COMPARATIVE
COGNITION & BEHAVIOR
REVIEWS
2012
Volume 7, pp 110 - 138

Cerebral and behavioural asymmetries in animal social recognition

Orsola Rosa Salva
Center for Mind/Brain Sciences, University of Trento, Italy

Lucia Regolin and Elena Mascalzoni
Department of General Psychology, University of Padova, Italy

Giorgio Vallortigara
Center for Mind/Brain Sciences, University of Trento, Italy

Evidence is here summarized that animal species belonging to distant taxa show forms of social recognition, a sophisticated cognitive ability adaptive in most social interactions. The paper then proceeds to review evidence of functional lateralization for this cognitive ability. The main focus of this review is evidence obtained in domestic chickens, the animal model employed in the authors' laboratories, but we also discuss comparisons with data from species ranging from fishes, amphibians and reptiles, to other birds and mammals. A consistent pattern emerges, pointing toward a right hemisphere dominance, in particular for discrimination of social companions and individual (or familiarity-based) recognition, whereas the left hemisphere could be specialized for "category-based" distinctions (e.g., conspecifics versus heterospecifics). This pattern of results is discussed in relation to a more general specialization and processing styles of the two sides of the brain, with the right hemisphere predisposed for developing a detailed, global and contextual representation of objects, and the left hemisphere predisposed for rapid assignment of a stimulus to a category, for processing releaser stimuli and for control of responses.

Keywords: social recognition, individual recognition, lateralization, comparative studies

Introduction: Visual social recognition in animals

In the last decades, a wide range of experimental studies in comparative cognition dealt with the investigation of animals' capability for social recognition (Special Issues in Behavioural Processes devoted to Social Recognition, 1994; Ligout and Porter, 2006). This comprises the distinction between individuals on the basis of features shared by some of them (e.g., recognition of conspecifics versus heterospecifics; Gheusi, Bluthe, Godall and Dantzer, 1994). At an intermediate level of sophistication, however, conspecifics can be discriminated simply on the basis of a familiarity effect (i.e., recognition of already known individuals versus strangers). Finally, animals may demonstrate the fine capability to recognize a given individual on the basis of its distinctive features (i.e., individual recognition, IR, the most precise form of social recognition; Gheusi et al., 1994, Tibbetts and Dale, 2007). In the literature this terminology has often been applied to cases in which it is not clear whether subjects are responding on the basis of true IR or simply on the basis of a familiarity judgement. For simplicity, in the rest of the paper we will therefore apply the term IR in this more general meaning

Corresponding author: Giorgio Vallortigara, Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, I-38068, Rovereto, Italy; e-mail address: giorgio.vallortigara@unitn.it

Recognition is an adaptive trait, required for a large spectrum of social behaviours such as creation of dominance hierarchies, territorial defence, cooperative breeding, monogamous pairing, parent/offspring recognition, et cetera (Tibbetts and Dale, 2007). In aggressive competitions, for example, previous experience with a certain subject has been demonstrated to play a role in modulating future conflicts. In this sense, IR might be used to predict the outcome of a conflict, to reduce the potential costs of aggression and consequently establish and maintain dominance hierarchies between a small number of individuals. In agreement with that, social recognition seems to be much more widespread than previously thought, having been demonstrated in several taxa, ranging from invertebrates to fishes, birds, and mammals (Tibbetts and Dale, 2007).

ISSN: 1911-4745 doi: 10.3819/ccbr.2012.70006 © Orsola Rosa Salva 2012

In contrast with previous claims that insects lack this cognitive ability (Anderson and McShea, 2001), evidence of social recognition has been found for wasps (*Polistes fuscatus*): queens and workers individually recognize nest mates by their facial and abdominal marks. This allows them to learn their relative ranks and consequently reduce aggression (in wasps a linear dominance hierarchy determines how resources, work, and reproduction are shared among individuals) (Tibbetts, 2002). Similar skills have been demonstrated in other invertebrates, such as the American lobster (*Homarus americanus*), which is able to visually recognize and discriminate familiar versus unfamiliar conspecifics on the basis of visual cues (Karavanich and Atema, 1998; Gherardi, Cenni, Parisi and Aquiloni, 2010). Similarly, the crayfish (*Cherax destructor*) visually recognizes an opponent encountered during previous fighting by its distinctive facial features (Van der Valden, Zheng, Patullo and Macmillan, 2008; see Seebacher and Wilson, 2007 for other data on crayfish).

Evidence of IR in invertebrates testifies to how widespread this capability is in the animal kingdom. However, in the rest of the review we will concentrate on vertebrate species, since to our knowledge there is no evidence of lateralized social recognition in invertebrates. In vertebrate species too, aggression toward strangers has been exploited as a measure to study social recognition. For example, among fish the rainbow trout (*Oncorhynchus mykiss*) demonstrated to discriminate between familiar and unfamiliar conspecifics by showing less aggression in contests with familiar conspecifics (Johnsson, 1997).

Besides aggressive competition and maintenance of dominance ranks, IR seems to be necessary in many other social contexts, such as monogamous pairing and parent/offspring interactions (Tibbetts and Dale 2007), which are widespread behaviours in animals. Partner recognition is a type of IR in which one distinguishes its own mating partner from others. This form of recognition is present even in monogamous species of fishes (Clark, Boersma and Olmsted 2006), probably due to the fact that it might favour territorial defence, reduce the time for courtship before spawning and prevent aggression against the partner (Tibbetts and Dale, 2007). Recently, IR has also been demonstrated in a non-territorial monogamous pipefish with paternal care (*Corythoichthys haematopterus*, Sogabe, 2011). Since this pipefish has ornamental traits on the thorax which are highly variable among individuals, it seems plausible that vision is the dominant modality in partner recognition for such species (Sogabe, 2011).

Although birds are usually thought to use vocal cues for social recognition, the possibility that they can also use visual cues for identity assessment has been recently investigated. Quelea males (*Quelea quelea*), for example, have been shown to distinguish between neighbours and strangers, allowing the former to approach more closely to their nests and avoiding costly conflicts of territorial defence (Dale, 2000). Similarly, ruffs (*Philomachus pugnax*) are more aggressive with neighbours having experimentally altered plumage, a sign that they do not recognize them as familiar conspecifics (Dale, Lank and Reeve, 2001). In pigeons (*Columba livia*), social groups are based on monogamous pair bonds between adults, with a clear dominance hierarchy regulating competition for optimal breeding sites. It is thus not surprising that pigeons are capable of IR and can distinguish between a social partner and strangers, discriminating photographs of familiar and unfamiliar conspecifics (Wilkinson, Specht and Huber, 2010; see also Watanabe and Ito, 1991). Similar evidence of the ability to discriminate two-dimensional visual images of conspecifics has also been observed in another social avian species, the budgerigar (*Melopsittacus undulatus*), that breeds in monogamous pairs within large colonies (Brown and Dooling, 1992; 1993).

Among avian species, responses to social stimuli have been widely investigated in the domestic chicken (*Gallus gallus*), the animal model employed in our laboratories (and one of the foci of this review). The domestic chicken is a social-living bird that searches for food in groups, avoids predators following warnings from other flock members, and forms stable social hierarchies (Mench and Keeling, 2001; Nicol, 2004; Rogers and Astiningsih, 1991; Schjelderup-Ebbe, 1935). All of these behaviors develop throughout ontogeny, largely during the very early stages post-hatch, and are demonstrated by the impressive social cognition abilities in young chicks (e.g., Beaugrand, Hogue and Lague, 1997; Rosa Salva, Daisley, Regolin and Vallortigara, 2009). Being the offspring of a precocial species, domestic chicks face the need to identify animate creatures in general, and social partners in particular, from the very first days after hatching. Chicks' early social interactions are thus guided by a set of experience-independent predispositions that determine preferential attention to animate creatures, such as a well-known predisposition for approaching and consequently imprinting on naturalistic (i.e., hen-like) with respect to artificial objects (Bolhuis and Honey, 1998). The crucial factor in eliciting this preference seems to be the configuration of features present in the hen's head region (Johnson and Horn, 1988), as recently confirmed by research using schematic or photographic face-like stimuli (Rosa Salva, Regolin and Vallortigara, 2010; Rosa Salva, Farroni, Regolin, Vallortigara and Johnson, 2011). Similarly, naïve chicks preferentially approach self-propelled objects, rather than objects whose motion is caused by physical contact with another object (Mascalzoni, Regolin and Vallortigara, 2010) and point-light displays representing a biological motion pattern (Vallortigara, Regolin and Marconato, 2005; Vallortigara and Regolin, 2006). It is worth noting that these early predispositions, which are observed in visually naïve chicks, seem to be devoted to the rapid detection of any animate creature present in the environment, but are not species-specific (e.g., chicks are equally attracted by the biological motion of conspecifics and by that of heterospecifics). More refined distinctions, such as recognition of conspecifics and of familiar individuals are later acquired through experience, thanks to the well-developed social-learning skills available to this species.

