

Core knowledge of object, number, and geometry: A comparative and neural approach

Giorgio Vallortigara

To cite this article: Giorgio Vallortigara (2012) Core knowledge of object, number, and geometry: A comparative and neural approach, *Cognitive Neuropsychology*, 29:1-2, 213-236, DOI: [10.1080/02643294.2012.654772](https://doi.org/10.1080/02643294.2012.654772)

To link to this article: <http://dx.doi.org/10.1080/02643294.2012.654772>



Published online: 31 Jan 2012.



Submit your article to this journal [↗](#)



Article views: 402



View related articles [↗](#)



Citing articles: 29 View citing articles [↗](#)

Core knowledge of object, number, and geometry: A comparative and neural approach

Giorgio Vallortigara

Center for Mind/Brain Sciences, University of Trento, Rovereto, Italy

Studies on the ontogenetic origins of human knowledge provide evidence for a small set of separable systems of core knowledge dealing with the representation of inanimate and animate objects, number, and geometry. Because core knowledge systems are evolutionarily ancient, they can be investigated from a comparative perspective, making use of various animal models. In this review, I discuss evidence showing precocious abilities in nonhuman species to represent (a) objects that move partly or fully out of view and their basic mechanical properties such as solidity, (b) the cardinal and ordinal/sequential aspects of numerical cognition and rudimentary arithmetic with small numerosities, and (c) the geometrical relationships among extended surfaces in the surrounding layout. Controlled rearing studies suggest that the abilities associated with core knowledge systems of objects, number, and geometry are observed in animals in the absence (or with very reduced) experience, supporting a nativistic foundation of such cognitive mechanisms. Animal models also promise a fresh approach to the issue of the neurobiological and genetic mechanisms underlying the expression of core knowledge systems.

Keywords: Core knowledge; Space; Geometry; Number; Objects; Intuitive physics; Animacy; Chicks.

According to a prominent hypothesis (Carey, 2009; Spelke, 2000), human cognition is composed of a set of core systems for representing significant aspects of the environment—namely, objects, persons, spatial relationships, and number. The hypothesis maintains that core knowledge systems are shared by other animals and are in place at birth. Studies on object, number, and space representation (e.g., Beran, Decker, Schwartz, & Schultz, 2011; Brannon, 2006; Cantlon & Brannon, 2006; Tommasi, Chiandetti, Pecchia,

Sovrano, & Valloirtigara, 2012; van Marle, Aw, McCrink, & Santos, 2006) in a variety of species provide evidence for the generality of the core knowledge systems in other animals. The hypothesis that core knowledge systems are available at birth is difficult to test in human infants, because of the unavoidable limitations on the control of early experience. It is important to note, however, that similar limitations are also apparent with other altricial species, whose young are born in a relatively immature state. Consider as an example

Correspondence should be addressed to Giorgio Vallortigara, Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, Rovereto, 38068 Italy. (E-mail: giorgio.vallortigara@unitn.it).

This work has been prepared thanks to the support from the Provincia Autonoma di Trento and the Fondazione Cassa di Risparmio di Trento e Rovereto. Thanks also to Dr Sang Ah Lee for commenting on a previous version of this paper.

the issue of preferential orientation of neonates to human faces. A complete absence of face stimulation could not be feasible even in neonates studied a few hours after birth. However, similar limitations arise in animal work. Sugita (2008) reported that infant Japanese monkeys reared with no exposure to any faces for 6–24 months showed nevertheless a preference for human and monkey faces. However, monkeys were separated from their mother within a few hours after birth (Sugita, 2008, p.1), making possible, in principle, very fast learning of face characteristics. Besides, it could be argued that monkeys (or other altricial animals) maintained for several months without exposure to faces might show an abnormal pattern of psychological development. On the other hand, testing monkeys soon after birth even in simple behavioural tasks would prove impractical because of their motoric immaturity.

Luckily enough, nature seems to have provided biologists with appropriate model organisms for investigation of every sort of scientific problem—“*God’s organisms*”, in the words of neuroscientist Steven Rose (2000). There are species that are extremely precocial with regard to their pattern of motor development, making possible quite sophisticated behavioural analyses at an early age (i.e., soon after birth or hatching) combined with a very precise control on the effects of past (even in utero or in ovo) sensory experiences, including a complete lack of some of them. Here I champion the use of the young domestic chick as a “*God’s organism*” for investigation of the origin of knowledge.

Criticisms concerning whether evidence for cognitive abilities available at birth indicate innateness stress that one cannot exclude a role of experience and learning in utero or in ovo (this was one of the arguments of Lehrman, 1953, in his debate with Lorenz, 1965, about so-called “instinctive behaviour”). Actually, control of stimulation in embryo would be possible to some degree using animal models. But there are reasons to doubt that evidence for a role of stimulation in embryo could produce *prima facie* evidence against innateness. An example comes from some work carried out recently in my lab.

We took advantage of the phenomenon of filial imprinting, the process by which animals like young chicks and ducks develop a strong social attachment to the first conspicuous visual object they are exposed to soon after hatching (see Natural-born physicists section). We found that newly hatched chicks show a spontaneous preference for consonant over dissonant intervals when coupled with a visual imprinting object to approach (Chiandetti & Vallortigara, 2011a). Chicks in these experiments were incubated and hatched in soundproof environments, but of course they could hear the sounds produced by themselves as embryos. However, chick vocalizations in embryo are produced spontaneously, and therefore their structure (consonant or dissonant) cannot be learned. Thus, if one assumes that the preference for consonance in newly hatched chicks cannot be said to be innately predisposed because it might actually arise from sensory stimulation in embryo, then it remains to be explained why the motor system of these embryos should be predisposed to produce consonant (rather than dissonant) intervals. The innateness that has been expunged from the sensorial side reappears in the motoric side.

I believe that we must be careful to keep separate the issue of the *origin* of information an organism appears to possess from the way in which information is actually encoded in the brain and exhibited in behaviour. We know very well that the road from genes to behaviour is a complex one and that development always implies a mixture of genetic, epigenetic, and experience factors (Bateson & Gluckman, 2011; Marcus, 2004). Nonetheless, the issue of the origin of information is different from that of the development of behaviour, because it should take into account the adaptiveness exhibited by organisms in behaviour. Consider the classical reply provided by Lorenz (1965) to Lehrman’s criticisms. Let’s assume, said Lorenz, that the aggressive behaviour exhibited by the famous three-spined stickleback fish to objects that are red on their belly is not innately predisposed but it is in some way learned in embryo as the empiricists would argue. Now, the issue is: How do the stickleback fish

know that attacking things that are red in their bellies is good for them? In fact the behaviour of attacking things that are red in their bellies is adaptive to the fish because it happens that things with red bellies are, in their natural environment, their male conspecifics. But what is the origin of *this* information that fish seem to possess? How do they possibly learn, in embryo, that they are going to meet male conspecifics with red bellies in their environment? Clearly, this cannot be learned during ontogeny. And, if we do not believe that there is some sort of pre-established harmony in the world that could account for biological adaptations, then this is knowledge that is part of their phylogenetic memory—knowledge that has been shaped by natural selection over the course of natural history and that resides in the animals' genome (Lorenz, 1965).

Similarly, in the case of the preferences of newly hatched chicks for consonance, the point is not *whether* some role of experience could be associated with exposure in embryo to consonant or dissonant stimuli but rather *why* it should be good for chicks to approach stimuli emitting consonant rather than dissonant sound intervals after hatching. My guess is that since harmonic spectra are prominent features of sounds in a natural environment, they could serve, as do certain visual cues (e.g., biological motion, self-propelled motion, to be discussed in the Natural-born "Life detectors" section), as a guide to newly hatched chicks to imprint preferentially on to animate rather than inanimate objects. (Recently, Johnson-Laird, Kang, & Leong, in press, argued that what determines the dissonance of chords—with harmonic partials—for human listeners is a combination of some basic principles of tonal music with "roughness", which occurs with sounds with harmonic partials and sounds with nonharmonic partials; the latter may be more frequent in the natural world: Philip Johnson-Laird, personal communication, 11 October 2011). And, again, *this* knowledge (that it is good for a newly hatched chick to approach animate rather than inanimate objects and to imprint on them) cannot have been acquired by learning during ontogeny; it is the

result of a "learning" that has occurred during phylogeny and has been incorporated into the genome.

In this review, I discuss evidence showing precocious abilities in very young chicks to represent basic mechanical properties of physical objects such as solidity, basic properties such as self-propelled motion that are used to identify certain objects as animate, cardinal, and ordinal/sequential aspects of numerical cognition and rudimentary arithmetic with small numerosness of discrete objects, and finally the geometrical relationships among these objects in the surrounding layout. Controlled rearing studies will provide evidence that these abilities are observed in chicks in the absence (or with very reduced) experience. I argue by comparison with the data available for the newborns of our own species that, overall, the empirical evidence supports a nativistic foundation of core knowledge cognitive mechanisms.

Natural-born physicists

When considering what aspects of knowledge are apparent in biological organisms prior to their first contacts with the objects of their experience and what then emerges thanks to the effects of experience with these objects, different theories seem to have been more or less successful in different domains. Historically, nativist theories have generally found greater favour in the domain of sensory development (e.g., Blakemore & Van Sluysters, 1975; Held & Hein, 1963; Walk, Gibson, & Tighe, 1957). Nativist and empiricist theories have generated acrimonious debates—and have found mostly equal favour until recently—in the domains of abstract concepts like number and geometry (see for the history of the debate reviews in Carey & Spelke, 1996; Platt & Spelke, 2009; Spelke, 1998). Empiricism has, however, always held major consideration in the domain of object mechanics (e.g., Mandler, 1988). For it seemed quite obvious that our knowledge of how objects behave comes from observing their behaviour, acting upon them, or both.

Consider a basic concept of object mechanics—the fact that a solid object cannot occupy the same

space as another solid object. In seminal experiments (Baillargeon, 1995; Baillargeon, Spelke, & Wasserman, 1985), it was shown that three-and-a-half-month-old infants form representations of hidden objects and make the inference that a solid object cannot move through the space occupied by another solid object. Evidence has since been collected that nonhuman animals also represent physical objects and reason about the motion of physical objects in accordance with the basic constraint of solidity of material bodies (Call, 2007; Kundey, De Los Reyes, Taglang, Baruch, & German, 2009; Pattison, Miller, Rayburn-Reeves, & Zentall, 2010). Nevertheless, the fact that human infants exhibit evidence for object permanence and inference about the physical properties of objects starting from three and a half months of age is compatible with both a nativist and an empiricist view, the former arguing for maturation and the latter for learning. Controlled-rearing studies of animals could help to disentangle the different views.

