on the screen of computers (see Hamilton et al., 2002, for an example). In the latter research line, for instance, the performance of humans has been compared to that of non-human animals in virtual adaptations of the Morris water maze, the radial maze and the rectangular arena used to test the 'geometric module' (see Section 4; Kelly and Gibson, 2007).

#### 3.4. Discriminating objects by geometry in an array

A novel approach has been introduced in recent years to investigate how human and non-human animals encode geometric cues in landmarks arrays. In a representative task based on this approach, the subjects are trained to locate a goal in the immediate vicinity of one of the objects in an array, or directly inside the array. The searching area is confined to a limited set of discrete alternatives, rather than distributed over a continuous substrate. The subjects are trained to discriminate the goal-object from the other, distracting objects in the array, on the basis of the geometric relationships it keeps in the configuration.

Gouteux and Spelke (2001) had found that children (3–4-year-old) systematically fail to locate a toy on the basis of purely configural geometric cues provided by a rectangular array of indistinguishable boxes. A large body of evidence have confirmed these findings using both different objects as hiding locations and other shape configurations (Gouteux and Spelke, 2001; Lee et al., 2006; Lee and Spelke, 2008, 2010, 2011). The children also fail to reorient when the shape of the array is made more salient by a two-dimensional figure flashed on the floor of the room. Apparently, the geometric arrangement specified by an array of discrete objects is an impervious cue for spatial reorientation in our species and our difficulties have been consistently detected up to 5 years of age. Further evidence in this respect has been obtained by Lee et al. (2006). The authors tested 4-year-old children in a circular room containing one distinctive and two identical containers. They found that whereas the distinctive container was used by children as a direct cue to a hidden object's location, it could not be used as a directional signal guiding reorientation. Comparable findings were obtained by Lew et al. (2006) in a peek-a-boo version of the task. In this study, 12–18-month-old children failed to use features as a cue to anticipate the location of the peek-a-boo after being disoriented.

In open contrast with predictions of explicit geometric mapping in birds (Cheng, 1988, 1989, 1990; Kamil and Jones, 1997), analogous observations have been reported in both the domestic chicks (Pecchia and Vallortigara, 2010a) and the Clark's nutcrackers (Kelly, 2010).

The difficulties observed in both human and non-human animals to reorient on the basis of the geometric cues specified by landmarks in arrays parallel a large body of evidence in rodents suggesting that the position of proximal objects is usually less effective than that of either distal or laterally placed objects in predicting the firing pattern of neurons in the hippocampal and in the parahippocampal circuitry (O'Keefe and Conway, 1978; Muller and Kubie, 1987; Knierim et al., 1995; Cressant et al., 1997, 1999; Taube, 1998; Zugaro et al., 2001). For example, Cressant et al. (1997) provided evidence that a triangular-shaped array of objects controlled the firing pattern of place cells in the rats' hippocampus when arranged in the vicinity of the perimeter wall of a circular arena, but not at all when it was arranged centrally within the searching space. Seemingly, while children fail to reorient by geometry in an array of freestanding boxes, Garrad-Cole et al. (2001) showed that young children (18–24 months) could reorient according to the geometric cues provided by a rectangular array of objects arranged in the vicinity of the perimeter wall of a circular room. Coherently, the hippocampal activation in adult humans appears to be selectively modulated by distal objects, whereas a spatial task based on proximal objects appears to selectively activate striatal nuclei (Doeller et al., 2008).

Several experiments have shown, however, that local cues made sufficiently salient can modulate the activation pattern of neurons in the rats' hippocampal region (Young et al., 1994; Gothard et al., 1996; Shapiro et al., 1997; Save and Poucet, 2000; Zinyuk et al., 2000; Knierim and McNaughton, 2001; Brown and Skaggs, 2002; Knierim, 2002a; Rivard et al., 2004; Knight et al., 2011). Indeed, rats could be successfully trained to locate a reward relative to freestanding objects in an arena (Gibson et al., 2007b; Benhamou and Poucet, 1998). Gibson et al. (2007b) tested the ability of rats to locate a reward in a rectangular array of cylinders. The reward could be accessed directly from an opening on cylinders, which position was maintained stable relative to the array throughout the experiment. Contrary to the results obtained in both children and birds, a number of tests revealed that rats successfully encoded the configural geometry together with the encoding of the non-geometric features. Furthermore, array expansion tests and landmark removal tests in the identical objects condition confirmed that rats could use the geometry provided by the arrangement of objects, the latter type of test (involving a transformation from the rectangular-shaped to a triangular-shaped enclosure) suggesting that rats possibly extracted the principal axis of the array during training.

Recent findings have revealed that both the nature of the task and the stability of openings on cylinders provide relevant indirect cues to reorient in the array. Contrary to previous studies in the rectangular array of objects in birds, it has been shown that both domestic chicks (Pecchia and Vallortigara, 2010b) and homing pigeons (Pecchia et al., 2011) reorient successfully in a rectangular array of indistinguishable cylinders when trained in an analogous version of the task used in rats by Gibson and colleagues. A distinctive feature characterizing this paradigm is that the reward site could be approached from a single direction, which in turn is imposed by the openings on cylinders. When that position was changed between the training series, both the domestic chicks and the homing pigeons failed to reorient. An analogous phenomenon has been recently observed in chicks trained in an array of cylinders arranged centrally within a rectangular-shaped arena (see Section 4.1). Since birds failed to reorient specifically in the variable access condition, the results suggest that spatial representation in both

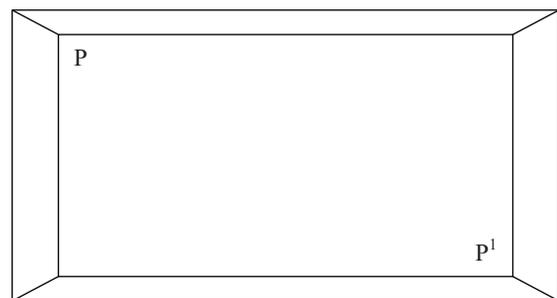
chicks and homing pigeons are anchored to an egocentered reference frame (Pecchia and Vallortigara, 2010b; Pecchia et al., 2011).

## 4. Geometry of enclosed spaces

### 4.1. The hypothesis of modularity in the spatial domain

Enclosures can be generally defined as environments surrounded by continuous (and contiguous) surfaces. On the human-sized scale, of course, an environment surrounded by surfaces is what we would call a room. Although non-human animals have not spent their evolutionary history hanging around in rooms, many experiments have recently made use of simple, more or less empty, animal-sized enclosures (real rooms or chambers in the case of humans), in order to study another aspect of geometric information processing involved in spatial orientation. The Morris water maze is an example of an enclosure in which rats trained to locate the goal are allowed to perceive objects external to the enclosure in order to orient. In this section we will focus on spatial memory in enclosed environments, although the majority of studies that have investigated spatial orientation depending on the shape of the environment have also compared it to situations in which the environmental shape was 'enriched' with the presence of a number of landmarks or cues located inside the environment, revealing interesting aspects on the relative importance that these two sources of information have for the orienting organism.

In a seminal study, Cheng (1986) investigated spatial reorientation of rats in a rectangular-shaped enclosure, developing an initial idea that had been tested using an X-shaped maze (Cheng and Gallistel, 1984). The experiments that made use of the rectangular enclosure (Cheng, 1986; see also Cheng, 1987 and Gallistel, 1990) were carried out both in a working memory and in a reference memory paradigm. In the working memory task, rats had to use the memory trace of one location over the surface of the enclosure where they dug to uncover a buried food reward; this trace had to be stored during one trial in the enclosure to be recollected in the next trial, carried out in an exact replica of the enclosure. The position to be remembered changed from trial to trial, thus requiring a short-lasting, although spatially precise, memory trace. In the reference memory task, the food reward was found in the vicinity of one corner of the rectangular enclosure and only in that location, throughout the whole duration of the experiment, thus requiring the formation of a stable, enduring memory trace of the corner where the food was to be found. If the reader is trying to imagine these situations, she or he might have already realized that the rats faced an unsolvable spatial ambiguity. If food had been found at location P in a trial of the working memory task, how could the rat tell the difference between location P and the rotational equivalent location P<sup>1</sup> in the following trial in the replica of the enclosure (see Fig. 2)? Similarly, if food had been found at one



**Fig. 2.** A rectangular enclosure in which the target position (P) and its rotational equivalent (P<sup>1</sup>) do share the same geometric attributes, i.e., maintain a left short wall with respect to a long right wall.

corner in the reference memory task, how could the rat tell it from the opposite corner in the next trial? It follows from trivial geometric considerations that P and P<sup>1</sup> are points that bear identical geometric relationships with respect to the shape of the enclosure when this is rotated 180°, and the same holds true for regions such as 'corners' that are opposite along the diagonal of the enclosure. Rats searched equally often at places P and P<sup>1</sup> in the trials carried out in the replica of the enclosure in the working memory task.