In line with the precocious development of social behaviour in this species, IR has also been demonstrated in subjects younger than one week. Chicks reared in pairs for the first 2 days of life discriminate between a familiar companion (cagemate) and an unfamiliar conspecific in a free choice task. However, in this task the two sexes exhibited opposite preferences: males chose to approach the strangers, females the companions (Vallortigara and Andrew, 1991; these results will be further discussed in detail in the section on “Laterality in social recognition”, because they are strongly related to lateralization effects). The presence of IR was also confirmed in a social pecking test, which relies on the marked xenophobia that socially-reared chicks show towards unfamiliar conspecifics (Zajonc, Wilson and Rajecki, 1975). Socially-reared chicks treated strangers and companions differently, with more aggressive pecks towards the stranger (Vallortigara, 1992a). It is interesting to note that, in adult chickens, IR seems to rely on the configuration of features present in the head region of the individual to be recognized, in line with what is observed for humans and other animals (see Brown and Dooling, 1992; 1993 for similar evidence in another avian species, the budgerigar; see below for evidence on non-avian species) (Candland, 1969; Dawkins, 1995; 1996; Guhl and Ortmann, 1953). Pigeons (*Columba livia*), however, seem to be predisposed to pay attention to local features of the head region rather than to the overall configuration (Patton, Szafranski and Shimizu, 2010). This behavioural difference between pigeons and humans in visual-facial analysis had been hypothesized to be related to anatomical differences between birds and mammals (Shimizu, Patton and Husband, 2010), but such a hypothesis does not fit to data collected in other bird species. It has to be considered, however, that in the study of Patton and colleagues (2010) pigeons were required to perform a spontaneous preference task. Pigeons were simultaneously presented with two static images of a female’s head, one image being a normal head, the other being the image of the same female with altered facial features. Subjects’ courtship responses to each image were recorded (Patton et al., 2010). Therefore, in contrast to the above research in other avian species in which subjects were required to recognize a given face amongst other faces, pigeons were not required to perform an IR task. Animals’ responses might in fact depend on the nature of the task employed. In the case of chickens, moreover, the tendency to use features present in the head region as a cue for IR could be due to the fact that hens establish their position in the dominance-hierarchy of the flock (the pecking order) by a form of fighting in pairs, which involves aggressive pecking at the head of another individual (Rushen, 1982). Thus, when learning the identity and dominance position of their opponent in a fight, hens would naturally pay great attention to the head region of the other bird and they would consequently store information on the appearance of this region. Such information will then be employed for future recognition of this same individual.

Among mammals, sheep (*Ovis aries*) have been thoroughly studied for their capability to perform social and IR, since they manifest a range of social behaviours which seem to require these abilities. For example sheep display a preference for maintaining social proximity with members of their own species and breed. Furthermore, they form individual consortships and selectively bond with their offspring (Kendrick, 1994). It has been shown that sheep succeed in such tasks because they are able to visually distinguish conspecifics on the basis of their distinctive face traits. Sheep, in fact, discriminate photographs of faces of their own breed from others of different species or breed (Kendrick et al., 1995), being able to detect the gender of the photographed individual, to distinguish faces of individual ewes (Kendrick, Atkins, Hinton, Heavens and Keverne, 1996) and even demonstrate transfer across faces of the same individual at different ages or in different orientations (Ferreira, Keller, Saint-Dizier, Perrin and Levy, 2004). In these studies sheep learned significantly faster to recognize sheep faces compared to geometrical symbols, even showing an inversion effect for faces but not for familiar objects (Kendrick et al., 1996). Moreover, familiar and unfamiliar faces are processed in a different fashion, with the former being identified by the configuration of inner face features, whereas unfamiliar faces are identified by the external features alone (Peirce, Leigh and Kendrick, 2000), in agreement with findings from human subjects (Ellis, Shepherd and Davies, 1979; Young, Hay, McWeeny, Flude and Ellis, 1985). This makes it likely that sheep are treating the face stimuli as social objects, rather than merely learning to discriminate them as any other complex visual pattern (Kendrick et al., 1996).

Sheep’s recognition memory is very efficient and not limited to faces of their own species: they can remember 50 conspecifics’ faces and up to 10 human faces over 2 years (Kendrick, da Costa, Leigh, Hinton and Peirce, 2001). Although sheep effectively discriminate between individual human faces at the same level they discriminate between sheep faces, when performing human face discriminations they use feature detection methods similar to those employed for object recognition, showing that the mere experience with faces of heterospecifics is probably not sufficient to match the natural predisposition for conspecifics’ faces (Peirce, Leigh, da Costa and Kendrick, 2001).

The capability to recognize conspecifics or individuals on the basis of their faces has also been demonstrated in mammals other than sheep, revealing some remarkable similarities with data obtained in this species. Heifers (*Bos taurus*), for instance, not only visually discriminate their own species from other species (Coulon et al., 2007) but also demonstrated to be able to recognize a certain individual (Coulon, Deputte, Heyman and Baudoin, 2009). Moreover, cattle easily discriminate among familiar conspecifics (Hagen and Broom, 2003), even using only visual cues from 2D images of conspecifics' heads (Coulon, Baudoin, Heyman and Deputte, 2011). Dogs (*Canis familiaris*) are capable of distinguishing faces of their own species from faces of other species, differentiating individual faces by visual cues alone (Racca et al., 2010). Similarly, dolphins (*Tursiops truncates*) clearly discriminate between familiar and unfamiliar humans (Thieltges, Lemasson, Kuczaj, Boye and Blois-Heulin, 2011).

Among non-human primates, which are considered a privileged model for comparative investigations due to their phylogenetic proximity to our species, chimpanzees (*Pan troglodytes*) readily discriminate unfamiliar conspecifics on the basis of the peculiar features of their faces (Parr and de Waal, 1999). Macaques (*Macaca mulatta*), whose dominance hierarchies are regulated by IR (Deaner, Khera and Platt, 2005), are able to recognize the faces of their kin among other conspecifics, spending more time looking at their offspring (Wu, Holmes, Medina and Sackett, 1980). Similar to sheep (and to humans) rhesus macaques show configural processing of conspecifics faces, but employ a feature-based recognition strategy when viewing faces of other species (i.e., human faces; Gothard, Brooks and Peterson, 2009). Therefore, the recognition of heterospecifics may involve different processes with respect to those applied to the recognition of conspecifics, even though the role played by experiential factors is still unclear. Recently, a study on another macaque species (Japanese monkeys, *Macaca fuscata*) (Sugita, 2008) attempted to clarify this issue. In this research, infant monkeys were reared without having any visual experience of faces, and then tested for their face processing abilities immediately before the end of this deprivation period and after one month of selective experience with human or with monkey faces. Naïve monkeys showed a spontaneous interest toward both types of faces (either monkey or human) compared to other objects, and were equally able to discriminate familiar versus unfamiliar human and monkey faces, using configural cues. However, after selective exposure to faces of one species only, the animals developed a preference for the species they were exposed to and lost the ability to discriminate faces of other species. Therefore, monkeys demonstrated to initially possess an experience-independent capability to attend to and process faces of different species, which is then shaped (tuned) by selective visual experience.

Laterality in social recognition

It is now well established that brain asymmetries occur throughout the animal kingdom (Rogers and Andrew, 2002; Vallortigara and Rogers, 2005; MacNeilage, Rogers and Vallortigara, 2009; Vallortigara, Chiandetti and Sovrano, 2010). Brain lateralization, that was once considered a uniquely human characteristic, has been found and studied in a wide range of species, including nonhuman primates (e.g., Fernandez-Carriba, Loeches, Morcillo and Hopkins, 2002a,b; Forrester, Leavens, Quaresmini and Vallortigara, 2011), birds (e.g., Rogers, 1997; Rugani, Kelly, Szelest, Regolin and Vallortigara, 2010; Vallortigara, 2000), amphibians (Vallortigara, Rogers, Bisazza, Lippolis and Robins, 1998), fish (e.g., Andrew et al., 2009; Sovrano, Rainoldi, Bisazza and Vallortigara, 1999; Sovrano and Andrew, 2006) and invertebrates (e.g., Ades and Ramires, 2002; Byrne, Kuba and Griebel, 2002; Cooper, Nudo, González, Vinson and Liang, 2011; Davison et al., 2009; Frasnelli, Vallortigara and Rogers, 2010; Hobert, Johnston and Chang, 2002; Kigth, Steelman, Coffey, Lucente and Castillo, 2008; Letzkus, Boeddeker, Wood, Zhang and Srinivasan, 2007; Rogers and Vallortigara, 2008; Pascual, Huang, Nevue and Préat, 2004). Lateralization at the individual level (i.e., not necessarily characterized by a consistent bias within the population) is associated with clear computational advantages, such as the possibility to avoid a costly reduplication of functions and slow interhemispheric interactions, while allowing for more efficient parallel processing. For example, an elevated predation rate seems to be associated with the development of more pronounced lateralization, suggesting that strongly lateralized individuals could be more fit to deal with predators (Brown, Western and Braithwaite, 2007), possibly also due to their facilitated social coordination. However, as a consequence of the increasing evidence of population level lateralization in animal species (in which most individuals are lateralized in the same direction, see Vallortigara, 2006), a debate arose about the origins of these phenomena. It seems reasonable that population-level lateralization would confer adaptive advantages that should compensate for its disadvantages (such as the predictability of the behaviour of the members of the population). It has been hypothesised that those advantages are, at least in part, linked to group living (Vallortigara and Rogers, 2005) and fixed genetically as evolutionarily stable strategies (Vallortigara, 2006). The alignment of asymmetries within a population would favour interactions needed for predators defence and for cooperation (Ghirlanda and Vallortigara 2004; Ghirlanda, Frasnelli and Vallortigara, 2009; Bisazza, Cantalupo, Capocchiano and Vallortigara, 2000), also by causing the presence of more stable social hierarchies (Rogers and Workman, 1989). An interesting related phenomenon is that more strongly lateralized chicks are advantaged in transitive inference tasks (Daisley, Regolin and Vallortigara, 2010). The ability to perform transitive inference can be interpreted as an adaptation to social groups organized by a relatively stable dominance hierarchy (the pecking order, in the case of domestic chickens). Transitive inference, in fact, allows chickens to gain information about the dominance status of their group members by the mere observation of agonistic encounters occurring between an individual whose status is already known and another bird whose status is still unknown. This reduces the number of fights required to determine the social hierarchy and could be one of the factors underlying the greater stability observed in groups of strongly lateralized chicks.