We recently investigated naïve physics conceptions in newborn chicks (Chiandetti & Vallortigara, 2011b). The domestic chick is a precocial species that has been largely used as a model system in ethology and neurobiology for the study of early learning (Andrew, 1991; Rogers, 1996), and recently it has become a focus of interest and insight with respect to several classical issues in developmental psychology, taking advantage in particular of the behavioural techniques made available by filial imprinting (for reviews see Vallortigara, 2004, 2006, 2009b; Vallortigara, Regolin, Chiandetti, & Rugani, 2010). Imprinting is the learning process by which the young of some animals learn the characteristics of an object—usually a social partner—by simply being exposed to it soon after hatching (Bateson, 2000; Horn, 2004). As in other forms of learning, there are biological predispositions that act to guide and facilitate imprinting in young chicks. We made use of both imprinting and its associated predispositions as a tool for investigation of the topic of the origins of knowledge.

In our experiments on intuitive physics, separate groups of chicks were imprinted on objects of

different size (see e.g., Figure 1 top). At test, chicks were placed (singly) in a transparent holding box and were able to see the imprinting object moving along a straight midline towards two identical screens (Figure 1 middle left). Their view was then obscured by an opaque partition, and the imprinting object was removed. The screens were replaced with two other screens that were no longer identical. For example, the height (middle right) or width (bottom left) or slant (bottom right) of the two screens was changed so that only one screen but not the other was large/tall/slanted enough (in different experiments) for the imprinting object to be hidden behind or beneath it. The partition was then removed, and the chicks were allowed to search for the object. Chicks typically choose to search only behind the screen that could hide the object.

We wondered whether the possibility of pecking at the imprinting object during rearing was instrumental to the chicks' intuition of impenetrability of the object. However, when a transparent polyester substrate screen prevented chicks from touching and pecking the object during exposure, the animals showed at test the same preference as chicks reared in direct contact with the imprinting object. Thus, apparently, chicks had very sophisticated abilities concerning physical objects and the properties of occlusion in the absence of specific experience. They seemed to be born with a sort of intuitive physics (and see also Regolin, Rugani, Stancher, & Vallortigara, *in press*).

I can anticipate an objection: The domestic chick and the human newborn are only remotely related from a phylogenetic point of view, and one could doubt whether these data have any relevance to the origins of human cognition. I return to discuss this issue in greater depth later on. But it should be stressed at this point that the choice of a successful animal system model in biology is not based on phylogenetic relatedness, but on the nature of the problem under investigation (otherwise fruit fly genetics would be totally irrelevant to human genetics). Thus, let us consider some other example of how fruitful the use of the

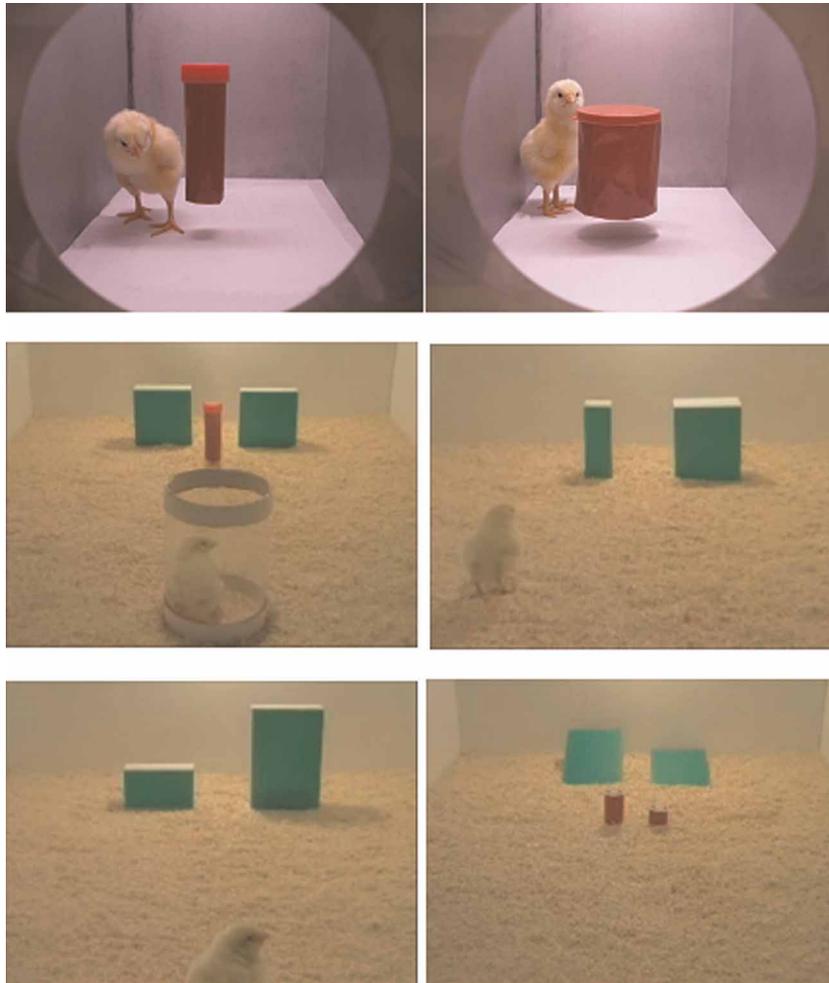


Figure 1. *Top: Examples of the imprinting objects that chicks were reared with. Middle and bottom: Photographs of the experiments (see text for details). To view a colour version of this figure, please see the online issue of the Journal.*

domestic chick as a system model for investigation of core knowledge mechanisms could be.

Natural-born “life detectors”

Physical objects comprise a category of entities that have special properties for biological organisms—namely, other living things. Converging evidence from neuropsychology (Caramazza & Shelton, 1998) and developmental psychology (S. C. Johnson, 2000) suggests that humans are

equipped with mechanisms for attending to and recognizing living things, in particular other animals. An example comes from a study by New, Cosmides, and Tooby (2007) showing that human observers are faster and more accurate at detecting change in animals than they are at detecting change in a variety of inanimate objects, ranging from vehicles to buildings and tools. However, we know little as to the extent to which these mechanisms are in place at birth and about the possible role of experience in shaping them. Even more importantly, we largely ignore the specific underlying

neural mechanisms (Mormann et al., 2011). As in other fields of biological sciences, animal models may be instrumental in providing clues to the nature and origin of internal mechanisms.

In 1988, Gabriel Horn and Mark Johnson carried out some groundbreaking studies showing that, contrary to widely held beliefs, filial imprinting seems to consist of two separate processes: an inborn predisposition of the young bird to attend to visual stimuli that resemble a broody hen, and a learning mechanism (which would be guided and supported by the innate predisposition) to learn by exposition about the specific, unique characteristic of a particular mother hen (M. H. Johnson & Horn, 1988). Subsequently, Johnson moved to studies on human infant face preferences and together with John Morton published a series of seminal papers (see for a review, M. H. Johnson & Morton, 1991) arguing that a similar two-mechanism device would be available to human neonates for face recognition. According to their model, infants are born with some information about the structure of faces. This structural information, termed *Conspéc*, guides the preference for face-like patterns found in newborn infants. *Conspéc* is contrasted with a device termed *Conlern*, which is responsible for learning about the visual characteristics of conspecifics.

Subsequent work, however, has cast some doubt as to the precise nature of the *Conspéc* mechanism. In particular, it has been argued that contrary to Johnson and Morton's (1991) theory, newborn infants' preferences for faces would be a secondary effect determined by nonspecific biases due to constraints imposed by the immature visual system of the child. Turati, Simion, Milani, and Umiltà (2002) provided evidence that the preference for face-like stimuli would be determined by an "up-down bias" that would direct baby's attention toward any configuration presenting more elements in the upper part (a "top-heavy configuration").

However, as noted above, human newborns cannot be completely prevented from being exposed to faces. Thus, it is unclear as to whether part of the controversy depends on an

effect of early learning or on transient effects related to the maturation of the visual system. In fact a recent study failed to show any top-heavy bias in 3- to 5.5-month-old infants (Chien, 2011). Carefully controlled studies with animals could help to resolve this issue.

Surprisingly, no further work after M. H. Johnson and Horn's (1988) paper had been done on newly hatched chicks to investigate what specific features of the head region stimulate *Conspéc*. We have recently undertaken such a research, and our results suggest that chicks have indeed an inborn preference to approach face-like stimuli, resembling their head region. Completely naïve, newly hatched chicks prefer face-like stimuli to features-on-top stimuli (e.g., they preferred the stimulus on the left in the pairs of figures shown in Figure 2; Rosa-Salva, Regolin, & Vallortigara, 2010). Note that in this case, the preference is not the outcome of exposure learning—that is, of filial imprinting—for chicks exhibit the preference to approach face-like stimuli without any previous experience. The preference, however, does affect the imprinting process by guiding and canalizing the range of objects the chicks are more likely to imprint to.

We also tested the prediction that both newly hatched chicks and human newborns will demonstrate similar preferences for face stimuli over spatial-frequency-matched structured noise (see, for example, Figure 3). This prediction was confirmed, providing strong converging evidence that many vertebrates have a domain-relevant bias toward faces shortly after hatching or birth

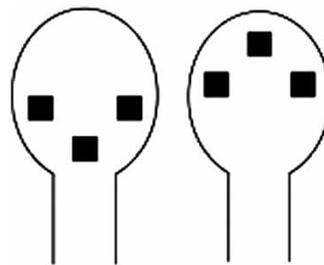


Figure 2. Examples of the stimuli used by Rosa Salva et al. (2010) for testing newborn chicks' preferences for face-like stimuli.



Figure 3. Example of stimuli (images of a face and of the scrambled noise control) used in the newborns' and chicks' study by Rosa Salva et al. (2011). To view a colour version of this figure, please see the online issue of the Journal.

(Rosa Salva, Farroni, Regolin, Vallortigara, & Johnson, 2011; and see also McKone et al., 2012 this issue, for a nativist position on face perception).

A second line of research involves work that was instead initiated in my own lab, concerning inborn preferences for biological motion. Even in this case, a route from initial research on the chick to subsequent research on the human newborn can be traced back. But first I shall consider some historical roots of my research.