The most striking result consisted in the fact that this expected confusion was observed despite the non-geometric features on the perimeter wall of the arena could be used as polarizing cues to break the environmental symmetry: i.e. salient colored markings in the form of one wall being painted differently from other walls, and distinctive panels attached to the corners (rectangular panels differing from each other for their color, texture and smell). These featural characteristics could be used, in principle, to discriminate between the rewarded location and its rotational equivalent, but rats appeared not to use them. In the reference memory task, rats eventually learned to search at the correct corner (which was kept constantly associated with a given panel from trial to trial), but still made errors more frequently in the rotationally opposite corner than in the two other corners. This proved that rats were able to use those featural characteristics to localize a place in the enclosure and, provided that the location of the reward was kept stable, they indeed used them. On the other hand the results of Cheng's experiment first showed that in the process of reorientation, rats are extremely sensitive to the overall geometric shape of the environment, to the point that this process, in some conditions, can be 'blind' to other sources of information. Many other tests were carried out by Cheng, involving transformations of the arrangement of featural information with respect to the shape of the enclosure. These tests confirmed the higher sensitivity of rats to the geometric information provided by the shape of the enclosure with respect to the non-geometric information provided by the panels. Among the various attempts by Cheng to put at test the resistance of rats' representation, affine, reflection, and transposition transformations were carried out. In the affine transformation, each panel was moved to the next corner in an orderly fashion. In the reflection transformation panels were swapped across opposite sides. In the transposition transformation, the correct panel and the one at the geometrically equivalent corner were swapped. These transformations altered one or two spatial properties (the metric structure in the affine transformation, the sense order in the reflection transformation, or both properties in the transposition transformation). In another experiment the panels associated with the geometrically correct corners were removed, to check whether the more distant information associated to the geometrically incorrect corners was used. Overall, the results of these transformations made even more evident the basic finding that the rats were using the shape of the enclosure as the primary cue to reorient themselves. The authors showed that rats confused the geometrically correct corners (i) when both the metric and sense properties as deduced from the arrangement of the panels were altered with respect to the training (transposition); (ii) when either of these properties was selectively altered with respect to the training (affine and reflection transformation); (iii) when both the panels marking the geometrically correct corners were removed, so that non-geometric information provided by the two residual distant panels could still be used to disambiguate the goal corner from the rotational equivalent corner in the arena.

One interesting aspect that emerged in the working memory task, and that was further analyzed by Margules and Gallistel (1988), had to do with the very idea of disorientation. In order to force the rats to rely solely upon the macroscopic (geometric) features, Cheng systematically rotated the enclosure from trial to trial. When such rotations were small, however, rats seemed to

better disambiguate the two geometrically correct corners. In the experiment carried out by Margules and Gallistel (1988) similar results were obtained, showing however that disorientation (which can be obtained by passive rotation of the animal in a restraining environment and/or by the rotation of the enclosure between trials) is a crucial factor for inducing rotational errors. This procedure allowed them to reduce at a minimum the likelihood that the rats relied on the inertial information accumulated during the passive transportation away from the enclosure and again inside it (path integration). Moreover they confirmed Cheng's result that geometric information prevails over non-geometric information in the process of reorientation.

Disorientation studies in humans have often used a procedure that involves rotating the participant (with eyes closed). Lourenco and Huttenlocher (2006) examined 18–25-month-olds' spatial encoding in two disorientation tasks – involving either participant or environment rotation (in both tasks rotational movements could not be tracked by the subjects). Children were tested in either task (participant- or environment-movement) from either inside or outside a triangle-shaped (isosceles) environment (with one unique and two equivalent corners). In the participant-movement task, performance was above chance, regardless of which corner contained the object, whereas in the environment-movement task, performance was above chance at only the unique corner. On both tasks, performance was better from inside the space than from outside. It is noteworthy, however, that in the environment-movement task, when the children were given the possibility of repeated trials, they could successfully learn to reorient. Comparative results have been collected only in chicks and this species showed to be unaffected by the two disorienting procedure adopted (Chiandetti and Vallortigara, 2010b). It seems that chicks are able to use the very same orienting mechanism from the beginning of learning; this can be explained by the fact that chicks are precocial, hence belong to a species that extremely needs to be able in managing stable external geometry without any sort of training.

The original experiment by Cheng has become a key paradigm used to test spatial representations based on the geometric shape of enclosures, and it has been considered an example of "cognitive modularity" (Fodor, 1983), in other words a mental faculty devoted to the analysis of only one source of information (in this case environmental geometry) and impenetrable to other sources (in this case the features associated with non-geometric information). This hypothesis (Cheng, 1986, 1987; Gallistel, 1990) had rested on those sole experimental data obtained in rats, until new experiments in humans and other species started to further test the notion of cognitive modularity (see Cheng and Newcombe, 2005 and Cheng, 2005b for reviews).

Vallortigara et al. (1990) performed some experiments (only in the reference memory task) using domestic chicks (*Gallus gallus*), providing the first inter-species comparison of Cheng's results. Chicks trained in the absence of non-geometric information (an empty rectangle-shaped enclosure) made rotational errors, showing that they could reorient relying upon the sole shape of the test enclosure. When non-geometric information (panels in the corners) was present during training and the test was carried out in the empty enclosure, chicks still reoriented toward the geometrically correct corners: apparently, geometric information had been encoded and used by chicks although not necessary to solve the task. The same result was obtained when only the two panels located at the geometrically correct corners were removed at test, showing that the distant information provided by the two residual panels was not used in the reorientation process. Interestingly, when tests were carried out moving each panel clockwise to the neighboring corner (an affine transformation) chicks searched mostly at the correct panel location, and therefore in a geometrically uncorrect corner relative to the shape of the arena, with

respect to the training trials. Thus, although chicks were shown to encode both geometric and non-geometric cues, they appeared to use principally the latter type of cue when the two sources of information were made to conflict, casting doubts on the universality, at least across major vertebrate groups, of the cognitive modularity hypothesis applied to the domain of environmental geometry. Another experiment on birds, carried out by Kelly et al. (1998) and again using a rectangle-shaped enclosure, provided similar results. These authors tested pigeons in many conditions involving the presence of both geometric and non-geometric cues. Pigeons, as chicks, reoriented predominantly relying upon the non-geometric cues in conflicting situations, although they could use the purely geometric cues in the case that no panel or object was present in the enclosure. Species (or group) discrepancies thus appear to be quite consistent, and perhaps partially explained when considering the differences in visual ecology of rodents and birds, although what appears to be confirmed is that the hypothesis of a strictly modular system, as had been suggested in the case of rats, would not be applicable to the avian species tested.

The controversy about the issue of modularity was further boosted after an experiment carried out by Hermer and Spelke (1994, 1996; see also Wang et al., 1999 for similar results). These authors tested young children (18–24-month-old) and adults in an adapted version of Cheng's task. Using a rectangular-shaped chamber as the testing environment and a toy concealed in one corner as the goal, they found that, after disorientation, children reoriented themselves making rotational errors and ignoring non-geometric cues provided in the form of a differently painted wall or the identity and appearance of objects located inside the chamber. Using other tasks, however, it was demonstrated that children could also encode and retrieve the featural information associated to those objects, provided that the setting where the search task took place did not involve reorientation also based on the geometry of the environment. The non-geometric cue had to be separated (or *disjoined*) from the geometric cue, thus, in order for the children to make some use of it. When the two cues were present in the chamber in the context of reorientation, children behaved in the same way as Cheng's rats. Adults, on the other hand, reoriented themselves correctly with respect to the location of the non-geometric information present in the chamber. In the absence of non-geometric information (in an empty white chamber), however, adults were shown to reorient using geometric information (making rotational errors). This pattern of results suggested to Hermer and Spelke that the human spatial representation involved in the process of reorientation entails a geometric module dedicated to the analysis of the macroscopic shape of the environment, and that this module is impenetrable to non-geometric information in the early stages of development (thus preventing the conjoint analysis of geometric and non-geometric information observed in children), a limitation which would be overcome with cognitive maturation. Exactly on this point, some works have been subsequently carried out to better understand on which *specific* cognitive process (or processes) the emergence of such a difference between children and adults would be based.

Hermer-Vazquez et al. (1999), performed a series of experiments on adults in the reorientation task, with the precise objective of inducing subjects to make rotational errors. This was attempted asking subjects to engage in a second task during the process of reorientation in the rectangular-shaped chamber. Such an experimental approach (dual-task interference or shadowing) is commonly used to determine whether some form of activity has a detrimental effect on a given task, in order to understand whether the resources or structures involved by the relevant task can be identified with those involved by the concurrent activity. The assumption is that if the processing resources dedicated to a given task are independent of the cognitive resources required

by a second task or if the two tasks do not share any processing mechanism, then the concurrent performance of the second task should not induce a deterioration in the performance of the first task, as compared to the first task carried out in isolation. On the other hand, if the two tasks share resources or structures, then the concurrent execution of the second task should bring to a deterioration of the performance of the first task. The interference tasks chosen by Hermer-Vazquez et al. (1999) consisted either in a verbal or in a nonverbal shadowing because it was hypothesized that the conjoint processing of geometric and non-geometric information observed in adults might depend on the possession and use of linguistic abilities (for instance labelling the goal as being "at the left of the blue wall"). When the dual-task involved verbal shadowing (reorienting while repeating verbal material played back from loudspeakers), subjects made rotational errors, their performance dropping down to the same level as children's. In the nonverbal shadowing task (reorienting while clapping at a rhythm heard from loudspeakers), on the other hand, subjects appeared able to reorient appropriately to the corner that was both geometrically and non-geometrically correct, as did the adult subjects that were not performing any shadowing task. According to Hermer-Vazquez et al. (1999), the difference in performance obtained in the two conditions could be easily attributed to the interference specifically ascribed to the linguistic processing present in the verbal shadowing task, and only to that level of processing, since other resources (like attention and working memory), were equally involved in both shadowing tasks, and deterioration of the performance would have then be observed also in the rhythmic shadowing task if the interference had an effect at those levels of processing. The inability of conjoining geometric and non-geometric information during reorientation, as observed in young children by Hermer and Spelke (1994, 1996), following this argumentation, would only be a consequence of linguistic immaturity. Hermer-Vazquez et al. (2001) further confirmed the hypothesis in an experiment carried out in children of different ages, in which a correlation between successful performance in the reorientation task and the possession of the linguistic tools necessary to describe space was found. Nonetheless, the different outcomes obtained in the verbal and the nonverbal shadowing tasks may reflect a difference in the overall attention requirement between the two procedures, rather than a specific linguistic component, with a minimal attention commitment in the latter than in the former procedure.