On the one hand lateralization favours social coordination and social-cognition abilities. On the other hand the evolution of sociality itself has been linked to the development of higher cognitive abilities. Some authors affirm that higher cognitive functions evolved as an adaptation for dealing with the challenges posed by group living (Humphrey, 1976; 1983; Jolly, 1966; Byrne and Whiten, 1988; Byrne and Bates, 2007). Individual recognition of conspecifics, decoding of their behavioural signals, learning and monitoring of social hierarchies are only some of the sophisticated cognitive operations that are needed for coping with social life. This social intelligence theory was initially developed for primates, but later extended to other species: for example, performance in a transitive inference task was influenced by the complexity of the early social environment experienced by individual greylag geese (Weiss, Kehmeier and Schloegl, 2010) or typical of some species of corvids (Bond, Kamil and Balda, 2003).

In the introduction we have summarized behavioural evidence showing that animal species belonging to phylogenetically distant taxa and characterized by central nervous systems with different levels of complexity, show some forms of social recognition (either IR, familiarity recognition or conspecific recognition), which is adaptive for them in various types of social interactions. In the following paragraphs we will review evidence of functional lateralization in this cognitive ability that seems to be necessary to the development of most aspects of social cognition. In doing so we will concentrate on evidence from studies on domestic chicks, the animal model employed in our laboratories and one of the main foci of this review, but we will also discuss studies from species ranging from primates to ungulates, other bird species, reptiles, fish and amphibians (See Table 1 for a summary of the principal studies on laterality and social recognition reviewed in the rest of the paper).

Face perception

When considering literature on human beings, the concept of lateralization in social recognition immediately evokes studies of right hemisphere dominance in face perception and IR. This is, in fact, one of the more notorious lateralization effects in our species (for behavioural results see Bradshaw and Nettleton, 1981; Geffen, Bradshaw and Wallace, 1971; Sergent, 1982; Hilliard, 1973; Finlay and French, 1978; Schwartz and Smith, 1980; Luh, Rueckert and Levy, 1991; Hellige et al., 1994; Burt and Perret, 1997; for neuroimaging studies see Kanwisher, Chunn, McDermott and Ledden, 1996; Kanwisher, Tong and Nakayama, 1998; for evidence on brain-damaged patients see De Renzi, Perani, Carlesimo, Silveri and Fazio, 1994). Similar results can be obtained also in non-human primates, even though evidence available in this direction is not as strong as for human beings. For example, like humans, apes exhibit a left visual field (LVF) advantage for the recognition of facial emotional expressions (Morris and Hopkins, 1993; see also Fernandez-Carriba et al., 2002a, b). This right hemispheric dominance for the processing of emotional expressions could be more pronounced for negative than for positive emotions (e.g., Parr and Hopkins, 2000; on the contrary, a right hemispheric bias for the production of emotional expressions seems to be independent from the valence of the displayed emotion, Hauser and Akre, 2001).

Another most prominent phenomenon associated with right hemispheric dominance in face perception is the Left Gaze Bias (LGB) (Guo, Meints, Hall, Hall and Mills, 2009). This bias can be expressed either as a tendency to spend a higher proportion of looking time exploring the left side of a centrally presented face, or as a tendency to direct the first fixation toward the left side of the face. A recent study compared the LGB in humans and in laboratory-raised rhesus monkeys (*Macaca mulatta*) (Guo et al., 2009). Notably, in adult humans a clear LGB (affecting both the direction of the first fixation and the overall looking time) was only elicited by upright conspecific faces, whereas monkeys showed a clear LGB for both human and monkey faces. It has been proposed that the LGB would emerge after extensive experience with faces (see below). This view fits well with the monkey data; being raised in the laboratory it is conceivable that they received a large amount of exposure to human faces, which could have determined a LGB for human faces.

***Table 1**. Summary of the principal studies on laterality and social recognition.*

Face perception		
Study	**Species**	**Task/behaviour tested**
Morris and Hopkins, 1993	chimpanzee (*Pan troglodites*)	recognition of facial expressions
Guo et al., 2009	dog (*Canis familiaris*); rhesus monkey (*Macaca mulatta*)	presence of the Left Gaze Bias
Peirce et al., 2000	sheep (*Ovis aries*)	discrimination between face pairs
Pinsk et al., 2005	macaque (*Macaca fascicularis*)	brain activation (fMRI) during exposure to face stimuli
Hamilton and Vermeire, 1988	rhesus monkeys (*M. mulatta*)	visual discrimination tests on split brain subjects
Broad et al., 2000	sheep (*O. aries*)	discrimination between face pairs and associated brain activation (c-fos mRNA expression)
Da Costa et al., 2004	sheep (*O. aries*)	brain activation (c-fos and zif/268 mRNA expression) during exposure to conspecific faces
Peirce and Kendrick, 2002	sheep (*O. aries*)	single-cell recording during exposure to face stimuli
Recognition of familiar social partners		
Vallortigara and Andrew, 1991; Deng and Rogers, 2002b	domestic chick (*Gallus gallus*)	simultaneous-choice test between familiar and unfamiliar social partners
McKenzie et al., 1998; Vallortigara, 1992a; Vallortigara et al., 2001	domestic chick (*G. gallus*)	social-pecking test (recording of pecks directed at familiar and unfamiliar conspecifics)
Vallortigara et al., 1999	domestic chick (*G. gallus*)	detour test (detouring an obstacle in order to reach or inspect a target social object)
Bisazza et al., 1997a; 1997b; 1998; Brown et al., 2007	fish species (*Brachyraphis episcopi, Brachyrhaphis roseni, Gambusia holbrooki, Gambusia nicaraguensis, Girardinus falcatus, Poecilia reticulata*)	detour test
Bobbo et al., 2006a; 2006b	domestic chick (G. gallus)	behavioural recording of monocular unihemispheric sleep episodes
Side asymmetries in social responses during naturalistic encounters		
Bisazza and de Santi, 2003	fish species (*Betta splendens, G. holbrooki, Xenotoca eiseni*)	aggressive behaviours
Deckel, 1995; Hews and Worthington, 2001; Hews et al., 2004	lizard species (*Anolis carol, Sceloporus virgatus, Urosaurus ornatus*)	aggressive behaviours
Robins et al., 1998; Vallortigara et al., 1998	toad species (*Bufo marinus, Bufo bufo*)	aggressive behaviours
Casper and Dunbard, 1996; Drews, 1996	non-human primates (*Papio cynocephalus, Theropitecus gelada*)	aggressive behaviours
Rogers et al., 1985; Ventolini et al., 2004	avian species (*G. gallus; Himantopus himantopus*)	sexual behaviours

An hypothesis about the role of experience in this kind of phenomena is that a form of perceptual tuning in favour of the type of face more often experienced during development could be at the basis of many well known effects that are considered hallmarks of specialized face processing (e.g., the face inversion effect, Diamond and Carey, 1986; the other species effect, Pascalis, de Haan and Nelson, 2002; see also Nelson, 2001). In line with that is the fact that 6-month-old babies displayed a much less selective LGB, which extended to non-face objects (Guo et al., 2009). The LGB has also been found in pet dogs (*Canis familiaris*) (Guo et al., 2009). Even though the dogs tested by Guo and colleagues were well socialized to both people and other dogs, a LGB was present for human faces, but not for dog faces. Therefore, at least in the case of dogs, the amount of visual experience with one kind of face does not seem to be the crucial factor determining the LGB. It is conceivable that the emergence of the LGB could be associated with different underlying mechanisms in primates and in domestic dogs. In dogs the LGB may have evolved during domestication as a specific adaptation to facilitate interactions with human beings (e.g., the LGB facilitates processing of the owner's hemiface that is more effective in expressing anger and whose emotional expressions can be more easily recognized, Indersmitten and Gur, 2003). According to this argument, the LGB can be considered limited to primates or to species that need to socialize with primates. To test this hypothesis further, studies should test the presence of the LGB in animals that were not selected to interact with humans and/or are not heavily socialized to humans (e.g., wolves and stray dogs).

At the electrophysiological (single neuron recording) level, the right hemisphere advantage for face processing seemed at first to be absent (or even reversed) in nonhuman primates. For example, in macaques tested in an identity recognition task, more responsive cells were found in the superior temporal sulcus (STS) of the left than of the right hemisphere (Perrett et al., 1988). However, a subsequent fMRI study demonstrated a more pronounced activation of the right STS, suggesting that previous conflicting results could have been influenced by the use of techniques different from those usually employed in humans (Pinsk, DeSimone, Moore, Gross and Kastner, 2005). Similar results favouring the right hemisphere in face recognition have also been obtained testing split-brain monkeys (Hamilton and Vermeire, 1988; Vermeire, Hamilton and Erdmann, 1998; Vermeire and Hamilton, 1998).

Somehow surprisingly, studies conducted in sheep revealed an even clearer right-hemisphere specialization for face processing, compared to research on non-human primates. Behavioural studies employing mirrored hemifaces and chimeric faces as stimuli demonstrated a LVF advantage for IR of faces of familiar conspecifics, but not for human faces (Kendrik, 2006; Peirce et al., 2000; 2001). It is interesting to note that this (familiar conspecifics) is exactly the category of face-stimuli that sheep can recognize thanks to the configuration of inner face features, in line with what is usually found in human beings for the processing of own-species faces. The right hemisphere advantage found in sheep can be explained by a general superiority of the left-eye-system for configural processing of visual stimuli (as hypothesized also for human beings, Levy et al., 1972; Rhodes, 1993). Most interestingly, Yamazaki, Aust, Huber, Hausmann and Güntürkün (2007) found evidence of an analogous configural processing style of the right hemisphere in pigeons trained to respond to pictures of human beings. In this study pigeons were reinforced for discriminating between pictures containing and pictures not containing human figures. After that they underwent a generalization test on novel exemplars of the same categories. Pigeons having their left eye (right hemisphere) in use were severely disturbed by manipulations altering the overall stimulus configuration (such as the use of scrambled stimuli), whereas subjects having the left hemisphere in use tended to base their choice on local category-defining cues.