If you look at ethology textbooks, you will find the general assertion that object motion facilitates imprinting. Curiously enough, however, no one has checked whether all types of motion are

identically effective or if animals are especially sensitive to particular types of motion. In order to disentangle the stationary visual characteristics of the mother hen (its shape) from the dynamic aspects of it (its motion), we used point-light displays. It is well known that when a small number of points of light are attached to the torso and limbs of a moving organism, and only such points of light are visible, the animation can correctly convey information as to the animal's activity (Johansson, 1973). We tested naïve, newly hatched chicks, lacking any previous visual experience, to investigate whether they showed a spontaneous preference to approach stimuli depicting biological rather than



Figure 4. Example of the point-light display stimuli used in the Vallortigara et al. (2005) study on predisposition for biological motion in chicks. To view a colour version of this figure, please see the online issue of the Journal.

nonbiological motion (Vallortigara, Regolin, & Marconato, 2005). One point-light sequence (see, e.g., Figure 4) represented a “walking hen” (13 points of light located on the digitalization of the video-recording of a real animal). Three other sequences were used as “foil sequences”. These were: “rigid motion” sequence (a single frame from the walking hen animation sequence was randomly selected and was moved rigidly about its vertical axis so as to produce the motion of a rotating rigid hen-like object); “random motion” sequence (the same set of points of light moved in arbitrary directions); and “scrambled hen” sequence (the same set of points of light as those employed for producing the walking hen and in the same set of frames as those used for the walking hen were used, only now the original position of each point was spatially displaced by a fixed amount consistently throughout the animation. Every single point of light, although displaced as compared with its position in the walking hen animation, moved identically in this sequence as it did in the walking hen. As a result, this last display no longer conveyed perception of a hen to human observers, though it retained the appearance of the biological motion of some kind of unidentified creature).

The results showed that naive chicks exhibit clear and consistent preferences in approaching certain types of movements. Intriguingly, however, chicks’ choices seemed to reflect a generic preference for the patterns of biological motion rather than a specific preference for the typical form of the motion of a hen. The walking hen was chosen as much as the scrambled hen, though both the walking hen and the scrambled hen were preferred to the rigid and random motion. This finding suggests that chicks preferentially approach semirigid motion, the type of motion that is exhibited by vertebrate animals. In semirigid motion, some points maintain a fixed distance from each other (e.g., two points placed close on the same limb), but can nonetheless vary their distance with respect to other points (e.g., with respect to points located on the torso). Such a pattern of semirigid motion is shared by the walking and the scrambled hen, even though the

latter does not match any existing biological creature. As a control for this hypothesis, we used the motion of a point-light cat, a species that can predate on young chicks. As predicted, chicks did not exhibit any preference between the walking hen and a walking cat point-light sequence, though they did prefer the walking cat to the random and to the rigid motion.

The predisposition found for certain kinds of motion shares characteristics in common with those earlier demonstrated for the head and neck region of a hen to artificial objects (M. H. Johnson & Horn, 1988). Similarly to this preference for form, the preference for movement is not species-specific. When considered together, these findings seem to fit a general scheme for cognitive development of recognition of other animals based on the interaction between two separate and independent systems. The first of these systems directs the attention of the young animal toward the appropriate class of objects to learn about, in the absence of any prior specific experience (e.g., in the case of motion, those objects that move semirigidly). The second system is concerned with learning about the peculiar characteristics of the objects to which attention has been directed by the first system. Given that in a natural environment it is more likely that the newly hatched chick would encounter a mother hen rather than a cat, a developing predisposition to pay attention to objects showing the characteristic motion of vertebrates would assure the highest probability to learn (by way of the imprinting mechanism) about the specific pattern of motion of the mother hen. Could these findings be generalized to the human species? As in the case of face-like preferences, the answer seems to be positive.

An inborn predisposition to attend to biological motion has long been theorized for the human species, but had so far not been demonstrated. In particular, no preference for biological motion was reported for human infants of less than 3 months of age (Fox & McDaniel, 1982). Recently, however, Simion, Regolin, and Bulf (2008) tested 2-day-old babies’ discrimination after familiarization and their spontaneous preferences for biological versus nonbiological point-

light animations, using the same type of stimuli (i.e., walking hens) as that used in our research with newly hatched chicks. Newborns were shown to be able to discriminate between the two different patterns of motion and, when first exposed to them, selectively preferred to look at the biological motion display. This preference was also orientation dependent: Newborns looked longer at upright displays than at upside-down displays (and the same result was previously reported for newly hatched visually naïve chicks; Vallortigara & Regolin, 2006). Overall, these parallel results in the two species strikingly support the hypothesis that detection of biological motion is an intrinsic capacity of the vertebrate visual system, which is presumably part of an evolutionarily ancient and non-species-specific system predisposing animals to preferentially attend to other animals (see J. Brown, Kaplan, Rogers, & Vallortigara, 2010, for evidence in other species, and Kaiser et al., 2010 for clinical implications for the study of autism).

Recent research on human infants has provided important evidence for early sensitivity to causal agency (animacy) and intention (for a review, see Biro et al., 2007, and see the seminal work by Leslie, 1982, 1984). We thus decided to investigate whether evidence for an inborn preference for objects conveying an impression of causal agency or intention can be observed in newly hatched visually inexperienced chicks (Mascalzoni, Regolin, & Vallortigara, 2010).

Chicks were presented with a video showing two objects, of different colours, on a stage, initially shown at rest. Then one object was shown to move slowly until contact with the other object, thus producing (to a human observer at least) the classical Michotte's (1963) launching effect (see O'Connell & Dunbar, 2005, for evidence that animals are sensitive to Michotte's perceived causality). The second object thus moved along a straight trajectory for the same length as the previous one, stopping before exiting from the stage. After this exposure phase, chicks were tested in a free-choice task for spontaneous preference for the two different objects. Complete balancing for use of different colours and left-right

direction of movement was ensured during exposure and at test. If chicks do attribute a notion of animacy to the object that starts moving and contacts the other object, then a preference for such an object would be evinced in free-choice preference tests, irrespective of its colour and direction of movement. This is precisely what we found. The results of other experiments showed that only when one of the two objects appeared as being self-propelled and the other not self-propelled did a preference emerge, as a choice for the self-propelled stimulus. Physical contact without physical causation (e.g., when both objects appeared as being self-propelled), or physical causation without any cues about the nature of the motion of "the causal object" (i.e., whether it is self-propelled or not), abolished any preference, showing that physical contact in itself was not capable of producing causal inference (Mascalzoni et al., 2010).

Chicks came from a dark incubator and hatchery; hence, they had not had any chance to be exposed visually to the motion of animate objects, apart for the controlled imprinting-exposure phase. Thus, the preference for the self-propelled object cannot be accounted for in terms of any specific learning. The minimal interpretation of our finding is that chicks are innately sensitive to self-propulsion as a crucial cue to animacy (or mechanical agency in the sense of having internal cause of action, see Leslie & Keeble, 1987).

The idea that sensitivity to self-produced motion could lie at the foundations of the clear-cut divide that the brain operates between the two basic domains of physical (inanimate) and intentional (animate) objects is not new—it dates back at least to Aristotle (*Physics*, translated by P.H. Wickstead and F.M. Cornford, Harvard University Press, Cambridge, 1980). The sensitivity to self-produced motion may be sufficient to adaptively constrain the early commitment of a highly precocious animal as to what to imprint on. It remains of course to be determined whether chicks are also innately endowed with a sensitivity to other movement properties, such as efficiency of goal approach (as humans and adult

primates seem to be, e.g., Rochat, Serra, Fadiga, & Gallese, 2008), which serve as cues to intentional agency. In any case, our findings are compatible with the idea that many vertebrate species, including humans, have primitive neural pathways that ensure a bias to attend to, or preferentially process, sensory information about other living entities.

The great advantage of an animal model such as the chick lies in the possibility of using invasive neurobiological techniques to investigate neural mechanisms in combination with the behavioural techniques described above. In nonhuman primates, a number of studies have reported neurons sensitive to occlusion and context in several brain areas (e.g., superior temporal sulcus, posterior parietal cortex, inferotemporal cortex; Assad & Maunsell, 1995; Duncan, Albright, & Stoner, 2000; Kovacs, Vogels, & Orban, 1995). For example, Baker, Keysers, Jellema, Wicker, and Perrett (2001) reported that neurons of the anterior superior temporal sulcus in the rhesus monkey show activity correlated to occlusion of objects. These responses could be hypothesized to contribute to the ability for object permanence and aspects of intuitive physics. However, it is difficult in primates to investigate these neural mechanisms in very young animals with precise control of past sensory experience. We are now trying to unveil these mechanisms in the chick. The first step involves the use of immediate early genes expression (such as *c-fos*) to identify target regions in the brain that appear to be stimulated by stimuli associated with specific predispositions. Our preliminary results suggest an involvement of the optic tectum. Interestingly, among the areas that have been hypothesized to be part of the human subcortical face-detection route (see M. H. Johnson, 2005), the superior colliculus, pulvinar, and amygdala all have homologues within the avian brain (respectively, optic tectum, nucleus rotundus, and amygdala).

Natural-born mathematicians

Number is another core domain of knowledge that might be encoded precociously in the vertebrate

brain. Again, we took advantage of filial imprinting for studying it in newborn chicks. Because of protection to predators and avoiding heat dissipation, young chicks tend to prefer to approach larger numbers of social partners. Thus, by exposing chicks to different numbers of artificial imprinting objects and then observing the animals in free-choice tests with sets of different number of objects, we could explore their numerical abilities. In a series of experiments (Rugani, Kelly, Szelest, Regolin, & Vallortigara, 2010), we imprinted separate groups of chicks on three or one imprinting objects and then tested chicks' choice between three and one objects. When chicks were reared with three objects, they preferred three objects at test; when they were reared with one object, they still preferred three objects at test. Apparently they went for more. When tested with two versus three, a more difficult task, the results were similar: Reared with three, they preferred three; reared with two, they preferred three again. Choice in a group of chicks tested without any imprinting did not yield any preference for the larger number of objects, thus showing that preference for the large number was clearly related to imprinting. However, it could be that chicks were not using number in this task but were simply estimating the overall volume or area or something like that. This has been shown to occur in human infants in some circumstances. For instance, when objects have similar properties or are from a domain in which physical extent can be particularly important (e.g., food, see Feigenson, Carey, & Hauser, 2002), infants seem to favour extent over number. When, however, a task requires reaching for individual objects (e.g., Feigenson & Carey, 2005) or objects contrasting in colour, pattern, or texture (Feigenson, 2005), then infants seem to respond to number and not to extent. Something similar seems to occur in chicks when they were imprinted on objects of different shape, colour, area, and volume and were then tested for choice with completely different novel objects (in size, colour, and shape with respect to the exposure imprinting phase). These novel objects were controlled in their continuous

extent (volume or surface area) such that they were the same in the three-element and in the two-element stimulus display. This time, when reared with three objects, chicks chose at test three objects; when reared with two objects, they chose two objects, showing their capacity to use number when continuous extent was equated (Rugani, Regolin, & Vallortigara, 2010).