Although the evidence obtained in toddlers and young children in all these works showed that reorientation 'blindly' depended on the geometric shape of the environment, other experimental works provided contradictory, if not contrary, evidence. Recent findings, for instance, provided evidence that adult aphasics successfully conjoin geometric and non-geometric cues in the blue-wall task (Bek et al., 2010). Learmonth et al. (2001), replicating the experiment by Hermer and Spelke (1994, 1996) with children aged 17–24 month, but using a larger chamber and comparably large non-geometric features, did not find any evidence of rotational errors. In a follow-up of the study, Learmonth et al. (2002) replicated the experiment using both a small and a large experimental chamber, and both 3–4-year-old and 5–6-year-old children. Their results showed that children younger than 6-year-old truly reoriented without making rotational errors in the large but not in the small room (which was comparable in size to that used by Hermer and Spelke, 1994), whereas 6-year-olds oriented correctly in rooms of both sizes. The results suggest therefore that a crucial factor determining the conjoint use of non-geometric information in the process of reorientation based on geometric cues, is the size of the environment, and that this ability develops at around 5 years of age (See Section 4.2). A result suggesting a similar developmental constraint was obtained by Gouteux et al. (2001a,b) in a table-top version of the task, which did not involve reorientation after

disorientation in a chamber or a room, but rather localization in a small rectangular-shaped box located on a table in front of which the subject sat and that could be rotated while the subject was asked to close eyes. The results also confirmed that joint analysis of geometric and non-geometric cues emerged at around 5 years of age. In a somewhat related study, [Huttenlocher and Vasilyeva \(2003\)](#) compared reorientation inside an isosceles triangular-shaped chamber (in the absence of non-geometric cues) in a group of 18–24-month-olds, with the performance of another group of children that had to search from outside a table-top box having the same shape. Interestingly, children in both conditions were equally able to localize the corner in which an object was hidden, confirming that reorientation based on shape is not limited to the case of the environment surrounding the children but extends also to enclose environments seen from outside (see also [Lourenco and Huttenlocher, 2006](#)).

The experimental paradigm described in Section 3.4 offers an interesting opportunity for studying the difference in geometry encoding between spaces defined by extended surfaces and discrete landmarks. Experiments in infants have shown that geometric computation of landmarks in an array is poorly developed in our species up to 5 years of age. Nevertheless, when portions of walls are placed between the objects in the arrays, making the arrangement more enclosure-like, children are able to reorient according to geometric cues in the scene ([Gouteux and Spelke, 2001](#); [Lee and Spelke, 2008, 2010, 2011](#)). When these portions of walls are placed around the objects at the corners of the configuration, leaving gaps on a side of the rectangle, children did not reorient correctly, suggesting that continuous surfaces are dramatically powerful in determining a reorientation process based exclusively on the geometric layout (see also [Lee and Spelke, 2008](#)).

The primacy of extended surfaces over freestanding objects for spatial reorientation is consistent with evidences in rodents indicating that the macroscopic surface layout of an environment is extremely powerful in controlling the response profile of neurons in both the hippocampus ([O'Keefe and Burgess, 1996](#); [Lever et al., 2002](#); [Wills et al., 2005](#)) and the medial entorhinal cortex ([Hafting et al., 2005](#); [Fyhn et al., 2007](#); [Barry et al., 2007](#)). Grid cells' grids present an intrinsic tessellating structure that is thought to represent, in conjunction with head direction, a computational module for path integration. Nonetheless, both class of cells are calibrated by external cues to correct for cumulating errors of the path integrator system ([Burgess et al., 2007](#)). Information gathered in the proximal space appears dominant in this respect ([Siegel et al., 2008](#)). Rescaling of a familiar environment causes grids to deform coherently ([Barry et al., 2007](#)). Under rescaling conditions, place cells fields stretch and compress accordingly ([O'Keefe and Burgess, 1996](#)). Recent findings suggest that remapping of the place cells fields might be controlled by grid orthogonalization, one synapse upstream the hippocampus ([Fyhn et al., 2007](#)), even though reciprocal modulation is also plausible on the basis of the anatomical connectivity between the hippocampus and the entorhinal cortex ([Moser and Moser, 2008](#)). Border cells, a class of entorhinal neurons selectively responsive to boundaries, might be instrumental in anchoring the grids to the external world, and in particular to the geometric shape of the environment ([Barry et al., 2006](#); [Solstad et al., 2008](#); [Savelli et al., 2008](#)). Despite the fact that extended surfaces provide relevant information cues for spatial reorientation, it remains unclear whether that primacy actually reflects computations operating selectively on extended surfaces as such, or rather if that primacy emerges as a by-product of a more generic computation process. Experiments in the array of discrete objects described in the previous section favor the latter interpretation. Domestic chicks and homing pigeons fail to integrate multiple local views of the surrounding into a unitary representation of the geometric cues defining an array of freestanding objects ([Pecchia and Vallortigara, 2010a,b](#); [Pecchia et al., 2011](#)).

These findings have been recently confirmed in a reference memory task even when extended surfaces defined the reward site. Chicks trained to locate a food reward in an array of cylinders arranged centrally within a rectangular-shaped arena were proved able to reorient as long as the position of openings on cylinders giving the access to the reward was maintained stable throughout the experiment. By contrast, the chicks chose at chance between cylinders at the geometrically correct and incorrect positions in the arena when the position of openings changed between the training series. The results suggest that borders defining the three dimensional surface layout geometry per se did not provide a unitary frame of reference for spatial reorientation ([Pecchia and Vallortigara, 2012](#)). Rather, the spatial representation appeared to be anchored to the openings on cylinders, suggesting that the primacy of extended surfaces over discrete objects might reflect a by-product of their general stability and placement underpinning the navigator, rather than the activation of a distinct computation module ([Lew, 2011](#)). It would be of interest examining whether the kinematic constraints offered by the opening on cylinders provide qualitatively comparable cues as a boundary (and an extended surface) in rodents.

Theoretical studies ([Cheung et al., 2008](#); [Stürzl et al., 2008](#); [Cheng, 2008](#); [Sheynikhovich et al., 2009](#)) and empirical evidences in arthropods ([Wystrach and Beugnon, 2009](#); [Wystrach et al., 2011](#)) have shown that spatial reorientation in enclosed spaces can be potentially exploited on the basis of a view-matching strategy, arguing that animals could match the view stored and captured while moving to the current view and without encoding any geometric cue ([Collett and Collett, 2002](#)). Egocentered frames of reference for spatial reorientation observed in chicks and pigeons are consistent with this hypothesis. Predictions based on a global matching, however, were not confirmed by a recent study with 44-month-old children ([Lee and Spelke, 2011](#)). In this study, reorientation was tested in a homogeneous rectangle located centrally within a circular room. When the rectangle was formed by short barriers or bumps on its perimeter, the children reoriented successfully. Conversely, the children failed to reorient both when the rectangle was formed by a two-dimensional figure flashed on the floor of the room and when the rectangle was formed by an array of four freestanding columns, connected together by a thin cord. The cord was intended to provide a physical constrain to the child's movement as the walls in a rectangular arena. The results indicate that children reorient regardless of boundaries confining the exploratory space. The authors concluded that children specifically rely on continuous perturbations in the three dimensional surface layout to reorient. The conditions under which these perturbations are encoded for reorienting purposes remain to be clarified.

Experiments testing the encoding of geometry have been carried out also in a number of touch-screen studies. [Kelly and Spetch tested adult humans \(2004a\) and pigeons \(2004b\)](#) in a task in which a goal was to be found in a rectangular picture presented on a computer screen with four distinctive objects near the corners. The goal kept a fixed position relative to object and geometric cues, whereas the position of the picture (and thus the absolute position of the goal) was moved about on the screen from trial to trial. Both humans and pigeons encoded geometric and non-geometric features: object features were predominantly used in searching during transformation tests that involved shifting the position of all objects, although tests that involved the removal of objects suggested that geometry was encoded spontaneously (see [Gibson et al., 2007a](#), for a similar study showing that 3–6-year-old children become progressively competent in handling geometric information in another touch-screen task).

Expanding the number of species compared insofar in Cheng's task, [Gouteux et al. \(2001a,b\)](#) tested rhesus monkeys (*Macaca mulatta*), adding important evidence to the analysis of the factors

that are crucial in inducing to conjoin geometric and non-geometric information during reorientation. Rhesus monkeys were shown to be able, as all species tested until then, to reorient using the purely geometric information provided by the shape of the enclosure (thus making rotational errors), when non-geometric information was absent. However, when one wall of the experimental chamber was painted a different color, monkeys appeared able to search at the correct corner without making rotational errors. Other crucial experiments were carried out including conditions in which distinctive panels at corners or along one of the walls were available. Importantly, the authors trained and tested the monkeys with panels of different size, observing that the number of rotational errors (in other words, the reliance on the sole geometry of the enclosure) was inversely proportional to the size of the non-geometric information available. Experiments carried out with cotton-top tamarins (*Saguinus oedipus*), a New World monkey, provided converging evidence to the idea that geometric and non-geometric information can be combined in primates, although the setting of these experiments was not based on an enclosure, but rather on a more complex “artificial jungle” (Deipolyi et al., 2001). Once again, however, departures from a strictly modular account of geometric processing were highlighted, although the accumulated evidence seems to point more precisely at the factors responsible of these discrepancies. The overall pattern of data has been interpreted (Wang and Spelke, 2002) as suggestive that the conjoint analysis of geometric and non-geometric information might become easier as a function of developmental and evolutionary transition: at the phylogenetic level of analysis, primates would do better than rodents, and at the developmental level adults would do better than children.