In the study of Peirce et al. (2001), the absence of any LVF advantage in sheep when using human faces as stimuli could either be due to the fact that the right hemisphere specialization is limited to the recognition of conspecific faces, or more simply to the fact that heterospecific faces are not processed configurally by sheep. In addition, the level of expertise that the subjects had with the faces of different species could play a role. Even though the sheep tested in the above mentioned study (Peirce et al., 2001) had a good degree of experience with human faces, it is difficult to deny that they probably had a more extensive and socially relevant experience with conspecific faces. The subjects stably lived in flocks of 30-50 individuals, whereas they interacted with no more than 10 different humans for 2-3h per day. Moreover, no information was provided about the age at which this human-sheep interaction had started for the first time after birth. This is particularly relevant since, as briefly mentioned above, a debated issue in the human literature concerns the role of experience in some characteristic phenomena typically associated with the perception of faces (such as configural processing and right hemispheric dominance). According to some authors faces would not be a special stimulus *per se*, but simply a most common object of expertise (e.g., Diamond and Carey, 1986; Nelson, 2001; Pascalis et al., 2002; but see Farah, Rabinowitz, Quinn and Liu, 2000 for an example of evidence supporting the opposite view). It has been theorized that faces acquire their special status as a consequence of extensive exposure to this sort of stimulus during a critical period of the early postnatal development (Johnson, 2005; Johnson, Grossman and Farroni, 2008). The lack of LVF advantage for the processing of human faces in sheep could thus be due to lack of (or not sufficient) exposure to human faces early after birth.

As suggested by an anonymous Referee, the discussion of the results from the study of Peirce et al. (2001) raises another intriguing issue: at which level does the distinction between conspecific versus heterospecific faces occur? A first possibility would be that top-down effects are primarily responsible for the mode of processing applied to each stimulus (and consequently for the hemisphere in charge of the task). This scenario however requires that a first analysis occurs, which determines the nature of the stimulus (is it a conspecific or not?), prior to the differential involvement of the two hemispheres. On the contrary, according to a bottom-up scenario, both hemispheres analyze face stimuli according to their preferred processing style. The right hemisphere, which applies a configural mode of elaboration, results more successful in recognizing faces belonging to the category of expertise. Obviously, this does not exclude the presence of top-down influences, such as attentional mechanisms, which may call into function left- or right-hemispheric processing, according to environmental or endogenous requirements.

Besides behavioural results, genetical markers of altered neuronal activity also revealed greater activation of the right hemisphere in individual sheep undergoing a discrimination task of upright faces, whereas the effect was absent for inverted faces (Broad, Mimmack and Kendrick, 2000). In this case, the task required to discriminate human versus sheep faces (the reward for a choice was gaining access to the photographed individual). Right hemisphere activation was observed also in individuals that did not demonstrate a preference for sheep faces in terms of the percentage of choices for the two kinds of faces (however, latency data revealed an advantage of sheep faces in all subjects, including this subgroup). Similar results were also obtained in a subsequent study, in which socially-isolated sheep were simply exposed to images of a conspecific face belonging to their own breed (Da Costa, Leigh, Man and Kendrick, 2004). Activation of the right hemisphere was elicited by faces of same-breed conspecifics, but not by exposure to goat faces. This effect appeared to be associated both with face processing and with emotional responses determined by the exposure to conspecific faces (having a calming effect on distressed animals).

Visual cells selective for faces are present in the temporal cortex of sheep, similar to what is usually found in monkeys (Kendrick and Baldwin, 1987; Kendrick et al., 2001). It is interesting to note that, while electrophysiological recordings in monkeys failed to reveal any dominance of the right hemisphere in response to face stimuli (see above), similar studies in sheep provided evidence of a temporal advantage of face-cells in the right hemisphere over left-hemisphere ones (Peirce and Kendrick, 2002), in line with event related potential results in humans (Seeck et al., 1997). In particular, cells that respond selectively to one type of face or to the face of one individual show a reduced response latency in the right hemisphere. This temporal advantage is limited to subtle discriminations between different faces, whereas the two hemispheres are equally fast in simply detecting the presence of a face in the visual field. Moreover, a certain number of neurons in the left hemisphere actually respond after the time necessary for sheep to identify a face is elapsed. It seems reasonable that these slower cells are not contributing critically to visual recognition, but rather are involved in later processing contingent on recognition (e.g. processing of behavioural responses appropriate to the recognized face).

Recognition of familiar social partners

Studies on non-human primates and sheep investigated asymmetries in social recognition mainly capitalizing on their remarkable face-processing abilities. Research in domestic chicks and other species has provided consistent evidence of behavioural lateralization of social recognition using a different approach. Even though evidence exists that faces are a relevant social stimulus for non-mammalian species, such as domestic chickens, the studies on lateralization of social recognition that will be reviewed in the following paragraphs were not focused on face-perception per se, but rather investigated the more general ability of the left- and right-eye system to recognize a familiar social companion from an unknown one. This approach has the advantage of being more ecologically relevant and allowing a direct comparison with data obtained in field-studies, since in the natural environment it is rare to perform social recognition on a face presented in isolation. In the following paragraphs we will offer a review of studies that applied this approach to domestic chickens, but also to other species tested under similar conditions and procedures.

The simultaneous choice test. The paradigms usually employed with chicks take advantage of the imprinting process, by which chicks develop a social attachment for the first conspicuous stimulus they are exposed to for at least a few hours. In the natural environment, imprinting usually leads the chick to memorize the distinctive features of the mother hen (or of one of its siblings), but in laboratory conditions imprinting can be directed to a great variety of artificial stimuli. The social attachment developed for the imprinting object leads the chick to regain contact or proximity with its imprinting object whenever they are separated, especially if in an unknown and potentially dangerous environment. One of the fundamental tests employed in most studies involves placing the chick in the centre of a rectangular corridor, with its imprinting object located on one side of the corridor and a similar, but unfamiliar, social object on the opposite side (e.g., the chick's cage-mate on one side and an unfamiliar same-breed chick on the other side) (see Figure 1 for a representation of the testing apparatus). The differential preference for staying on one of the two sides of the corridor is an index of the capacity to discriminate the two stimuli. In general, chicks' behaviour in this kind of test is markedly influenced by gender effects. As mentioned above, even though both sexes are generally able to discriminate the stranger chick from their social companion, males tend to choose the stranger and females the companion (Vallortigara and Andrew, 1991; 1994).

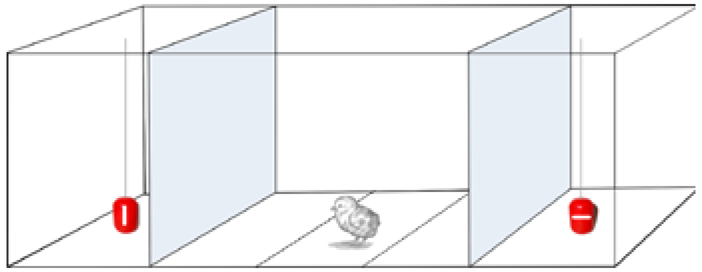

Figure 1. *Schematic representation of the testing apparatus employed in the spontaneous preference test for domestic chicks (e.g., Vallortigara and Andrew, 1991). The experimental subject is represented in the starting position in the central sector of the apparatus. Two stimuli are simultaneously placed at opposite ends of the runway. Typically, one stimulus is identical to the subjects' artificial imprinting object and the other is a novel, but similar, object.*

However, this overall pattern appears to be modulated by the degree of perceptual difference between the familiar and unfamiliar object, by the type of social companion employed (either natural or artificial imprinting object) and, more importantly, by lateralization effects. In a seminal study (Vallortigara and Andrew, 1991), lateralization effects were directly assessed thanks to the employment of a monocular occlusion procedure. In birds, as in many other species with laterally placed eyes, each eye projects mainly to the contralateral hemisphere: the avian brain does not have a corpus callosum and displays a virtual complete decussation at the optic chiasm (Deng and Rogers, 2002a; Csillag and Montagnese, 2005). Methodologically speaking, this means that visual input to the chick's brain can be easily restricted to one hemisphere and a simple patch over one eye can be used to test lateralization effects (Rogers, 1997; Gülbetekin, Güntürkün, Dural and Cetinkaya, 2007). According to a monocular occlusion procedure, chicks can be defined as binocular subjects (BIN-chicks) when they are not eye patched and view freely with both eyes. Subjects having the left eye in use (i.e., the right eye occluded) are labelled as LE-chicks and are supposed to process visual information mainly with their right hemisphere. RE-chicks use their right eye and thus are employing mainly their left hemisphere. In addition, birds can use their eyes independently allowing, for example, the scanning for predators with one eye whilst categorizing food and non-food items with the other (Rogers, 2000). This spontaneous eye use can also allow us to discern hemispheric specializations.

In male chicks tested by Vallortigara and Andrew (1991), both binocular subjects (BIN-chicks) and chicks using the left eye (LE-chicks) prefer to approach their artificial imprinting object to moderate or large transformations of it. For example, BIN- and LE-chicks imprinted on a red ball with an horizontal white stripe, when faced with the choice between an identical object or a red ball in which the white stripe had been rotated by 90°, chose the familiar one. A similar result was also obtained when the white stripe was still horizontally oriented but moved to a markedly different position on the red ball. However, LE-chicks preferred the novel object when choosing between their artificial imprinting stimulus and small transformations of it, such as a rotation of the white stripe by only 45°. A preference for the novel object in BIN- and LE-chicks was observed also when choosing between a familiar and an unfamiliar chick (possibly the visual difference between two chicks is comparable to a small transformation of the artificial imprinting object in terms of the degree of perceptual change). On the contrary, male RE-chicks (having the right eye in use) did not express any preference, except for large transformations of the appearance of the imprinting object (in this case they chose the familiar individual). For example, a significant choice for the familiar stimulus was observed in RE-chicks when the aspect of the red ball was dramatically altered by removing the white stripe or by changing the overall colour of the ball itself. Similarly, when the relevance of the white stripe for the appearance of the imprinting object was increased by augmenting its dimension to completely cover the equator of the red ball, RE-chicks also became sensitive to changes in its orientation. Finally, females demonstrated a simpler pattern of results, since they always chose the familiar social object, with the exception of RE-subjects that did not express any significant preference when choosing between familiar and unfamiliar chicks (Vallortigara and Andrew, 1991).