Early availability of small numerosity discrimination by chicks strongly suggests that these abilities are in place at birth. Even basic arithmetic seems available at birth in chicks. In some experiments (Rugani, Fontanari, Simoni, Regolin, & Vallortigara, 2009), we reared chicks with five identical imprinting objects. At test, each chick was confined to a holding pen, behind a transparent partition, from where it could see two identical opaque screens. The chick saw two sets of imprinting objects—a set of 3 objects and a set of 2 objects; each set disappeared (either simultaneously or one by one) behind one of the two screens. Immediately after the disappearance of both sets, the transparent partition was removed, and the chick was left free to move around and search within the arena. Chicks spontaneously inspected the screen occluding the larger set of 3 (and did so even when continuous physical variables were controlled for). In further experiments, after an initial disappearance of two sets (i.e., 4 objects disappeared behind a screen and 1 behind the other), some of the objects were visibly transferred, one by one, from one screen to the other before the chick was released into the arena. Even in this case, chicks spontaneously chose the screen hiding the larger number of elements, and they did so irrespective of the directional cues provided by the initial and final displacements. Thus, chicks could compute, at their very first experience, a series of subsequent additions or subtractions of objects that appeared and disappeared over time, suggestive of early proto-arithmetic capacities. Intriguingly, whereas evidence using conditioning procedures in this species suggest a set size effect for small numerosities at about 3 items (Rugani, Regolin, & Vallortigara, 2008), in the imprinting experiments by Rugani et al. (2009), computation is done for larger sets (up to 5 items).

Currently nothing is known about the neural mechanisms underlying these abilities (and others, e.g., Pepperberg, 1994, 2006a, 2006b) in the avian brain, and it would certainly be interesting to investigate the existence of nerve cells tuned to number, as those described in the monkeys brains in parietal and frontal cortex (Nieder, Freedman, & Miller, 2002; Nieder & Miller, 2004). Candidate areas in the avian brain include the mesopallium and nidopallium caudolaterale (e.g., Butler & Cotterill, 2006). However, suggestive evidence of basic mechanisms shared and possibly homologous in the vertebrate brain comes from studies involving the ordinal/sequential aspects of numerical cognition.

Like other animal species (e.g., Chittka & Geiger, 1995; Dacke & Srinivasan, 2008; Davis & Bradford, 1986), chicks have been shown to possess the ability to identify an object on the exclusive basis of its position in a series of identical objects. When trained to peck at, for example, the 3rd, 4th, or 6th position in a series of 10 identically spaced locations, chicks learned accurately to identify the correct position (Rugani, Regolin, & Vallortigara, 2007). Control experiments ruled out the possibility they were using distances as a cue. For instance, when chicks were trained to peck at the fourth position and were then tested with a new sequence in which the distance from the starting point to each position was manipulated in such a way that ordinal position and distance from the starting point were different from those during initial training, chicks correctly pecked at the fourth serial position, even if that position was now located much farther away than before.

Interestingly, a bias for the left hemispace was found in these experiments. Chicks were trained to peck a selected position in a sagittally oriented series of identical elements. During test, the array was rotated by 90 degrees and oriented in a fronto-parallel fashion with respect to the chick's starting point, such that the correct position could not be located on the basis of absolute distances from the starting point. Chicks selected only the fourth position from the left end, and not the fourth from the right end, which was

chosen at chance level. In subsequent work, adult nutcrackers (*Nucifraga columbiana*) and newborn domestic chicks were compared in a similar task in which they were trained to peck at either the 4th or the 6th element in a series of 16 identical and aligned positions. Again, when the array was rotated 90 degrees, both species showed a bias for the correct position from the left but not from the right end (Rugani, Kelly, et al., 2010).

The birds' bias is reminiscent of the human mental number line phenomenon. As early as 1880, Galton (Galton, 1880) showed that humans describe and think of numbers as being represented on a mental number line, which is usually oriented from left to right (see also Dehaene, 1997). It is typically maintained that the spatial orientation of the human mental number line is linked to writing and reading habits. We wondered, however, if it may depend, at least in part, on biologically specific biases in the allocation of attention in extracorporeal space. A preference for targets located on the left hemispace may be due to a bias in the allocation of attention, somewhat similar to that shown by humans and dubbed as "pseudoneglect" (e.g., Jewell & McCourt, 2000). In fact, "pseudoneglect" phenomena have been described in birds with selective allocation of attention to the left hemifield during free foraging (Chiandetti, 2011; Diekamp, Regolin, Gunturkun, & Vallortigara, 2005). Somewhat similar phenomena of pseudoneglect favouring the left hemifield have been described also for amphibians (Vallortigara, Rogers, Bisazza, Lippolis, & Robins, 1998; and see for general reviews, MacNeilage, Rogers, & Vallortigara, 2009; Vallortigara, 2000; Vallortigara & Rogers, 2005).

We thus embarked on a series of systematic studies in order to better understand the nature of the bias shown by the chicks in the ordinal number task (Rugani, Vallortigara, Vallini, & Regolin, 2011). We found that when accustomed to systematic changes in interelement distances during training or when faced with similar spatial changes at test, chicks identify as correct the target positions from both the left and the right end. Experiments also showed, however, that ordinal position was spontaneously encoded

even when interelement distances were kept fixed during training (in spite of the fact that distances between elements sufficed for target identification without any numerical computation).

We thus believe that asymmetries in these serial ordering tests can be accounted for with a simple model that assumes differential encoding and coupling in the two hemispheres for spatial and numerical information. The finding that, even after training with fixed interelement distances, chicks encoded serial ordering and not just distances between the elements suggests that two separate representations are formed during training. The first representation concerns serial ordering as such—that is, without any association with magnitude of distances on a spatial scale. Such a representation would encode something like: The target is in the 4th position—that is, after the 3rd container and before the 5th container—without any specification of the distances between the ordinal positions of the containers. The second representation, on the other hand, would be of a spatial nature, encoding magnitude of distances between containers in a relational fashion. Association of the purely ordinal and the purely spatial representation would provide the animal with a mental line of number.

The purely ordinal representation would be bilaterally represented in the left and right cerebral hemispheres, and activation of this representation would not produce any imbalance in the activity of the two hemispheres. As a result, allocation of attention would be identically directed towards both the left and the right visual hemifields. This is supported by the fact that when following fronto-parallel presentation of the line of elements, distances are changed at test, chicks could choose the correct target from both the left and the right ends. In contrast, the purely spatial representation would be unilaterally represented in the right hemisphere. This is supported by independent evidence provided by both behavioural (Tommasi & Vallortigara, 2001; Vallortigara, Pagni, & Sovrano, 2004) and lesion (Tommasi, Gagliardo, Andrew, & Vallortigara, 2003) studies showing that spatial information is encoded selectively into the right hemisphere in

the chick forebrain (review in Vallortigara, 2009a, and see also next section). As a result, when at test chicks are faced with a fronto-parallel line of elements whose relational spatial encoding matches the serial ordering, extra activation of the right hemisphere would occur, favouring allocation of attention to the left hemispace and thus producing a bias to “count” selectively from left to right. When, however, because of a change in the spatial arrangement of the distances, chicks are faced with a line of elements in which spatial properties do not match those acquired during training, the chicks rely on serial ordering alone. The outcome in this case is the bilateral activation of both cerebral hemispheres and the unbiased allocation of attention along both hemifields, resulting in chicks showing identical propensity “to count” from left to right and from right to left. Possible implications of these findings from animal models to human asymmetries in spatial attention deserve scrutiny (see, e.g., Loetscher, Schwarz, Schubiger, & Brugger, 2008; Siman-Tov et al., 2009).

Natural-born geometers

Animals show very sophisticated knowledge of their spatial layout, with some rudimentary understanding of geometric properties (Vallortigara, 2009a). This has been originally shown in seminal studies by Cheng (1986) with rats and

by Spelke (Hermer & Spelke, 1994, 1996) with children. A simple example is shown in Figure 5. Imagine you are located in an empty rectangular room, with identically coloured walls and no external cues. In a corner there is a visible goal. Then you are displaced from the room and, with your eyes covered, turned around passively a few times. Finally, you are reintroduced into the room. The goal object is no longer visible. Your task is to figure out the corner where the goal object was previously located. Apparently, all corners look identical, and perhaps you would search at random among the four corners. However, if you ponder a little bit on the problem you could realize that there is a partial—though not complete—solution to the disambiguation of the corners. This is because you can make use of the geometry of the enclosure—its rectangular shape. For instance, when you are facing the corner indicated by the small blue square on top (see Figure 5), there will be on your right side a short wall and on your left side a long wall. Only another location will stand in the same geometric relationships with respect to the shape of the room—namely, the rotationally equivalent corner located on the opposite side along the diagonal (indicated by the small blue square on the bottom of Figure 5). These two corners cannot be distinguished from each other as they are geometrically equivalent, but they can be distinguished from the remaining two other

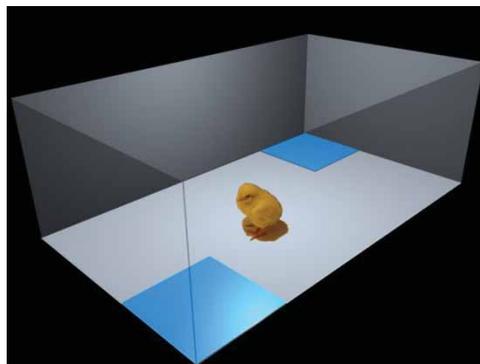


Figure 5. Schematic representation of the rectangular enclosure task to study use of geometry in spatial reorientation in animals and children (image courtesy of Cinzia Chiandetti). To view a colour version of this figure, please see the online issue of the Journal.

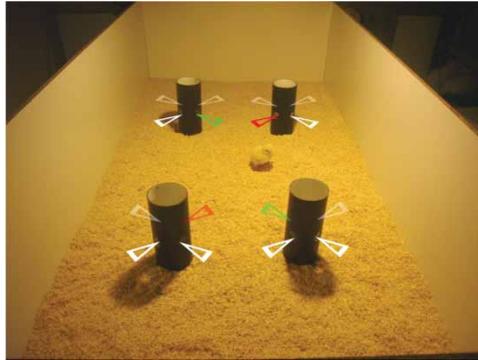


Figure 6. Schematic representations of the arrangements of the accessible openings on pipes (correct cylinders: darker arrows; incorrect cylinders: lighter arrows) during training in the fixed access and in the variable access condition. To view a colour version of this figure, please see the online issue of the *Journal*.

corners. In order to solve the task, therefore, two very simple forms of geometric knowledge are needed: the ability to discriminate *metric properties* of surfaces as surfaces (short wall vs. long wall) and the ability to discriminate what is called *sense* in geometry (left vs. right).