However, this account leaves out the evidence obtained in birds and the even more dramatic discrepancies obtained from replications of Cheng’s paradigm in fish species. A number of recent studies have investigated the issue. Sovrano et al. (2002, 2003) demonstrated that a species of goodeid fish, the redbtail splitfin (*Xenotoca eiseni*), when tested in an adapted version of the task (in a rectangular-shaped tank provided with escape points at the four corners), were shown perfectly able to use geometric information in the case that non-geometric information was absent, but used non-geometric over geometric information when the two sources of information were both available and made to conflict. Similar results were obtained subsequently in the common goldfish (*Carassius auratus*) using a similar version of the task and showing that fish used both geometric and non-geometric information when reorienting (Vargas et al., 2004a,b). However, the use of non-geometric information (differently painted walls) was shown to depend on how distinctively it was “attached” to the surfaces of the tank. Escape doors in the corners of a rectangular-shaped tank were used as search regions, and only one would open (the goal). Two adjacent walls were painted a different color than the other walls. Importantly, for one group of fish the correct corner was located left of these two walls (so that it was at the intersection of two walls of different colors), whereas for a second group of fish the correct corner was at the intersection of the two identically colored walls. For both groups the crucial transformation consisted in a test after that the colored walls were moved one adjacent position clockwise. In this test, only fish in the group trained with the goal included between the two identically colored walls chose the correct corner (which was in the geometrically wrong position), whereas the performance of fish in the other group did not depart from chance level. These results add evidence to the fact that purely geometric encoding is shared by a wide variety of species and that it does not exclude access to other sources of information, making the claim on cognitive modularity less and less tenable (although see Cheng, 2005a, for an alternative account). Whether or not the conjoining of geometric and non-geometric cues depends on the

acquisition of spatial linguistic terms in humans, and despite the discovery of factors modulating such interaction in non-human animals, some sensitivity to the macroscopic shape of the environment has been reported in all species studied so far, in that all species make rotational errors in tests where only geometric information is available during training, and especially in those tests in which non-geometric information is available during training but is then removed during tests. The original observations by Cheng (1986) and Margules and Gallistel (1988), have thus initiated a rich line of research that, bringing together data from experiments in animals, humans and infants, provided a brilliant example of interdisciplinary cross talk revolving around a simple and inexpensive experimental paradigm. The striking results that had been obtained with rats, however, could not escape further and independent research on the same species in other laboratories. Golob and Taube (2002) for instance, in the light of previous results concerning the role of motivation in spatial tasks (Dudchenko et al., 1997), tested rats in two motivationally opposite versions of Cheng’s task. Their rats were trained both in an appetitive ‘dry maze’ condition (they were thirsty, and searched for water in one corner of a rectangular-shaped enclosure) and in an aversive ‘water maze’ condition (in this case rats were swimming, and tried to escape to a hidden platform in one corner of the same enclosure filled with water). In both cases non-geometric information was present in the enclosure in the form of a differently painted wall. In the appetitive condition rats made rotational errors (although at a lower rate than in any previous study), whereas rats in the aversive condition searched only in the corner that was both geometrically and non-geometrically correct, showing that, depending on the type of motivation, rats could differently conjoin the two types of information.

Hayward et al. (2003), using a black sphere near the escape platform in a corner of a rectangular-shaped water maze as the non-geometric information, found out that removal of the sphere during test trials induced rats to make rotational errors, as happened in the case of rats trained without any non-geometric information nearby the platform. However, the authors report that at the end of training, rats in the condition with the sphere reached 90% choices in the correct corner and only 7% in the rotationally opposite corner. It is thus evident that both motivational aspects of the task (aversive vs. appetitive) and the nature (relative size) of the non-geometric information have a role in determining how strongly (or weakly) rats would rely on the purely geometric information conveyed by the shape of an enclosure.

In a larger experimental framework aimed at examining the relationships between environmental shape and landmark information in terms of cue competition, however, other experiments by the same authors established that shape has almost always a major role in rats’ reorientation. Experiments in which the effects of beacons and landmarks were assessed by designs meant to reveal overshadowing or blocking (Pearce et al., 2001; Hayward et al., 2003, 2004), and to pit shape against extra-maze cues (Hayward et al., 2003), generally failed to knock-out learning based on the shape of the environment (Wall et al., 2004; but see Cheng, 2008 and Pearce, 2009).

A remarkable exception has been observed by Graham and colleagues in rats (2006). Rats were trained to locate a submerged platform in a kite-shaped pool with adjacent walls at the right-angled corners presenting a homogeneous black and a homogeneous white color, respectively. For one group of rats, both the geometric cues and the color on the walls predicted the position of the platform. Another group of rats was trained to locate the platform at constant geometric position relative to the shape of the pool, but the color on walls was made inconsistent between trials alternating their position between the two alternatives during the training. For the third group of rats only the color on walls reliably

predicted the position of the platform. Contrary to prediction of an obligatory process for the analysis of the geometric surface layout, the group of rats trained in a fixed geometric position, but a variable color on walls, failed to learn the task (Graham et al., 2006).

Since environmental geometry had proven such a powerful source of information in the process of spatial reorientation, it seemed reasonable that the representations and computations required to encode and use shape should also be studied per se, aside of investigating the interaction between shape and landmarks. In this respect, one research line that until now has seen few but interesting developments, made deliberate use of transformations involving exclusively the shape of enclosed environments. Kelly and Spetch (2001), for instance, devised an experiment aimed at understanding at what extent pigeons' performance in Cheng's task is based on the encoding of relative geometry. To this aim they trained pigeons to find a food reward in a corner of a rectangular-shaped enclosure (2 m × 1 m) and then tested them in a number of different enclosures. For two test enclosures, the ratio between the lengths of the two sides was identical to the training enclosure (thus the enclosures had the same relative geometry; i.e., shape): both enclosures were smaller in absolute size, one of them having walls halved in length (1 m × 0.5 m), the other having walls of an intermediate length (1.33 m × 0.66 m). One last test enclosure was square-shaped (1 m × 1 m): in this case the relative geometry was overtly altered. As expected, search in the square-shaped enclosure was distributed equally in the four corners. Pigeons transferred their searching behavior in the geometrically correct corners of the intermediate rectangular-shaped test enclosure, despite all walls had a different absolute length than the training enclosure, but showing that the task could be accomplished just on the basis of relative geometry. In the smaller rectangular-shaped enclosure, however, searching behavior appeared to be influenced by absolute geometry: despite pigeons searched more in the geometrically correct corners, this transfer appeared to be weaker than in the intermediate case. It thus seems that spatial reorientation in an enclosed environment, at least for what concerns search at geometrically correct corners in Cheng's paradigm, and at least in pigeons, can be thought as based upon the encoding of relative geometry. Considering this result in the light of the negative evidence reviewed above on the ability of pigeons to transfer geometric relationships in the domain landmark arrays (i.e., Spetch et al., 1997), it is clear that differences in spatial abilities can be ascribed right to the nature of the spatial environment considered, relative geometry being more easily encoded in the case of continuous surfaces than in the case of discrete landmarks.

Another example of this shape-transformation approach is provided by the study of Tommasi and Polli (2004) with chicks. Disoriented chicks were trained to find a corner of a parallelogram-shaped enclosure that had pairs of opposite walls in a length ratio of 1:2 (two walls being 35 cm long and the other two being 70 cm long) and pairs of opposite corners in an analogous 1:2 ratio (two corners were 60° in amplitude and the other two were 120° in amplitude).

One group of chicks was trained to find a food reward in the 60° corner and another group of chicks was trained to find the reward in the 120° corner. Chicks in both groups had thus two cues available to reorient, the amplitude of the corner and the relative length of walls. Two tests in shape-transformed enclosures were devised to ascertain whether either cue had been encoded and used by chicks. The first test was carried out in a rectangular-shaped enclosure having walls of the same length as the training enclosure. Corners, being all 90° in amplitude, were thus made irrelevant cues for the chicks in order to reorient. The second test was carried out in a rhombus-shaped enclosure having opposite corners of the same amplitude as the training enclosure (two corners 60° and the other two 120°). Walls, being all of equal length (52 cm), were in this case made irrelevant cues. Chicks in both training groups reoriented

correctly with respect to the residual information available in the test enclosures. A third test was devised to assess which of the two cues had, if any, a stronger control on chick's reorientation. This test was carried out in a mirror image replica of the training enclosure, that thus had the same lengths of walls and the same amplitude of corners as the training enclosure, but in a mismatched fashion. If chicks relied on one cue more strongly than the other, they would show a preference for those corners of this test enclosure that presented that cue despite the presence of the conflicting (and wrong) other cue. The result was at first sight puzzling: all chicks searched in the 60° corners of this test enclosure. Thus, although chicks in the two groups had encoded both the geometric relationships between walls and the amplitude of corners (as suggested by the first two tests), these cues appeared to be assigned different priorities. Since previous results had shown that disoriented chicks facing a conflict between geometric and non-geometric information relied upon the latter source of information (Vallortigara et al., 1990), it might be speculated that corner amplitude, although ultimately a geometric information in nature, is encoded and treated by chicks as *local* information. This appears realistic when considering the relatively small visual angle subtended by *one corner* perceived as such vs. that subtended by *two adjacent surfaces* perceived in their entirety. The experiment was recently replicated in pigeons (Lubyk and Spetch, 2011), that also showed to encode both types of information, but relied preferentially on the learned angular information when tested in the mirror-enclosure.