Results obtained by Vallortigara and Andrew (1991) show that the right hemisphere is in control of behaviour in normal vision conditions, since the performance of BIN- and LE-chicks is usually indistinguishable. In RE chicks, the absence of significant choice displayed in some tests does not seem to be due to a lack of motivation for social reinstatement. In fact, RE-chicks approached the two social objects present in the corridor to the same extent as LE- subjects did, even though they did not express any preference between the familiar and unfamiliar object. It is thus reasonable to assume that RE-subjects simply decide whether a given stimulus is a social companion or not, i.e., belongs to the category of social companions, without determining if it is the familiar individual they have been reared with or a novel one. Evidence that RE-chicks tend to group stimuli that differ on one parameter (as long as this parameter is not a defining one for the category, such as the presence of the white bar on the red ball) but are otherwise similar has also been obtained in radically different tasks (e.g., Andrew, 1988). This specialization of the left hemisphere is adaptive whenever an organism needs to make a rapid decision that will influence the response emitted (in this case whether a stimulus is a social companion or not). On the other hand, the right hemisphere possesses a complementary specialization for novelty detection, based on the fact that it seems to build up cognitive representations of what is specific to a particular stimulus as opposed to invariant features of all the members of the category. This specialization of the right hemisphere for subtle forms of within-category visual discriminations is consistent with response properties of neurons in areas specialized for encoding visual features of the imprinting object in the two hemispheres (Nicol, Brown and Horn, 1995). After imprinting, there is greater neuronal responsiveness to the sight of the imprinting object in imprinted chicks compared to non-imprinted chicks. This effect is evident in both the right and the left hemisphere. However, only in the right hemisphere, there is also evidence that a smaller number of neurons are responding to an alternative stimulus (not used in imprinting). As a consequence, the signal-to-noise ratio at the cellular level would favour discrimination of the two objects (familiar vs. unfamiliar) in the right hemisphere over the left one.

It is worth noting that, in a subsequent study, Deng and Rogers (2002b) employed a similar paradigm to that developed by Vallortigara and Andrew (1991) and confirmed the presence of lateralized IR in favour of the right hemisphere in chicks of a Black Australorp-White Leghorn breed. In this case, LE-chicks showed stronger individual preferences for approaching either a familiar or an unfamiliar chick (even though no preference was evident at the group level), whereas RE- and BIN-chicks showed an absence of preference even at the individual level. The absence of significant choice, even at the individual level, in BIN-chicks of the strain tested by Deng and Rogers (different from that previously employed by Vallortigara and Andrew, 1991) is one of the puzzling results reported in this paper. In fact, the behaviour of binocular individuals is supposed to be guided by the right hemisphere in this task, and it is surprising that in normal vision conditions chicks do not discriminate familiar subjects. However, subsequent experiments, demonstrated that visual experience of a group of conspecifics (provided before the subjects start to be reared in pairs) improves the discrimination performance of BIN- and RE-subjects, which become able to express a choice between familiar and unfamiliar chicks, at least at the individual level. From the results of this study, it seems that LE-chicks pay attention to the visual cues that differentiate individuals without requiring visual experience of a number of conspecifics, whereas RE-chicks do need such visual experience (Deng and Rogers, 2002b). It is interesting to note that this result is in striking contrast to what found in human beings. Evidence suggests that in our species right-hemispheric social recognition depends on visual input. For example, a study by Le Grand, Mondloch, Maurer and Brent (2003) showed that early deprivation of visual input to the right hemisphere, due to unilateral congenital cataracts, severely impairs the development of expert face processing in humans. The reason for these partially-discrepant results in humans and chicks is not known. A reasonable hypothesis is that the discrepant results could be due, at least in part, to the different developmental rates of the two species, since humans are one of the most altricial animal species whereas chicks are possibly one of the most precocial animal species. However, it is also possible that the crucial factor determining this apparently conflicting evidence is the quantity and quality of visual deprivation in the different studies. In fact human infants suffering from congenital cataracts do not experience any form of visual patterned input during the first months of life. On the contrary, in the study of Deng and Rogers (2002b) all chicks had unrestricted visual experience of their rearing environment and of at least one cagemate; the deprived subjects only lacked visual experience of a group of conspecifics.

Sex differences in motivation and lateralization in the simultaneous choice test. When discussing the sex differences observed in the study of Vallortigara and Andrew (1991), it should be noted that the existing literature suggests that female chickens are more motivated to re-establish contact with social partners and are more conservative in their social preference (Vallortigara, 1992b; Vallortigara, Cailotto and Zanforlin, 1990). Female chickens tend to choose the familiar social companion if they can detect any difference between the two objects. Males demonstrate more exploratory behaviour than females do (Workman and Andrew, 1989) and will approach stimuli that are not too different from their imprinting object. This may seem a disadvantageous behaviour in a young animal, regardless of its sex, but it is likely to actually be adaptive under some circumstances. For example, it can ensure the possibility to more rapidly develop a complete representation of the imprinting object itself; stimuli that are similar, but not identical, to the memorized aspect of the familiar social companion may be different views of the companion itself (e.g., frontal and profile views of the mother hen). It is conceivable that male chicks will develop such a complete representation of a social object sooner than females and this will in turn compensate for the potential risks associated with their stronger exploratory tendency. Moreover, in males the need to familiarize with unknown conspecifics could be adaptive per se, since in natural conditions males will probably have to leave the original brood once adulthood is reached, whereas females would probably form a group with their sisters within their natal territory (see Vallortigara and Andrew, 1994, for a discussion, pp. 46-49). However, some of the sex differences observed by Vallortigara and Andrew (1991) seemed to be related to differences in lateralization, rather than in motivation, between males and females. In particular, female chicks were more likely than male chicks to show identical behaviour in LE- and RE-subjects. It has been theorized that, in females, the hemisphere that is normally in control of the task in binocular vision conditions (the right hemisphere, in this case) would be able to direct behaviour even when sight is limited to the ipsilateral eye (see also Andrew and Brennan, 1984; Andrew, 1988; see below for a discussion of a similar phenomenon occurring in male chicks, Vallortigara, Regolin and Pagni, 1999). A prerequisite for this phenomenon is a process termed metacontrol, i.e., the mechanism by which one hemisphere takes charge of behaviour by inhibiting conflicting responses from the contralateral side of the brain. Until a recent study in pigeons (Adam and Güntürkün, 2009), which demonstrated that this process occurs also in avian species, metacontrol had been directly investigated only in primates (mostly humans, Hellige, Jonsson and Michimata, 1988; Urgesi, Bricolo and Aglioti, 2005; for evidence from macaques see Kavcic, Fei, Hu and Doty, 2000). However, indirect evidence of metacontrol in avian species was already available in the literature (e.g., see the above reviewed research in chicks) since this process is even more relevant for animals, like birds, with laterally placed eyes and complete chiasmatic decussation, in which visual input to the hemispheres is largely independent.

A paradigm free of sex differences: The social pecking test The study of Vallortigara and Andrew (1991) revealed a fundamental difference between the behaviour of LE- and RE-chicks, that is to say, the inability or lack of interest of RE-chicks for discriminating between familiar and unfamiliar conspecifics. This result has been replicated with a slightly different paradigm (Vallortigara, 1992a). This procedure exploits chicks' tendency to direct aggressive/exploratory pecks to unfamiliar conspecifics. One of the advantages of this paradigm is that females and males (in normal binocular vision conditions) behave similarly (pecking more at strangers than at their cage-mate). Thus, lateralization effects can be studied without being complicated by interactions with social-motivational differences between in the two sexes. In this case, both sexes showed the identical pattern of results, with BIN- and LE-subjects pecking more at strangers and RE-chicks directing the same number of pecks to both cage-mates and unfamiliar individuals.

A similar procedure, based on the analysis of pecking responses toward familiar or unfamiliar conspecifics, has been employed in a subsequent study that investigated lateralization in the use of both the central and the lateral visual field of young chicks (Vallortigara, Cozzutti, Tommasi and Rogers, 2001). In this case, the authors measured not only the number of pecks directed at familiar versus unfamiliar social companions, but also the frequency with which each chick used its lateral and frontal fields of vision of each eye to fixate before pecking. When pecking at strangers, but not at cage-mates, chicks showed a preference for using the left lateral visual field to fixate on the unfamiliar individual. Thus, the dominance of the left-eye-system (right hemisphere) is evident even when no visual restriction is performed and chicks are experiencing their natural vision condition. However, in this experiment chicks also showed a most interesting preference for using the right frontal visual field to fixate on the stranger to be pecked (such a preference was probably mediated by transfer of information between the two sides of the brain, thanks to interhemispheric commissural fibers, or by ipsilateral projections from the frontal fields of vision). This reversed (and complementary) asymmetry in the use of the lateral and frontal visual fields could reduce the disadvantages associated with behavioural lateralization in a non-asymmetrical word. It has been argued that being more prepared to respond to a given stimulus when presented on the left rather than on the right side can be problematic since, other things being equal, in the natural environment social stimuli are equally likely to appear from either direction. Moreover, if a side bias is consistent at the population level, the consequent predictability of the behaviour of the members of the population can be exploited by other organisms. This issue does not pertain only to asymmetries in social cognition but applies to every kind of behavioural asymmetry. If a similar complementary specialization of frontal versus lateral visual fields could also be demonstrated in other domains, this could reveal a putative mechanism able to compensate for the above mentioned ecological disadvantages.