Several species have been proved able to solve this geometrical task. For instance, we demonstrated this in domestic chicks (Vallortigara, Zanforlin, & Pasti, 1990), in fish (redtail splitfins, *Xenotoca eiseni*; Sovrano, Bisazza, & Vallortigara, 2002, 2003), and, very recently, in bumblebees (Sovrano, Rigosi, & Vallortigara, 2011).

Competing theories have been formulated as to how organisms reorient themselves in these circumstances (see Spelke, 2011). One key finding has been that whereas computation of geometric properties is commonly observed with extended surfaces (such as enclosures similar to that of Figure 5), using freestanding objects arranged in the shape of rectangular arrays results are more variable (see Pecchia & Vallortigara, 2010a). Recently we provided evidence that a key determinant of animals' abilities to compute geometrical properties to reorient is not whether the landmarks are discrete objects or environment boundaries, but whether the animals are exposed to the same view while retrieving the goal or not (Pecchia, Gagliardo, & Vallortigara, 2011; Pecchia & Vallortigara, 2010b, in press). Usually retrieving a goal at an enclosure corner constrains the

animal's viewpoint (promoting viewpoint-dependent learning), whereas retrieving it at a freestanding object usually does not. To allow comparison of similar versus different viewpoints while retrieving goals at otherwise identical locations, we used a task in which the goal (food) was hidden in cylinders, each with four openings on different sides, only one of which was accessible (see Figure 6). The spatial location—cylinder—was then dissociated from the viewpoint experienced while retrieving food from it, which was determined by the side of the opening that was accessible. Chicks that saw fixed views during training (i.e., had the same perspective on the layout when retrieving food) could recall locations using either boundaries or discrete objects, whereas chicks that saw variable views could not succeed even with both cues available at the time. This provides evidence for view-based reorientation to either boundaries or configurations of objects, at least in chicks.

According to this theoretical approach, movements in space are deduced by comparing specific contents of panoramic views (visual snapshots) at the target and at the current location, following a minimal mismatch criterion (Cartwright & Collett, 1982, 1983). The hypothesis of a view-based strategy for spatial reorientation does not make any assumption of separate computation processes between information provided by extended surfaces and those provided by

freestanding objects in an array. However, it remains to be seen whether this also holds true for humans (and children). An important limitation to the generality of these findings concerns the methods used. Typically in animal studies a “reference memory” paradigm is used in which subjects learn over reinforced training to navigate to a goal location, such as a food source (as in the studies with the cylinders described above). In other studies, especially in those of human navigation, a spontaneous “working memory” procedure is used in which subjects are shown, without repeated reinforcement training, the goal at a particular location and then are observed after some time has passed, from a different viewpoint, or after they have been inertially disoriented. Using working memory tasks, evidence against purely image-matching theories has been obtained. For instance, in contrast to the prediction based on global matching, it has been shown that children fail to reorient by sharp contrast borders produced by a two-dimensional rectangle flashed against the floor of a circular-shaped room (Lee & Spelke, 2011). Children also fail to reorient by geometry in an array of freestanding objects (Lee, Shusterman, & Spelke, 2006; Lee & Spelke, 2008, 2010) even when the objects are connected together by a thin cord (Lee & Spelke, 2011). Similar results have been obtained in chicks in a working memory task (Lee, Spelke, & Vallortigara, 2012). Thus, it could be that a panoramic view (snapshot) approach to spatial

reorientation only holds for those circumstances in which repeated trials and learning allow organisms to form such snapshot memories.

As in the case of intuition of physical properties of objects and of number, we found that little, if any, experience is needed to young chicks to deal with geometry (Chiandetti & Vallortigara, 2008). We tested the navigational abilities of newborn chicks reared in enclosures of different shapes and metrical properties (Figure 7). Rectangular enclosures provided metrically distinct surfaces connected at right angles and two principal axes of symmetry (Figure 7, left). Geometric information was not available, in contrast, in circular enclosure (Figure 7, right), in which there was also an infinite number of principal axes. In C-shaped enclosures (Figure 7, middle), neither right angles nor differences in wall length were available, although the first principal axis was available to encode shape. Chicks proved to be equally capable of learning and performing navigational tasks based on geometric information irrespective of rearing in different environments

In a particularly revealing experiment, chicks were trained in a rectangular-shaped enclosure with panels at the corners providing salient featural cues (as shown in Figure 8a). Rectangular-reared and circular-reared chicks proved equally able to learn the task. Nonetheless, one could have expected that encoding of purely geometric information was stronger in animals reared in a

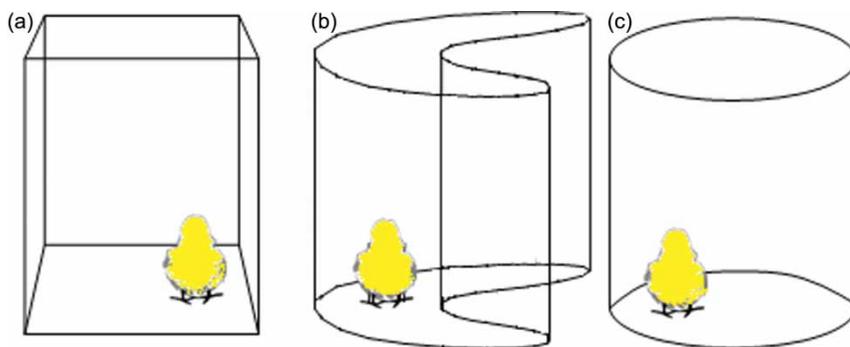


Figure 7. An illustrative representation of the rearing condition used to raise single chicks in controlled rearing experiments of geometry; (a) rectangular, (b) C-shaped, and (c) circular home cages. To view a colour version of this figure, please see the online issue of the Journal.

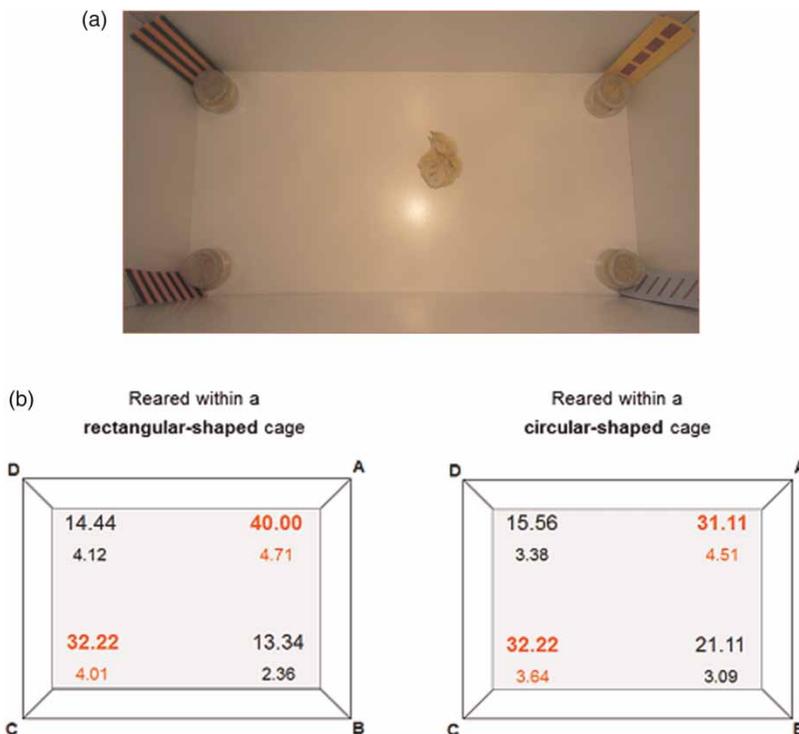


Figure 8. Set-up for training chicks with panels at the corners. (a) Panels were removed at test, revealing similar choice for the two geometrically correct corners in chicks reared in a rectangular or in a circular enclosure. (b) Numbers indicate means of choices with standard errors below. To view a colour version of this figure, please see the online issue of the Journal.

rectangular environment. In contrast, when tested after removal of the panels, both rectangular- and circular-reared chicks showed similar evidence that they had spontaneously encoded geometric information, choosing the two geometrically correct corners (Figure 8b). 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 have been obtained in fish. A. A. Brown, Spetch, and Hurd (2007) reared fish (*Archocentrus nigrofasciatus*) in rectangular or circular tanks and then tested their reorientation abilities in a rectangular tank without any featural cues. Similarly to chicks, results revealed no differences in learning abilities between circular- and rectangular-reared fish. When trained with featural information present, fish proved able to

learn both types of information. However, when these cues were in conflict, fish raised in a circular tank showed greater reliance on featural information than fish raised in a rectangular tank. This would suggest that rearing experience, though not affecting the ability to encode geometry, might affect the relative dominance in the use of geometric and nongeometric cues when animals are facing conflicting information. Intriguingly, such an effect was not observed in chicks (Chiandetti & Vallortigara, 2010). Perhaps this discrepancy between the species could be accounted for in terms of distinction between altricial and precocial organisms (Vallortigara, Sovrano, & Chiandetti, 2009). The species of fish used by A. A. Brown et al. (2007) shows biparental, prolonged care, whereas domestic chicks are immediately largely independent from parental care. Altricial species may therefore be more

sensitive to external stimulation (or to be open to such stimulation for a more extended period of time); hence, fish may be affected by rearing experience concerning nongeometric cues.

Overall our findings suggest that the foundation of natural geometry, at least in its most basic aspects, is far removed from any strictly linguistic and cultural constraint (see also Dehaene, Izard, Pica, & Spelke, 2006; Izard, Pica, Spelke, & Dehaene, 2011; Spelke, Lee, & Izard, 2010) and is deeply rooted in phylogenetic history. Education certainly determines our refinement in geometric skills—namely, our engaging in symbolic, exact manipulation of geometric concepts and measurements. However, *basic* metric and geometry emerge from nonsymbolic abilities that are widespread across different species and developmental levels (Spelke & Kinzler, 2009) and that are not experience dependent. Further support to this view comes from evidence that when such a core knowledge system is not working in the proper way, the use of geometry alone may be severely compromised. This is the case of Williams syndrome (WS), a genetic disorder in which patients exhibit impaired spatial abilities with relatively preserved language abilities (Landau, 2011). Lakusta et al. (2010) recently found that adults with WS searched at random in the standard task of the rectangular enclosure (with the walls uniformly coloured) though they were able to use featural information (with one wall of a different colour) to reorient themselves.

The use of simple animal models, which allow scientists to perform controlled-rearing studies, may open the door to research linking specific genes (Osborne, 2006) and elderly related spatial detriments (Fellini, Schachner, & Morellini, 2006) to reorientation impairment.