In another study Pearce et al. (2004) used a rectangular-shaped water maze, in which rats had to swim to find a hidden platform in one corner. Once learned the task, the rats were transferred to a kite-shaped water maze, obtained by juxtaposing one half of the training water maze and its mirror image.

The kite-shaped water maze had walls the same length as the rectangular-shaped enclosure but in the wrong order (i.e., in the sequence short-short-long-long instead of short-long-short-long); moreover there were two corners that were absent in the rectangular-shaped enclosure: one acute corner (between the two long walls) and one obtuse corner (between the two short walls); whereas there was only one geometrically correct and one geometrically incorrect corner. In the transfer test, rats searched equally often in the correct corner and in the acute corner between the two long walls. Rats trained first in the kite-shaped water maze (in one of the two right-angled corners), searched in the equivalent two corners when transferred in the rectangular-shaped water maze. According to the authors, this search pattern shows that rats had correctly encoded the local characteristics of the region where the platform was found (at the intersection of a long and a short wall) and the associated sense order (which wall was on the left and which was on the right). The search at the acute corner observed in the rats tested in the kite-shaped water maze, was explained as the outcome of a strategy which would lead rats to search along a long wall and stop at either its right or left end, according to which end of the long wall the platform was usually found during training in the rectangle-shaped water maze.

Cheng and Gallistel (2005) opposed the idea that geometric encoding in the previous two works on chicks (Tommasi and Polli, 2004) and rats (Pearce et al., 2004) could be explained by the use of local information, and proposed an alternative explanation based on the extraction of the principal axes of the enclosures, a process based on the form of the whole environment rather than on localities and accidents, however they might appear salient to human (and perhaps non-human) perception. Principal axes would instead provide a single parameter conveying the overall orientation of the global shape, and animals would thus use this parameter as a directional cue against which the specific location of places could be determined, even across different shapes. Although this account

would easily explain the results of Tommasi and Polli (2004) and Pearce et al. (2004), the idea on which it rests (i.e., the extraction of the principal axes) has little backing from other data about the nature of the geometric determinants in place learning used by chicks and rats. It seems unlikely that the bias to anchoring points (i.e., edges and discontinuities) known to be present in chicks and rats in place learning tasks, would allow for the extraction of principal axes, which would instead require the computation of the whole perimeter of the enclosure (Tommasi, 2005; see also Kelly et al., 2010, 2011; Sturz and Bodily, 2011 for a recent debate).

Esber et al. (2005) and McGregor et al. (2006) provided evidence against Cheng and Gallistel's (2005) explanation based on principal axes, using respectively a landmark array-based- and an enclosure-based-procedure: in both cases, local explanations were shown to be sufficient to explain rats' search behavior. On a similar vein, in a rhombic environment, children of 4 years of age are capable of using angular information to reorient and also to integrate it with featural cues whenever available (Hupbach and Nadel, 2005).

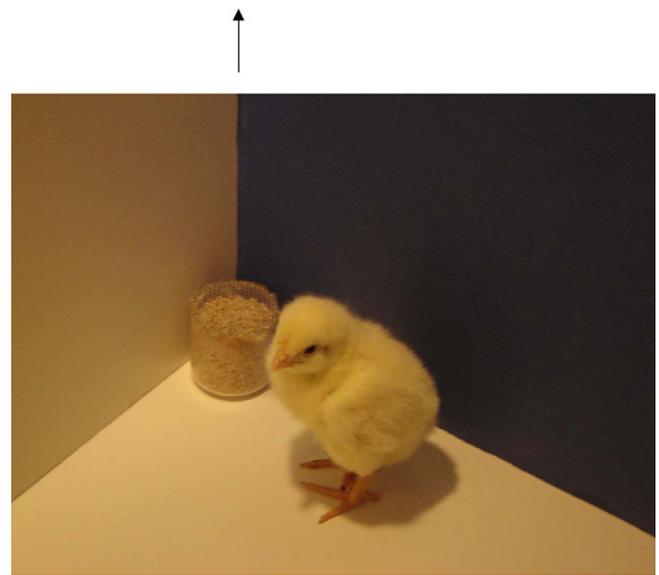
#### 4.2. Reorienting in large and small spaces

As mentioned above, the studies by Learmonth et al. (2001, 2002) provided an interesting finding that relates the ability to conjoin geometric and non-geometric information to the spatial scale of the environment (see also Vallortigara, 2009, for a review).

Work with non-human animals recently provided more complex results, but also pointed to a role of the spatial scale of the environment on the ability to integrate geometric and non-geometric information. Fish (redtail splitfins, *X. eiseni*) tested in the same task used with children proved able to conjoin geometric and non-geometric information to reorient in both the large and the small space used (Sovrano et al., 2005). Moreover, fish proved able to reorient immediately when transferred from a large to a small experimental space and vice versa. However, they tended to make relatively more errors based on geometric information when the transfer occurred from a small to a large space, and to make relatively more errors based on landmark information when transfer occurred from a large to a small space.

One-week old domestic chicks also seemed to be able to conjoin geometric and non-geometric (landmark) information to reorient in both a large and a small space (Vallortigara et al., 2005; Chiandetti et al., 2007). Moreover, chicks reoriented immediately when displaced from a large to a small environment and vice versa, without showing any difference in amount of geometric and non-geometric errors. However, when tested after a transformation (affine) that altered the geometric relations between the target and the shape of the environment, chicks tended to make more errors based on geometric information when tested in the small than in the large space. Overall, these findings suggest that the relationship between the reliance of the use of geometric information and the spatial scale of the environment is not restricted to the human species (see Chiandetti and Vallortigara, 2008a for a review).

Why should the ability of conjoining geometric and non-geometric information depend on the size of the experimental space? One explanation suggested by various authors is that organisms are prepared to use only distant featural information as landmarks (Wang and Spelke, 2002; Spelke, 2000; Spelke and Tsivkin, 2001; Hupbach and Nadel, 2005; Nadel and Hupbach, 2006). However, there is one problem with this view. Several data have provided evidence of a "primacy" of geometric information over non-geometric information (see Vallortigara and Sovrano, 2002 and Cheng and Newcombe, 2005 for reviews). For instance, after training with local landmark information at the corners that would suffice to completely disambiguate the task, a test with complete removal of the local landmarks does not result in random search: animals search on the basis of geometric information (see

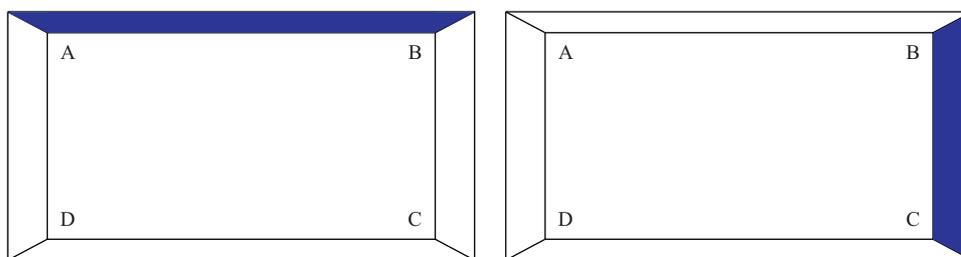


**Fig. 3.** Sense (i.e., left and right distinction) linked to non-geometric information (color): the location of the food jar is identifiable taking the blue wall on the right and the white wall on the left. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

e.g. Vallortigara et al., 1990; Kelly et al., 1998). This suggests that geometric information is encoded anyway, even when not strictly necessary to solve the task (see Cheng and Newcombe, 2005 for a general review of the evidence). Therefore, the basic issue as to the effects of size on spatial reorientation is not to explain why organisms do not use featural information in small spaces (they could do that simply because of the primacy of geometric information), but rather to explain why they do not continue to use geometric information even when tested in large spaces. The latter issue is difficult to understand in terms of the simple hypothesis that animals tend to use as landmarks distal rather than proximal objects. There seems to exist some factor that is specifically associated with a more reduced reliance of geometric information in large spaces.

Sovrano and Vallortigara (2006) have put forwards a hypothesis in this regard. The solution of the differently colored-wall task actually encompasses the combined use of two sources of information, geometric information provided by the shape of the room (i.e., the arrangements of surfaces as surfaces) and non-geometric, landmark information provided by the differently colored-wall. However, geometric information actually comprises two aspects: i.e., metric information and sense. Metric information refers to the ability of the animal to distinguish between a shorter and a longer wall (irrespective of any other non-geometric property associated with the walls' surfaces, such as color, brightness, scent and so on). Sense refers in geometry to the ability to distinguish between left and right. The important point to note is that in certain conditions animals might make use of a combination of non-geometric information and sense in order to reorient, without making any use of truly metric properties of the environment (for a visual representation of sense linked to color, see Fig. 3).