Similar results were also obtained in hens with a slightly different procedure based on the use of blinkers that covered only the frontal visual fields (McKenzie, Andrew and Jones, 1998). The presence of this effect in adult subjects was not unexpected, due to the clear adaptive value of this complementary specialization during the whole life-span of an individual (even though some anatomical asymmetries of the visual pathways are marked in young chicks, but reduce or disappear with development, Rogers and Sink, 1988).

The use of the right-frontal visual field to inspect social partners and guide pecking responses (Vallortigara et al., 2001) is not the only instance of left-hemisphere involvement in social responses of domestic chicks. On their first encounter with a potential social companion (i.e., the stimulus that will later become their imprinting object) chicks (females in particular) show a bias to inspect it using their right eye (left hemisphere) (Dharmaretnam and Andrew, 1994; McKenzie, Andrew and Jones, 1998). In this situation the potential social companion is intrinsically attractive, but it is not yet a familiar stimulus. It has been hypothesized that the use of the left hemisphere, specialized in response control, is associated with the need to refrain from approaching this novel object until categorization of the new stimulus as a potential social companion (another left hemisphere function) has been achieved. Other cases of left-hemispheric participation in responses toward familiar/unfamiliar social companions will be described in the following two paragraphs (The detour test; Monocular-unihemispheric sleep).

The detour test. Lateralization of social recognition in chicks has also been studied employing paradigms based on the detour test, in which the subject has to circle around an obstacle in order to reach a familiar or an unfamiliar social object (Vallortigara, Regolin and Pagni, 1999). In this study, a bias for monitoring the target social object with the left eye (right hemisphere) emerged for unfamiliar social companions (either stranger chicks or moderately-altered versions of an artificial imprinting object), whereas when reaching for the familiar social object, chicks tended to monitor it with their left hemisphere. Also in this case the preferential use of the right hemisphere is influenced by chicks' gender and by the degree of novelty of the stimulus, with females using the right hemisphere for increasing degrees of novelty, and males reverting to the use of the left hemisphere in cases of extreme alterations of the original stimulus, possibly in order to inhibit fear reactions associated with novel objects. The authors hypothesise that, in males experiencing pronounced changes in their imprinting stimulus, the right hemisphere would be still in control of behaviour, but it would use the left hemisphere (fed by the right eye) in order to monitor the partially-frightening altered stimulus. In this circumstance, the dominant hemisphere would be ipsilateral to the eye in use for viewing during the detour, and the task of monitoring the stimulus would be delegated to the subordinate hemisphere because this is less fearful of the novel stimulus.

The preferential use of the left-hemisphere to monitor for familiar social companions observed by Vallortigara and his colleagues (1999) may seem at odds with other evidence of right hemispheric dominance for social recognition, but this result should be interpreted considering the task employed in this study and the problems that it poses to a young organism. In a detour task, the main difficulty for chicks is to inhibit responses along the straight route (chicks have to be able to momentary increase their distance from the social companion they want to reach, taking the long route in order to detour the obstacle). The left hemisphere is better suited for the control of responses (e.g., Miklosi and Andrew, 1999), and thus, in this task, it remains in charge of behaviour unless the presence of alterations in the appearance of the target social object calls into function circuits of the right hemisphere specialized for novelty detection and IR. Overall, with regard to the role of the right hemisphere, results obtained by Vallortigara, Regolin and Pagni (1999) are consistent with those of previous studies reviewed above in that they suggest that its specialization for discrimination of social companions seems to be based on its dominant role in the assessment of novelty, which in turn is due to its ability to encode the peculiar and distinctive features of individual objects.

It must be noted that a subsequent study, testing the performance of adult quail in a similar detour task, revealed a bias to use the left hemisphere to monitor unfamiliar social companions (stranger chicks or the subject's own mirror reflection), whereas the right hemisphere was used for monitoring the familiar social object (Zucca and Sovrano, 2008). Similarly, lambs and ewes show right hemisphere dominance for monitoring familiar social partners during the partial detour of an obstacle (Versace, Morgante, Pulina and Vallortigara, 2007). The discrepancies between such results and those obtained by Vallortigara and colleagues (1999) might be due to subtle differences in the way adult quail and newly-hatched chicks process social stimuli. It has been suggested that for an adult bird (such as those tested by Zucca and Sovrano, 2008) the sight of an unfamiliar conspecific could require a more considered response-selection to decide between alternatives such as attack versus approach, activating the left-hemispheric specialization for visual control of responses. With regard to sheep, it has to be considered that the detour task employed was less demanding than the version employed with chicks, since it allowed the animals to proceed along a nearly straight route to reach the social companion (Versace et al., 2007, see Figure 2). Thus, recruitment of the left hemisphere for response inhibition would probably be unnecessary

The detour test has also been employed with fish species. However, studies on detour in fish were not focused on the distinction between approach of familiar versus unfamiliar social partners, but rather on the investigation of the different behaviour elicited by sexual versus affiliative motivation. For example, it has been found that female poeciliid fish (*Gambusia holbrooki, Girardinus falcatus*) detouring an obstacle behind which a group of other females was visible, preferentially kept the target in view with their left eye (Bisazza, Facchin, Pignatti, and Vallortigara, 1998). However, when males were tested with same-sex conspecifics as target object, they showed no bias (Bisazza et al., 1998), dis-

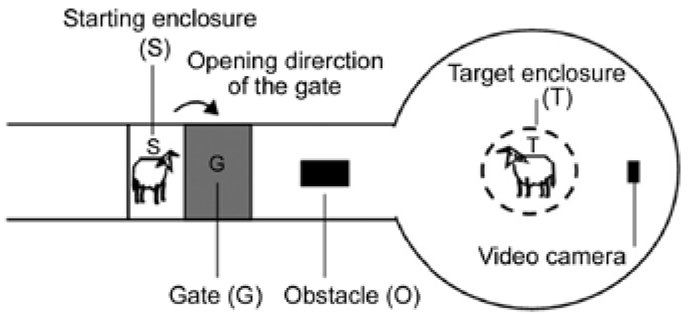

Figure 2. *The experimental setup used for the detour test in the study of Versace et al. (2007). Adapted from Behavioural lateralization in sheep (Ovis aries) by E. Versace, M. Morgante, G. Pulina and G. Vallortigara, 2007, Bheavioural Brain Research, 184, p. 72-80. Adapted with permission.*

playing preferential use of one eye only when the target was a group of females, a sexual stimulus (Bisazza, Pignatti and Vallortigara, 1997a; 1997b; Bisazza et al., 1998). It is interesting to note that the direction of the bias showed by males in this circumstance varied according to the degree of fear (and consequent motivation to gregarious behaviour) versus sexual motivation characterising subjects of each species (*Brachyrhaphis roseni, G. holbrooki, Gambusia nicaraguensis, G. falcatus, Poecilia reticulata*) when tested in a novel environment: higher sexual motivation was associated with right eye use and higher affiliative motivation with left eye use. In line with this, sexually deprived females showed a bias in favour of the right eye to scrutinize target males (Bisazza et al., 1998).

An interesting set of studies conducted by Brown and his collaborators investigated how early experience and emotional context influence laterality in the detour test (Brown et al., 2007). Brown et al. (2007) investigated the detour behaviour of wild-caught fish (*Brachyraphis episcopi*) obtained either from high- or from low-predation areas. The behaviour of wild-caught female fish was compared with the performance of their laboratory-raised offspring. This approach enabled the authors to disentangle the role of early experience from that of inheritable adaptations to stable environmental contingencies. The turning preference displayed by wild-caught subjects while facing novel objects or potential predators seemed to vary according to their original predation rate (Brown, Gardner and Braithwaite, 2004; Brown et al., 2007). However, when a same sex conspecific was used as a target, wild-caught females showed a symmetrical turning response (i.e., they did not display any significant turning bias), regardless of whether they came from a high- or a low-predation area. On the contrary, previous experience had a clear effect even when conspecifics were used as targets. In fact, laboratory-raised highly-predated females showed a bias to use the right eye to view unfamiliar conspecifics, which was not significant for wild-caught highly-predated females. The direction of lateralization observed in this occasion is the opposite of that reported by Bisazza et al. (1998), possibly indicating interspecies variability. Another possibility is that the crucial element determining the difference between the results of Bisazza et al. (1998) and those of Brown et al. (2007), is that Brown and collaborators used a single unfamiliar conspecific as a stimulus, instead of the group of conspecifics employed by Bisazza and colleagues. In the context of these studies, a single unknown conspecific may represent a remarkably different stimulus, with respect to a group of conspecifics. An isolated conspecific could, in fact, elicit a lower degree of gregarious behaviour, since in it can offer limited dilution effect (i.e., limited protection against predation). However, the most interesting element revealed by the work of Brown et al. (2007) is that the pattern of expression of lateralized responses was influenced by early experiences, such as being raised in an environment rich in predators or in a predator-free laboratory tank. In the reasoning proposed by the authors is that such early experiences are going to affect the motivational and emotional valence of a given stimulus for different subjects, influencing which hemisphere will be used to analyze and respond to the stimulus.