Comparative research investigating the role of hippocampus as a crucial area for representing space is long dated (O'Keefe & Nadel, 1978); however, the hippocampal involvement in the geometric module task is controversial (Bingman, Erichsen, Anderson, Good, & Pearce, 2006; Burgess, 2008; Vargas, Bingman, Portavella, & Lopez, 2006; Vargas, Petruso, & Bingman, 2004). In the chick brain, we found evidence for

a role of the hippocampal formation in place-finding tasks in which birds were required to find the centre of an enclosure (Tommasi et al., 2003). Whether this could be generalized to the rectangular geometry task is unclear, because place-finding tasks lack the essential component of the spatial disorientation of the animals. Evidence is clear, on the other hand, for a predominant role of the right hemisphere in using geometry in the rectangular reorientation task in experiments with monocularly tested chicks, which took advantage of complete decussation at optic chiasma and limited interhemispheric communication in the chicken's brain (Vallortigara et al., 2004). Interestingly, a lateralization favouring the right hippocampus was also reported in place finding tasks involving estimation of distances between the walls and the centre of a square-shaped enclosure (Tommasi et al., 2003).

Different families of cells strictly related to specific spatial demands have been discovered in the parahippocampal circuit (place cells: O'Keefe & Dostrovsky, 1971; head direction cells: Taube, Muller, & Ranck, 1990; grid cells: Fyhn, Molden, Witter, Moser, & Moser, 2004; border cells: Barry et al., 2006; Solstad, Boccara, Kropff, Moser, & Moser, 2008). Single cell recording when rat pups explore an open environment outside the nest for the first time showed that head-direction cells show adult-like properties from the beginning; place and grid cells are also present from the beginning but their selectivity is refined gradually (Langston et al., 2010; Wills, Cacucci, Burgess, & O'Keefe, 2010). Thus, electrophysiological data clearly support evidence from controlled rearing studies.

Conclusion

Chicks show sophisticated core knowledge mechanisms at a very precocial age, when the chances that they have acquired them by exposure to objects and events properties, if any, are extremely reduced. Of course it is impossible to prevent an organism from having sensory and motor experience of some sort. One could argue that our chicks at least should have had the experience of

pecking (which is a behaviour occurring also in ovo in order to hatch). However, it should be stressed that any empiricist interpretation should be specific about the type of experience that is needed in order to account for evidence of early core knowledge mechanisms (see also Spelke, Breinlinger, Macomber, & Jacobson, 1992). Consider the case of intuitive physics described in the Natural-born physicists section. Generic experience of pecking in itself cannot explain our findings: Chicks could encounter different types of physical materials: some soft, some liquid, and some offering resistance to pecking in their environment. Thus, one must argue that it is the specific experience of touching and pecking the solid imprinting object that is crucial. However, even when chicks were prevented from any direct physical contact with the imprinting object, they chose the screen with the proper physical features (note also that the imprinting object that was visually available to the chicks was never observed to contact other objects, thus ruling out the possibility that chicks learned about object solidity by observing the ways in which moving objects interact with each other).

It seems to me that a reasonable account of these findings is to argue that, although animals can certainly learn a lot about the physical properties of objects, they seem to do so precisely because they possess inborn core knowledge mechanisms that guide and constraint their intuitive inferences concerning material object properties such as solidity. Similar Kantian arguments can be put forward for the evidence I described concerning number and space cognition.

One could argue that the pattern of development of precocial species may be peculiar and that it does not generalize to humans. However, the evidence I discussed constitutes a sort of “proof of existence”. The findings provide evidence that a certain capacity can fully develop in the absence of a *specific* experience contribution. One could argue of course that humans are different, and that although it is possible, in principle, for natural selection to shape creatures that are able to deal with basic object, number, and space knowledge without resorting to specific

experiences with objects and events in the environment, a different path was followed with our species; I doubt this should be so, however. Certainly our species depends on learning and experience to a degree that is incommensurable in comparison to other species, especially in the form of language and cultural transmission. But exactly because we are so dependent on learning we need some “necessary knowledge” that is inborn and that could operate as a guide for learning by experience (see Natural-born “life detectors” section on how biological predispositions guide exposure learning about animate objects).

Chicks and human newborns are different in the pattern of development. Humans are the most altricial of the species. However, it should be considered that some differences between altricial and precocial species may turn out to be the by-product of maturation rather than learning. For instance, the ability to mentally complete partly occluded objects (*amodal completion*) is apparent in chicks soon after hatching (Lea, Slater, & Ryan, 1996; Regolin & Vallortigara, 1995) whereas in human infants it is only from about 4 months of age (Kellman & Arterberry, 1998). One could argue that perhaps chicks are equipped from the start with the mechanisms for completing partly occluded objects, whereas humans would learn about it in a period of about 4 months, taking advantage of experience with occluding events in the world. Recently, however, it has been shown that when stroboscopic motion is used instead of continuous motion (the former being processed early in development by subcortical structures), neonates of only a few hours of life show evidence of amodal completion similarly to chicks (Valenza & Herman, 2011; Valenza, Leo, Gava, & Simion, 2006). Thus, maturation of certain other areas of the brain seems to be necessary in altricial species in order to exhibit in behaviour mental competencies that are actually already available from the start—that is, competencies that are predisposed in the brain at birth.

All this is not to detract from human uniqueness. Clearly, human language and other types of experience may influence the development of

uniquely human forms of physical, numerical, and spatial knowledge (Landau & Lakusta, 2009; Spelke, 2003; Spelke et al., 2010). But they can operate that way because of inbuilt necessary knowledge largely shared by all vertebrate brains.

REFERENCES

- Andrew, R. J. (Ed.). (1991). *Neural and behavioural plasticity: The use of the chick as a model*. Oxford, UK: Oxford University Press.
- Assad, J. A., & Maunsell, J. H. (1995). Neuronal correlates of inferred motion in primate posterior parietal cortex. *Nature*, *373*, 518–521.
- Baillargeon, R. (1995). Physical reasoning in infancy. In M.S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 181–204). Cambridge, MA: MIT Press.
- Baillargeon, R., Spelke, E. S., & Wasserman, S. (1985). Object permanence in five-month-old infants. *Cognition*, *20*, 191–208.
- Baker, C. I., Keysers, C., Jellema, T., Wicker, B., & Perrett, D. I. (2001). Neuronal representation of disappearing and hidden objects in temporal cortex of the macaque. *Experimental Brain Research*, *140*, 375–381.
- Barry, C., Lever, C., Hayman, R., Hartley, T., Burton, S., O'Keefe, J., et al. (2006). The boundary vector cell model of place cell firing and spatial memory. *Reviews in the Neurosciences*, *17*, 71–97.
- Bateson, P. (2000). What must be known in order to understand imprinting? In C. Heyes & L. Huber (Eds.), *The Evolution of Cognition* (pp. 85–102). Cambridge, MA: The MIT Press.
- Bateson, P., & Gluckman, P. (2011). *Plasticity, robustness, development and evolution*. New York, NY: Cambridge University Press.
- Beran, M. J., Decker, S., Schwartz, A., & Schultz, N. (2011). Monkeys (*Macaca mulatta* and *Cebus apella*) and human adults and children (*Homo sapiens*) enumerate and compare subsets of moving stimuli based on numerosity. *Frontiers in Comparative Psychology*, *2*, Article 61.
- Bingman, V. P., Erichsen, J. T., Anderson, J. D., Good, M. A., & Pearce, J. M. (2006). Spared feature-structure discrimination but diminished salience of environmental geometry in hippocampal-lesioned homing pigeons (*Columba livia*). *Behavioral Neuroscience*, *120*, 835–841.
- Biro, S., Csibra, G., & Gergely, G. (2007). The role of behavioral cues in understanding animacy, agency and goal-directed actions in infancy. In C. von Hofsten & K. Rosander (Eds.), *Progress in brain research: From action to cognition* (p. 303). Elsevier.
- Blakemore, C., & Van Sluylers, E. C. (1975). Innate and environmental factors in the development of the kitten's visual cortex. *Journal of Physiology*, *248*, 663–716.
- Brannon, E. M. (2006). The representation of numerical magnitude. *Current Opinion in Neurobiology*, *16*, 222–229.
- Brown, A. A., Spetch, M. L., & Hurd, P. L. (2007). Growing in circles: Rearing environment alters spatial navigation in fish. *Psychological Science*, *18*, 569–573.
- Brown, J., Kaplan, G., Rogers, L. J., & Vallortigara, G. (2010). Perception of biological motion in common marmosets (*Callithrix jacchus*): By females only. *Animal Cognition*, *13*, 555–564.
- Burgess, N. (2008). Spatial cognition and the brain. *Annals of the New York Academy of Sciences*, *1124*, 77–97.
- Butler, A.B., & Cotterill, R. M. J. (2006). Mammalian and avian neuroanatomy and the question of consciousness in birds. *Biological Bulletin*, *211*, 106–127.
- Call, J. (2007). Apes know that hidden objects can affect the orientation of other objects. *Cognition*, *105*, 1–25.
- Cantlon, J., & Brannon, E. M. (2006). Shared system for ordering small and large numbers in monkeys and humans. *Psychological Science*, *17*, 401–406.
- Caramazza, A., & Shelton, J. R. (1998). Domain-specific knowledge systems in the brain: The animate–inanimate distinction. *Journal of Cognitive Neuroscience*, *10*, 1–34.
- Carey, S. (2009). *The origin of concepts*. New York, NY: Oxford University Press.
- Carey, S., & Spelke, E. S. (1996). Science and core knowledge. *Philosophy of Science*, *63*, 515–533.
- Cartwright, B. A., & Collett, T. S. (1982). How honey bees use landmarks to guide their return to a food source. *Nature*, *295*, 560–564.
- Cartwright, B. A., & Collett, T. S. (1983). Landmark learning in bees—Experiments and models. *Journal of Comparative Physiology*, *151*, 521–543.

- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, *23*, 149–178.
- Chiandetti, C. (2011). Pseudoneglect and embryonic light stimulation in the avian bra. *Behavioral Neuroscience*, *125*(5), 775–782. doi:10.1037/a0024721
- Chiandetti, C., & Vallortigara, G. (2008). Is there an innate geometric module? Effects of experience with angular geometric cues on spatial reorientation based on the shape of the environment. *Animal Cognition*, *11*, 139–146.
- Chiandetti, C., & Vallortigara, G. (2010). Experience and geometry: Controlled-rearing studies with chicks. *Animal Cognition*, *13*, 463–470.
- Chiandetti, C., & Vallortigara, G. (2011a). Chicks like consonant music. *Psychological Science*, *22*, 1270–1273.
- Chiandetti, C., & Vallortigara, G. (2011b). Intuitive physical reasoning about occluded objects by inexperienced chicks. *Proceedings of the Royal Society of London, B*, *278*, 2621–2627.
- Chien, S. H.-L. (2011). No more top-heavy bias: Infants and adults prefer upright faces but not top-heavy geometric or face-like patterns. *Journal of Vision*, *11*(6), 1–14.
- Chittka, L., & Geiger, K. (1995). Can honey bees count landmarks? *Animal Behaviour*, *49*, 159–164.
- Dacke, M., & Srinivasan, M. V. (2008). Evidence for counting in insects. *Animal Cognition*, *11*, 683–689.
- Davis, H., & Bradford, S. A. (1986). Counting behavior by rats in a simulated natural environment. *Ethology*, *73*, 265–280.
- Dehaene, S. (1997). *The number sense*. New York, NY: Oxford University Press.
- Dehaene, S., Izard, V., Pica, P., & Spelke, E. S. (2006). Core knowledge of geometry in an Amazonian indigene group. *Science*, *311*, 381–384.
- Diekamp, B., Regolin, L., Gunturkun, O., & Vallortigara, G. (2005). A left-sided visuospatial bias in birds. *Current Biology*, *15*, R372–R373.
- Duncan, R. O., Albright, T. D., & Stoner, G. R. (2000). Occlusion and the interpretation of visual motion: Perceptual and neuronal effects of context. *Journal of Neuroscience*, *20*, 5885–5897.
- Feigenson, L. (2005). A double dissociation in infants' representation of object arrays. *Cognition*, *95*, B37–B48.
- Feigenson, L., & Carey, S. (2005). On the limits of infants' quantification of small object arrays. *Cognition*, *97*, 295–313.
- Feigenson, L., Carey, S., & Hauser, M. (2002). The representations underlying infants' choice of more: Object files vs. analog magnitudes. *Psychological Science*, *13*(2), 150–156.
- Fellini, L., Schachner, M., & Morellini, F. (2006). Adult but not aged C57BL/6 male mice are capable of using geometry for orientation. *Learning and Memory*, *13*, 473–481.
- Fox, R., & McDaniel, C. (1982). The perception of biological motion by human infants. *Science*, *218*, 486–487.
- Fyhn, M., Molden, S., Witter, M. P., Moser, E. I., & Moser, M. B. (2004). Spatial representation in the entorhinal cortex. *Science*, *305*, 258–264.
- Galton, F. (1880). Visualised numerals. *Nature*, *21*, 252–256. doi:10.1038/021252a0
- Held, R., & Hein, A. (1963). Movement-produced stimulation in the development of visually guided behavior. *Journal of Comparative and Physiological Psychology*, *56*, 872–876.
- Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature*, *370*, 57–59.
- Hermer, L., & Spelke, E. S. (1996). Modularity and development: The case of spatial reorientation. *Cognition*, *61*, 195–232.
- Horn, G. (2004). Pathways of the past: The imprint of memory. *Nature Reviews Neuroscience*, *5*, 108–120.
- Izard, V., Pica, P., Spelke, E. S., & Dehaene, S. (2011). Flexible intuitions of Euclidean geometry in an Amazonian indigene group. *Proceedings of the National Academy of Sciences*, *108*, 9782–9787.
- Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisections tasks. *Neuropsychologia*, *38*, 93–110.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception and Psychophysics*, *14*, 201–211.
- Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience*, *6*, 766–774.
- Johnson, M. H., & Horn, G. (1988). Development of filial preferences in dark reared chicks. *Animal Behaviour*, *36*, 675–683.
- Johnson, M. H., & Morton, J. (1991). *Biology and cognitive development: The case of face recognition*. Oxford, UK: Basil Blackwell.
- Johnson, S. C. (2000). The recognition of mentalistic agents in infancy. *Trends in Cognitive Sciences*, *4*, 22–28.

- Johnson-Laird, P. N., Kang, O. E., & Leong, Y. C. (in press). On musical dissonance. *Music Perception*.
- Kaiser, M. D., Hudac, C. M., Shultz, S., Lee, S. M., Cheung, C., Berken, A. M., et al. (2010). Neural signatures of autism. *Proceedings of the National Academy of Sciences USA*, *107*, 21223–21228.
- Kellman, P. J., & Arterberry, M. E. (1998). *The cradle of knowledge*. Cambridge, MA: MIT Press.
- Kovacs, G., Vogels, R., & Orban, G. A. (1995). Selectivity of macaque inferior temporal neurons for partially occluded shapes. *Journal of Neuroscience*, *15*, 1984–1997.
- Kunder, S. M. A., De Los Reyes, A., Taglang, C., Baruch, A., & German, R. (2009). Domesticated dogs' (*Canis familiaris*) use of the solidity principle. *Animal Cognition*, *13*, 497–505. doi:10.1007/s10071-009-0300-6
- Lakusta, L., Dessalegn, B., & Landau, B. (2010). Impaired geometric reorientation caused by genetic defect. *Proceedings of the National Academy of Sciences*, *107*(7), 2813–2817.
- Landau, B. (2011). The organization and development of spatial cognition: Insights from Williams syndrome. In J. Burack, R. M. Hodapp, G. Iarocci, & E. Zigler (Eds.), *Handbook of intellectual disabilities and development* (2nd ed.). New York, NY: Oxford University Press.
- Landau, B., & Lakusta, L. (2009). Spatial representation across species: Geometry, language, and maps. *Current Opinion in Neurobiology*, *19*(1), 12–19.
- Langston, R. F., Ainge, J. A., Couey, J. J., Canto, C. B., Bjerknes, T. L., Witter, M. P., et al. (2010). Development of the spatial representation system in the rat. *Science*, *328*, 1576–1580.
- Lea, S. E. G., Slater, A. M., & Ryan, C. M. E. (1996). Perception of object unity in chicks: A comparison with the human infant. *Infant Behavior and Development*, *19*, 501–504.
- Lee, S. A., Shusterman, A., & Spelke, E. S. (2006). Reorientation and landmark-guided search by young children: Evidence for two systems. *Psychological Science*, *17*, 577–582.
- Lee, S. A., & Spelke, E. S. (2008). Children's use of geometry for reorientation. *Developmental Science*, *11*, 743–749.
- Lee, S. A., & Spelke, E. S. (2010). A modular geometric mechanism for reorientation in children. *Cognitive Psychology*, *61*, 152–176.
- Lee, S. A., & Spelke, E. S. (2011). Young children reorient by computing layout geometry, not by matching images of the environment. *Psychological Bulletin and Review*, *18*, 192–198.
- Lee, S. A., Spelke, E. S., & Vallortigara, G. (2012). *Spontaneous reorientation behavior in chicks: Evidence for evolutionary continuity across distantly related species*. Manuscript in preparation.
- Lehrman, D. S. (1953). Critique of Konrad Lorenz's theory of instinctive behavior. *Quarterly Review of Biology*, *28*, 337–363.
- Leslie, A. M. (1982). The perception of causality in infants. *Perception*, *11*, 173–186.
- Leslie, A. M. (1984). Spatiotemporal continuity and the perception of causality in infants. *Perception*, *13*, 287–305.
- Leslie, A. M., & Keeble, S. (1987). Do six-month-old infants perceive causality? *Cognition*, *25*, 265–288.
- Loetscher, T., Schwarz, U., Schubiger, M., & Brugger, P. (2008). Head turns bias the brain's internal random generator. *Current Biology*, *18*, R60–R62.
- Lorenz, K. (1965). *Evolution and the modification of behaviour*. Chicago, IL: University of Chicago Press.
- MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Origins of the left and right brain. *Scientific American*, *301*, 60–67.
- Mandler, J. M. (1988). How to build a baby: On the development of an accessible representational system. *Cognitive Development*, *3*, 113–136.
- Marcus, G. F. (2004). *The birth of the mind: How a tiny number of genes creates the complexities of human thought*. New York, NY: Basic Books.
- Mascalzoni, E., Regolin, L., & Vallortigara, G. (2010). Innate sensitivity for self-propelled causal agency in newly hatched chicks. *Proceedings of the National Academy of Sciences*, *107*, 4483–4485.
- McKone, E., Crookes, K., Jeffery, L., & Dilks, D. D. (2012 this issue). A critical review of the development of face recognition: Experience is less important than previously believed. *Cognitive Neuropsychology*, *29*, 174–212.
- Michotte, A. (1963). *The perception of causality*. New York, NY: Basic Books.
- Mormann, F., Dubois, J., Kornblith, S., Milosavljevic, M., Cerf, M., Ison, M., et al. (2011). A category-specific response to animals in the right human amygdala. *Nature Neuroscience*, *14*, 1247–1249.
- New, J., Cosmides, L., & Tooby, J. (2007). Category-specific attention for animals reflects ancestral priorities, not expertise. *Proceedings of the National Academy of Sciences USA*, *104*, 16598–16603.
- Nieder, A., Freedman, D. J., & Miller, E. K. (2002). Representation of the quantity of visual items in