Consider now the situation depicted in Fig. 4. The correct corner (A) can be distinguished from both its geometric equivalent (C) and its featural equivalent (B) without relying on the use of metric information. It suffices that the animal encodes the information that the correct corner is the corner with a white-blue arrangement (featural information) in which the blue is "on the right" (geometric information). This combination of featural information and sense (without any reference to the metric of the environment) would suffice to disambiguate the problem, because the corner A can now be distinguished easily from both corner C (because corner C lacks



**Fig. 4.** The geometric module task in its blue-wall version: animals trained to locate a goal in A (leftmost panel) are subsequently tested after a displacement of the colored wall (rightmost panel). Different choices are available depending on the combination of long–short and white–blue information with left–right sense (see the text). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

any blue color) and corner B (because in corner B the blue color, although present, is located in the wrong sense order).

Sovrano and Vallortigara (2006) devised a test in chicks (Fig. 4) in which such a dissection of sense and metric information was made possible. After training (Fig. 4, left), at test (Fig. 4, right) the blue wall was dislocated from the AB to the BC wall (given that the transformation also implied a change in size of the feature, that was accounted for experimentally by counterbalancing the two types of changes, from a large to a small blue wall and vice versa). As a result of the transformation, it would appear impossible for the animal to find a corner that exactly matches featural and geometric information (sense and metric properties) as experienced during initial training (Fig. 4, left). If animals take into consideration both sources of information, geometric and non-geometric, then choices should be expected to be concentrated along corners in the BC wall, because these are the only locations which possess the correct featural information. However, given that geometric information actually comprises two distinct aspects, metric properties and sense, there are two possibilities (or combinations of them). Firstly, if animals rely mainly on metric properties but tend to ignore sense with regard to featural information, then corner C should be preferred. This is because corner C has the same featural information (the blue color – even though with the wrong sense because the blue is on the left rather than on the right) and the same metrical arrangement of surfaces as during the initial test (i.e., long wall on the left and short wall on the right). Secondly, if, on the contrary, animals rely mainly on the sense of the feature and tend to ignore metric properties of surfaces, then corner B should be preferred. This is because corner B possess the same featural information (the blue color) with the same sense properties (i.e., blue on the left) as during the initial test, even though it does not possess the same metrical arrangement of surfaces (i.e., in this case the long wall is on the right and the short one on the left). Results were striking: in the large enclosure chicks chose the corner that maintained the correct arrangement of the featural cue with respect to sense (B in Fig. 4), whereas in the small enclosure they chose the corner that maintained the correct metric arrangement of the walls with respect to sense (C in Fig. 4; see Sovrano and Vallortigara, 2006). These findings suggest that there would be a different linkage of sense information with either metric or landmark information depending on the spatial scale of the environment: in small spaces animals link sense with metric properties of surfaces, in large spaces animals link sense with local landmark cues (see Learmonth et al., 2008 for a different point of view).

An associative model of geometry learning developed to study reorientation in a geometric environment (Miller and Shettleworth, 2007, 2008; Dawson et al., 2008), for instance, may reproduce the behavioral pattern of data obtained in dependence of the size of the environment by simply adjusting the saliency of either geometric or featural information or both due to the change in environmental size (Miller, 2009).

However, before any generalization can be drawn it should be considered that the evidence currently available suggests that the relative role of geometric and non-geometric (landmark) information can vary in different species (likely because of differences in ecology and sense organs properties). Fish and birds can provide an interesting case in point. Although in species of both classes it has been demonstrated the capacity to integrate geometric and non-geometric information in the differently colored-wall task (e.g., chicks: Vallortigara et al., 2004; redbill splitfins: Sovrano et al., 2002), the effects of tests in which geometric and non-geometric cues provided contradictory information produced very different results: chicks, for instance, seemed to be little affected by geometric cues and tended to rely mainly on local landmark information (Vallortigara et al., 1990), whereas redbill splitfins tended to be severely affected by the metric properties of the surfaces of the environment (Sovrano et al., 2003). Recently, Sovrano et al. (2007) tested redbill splitfins in the same task studied in chicks. There were interesting differences between the two species. In the large enclosure chicks chose the corner that maintained the correct arrangement of the featural cue with respect to sense, whereas in the small enclosure they chose the corner that maintained the correct metric arrangement of the walls with respect to sense (Sovrano and Vallortigara, 2006). Fish tested in the large tank also chose the corner that maintained the correct arrangement of the featural cue with respect to sense. However, in the small enclosure fish did not limit themselves to choosing the corner that maintained the correct metric arrangement of the walls with respect to sense among the two corners with the blue feature, but also chose the corner in the geometric position lacking any featural cue.

All this seems to suggest that, although the general hypothesis put forwards by Sovrano and Vallortigara (2006) appears to be correct, i.e., that in small spaces animals tend to link sense with metric properties of surfaces and in large spaces animals tend to link sense with local landmark cues, there seem to be species differences in the reliance of using prevalently geometric or landmark information. Basically, it seems that for redbill splitfins geometric information is relatively more important than featural information than it is for chicks. Perhaps such a difference could be expected considering that birds are highly visual animals with considerable spatial resolution capabilities; fish, in contrast, because of adaptation to an aquatic environment, show comparatively more reduced spatial resolution because of the spatial filtering produced by water [but see recent evidences collected with rats (*R. norvegicus*) which used more featural than geometric information with increasing arena size (Maes et al., 2009)].

#### 4.3. Middle, center and other singularities

Reorientation in an enclosed environment is a task that depends on the shape of the search space in order to obtain the directional information needed to localize a goal. Moreover, in almost all the experiments described in the last section the disoriented

participant – animal or human – just had to decide which, out of a couple of geometrically equivalent regions of space (most commonly corners), was the correct one. However, as in the case of Cheng's working memory task with rats (Cheng, 1986), involving search all over the surface of an enclosure, animals may exploit the shape of an enclosure in order to localize a specific position out of a theoretically infinite number of alternatives. The same applies to all the experiments involving landmarks described above, as well as in the water maze: the behavior of the animals in these cases is not restricted to two choices, but it is expressed as a continuous, two-dimensional distribution of spatial search over the environment. One could thus wonder whether and how place learning could take place in the situation where the shape of the environment acts as the only cue guiding the animal to a unique, invisible, goal. In Cheng's (1986) example, the unequivocal position of the goal and the resulting rotational errors observed could be predicted by the symmetrical shape of the enclosure that had been used. An asymmetrical environment might thus allow the experimenter to train an animal to a single location without spatial ambiguities. However, there is a position that would not possess ambiguous rotational equivalents even in a regular, symmetrical enclosure: the center.

Tommasi et al. (1997) trained domestic chicks to find a goal in the center of symmetrical, regular-shaped enclosures in which the vision of stimuli external to the enclosure was prevented, thus forcing the animals to rely exclusively upon the shape of the environment. Chicks easily learned the task, that consisted in ground-scratching over a layer of sawdust to uncover some buried food. This experimental paradigm called for a genuine use of the transformational approach, given that the center is a robust geometric entity across a number of transformations: size and shape transformations were thus studied. Different groups of animals were trained with different shapes of enclosures (a square-shaped, a circular-shaped and an equilateral triangular-shaped enclosure) and subsequently tested in enclosures that were made double in linear size. Chicks trained in a square-shaped enclosure and tested in a larger one, searched both in the center of the test enclosure, but also at the same distance from the walls as the distance from the walls to the center learned in the training enclosure. A similar result was obtained with chicks trained in the triangular-shaped enclosure, whereas in the case of the test in an enlarged circular shape, chicks searched in an annulus halfway between the center and the absolute distance of the center from the walls as learned during training in the smaller enclosure. This seemed to suggest that, in learning the task, chicks had encoded the central position both as the output of a relational computation (same distance from multiple points along the walls), and as the absolute distance from the walls to the center, as evidenced by the bimodal search pattern observed in the enlarged square- and the triangular-shaped enclosure. The absence of an analogous pattern in the case of the circular-shaped enclosure, suggested that these spatial computations could benefit from the presence of discontinuities, like edges at corners, which were lacking in the continuous surface of the circular-shaped enclosure. Another group of chicks was tested for transfer involving shape transformations. They were all trained in a square-shaped enclosure and tested in four differently shaped enclosures: a circular-, an equilateral triangle-, an isosceles triangle-, and a rectangular-shaped enclosure. All chicks showed central searching behavior in the four novel enclosures, although the distribution of ground-scratching presented three peaks in the rectangular-shaped enclosure (one in the center and the other two in the squares composing the rectangle, which was obtained doubling one side of the training enclosure). In the isosceles triangle-shaped enclosure, search appeared to be localized in a single location, which turned out to be statistically equivalent to the center of gravity of the shape. Overall, chicks seemed to encode both absolute and relative distances in the task, and the features

upon which chicks appeared to rely upon might really be the discontinuities over the surfaces defining the enclosure. This result was confirmed in further studies (Tommasi and Vallortigara, 2000, 2001), that also tested for transfer in a smaller enclosure than that used during training: in this case chicks trained in a square-shaped enclosure were tested in a smaller (halved in side) enclosure of the same shape, and showed only central search.

Analogous experiments carried out in rats (Tommasi and Thinus-Blanc, 2004; Tommasi and Save, 2005; transfer across different shapes and sizes) and in pigeons (Gray et al., 2004; transfer across different sizes) provided similar results, thus suggesting that (i) the center is encoded by means of relational computations based on shape alone in species that had all shown to be sensitive to this cue in reorientation tests; and that (ii) shape, as defined by continuous surfaces, is a more powerful source of information in inducing encoding based on relative distances, than are discrete landmarks. The latter conclusion derives from comparing experiments on landmark expansion and experiments on enclosure expansion in pigeons (Spetch et al., 1997; Gray et al., 2004), but also from comparing the results of landmark transformations in gerbils and the results on enclosure transformation in rats (Collett et al., 1986; Tommasi and Thinus-Blanc, 2004). Recent data seem to suggest that similar differences in place learning in the case of search based on enclosure geometry or landmark geometry might apply also to the case of domestic chicks (Della Chiesa et al., 2006a).