Brown and collaborators (2007) also observed gender differences in the strength of lateralization of laboratory-raised subjects, with males more strongly lateralized than females (this pattern is in line with evidence available in chicks, e.g., Vallortigara and Andrew, 1991). In particular, males originating from the highly-predated population showed a remarkably-different pattern of lateralization depending on the nature of the stimulus used as a target for the detour test, whereas this pattern was much less pronounced in females from the same population. Interestingly, for males, the target stimulus that elicited the stronger lateralization of response was the unknown conspecific. This study confirms previous evidence that males and females diverge in the way they process unfamiliar conspecifics, even though this was evident only for the highly-predated subjects. A possible interpretation of these findings is based on the fact that male *B. episcopi* are more aggressive than females (both sexes are generally quite aggressive). This difference is likely to affect the way the males and females react to the sight of same-sex conspecifics, the way visual stimulation coming from conspecifics is processed, and consequently the differential involvement of the two hemispheres. In low-predation areas, females are more territorial and may behave in a similar way to males. Moreover, males are less numerous in low-predation areas, where the sex-ratio is particularly biased in favour of females, making male-male encounters less frequent. Thus sex differences might be more prominent in populations coming from a highly-predated area.

Monocular-unihemispheric sleep Recent studies exploited a peculiar behavioural and electrophysiological state exhibited by domestic chicks, monocular-unihemispheric sleep, to further investigate asymmetries in social recognition. During monocular sleep episodes, one eye is open while the other remains shut. The hemisphere contralateral to the open eye shows an EEG pattern typical of wakefulness states, whereas the hemisphere contralateral to the closed eye presents an EEG pattern typical of slow wave deep sleep. Episodes of monocular sleep in one hemisphere seem to be associated either with the need to monitor environmental stimuli with the other hemisphere, according to its specialization, or with the need to consolidate memory traces encoded by the sleeping hemisphere. During the first week of exposure to an imprinting object (a cagemate), female chicks present a bias toward right-hemisphere monocular sleep, probably as a consequence of intense social-interaction and encoding of the distinctive features of their cagemate (Bobbo, Vallortigara and Mascetti, 2006a). Interestingly, experiencing changes in the appearance of the imprinting object caused a bias for left hemisphere monocular unilateral sleep (Bobbo, Vallortigara and Mascetti, 2006b). The interpretation of this last result is less clear, since it could be explained as either a tendency to open the left eye in order to monitor the novel stimulus with the right hemisphere, or as an activation of the left hemisphere for initial encoding of the features of a secondary imprinting object (the modified stimulus), with consequent left-hemispheric sleep in order to achieve memory consolidation. Secondary imprinting refers to the learning and social-attachment processes occurring when a chick is exposed to a novel object appropriate for imprinting, after it has already become imprinted on a given stimulus. In his original theorization Lorenz (1935) claimed that imprinting was irreversible. Subsequent research demonstrated that, if the first imprinting object is removed and substituted with a new one, imprinting can be directed toward this second object (even though memory for the first object may not disappear) (Kent, 1987; Bolhuis and Trooster, 1988; Cherfas and Scott, 1981). Why should the left hemisphere be particularly involved in the initial encoding of the features of a secondary imprinting object (as hypothesised in the study of Bobbo et al., 2006b)? Lesion and electrophysiological studies demonstrated that an associative forebrain structure, known as IMM (Intermediate Medial Mesopallium), is part of a memory system that encodes a representation of the imprinting object (Horn, 1990; 2004). It seems that both the right and the left IMM act as long-term stores of memory traces about the appearance of the imprinting object (Nicol et al., 1995), but the right IMM is also crucial in establishing another store outside this region (McCabe, 1991). The right IMM passes information to this other store (whose location is unknown) over a period of several hours (Horn, 1990). It seems likely that, while the left IMM establishes an initial representation of the appearance of the imprinting object, the right IMM would be involved in a later process of enrichment of this simple initial representation (Horn and Johnson, 1989). An initial recruitment of circuits and functions of the left hemisphere in the first encounter with a potential social companion can be easily explained considering, as theorized for example by Vallortigara and Andrew (1994), that the right-eye system is crucially involved whilst behaviour is dominated by a response to releaser stimuli. According to this, the left hemisphere responds to selected properties of a stimulus that can be used to assign it to a category, such as releaser cues. When a chick first encounters the mother hen or a sibling, its behaviour is likely to be mainly affected by releasers evoking approach and affiliative responses, determining left-hemisphere dominance. This view is strengthened by the fact that, during chicks' development, days of left-hemispheric dominance are associated with points of first or greatly-increased exposure to a new category of social object (or to a new aspect of an already known category) (see Vallortigara and Andrew, 1994). Moreover, as noted previously, the use of the left hemisphere could also help to prevent premature approach of an attractive object, until it is stably recognized as a social companion.

Side asymmetries in social responses during naturalistic encounters

A simple methodology to reveal the presence of behavioural asymmetries, which has been extensively employed in species such as fish, amphibians and reptiles, involves recording the frequency of social responses (e.g., aggressive or sexual behaviours) occurring toward conspecifics when they appear on the left versus on the right side of the subject (i.e., fall within the LVF or the RVF). In most cases, aggressive and sexual displays are performed toward conspecifics and imply recognition of the other organism as belonging to the same species of the subject (sometimes also recognition of the gender or individual identity of the other organism is required). With this procedure it has been demonstrated that, in female striped plateau lizards (*Sceloporus virgatus*, males were not tested), aggressive displays toward courting males are more frequent if the male appears on the left side of the subject or on its binocular visual field, than if the male appears in its right side (Hews, Castellano and Hara, 2004). Similarly to that described above for chicks, performance of lizards under the guidance of their binocular visual field resembled that observed under the guidance of the LVF, suggesting that the right hemisphere could determine performance in binocular vision conditions. Moreover, female lizards also show a bias for orienting in such a way to view conspecifics with their LVF before performing a charge (a strongly aggressive act) (Hews et al., 2004). This general pattern of behaviour was evident both in controlled laboratory conditions and in unmanipulated natural encounters. Similar data to those obtained in females by Hews and collaborators (2004) are also available for male three-lizards (*Urosaurus ornatus*), that show more aggression toward other males when in the LVF (Hews and Worthington, 2001; see also Deckel, 1995 for evidence on male green anoles, *Anolis carolinensis*). Moreover, studies on lizards suggest that individuals with different motivational states may use brain lateralization to alter the nature of social encounters. That is to say, lizards that are likely to be aggressive (e.g., because they are bigger than their opponent, see Hews and Worthington, 2001) could decide to use the LVF for their aggressive display. This could in turn modify their own behavioural response (determining increased aggressiveness) and signal to the opponent that they are unlikely to give up the fight.

Research conducted with lizards also revealed that an asymmetry in endogenous serotonin (5-HT) levels (possibly in the raphe nucleus), is likely to contribute to the behavioural asymmetries described in the previous paragraph. Consistent with this is the fact that quipazine, a 5-HT2 agonist, decreases selectively right hemisphere-stimulated aggression (Deckel and Fuqua, 1998). Other evidence consistent with this idea comes from the fact that mild stressors and experimentally-induced alcohol withdrawal can decrease the leftward bias in aggression (Deckel, 1997; 1998; Deckel, Lillaney, Ronan and Summers, 1998). Both these manipulations might act on the asymmetry in endogenous serotonin. In line with this idea, evidence available in the literature suggests a greater sensitivity to alcohol administration of the right hemisphere than of the left one (e.g., Erwin and Linnoila, 1981), with a consequent impairment in right hemisphere's cognitive functions other than social recognition (e.g., spatial abilities in rats, Blanchard, Riley and Hannigan, 1987).

A left-eye bias during aggressive or courtship behaviour has been demonstrated in toads (*Bufo marinus*, Robins, Lippolis, Bisazza, Vallortigara and Rogers, 1998; *Bufo bufo*, Vallortigara et al., 1998), but also in avian species (e.g. Rogers, Zappia and Bullock, 1985; Ventolini et al., 2005) and nonhuman primates (*Theropitecus gelada, Macaca mulatta, Papio cynocephalus,* Casper and Dunbard, 1996; Drews, 1996). Studies of side biases in courtship and aggressive displays in fish revealed a less-clear pattern of results than in lizards, toads and other species. Siamese fighting fish (*Betta splendens*) showed individual-level, but not population-level, lateralization in aggressive displays toward an unfamiliar conspecific (the subject's mirror reflection) and in courtship displays toward live females (Cantalupo, Bisazza and Vallortigara, 1996). Subsequent research on two further species of teleost fish (*G. holbrooki, Xenotoca eiseni*) and again on Siamese fighting fish, showed an unexpected population level bias in favour of the right eye in aggressive responses toward other males (both mirror reflections and live males) (Bisazza and de Santi, 2003). This contradicts the absence of lateralization at the population level obtained by Cantalupo et al. (1996), possibly due to methodological improvements with respect to the procedure used in the former study, which forced fishes to swim in unnatural positions when performing aggressive responses. More surprisingly, the side bias observed by Bisazza and de Santi (2003) is in the opposite direction with respect to that demonstrated in the tetrapod species tested in other studies (see above). The authors suggest that this should be explained not as a shift in the direction of laterality during phylogeny but rather as an index of the fact that the same behaviour (performance of attack responses) involves different cognitive operations in fish compared to most tetrapod species tested. For instance, due to indeterminate growth, fish show large individual variations in body size (a main predictor of fight outcome). Probably, fish must enact a continuous inhibition of attack responses (a left hemisphere function) until a correct short-distance assessment of the opponent size has been accomplished.