- the primate prefrontal cortex. *Science*, 297, 1708–1711.
- Nieder, A., & Miller, E. K. (2004). A parieto-frontal network for visual numerical information in the monkey. *Proceedings of the National Academy of Sciences USA*, 101, 7457–7462.
- O'Connell, S., & Dunbar, R.I. M. (2005). The perception of causality in chimpanzees (*Pan spp.*). *Animal Cognition*, 8, 60–66.
- O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, 34, 171–175.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, UK: Oxford University Press.
- Osborne, L. R. (2006). Molecular basis of a multisystem disorder. In C. A. Morris, H. M. Lenhoff, & P. P. Wang (Eds.), *Williams-Beuren syndrome: Research, evaluation, and treatment* (pp. 18–58). New York, NY: JHU Press.
- Pattison, K. F., Miller, H. C., Rayburn-Reeves, R., & Zentall, T. (2010). The case of the disappearing bone: Dogs' understanding of the physical properties of objects. *Behavioural Processes*, 85, 278–282.
- Pecchia, T., Gagliardo, A., & Vallortigara, G. (2011). Stable panoramic views facilitate snap-shot like memories for spatial reorientation in homing pigeons. *PLoS ONE*, 6(7), e22657. doi:10.1371/journal.pone.0022657
- Pecchia, T., & Vallortigara, G. (2010a). Re-orienting strategies in a rectangular array of landmarks by domestic chicks (*Gallus gallus*). *Journal of Comparative Psychology*, 124, 147–158.
- Pecchia, T., & Vallortigara, G. (2010b). View-based strategy for reorientation by geometry. *Journal of Experimental Biology*, 213, 2987–2996.
- Pecchia, T., & Vallortigara, G. (in press). Spatial reorientation by geometry with freestanding objects and extended surfaces: A unifying view. *Proceedings of the Royal Society of London B*. doi:10.1098/rspb.2011.2522
- Pepperberg, I. M. (1994). Evidence for numerical competence in an African Grey parrot (*Psittacus erithacus*). *Journal of Comparative Psychology*, 108, 36–44.
- Pepperberg, I. M. (2006a). Gray parrot numerical competence: A review. *Animal Cognition*, 9, 377–391.
- Pepperberg, I. M. (2006b). Grey parrot (*Psittacus erithacus*) numerical abilities: Addition and further experiments on a zero-like concept. *Journal of Comparative Psychology*, 120, 1–11.
- Platt, M. L., & Spelke, E. S. (2009). What can developmental and comparative cognitive neuroscience tell us about the adult human brain? *Current Opinion in Neurobiology*, 19, 1–5.
- Regolin, L., Rugani, R., Stancher, G., & Vallortigara, G. (in press). Spontaneous discrimination of possible and impossible objects by newly hatched chicks. *Biology Letters*. Advance online publication. doi: 10.1098/rsbl.2011.0051.
- Regolin, L., & Vallortigara, G. (1995). Perception of partly occluded objects by young chicks. *Perception and Psychophysics*, 57, 971–976.
- Rochat, M.-J., Serra, E., Fadiga, L., & Gallese, V. (2008). The evolution of social cognition: Goal familiarity shapes monkeys' action understanding. *Current Biology*, 18, 227–232.
- Rogers, L. J. (1996). Behavioral, structural and neurochemical asymmetries in the avian brain: A model system for studying visual development and processing. *Neuroscience Biobehavioral Reviews*, 20, 487–503.
- Rosa-Salva, O., Farroni, T., Regolin, L., Vallortigara, G., & Johnson, M. H. (2011). The Evolution of social orienting: Evidence from chicks (*Gallus gallus*) and human newborns. *PLoS ONE*, 6(4), e18802.
- Rosa-Salva, O., Regolin, L., & Vallortigara, G. (2010). Faces are special for newly hatched chicks: Evidence for inborn domain-specific mechanisms underlying spontaneous preferences for face-like stimuli. *Developmental Science*, 13, 565–577.
- Rose, S. (2000). God's organism? The chick as a model system for memory studies. *Learning & Memory*, 7, 1–17.
- Rugani, R., Fontanari, L., Simoni, E., Regolin, L., & Vallortigara, G. (2009). Arithmetic in newborn chicks. *Proceedings of the Royal Society B*, 276, 2451–2460.
- Rugani, R., Kelly, D. M., Szelest, I., Regolin, L., & Vallortigara, G. (2010). Is it only humans that count from left to right? *Biology Letters*, 6, 290–292.
- Rugani, R., Regolin, L., & Vallortigara, G. (2007). Rudimentary numerical competence in 5-day-old domestic chicks: Identification of ordinal position. *Journal of Experimental Psychology: Animal Behavior Processes*, 33, 21–31.
- Rugani, R., Regolin, L., & Vallortigara, G. (2008). Discrimination of small numerosities in young chicks. *Journal of Experimental Psychology: Animal Behavior Processes*, 34, 388–399.
- Rugani, R., Regolin, L., & Vallortigara, G. (2010). Imprinted numbers: Newborn chicks' sensitivity to

- number vs. continuous extent of objects they have been reared with. *Developmental Science*, *13*, 790–797.
- Rugani, R., Vallortigara, G., Vallini, B., & Regolin, L. (2011). Asymmetrical number-space mapping in the avian brain. *Neurobiology of Learning and Memory*, *95*, 231–238.
- Siman-Tov, T., Papo, D., Gadoth, N., Schonberg, T., Mendelsohn, A., Perry, D., et al. (2009). Mind your left: Spatial bias in subcortical fear processing. *Journal of Cognitive Neuroscience*, *21*, 1782–1789.
- Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences USA*, *105*, 809–813.
- Solstad, T., Boccara, C. N., Kropff, E., Moser, M. B., & Moser, E. I. (2008). Representation of geometric borders in the entorhinal cortex. *Science*, *322*, 865–868.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2002). Modularity and spatial reorientation in a simple mind: Encoding of geometric and nongeometric properties of a spatial environment by fish. *Cognition*, *85*, B51–B59.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2003). Modularity as a fish views it: Conjoining geometric and nongeometric information for spatial reorientation. *Journal of Experimental Psychology: Animal Behavior Processes*, *29*, 199–210.
- Sovrano, V. A., Rigosi, E., & Vallortigara, G. (2011). *Spatial reorientation by geometry in bumblebees*. Manuscript submitted for publication.
- Spelke, E. S. (1998). Nativism, empiricism, and the origin of knowledge. *Infant Behavior and Development*, *21*, 181–200.
- Spelke, E. S. (2000). Core knowledge. *The American Psychologist*, *55*, 1233–1243.
- Spelke, E. S. (2003). What makes us smart? Core knowledge and natural language. In D. Gentner & S. Goldin-Meadow (Eds.), *Language in mind: Advances in the investigation of language and thought*. Cambridge, MA: MIT Press.
- Spelke, E. S. (2011). Natural number and natural geometry. In E. Brannon & S. Dehaene (Eds.), *Space, Time and Number in the Brain: Searching for the Foundations of Mathematical Thought* (pp. 287–317). Attention & Performance XXIV, Oxford University Press.
- Spelke, E. S., Breinlinger, K., Macomber, J., & Jacobson, K. (1992). Origins of knowledge. *Psychological Review*, *99*, 605–632.
- Spelke, E. S., & Kinzler, K. D. (2009). Innateness, learning, and rationality. *Child Development Perspectives*, *3*, 96–98.
- Spelke, E. S., Lee, S. A., & Izard, V. (2010). Beyond core knowledge: Natural geometry. *Cognitive Science*, *34*, 863–884.
- Sugita, Y. (2008). Face perception in monkeys reared with no exposure to faces. *Proceedings of the National Academy of Sciences USA*, *105*, 394–398.
- Taube, J. S., Muller, R. U., & Ranck, J. B. (1990). Head-direction cells recorded from the post-subiculum in freely moving rats. I. Description and quantitative analysis. *Journal of Neuroscience*, *2*, 420–435.
- Tommasi, L., Gagliardo, A., Andrew, R. J., & Vallortigara, G. (2003). Separate processing mechanisms for encoding geometric and landmark information in the avian hippocampus. *European Journal of Neuroscience*, *17*, 1695–1702.
- Tommasi, L., Chiandetti, C., Pecchia, T., Sovrano, V. A., & Vallortigara, G. (2012). From natural geometry to spatial cognition. *Biobehavioral and Neuroscience Reviews*, *36*(2), 799–824.
- Tommasi, L., & Vallortigara, G. (2001). Encoding of geometric and landmark information in the left and right hemispheres of the avian brain. *Behavioral Neuroscience*, *115*, 602–613.
- Turati, C., Simion, F., Milani, I., & Umiltà, C. (2002). Newborns' preference for faces: What is crucial? *Developmental Psychology*, *38*, 875–882.
- Valenza, E., & Herman, B. (2011). Early development of object unity: Evidence for perceptual completion in newborns. *Developmental Science*, *14*, 799–808.
- Valenza, E., Leo, I., Gava, L., & Simion, F. (2006). Perceptual completion in newborn human infants. *Child Development*, *77*, 1810–1821.
- Vallortigara, G. (2000). Comparative neuropsychology of the dual brain: A stroll through left and right animals' perceptual worlds. *Brain and Language*, *73*, 189–219.
- Vallortigara, G. (2004). Visual cognition and representation in birds and primates. In L. J. Rogers & G. Kaplan (Eds.), *Vertebrate comparative cognition: Are primates superior to non-primates?* (pp. 57–94). New York, NY: Kluwer Academic/Plenum Publishers.
- Vallortigara, G. (2006). The cognitive chicken: Visual and spatial cognition in a non-mammalian brain. In E. A. Wasserman & T. R. Zentall (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 41–58). Oxford, UK: Oxford University Press.

- Vallortigara, G. (2009a). Animals as natural geometers. In L. Tommasi, M. Peterson, & L. Nadel (Eds.), *The biology of cognition*. Cambridge, MA: MIT Press.
- Vallortigara, G. (2009b). Original knowledge and the two cultures. In E. Carafoli, G. A. Danieli, & G. O. Longo (Eds.), *The two cultures: Shared problems* (pp. 125–145). New York, NY: Springer Verlag.
- Vallortigara, G., Pagni, P., & Sovrano, V. A. (2004). Separate geometric and non-geometric modules for spatial reorientation: Evidence from a lopsided animal brain. *Journal of Cognitive Neuroscience*, *16*, 390–400.
- Vallortigara, G., & Regolin, L. (2006). Gravity bias in the interpretation of biological motion by inexperienced chicks. *Current Biology*, *16*, R279–R280.
- Vallortigara, G., Regolin, L., Chiandetti, C., & Rugani, R. (2010). Rudiments of mind: Insights through the chick model on number and space cognition in animals. *Comparative Cognition and Behavior Reviews*, *5*, 78–99.
- Vallortigara, G., Regolin, L., & Marconato, F. (2005). Visually inexperienced chicks exhibit spontaneous preference for biological motion patterns. *PLoS Biology*, *3*, 1312–1316.
- Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, *28*, 575–589.
- Vallortigara, G., Rogers, L. J., Bisazza, A., Lippolis, G., & Robins, A. (1998). Complementary right and left hemifield use for predatory and agonistic behaviour in toads. *Neuroreport*, *9*, 3341–3344.
- Vallortigara, G., Sovrano, V. A., & Chiandetti, C. (2009). Doing Socrates experiment right: Controlled rearing studies of geometrical knowledge in animals. *Current Opinion in Neurobiology*, *19*, 20–26.
- Vallortigara, G., Zanforlin, M., & Pasti, G. (1990). Geometric modules in animal's spatial representation: A test with chicks. *Journal of Comparative Psychology*, *104*, 248–254.
- van Marle, K., Aw, J., McCrink, K., & Santos, L. R. (2006). How monkeys (*Cebus apella*) enumerate objects and substances. *Journal of Comparative Psychology*, *120*, 416–426.
- Vargas, J. P., Bingman, V. P., Portavella, M., & Lopez, J. C. (2006). Telencephalon and geometric space in goldfish. *European Journal of Neuroscience*, *24*, 2870–2878.
- Vargas, J. P., Petruso, E. J., & Bingman, V. P. (2004). Hippocampal formation is required for geometric navigation in pigeons. *European Journal of Neuroscience*, *20*, 1937–1944.
- Walk, R. D., Gibson, E. J., & Tighe, T. J. (1957). Behavior of light- and dark-reared rats on a visual cliff. *Science*, *126*, 80–81.
- Wills, T. J., Cacucci, F., Burgess, N., & O'Keefe, J. (2010). Development of the hippocampal cognitive map in preweanling rats. *Science*, *328*, 1573–1576.