One aspect of place learning based on enclosure shape that has been investigated extensively in chicks, concerns the case in which a single landmark (a beacon) was also present in the center of the enclosure, thus providing, along with the geometric information, local non-geometric information that might be sufficient to localize the goal. Chicks trained in this way, consistently with data on reorientation and overshadowing in rats (but less consistently with data on chicks' reorientation), searched in the center of the enclosure when the beacon was removed during tests (Tommasi and Vallortigara, 2000, 2001, 2004), and even when the beacon was simply displaced toward a corner (Tommasi and Vallortigara, 2001, 2004; see also Tommasi et al., 2003), providing another compelling instance of the primacy of environmental shape information over landmark information. Why should this outcome be consistent with data on rat's reorientation and navigation in the water maze, while at the same time being at variance with data on chicks' reorientation is not clear, although experiments in which a landmark array was used instead of a single central beacon, suggest that chicks attend to the non-geometric information more than the geometry of the enclosure (Della Chiesa et al., 2006b). A fixed path length separated the starting point from the goal-spot in all of these studies, so that inertial guidance cues, together with the visual cues, provided additional spatial information to the subjects. It could be argued that translating the beacon from the center toward the perimeter wall of the arena set into conflict these information, whereas translating the beacon between corners in a rectangular room task did not substantially altered the linkage between these information sources.

On the other hand, a recent work by Gray and Spetch (2006) seems to suggest that the difference between individual landmarks and extended surfaces may be limited to the visibility of external cues. As mentioned before, pigeons seem to use absolute distance from landmarks, whereas when trained in enclosures with extended surfaces, they tend to use relational distances (as chicks do, Tommasi and Vallortigara, 2000). However, Gray and Spetch (2006) showed that after training to find the center of an array of landmarks or a set of short walls that did not block external cues, when tested in expansion tests pigeons used an absolute distance strategy in both cases. The authors suggested that the presence of external cues alters the set of cues that constitute global information. When external cues are not blocked, as in the case of

a set of short walls, the shape and features of the larger experimental room would make the set of global cues, and the array of short walls or landmarks would serve as local cues to indicate the goal location. In contrast, when external cues are visible, as in the case of high-extended walls, the walls themselves may provide the only global information available. Counter evidence, however, have been obtained suggesting that pigeons rely on absolute metric to locate the center of a square-shaped enclosure as well, indicating that vector strategies may represent the default searching strategies in both landmarks arrays and enclosed spaces in this avian species (Wilzeck et al., 2009).

## 5. Natural geometry: the role of experience and innate factors

Curiously, enough, little research has been carried out on the role of experience on the ability to deal with geometric information in animals. Although modules need not be necessarily innate (Karmiloff-Smith, 1992), the issue of whether the ability of encoding geometric information would require environmental triggering or some sort of experience with angled surfaces of different lengths appears to be interesting. This is particularly true in the light of evidence from human studies that more than rudimentary knowledge of geometry seems to be available even in the absence of specific linguistic training and use of symbolic maps (Dehaene et al., 2006).

Recent evidence has revealed species differences in the ability to deal with geometric and non-geometric information in birds that could be suggestive of a role of experience. Differently than domestic chicks and pigeons, wild-caught mountain chickadees (*Poecile gambeli*) do not spontaneously encode the geometry of an enclosure when salient features are present near the goal; moreover, when trained without salient features they do encode geometric information but this encoding is overshadowed by features (Gray et al., 2005). It is unclear at present why these differences may occur. One possible explanation could be that wild-caught birds have little experience with small enclosures and right corners which are familiar to laboratory animals, thus leading to reliance on featural over geometric information. Somewhat the reverse could be true for small fish that live in shallow, transparent water with pebbles and rich vegetation such as redbellied splitfins (see Meyer et al. (1985); and see also Burt de Perera (2004) for evidence of use of geometric information in a species of blind fish that obviously cannot make any use of visual featural information).

Some recent results obtained in chicks and in fish suggest, however, that the encoding of geometry could be predisposed and little affected by experience. Chiandetti and Vallortigara (2008b) tested the navigational abilities of newborn domestic chicks hatched in the dark and reared soon after hatching in either a circular or rectangular cage. Chicks were trained in a rectangular-shaped enclosure with panels at the corners providing salient featural cues. Circular-reared and rectangular-reared chicks proved identically able to learn the task. When tested after removal of the featural cues, both circular- and rectangular-reared chicks showed evidence of having spontaneously encoded geometric information. These results strongly suggest that effective use of geometric information for spatial reorientation does not require experience in environments with right angles and metrically distinct surfaces.

Similar results were obtained by Brown et al. (2007) in the convict cichlid fish (*Archocentrus nigrofasciatus*). Fish reared into circular or rectangular tanks were identically able to use geometric information to navigate when no features were present. With features present, fish encoded both geometric and featural information. Interestingly, when geometric and featural cues were set in conflict, fish raised in a circular tank showed less use of geometric information than fish reared in a rectangular tank. Thus,

although the ability to use geometry to reorient does not require exposure to angular geometric cues during rearing, the rearing environment can affect the relative dominance of features and geometry. This could explain the results obtained with wild-caught mountain chickadees by Gray et al. (2005) mentioned above, but an alternative explanation resides in the species-specific difference in assigning the primacy to geometry. Both wild-caught and hand-reared individuals of two sister families [mountain chickadees (*P. gambeli*) and black-capped chickadees (*Poecile atricapillus*)] have been recently compared while reorienting, and all groups resorted to geometry use in the geometric test (Batty et al., 2009). Both black-capped and mountain chickadees showed to perform the test in the same way as to the ability to rely to geometry, independently from experience; but mountain chickadees were less disposed to use geometry, indicating a species-specific leaning toward reference to other sources of information. Support to this view comes from data obtained in further experiments with differently reared chicks. The critical condition for fish was the reorientation while in the presence of conflicting geometrical and featural information. When this situation was replicated in chicks, this species showed any difference in choices depending on previous exposure (Chiandetti and Vallortigara, 2010a). The species-specific difference may in this case account for the discrepancy of results with fish since chicks are precocial whereas fish need prolonged parental care; most noteworthy this explanation can explain the species-specific difference in chickadees as well (Vallortigara et al., 2009).

Recently, further evidence that at least some aspects of spatial representations are present at birth, even in altricial species, has appeared from single cell recording studies. It has been found that when rat pups explore an open environment outside the nest for the first time head-direction cells (see next section) show adult-like properties from the beginning; place and grid cells are also present from the beginning but their selectivity refine gradually (Langston et al., 2010; Wills et al., 2010; see also for a discussion of these results Haun et al., 2010).

Fellini et al. (2006) recently tested whether aging could affect encoding of geometry in spatial reorientation. They compared the behavior of adult (3–5-month-old) and aged (20–21-month-old) C57BL/6 male mice in a water maze task in which spatial information was provided by one landmark proximal to the target (featural information) and by the rectangular shape of the maze (geometric information). By means of probe trials in which they manipulated the presence of these two kinds of information, they showed that adult mice can use both geometry and landmark to orient. By contrast, aged mice do not use geometry and rely exclusively on the landmark to locate the platform. This study provides the first evidence that use of geometric information declines in aged animals. It would be interesting to study even other species, including non-mammals.

## 6. Neural mechanisms underlying the encoding of geometry in enclosed spaces

Little is known even on the neural mechanisms that deal with the treatment of geometric information. A strategy for assessing to what extent the mechanisms that process geometric and non-geometric information are segregated has been to look at the asymmetry of function between the left and right side of the animal brain (see for a review Vallortigara and Rogers, 2005; Vallortigara et al., 2011).

In animals with laterally placed eyes, such as fish and most species of birds, there is a virtually complete decussation at the optic chiasm. In the optic nerves less than 0.1% of the fibers proceed to the ipsilateral side (Weidner et al., 1985). Since only a limited number of axons re-cross via the mesencephalic and

thalamic commissures, the avian visual system is remarkably crossed. This means that information entering each eye is largely, though not completely (see Rogers and Deng, 1999; Deng and Rogers, 2002), processed by the contralateral side of the brain. Thus, by simply temporarily occluding one eye we can obtain some insights on lateralized functions of the avian brain.

Vallortigara et al. (2004) trained chicks binocularly in a rectangular enclosure with panels at the corners providing non-geometric cues. When tested after removal of the panels, left-eyed chicks, but not right-eyed chicks, reoriented using the residual information provided by the geometry of the cage. When tested after removal of geometric information (i.e., in a square-shaped cage), both right- and left-eyed chicks reoriented using the residual non-geometric information provided by the panels. When trained binocularly with only geometric information, at test left-eyed chicks reoriented better than right-eyed chicks. Finally, when geometric and non-geometric cues provided contradictory information (because of an affine transformation on the spatial distribution of panels), left-eyed chicks showed more reliance on geometric cues, whereas right-eyed chicks showed more reliance on non-geometric cues. The results suggest therefore separate mechanisms for dealing with spatial reorientation, with the right hemisphere taking charge of large-scale geometry of the environment and with both hemispheres taking charge of local, non-geometric cues when available in isolation, but with a predominance of the left hemisphere when competition between geometric and non-geometric information occurs.

As to the extent these data obtained with the avian brain can be generalized to mammals, and to humans in particular, little evidence is currently available. Birds are special in having complete decussation at the optic chiasma, lack of corpus callosum and (relatively) reduced inter-hemispheric communication (Vallortigara, 2000). Nonetheless, hemispheric differences comparable to those reported here for chicks have been observed in rats. LaMendola and Bever (1997) tested rats in an eight-arm radial maze, the same five arms of which were always baited. Fewer errors (scored as returns to a baited arm which had already been visited, or entry of one of three arms that were never baited) were made when left whiskers were anesthetized (and so only right whiskers were in use) than when only left whiskers were in use. The dependence of this effect on a left-hemisphere involvement in the analysis of right whisker input was confirmed by unilateral spreading depression of the left or right cortex, with left-hemisphere depression producing more errors in rats with both sets of whiskers in use. This left hemisphere dominance was likely due to the fact that local intramaze cues provided a unique and conspicuous label for each arm. When the maze was rotated, so that intramaze and extramaze cues were no longer in their usual relationship, a reversal in the relative performance of right- and left-whisker rats was observed; use of extramaze cues seems to favor dependence on a record based on the overall layout of the maze and thus dominance of the right hemisphere.

Some recent data may suggest dissociations along similar lines in humans. For instance, right hippocampal activation has been documented in taxi drivers asked to mentally navigate the streets of London (Maguire et al., 1997, 2006). Using the rectangular room task, Pizzamiglio et al. (1998) showed that patients with right brain damage with hemineglect are deficient in reorienting (though it proved difficult to establish a precise correlation between the site of the lesion and the deficit in the use of geometric and/or non-geometric information). More recently, however, Guariglia et al. (2000) found that in neglect patients transcutaneous electrical neural stimulation significantly improved the ability to code geometric information, but was ineffective with non-geometric information. All this suggests the existence of separate systems for processing geometric and non-geometric information similar to those found in the avian brain. Similar evidence derives from Williams

syndrome patients, who maintain language skills whereas display severe detriment in spatial abilities: if affected by this genetic disorder, the subjects are profoundly compromised in the selective use of geometry to reorient (Landau and Lakusta, 2009; Lakusta et al., 2010).

However, the presence of a structure of the brain devoted to spatial processing seems an ancient feature of the vertebrate brain indeed, phylogenetically preserved. Lesions to the lateral pallium (a forebrain structure of teleost fish which is considered neuroanatomically equivalent to the mammalian and avian hippocampus) of goldfish (*C. auratus*) selectively impair the processing of geometric spatial information (Vargas et al., 2004a,b, 2006; Rajan et al., 2011). Further evidence for specific mechanisms dealing with geometric information in the brain arise from place finding tasks in which the abilities of young chicks to localize the central position of a closed environment in the absence of any external cues were investigated (see previous sections). Tommasi and Vallortigara (2001) tested chicks under environmental changes that involved a substantial modification in the size of the arena. For instance, after training in a square-shaped arena chicks were tested in an arena of the same shape but of a larger size. As mentioned above, the search behavior of chicks in the test (larger) arena was localized in two regions: in the actual center of the test arena and (in part) at a distance from the walls that was equal to the distance from the walls to the center in the training (smaller) arena. Apparently, two behavioral strategies seem to be available to the chicks, i.e. encoding a goal location in terms of absolute distance and direction to the walls, and encoding a goal location in terms of ratios of distances (whatever their absolute values) from the walls. Tests carried out under monocular viewing (after binocular training) revealed striking asymmetries 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 Tommasi and Vallortigara, 2001; Vallortigara, 2006).

Encoding of large-scale information based on the shape of the arena in place finding tasks seems to be based on hippocampal function. Tommasi et al. (2003) tested chicks bilaterally or unilaterally lesioned to the hippocampus which were trained to search for food hidden beneath sawdust by ground-scratching in the center of a large enclosure, the correct position of food being indicated by a local landmark in the absence of any extra-enclosure visual cues. At test, the landmark was removed or displaced at a distance from its original position. Results showed that sham-operated chicks and chicks with a lesion of the left hippocampus searched in the center, relying on large-scale geometric information provided by the enclosure, whereas chicks with a lesion of either the right hippocampus or both hippocampi were completely disoriented (landmark removed) or searched close to the landmark shifted from the center (landmark displaced). These results indicate that encoding of geometric features of an enclosure occurs in the right hippocampus even when local information provided by a landmark would suffice to localize the goal; encoding based on local information, in contrast, seems to occur outside the hippocampus.

A role of the avian hippocampal formation in the encoding of geometric information in reorientation task has been suggested by work of Bingman and colleagues with homing pigeons, though in this case the results were more complicated. Evidence in the field suggest that spontaneous flight around the home-loft, as well as repeated homing experience from distant release site, allow the homing pigeons to learn a mental representation of the prominent landmarks in the surrounding and to rely on these landmarks in the subsequent homing flight (Holland, 2003). Lesion studies also suggest that the hippocampus mediates the familiar landmark based navigation (Bingman and Mench, 1990; Bingman et al., 2005; Gagliardo et al., 1999, 2009). It is a matter of debate whether

pigeons take into account metric information when navigating over familiar terrains. This issue has been tackled recently in a series of small scale spatial task.

In a first study Vargas et al. (2004b) trained pigeons to find food in a rectangular arena in which one of the short walls was of a different color (red). During a conflict test in which one of the long wall was red and the other remained all white, control pigeons relied on geometric information to search for food, whereas pigeons with bilateral lesions to the hippocampus relied completely on the colored wall (featural information). This in spite of the fact that during training lesioned pigeons learned even faster than control pigeons.

In a subsequent study, however, Bingman et al. (2006a) trained homing pigeons (*C. livia*) to locate a goal in one corner of a rectangular arena by either its shape (geometry) or the left–right configuration of colored features located in each corner (feature structure). Although control and hippocampal-lesioned pigeons proved to learn at a similar rate, the control birds made proportionally more geometric errors during acquisition. In conflict probe trials, the control birds preferred geometrically correct corners, whereas the hippocampal-lesioned birds displayed a greater preference for the correct corner defined by feature structure. However, differently than in Vargas et al. (2004b), geometry-only probe trials revealed that both groups demonstrated an ability to identify the goal location. Thus, in this study hippocampal lesions do not interfere with encoding of featural information (as shown also in chicks by Tommasi et al., 2003), but also do not abolish encoding of geometric information: rather, it seems that lesions to the hippocampus diminished the salience of geometric information. The reason for these discrepancies is unclear. One possibility put forwards by Bingman et al. (2006a) is relative to the fact that the arena used by Vargas et al. (2004b) was 50% larger in size than that used by Bingman et al. (2006a), suggesting a reduced reliance on geometric cues (see previous sections for the role of size in encoding of geometric information). However, histology also suggest differences in the site of the lesion, in that substantial sparing of parahippocampus could be observed in the lesions of Vargas, Petruso and Bingman whereas this structure was lesioned in the pigeons of Bingman et al.

It is interesting to note that work by Pearce et al. (2005) has shown that hippocampal lesions in pigeons do not abolish the capacity to discriminate between different pairs of colored cards on the basis of the structural relationship between their components in an open-field arena. Thus, pigeons without a hippocampus can make discrimination of the type “pink to the left of green”. Thus, it is perhaps not surprising that they could discriminate something like “short wall to the left of the long wall”. Nonetheless, it remains unclear why they should be unable to do so in the Vargas et al. (2004b) test. The data of Vargas et al. (2004b) seem also to agree with evidence obtained in mammals. McGregor et al. (2004) showed that lesions to the hippocampus prevented the ability of rats to navigate to a goal using the geometric information provided by a solid-walled arena or a rectangular array of identical landmarks. These authors also attempted to link these findings with the pattern of firing of hippocampal neurons (place cells) that are known to correlate with an animal's position in the environment. According to O'Keefe and Burgess (1996) a key feature that affects place cells activity is the distance of the animal from the wall of an arena, i.e., place cells would encode the location of the animal from the edge of an arena in the form of a Gaussian distribution with a peak level of firing located at a fixed distance from the arena wall. A particularly suited class of cells for the metric analysis of an environment has been very recently added in the spatial neural circuit: the border cells (Solstad et al., 2008). Their existence was first posited in computational models as boundary vector cells (Barry et al., 2006); border cells seem to encode obstacles and borders of the surroundings allowing the definition of the perimeter of an

environment. Whether or not they represent the firing expression of capturing distances and directions from surfaces, border cells may be an instrumental step in deepening our understanding of spatial cognition of geometry.

It is unclear, however, whether in the avian hippocampus place cells with similar selectivity of response as those found in the rodents hippocampus are present (Siegel et al., 2005), although evidence has been recently found that cells in the left and right hippocampal formation of pigeons have different properties, apparently supporting the evidence collected in lesion experiments (Siegel et al., 2006; Bingman et al., 2006b).

A further complication with pigeons is that they seem to show a different pattern of lateralization with respect to chicks, for when faced with a conflict between geometric and non-geometric information, pigeons with lesion to the left hippocampus seem to favor featural over geometrical cues (Nardi and Bingman, 2007). It seems likely that this is due to a basic difference in the neural circuits involved in cerebral lateralization in the two species, the thalamofugal pathway in the chick and the tectofugal pathway in the pigeon (see reviews in Güntürkün, 1997; Rogers, 1996; Rogers and Andrew, 2002; Vallortigara and Rogers, 2005; Chiandetti et al., 2005).

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