Results in line with the general evidence of a left hemi-visual-field bias for guiding social responses and social recognition have been obtained testing fish with slightly different procedures that investigate side preferences without involving clear aggressive or sexual behaviours. For example, eight species of fish (eastern mosquito fish, scientific name *G. holbrooki,* redtail splitfin X. *eiseni,* eurasian minnow *Phoxinus phoxinus,* angelfish *Pterophyllum scalare,* sarasins minnow *Xenopoecilus sarasinorum,* zebrafish *Danio rerio,* elephant-nose fish *Gnathonemus petersii* and blue gourami *Trichogaster trichopterus*) as well as the tadpoles of five anuran species (common toad *B. bufo,* European green toad *Bufo viridis,* common frog *Rana Temporaria,* edible frog *Rana esculenta,* yellow-bellied toad *Bombina variegata*) show a left-eye preference for inspection of their mirror image, perceived as an unfamiliar conspecific (Bisazza, De Santi, Bonso and Sovrano, 2002; Sovrano et al. 1999; Sovrano, BIsazza and Vallortigara, 2001; De Santi, Sovrano, Bisazza and Vallortigara, 2001). The mirror test exploited in these studies, initially used to prove that fish (*G. holbrooki*) are more prone to show predator inspection when sharing with a social partner the risk of being predated upon, has also revealed that predator inspection is more frequent when the social companion (either a mirror image or a video recorded stimulus) is visible on the left side (Bisazza, De Santi and Vallortigara, 1999).

Such a left visual field bias, observed in mirror studies on fishes and anurans, changes over time with prolonged testing, under the influence of changes in the motivation to establish and maintain proximity with social companions (Sovrano et al., 2001; see also Dadda, Sovrano and Bisazza, 2003). This laterality effect seems to strongly depend on the presence of gregarious behaviour and affiliative motivation, that in fishes differ strongly between males and females, with males being gregarious only when at risk of predation or in a novel environment (in anuran species gregariousness is shown by juvenile subjects, mainly on the basis of kin or familiarity recognition). See the paragraph (The detour test) for a discussion of motivational and experiential factors influencing the expression of laterality in fish species.

Also in this case, as previously discussed for face perception studies, an important issue regards the role of experience with a given stimulus (or stimulus category) in determining the preferential involvement of the right hemisphere. It is worth mentioning that, in fish, the same left-eye bias demonstrated in the mirror test is evident also for the inspection of familiar abstract patterns, but not for unfamiliar ones (Sovrano, 2004). However, when social stimuli are employed, such as in the mirror test, fish display a preferential left-eye-use regardless of whether they have been directly familiarized with their own mirror reflection: a period of visual experience either with other conspecifics or with their own mirror reflection is sufficient to determine this effect (Sovrano, 2004). Thus, for fish, visual familiarity with the category to which the stimulus belongs to (e.g., same-sex conspecifics) is enough to determine a right-hemisphere involvement. This would be remarkably similar to what hypothesised for face perception in primates and sheep. In fact, such species seem to develop a special expertise for the type of face more extensively experienced during (early) life, with preferential involvement of the right hemisphere for this kind of face only (see the paragraph Face perception). Nevertheless, it is also possible to hypothesise that fishes would use their left eye when looking at familiar stimuli or at stimuli containing only a limited degree of novelty: unknown conspecifics could be characterized exactly by this moderate degree of novelty. In general, results obtained with the mirror test in fishes are in agreement with those previously reviewed for other species in that the right hemisphere dominance (for monitoring conspecifics according to an affiliative motivation) seems to be linked to the specialization of this hemisphere for the evaluation of stimuli's familiarity.

Evidence of side biases in naturalistic encounters that are neither sexual nor aggressive is also present in avian species and in mammals. One notable example is that of pigeons; when homing in flocks, pigeons tend to fly to the right of their favourite flight-partners, monitoring them with their left-eye (i.e., the longer a bird had spent behind another individual, the more likely it was to be flying to the partner's right side) (Nagy, Àkos, Biro and Vicsek, 2010). Thanks to sophisticated analyses of pigeons' flight trajectories, Nagy and collaborators concluded that when pigeons observe visual cues from a given conspecific predominantly with their left eye, they are more responsive to its movements, which influence the pigeon's own flight trajectory. Similarly, gelada baboons (*Theropithecus gelada*) prefer to process social visual cues from conspecifics with their right hemisphere even during non-aggressive approaches (Casperd and Dunbar, 1996). In sea mammals, a bias to monitor social signals from conspecifics with the left eye has been observed during mother-offspring interactions; in the natural environment calves of the wild beluga whale (*Delphinapterus leucas*) swim keeping their mother on the left side (Karenina et al., 2010; see also Sakai, Hishii, Takeda and Kohshima, 2006 for similar evidence of more pronounced social rubbing behaviour with the left than with the right flipper, associated with a preferential left-eye use, in bottlenose dolphins *Tursiops aduncus*).

Environmental and genetic factors underlying the development of lateralization

Previous work revealed that, in chicks, structural and functional lateralization is triggered by exposure of the embryo in the egg to light (Rogers and Sink, 1988). During development, the embryo turns so that the right eye faces outward, toward the translucent eggshell and to any available light. On the contrary, the left eye is turned toward the body mass and receives little or no light during this last stage of development (when the embryo becomes too large to move within the egg). Whilst still in the egg the thalamofugal visual pathway of the chick undergoes differentiation. During a critical period (from embryonic day 17 to 21; Rogers, 2008) exposure to light produces an asymmetrical stimulation of the two eyes causing an increase in forebrain projections from the left side of the thalamus (fed by the light-stimulated right eye) compared with the right side (Rogers and Deng, 1999; Koshiba, Nakamura, Deng and Rogers, 2003). If the chick does not receive light during incubation, both this structural lateralization as well as its behavioural consequences is largely prevented (Rogers and Bolden, 1991; Rogers, 1990; 1995). Similar evidence has also been obtained in pigeons: the development of asymmetries in the tectofugal pathway crucially depends on light exposure during incubation (Güntürkün, 1993).

The effect of light-exposure on functional asymmetries has been investigated for the social-recognition tasks described in the previous paragraphs. In the study of Vallortigara et al. (2001) the behaviour of chicks hatched from light- and dark-incubated eggs was compared, revealing unexpected results. Dark-incubated chicks were even more lateralized than light-incubated ones. In particular, the bias for using the right-frontal visual field was evident only in dark-incubated chicks, in striking contrast with results obtained for other tasks (see above). The absence of this trait in light-incubated chicks has been interpreted as an index of the fact that they better integrate information in the two hemispheres, due to early light-stimulation allowing a better coordination of visual input from the two eyes. This is consistent with evidence of how light-exposure affects the development of visual pathways in chicks. In particular, input from the right eye via the thalamofugal pathway differs in light- and dark-incubated chicks. In chicks exposed to light during incubation, the right eye sends strong input to both hemispheres, thanks to a greater number of fibres projecting from the left side of the thalamus to the contralateral hemisphere, determining increased integration between information in the frontal visual fields (Deng and Rogers, 1998; Rogers and Deng, 1999).

A subsequent study, this time employing the standard procedures based on free choice test and monocular occlusion, confirmed that lateralization of social recognition is not dependent on light-exposure, in contrast to other forms of behavioural asymmetry previously documented in this species. Deng and Rogers (2002b) found right hemispheric dominance for IR in both light- and dark-incubated subjects: LE-chicks showed individual preferences for approaching either the familiar or the unfamiliar chick, whereas RE- and BIN-chicks showed an absence of preference. An important question that emerges from the studies reviewed above is why lateralization of social recognition should be independent from light exposure, in contrast to what is observed for other tasks. An interesting possibility is that, while lateralization of functions controlled by the left-hemisphere is established thanks to the stimulation of the right-eye by the light passing through the eggshell, social recognition is not controlled by this environmental factor since it is a right hemisphere specialization. In fact, the left eye (projecting to the right hemisphere) receives limited stimulation during the last stage of development even if the eggs are exposed to light, because it is occluded by the embryo's body (see above). In this case, however, the existing evidence does not distinguish whether lateralization of social recognition in favour of the right hemisphere might be dependent on other environmental factors providing asymmetrical stimulation or whether it could be expressed in an experience-independent manner. For evidence on the role of embryonic light-stimulation on the development of spatial abilities (a specialization of the right hemisphere) see Chiandetti, Regolin, Rogers and Vallortigara (2005), Chiandetti and Vallortigara (2009). In the former study, the possibility for the non-seeing hemisphere (fed by the occluded eye) to take part in the control of overt behaviour seemed to depend on light exposure. According to this result, asymmetric light stimulation might be more involved in interhemispheric communication rather than in the development of different specializations for the two hemispheres, in line with what discussed above for the study of Vallortigara et al. (2001).

While the studies reviewed above concentrated on the role of environmental factors in the development of functional asymmetries, another crucial issue involves the contribution of genetic factors and their interaction with the environmental ones. Moreover, variations in light stimulation of the embryo can influence the strength of the brain asymmetry but cannot reverse its direction, unless the position of the embryo itself is changed during the critical period. The positioning of the embryo is determined by genes of the so-called "Nodal cascade". Transplantation experiments with chick heart mesoderm have shown that heart sidedness is determined during gastrulation (Hoyle, Brown, Wolpert, 1992). Levin, Johnson, Stern, Kuehn and Tabin (1995) characterized a set of genes, which are asymmetrically expressed in the gastrulating embryo and regulate each other's expression to ultimately determine cardiac situs. These genes, along with others, regulate not only the heart asymmetry but also the asymmetry of viscera (situs viscerum) and embryonic turning (body rotation of the chick embryo in the egg, Levin et al., 1997). Many other asymmetric genes have been found to participate in this cascade (review in Levin et al., 1997). Certain asymmetric genes (e.g., FGF8, FGF18) are expressed in the isthmus zone of the chick's brain (Ohuchi, Kimura, Watamoto and Itoh, 2000), however, it is not known whether this expression produces any of the lateralized behaviours or is the primary source for the stable left-right differences between the telencephalic hemispheres. Therefore, the relevance of the asymmetric gene cascade to cerebral lateralization is not known. However, studies in fish provided a valuable insight on the genetic mechanisms determining the development of the described behavioural asymmetries. Recent work done on zebrafish has shown an asymmetric organization of diencephalic forebrain regions, regulated by the nodal signalling pathway (Concha, Burdine, Russel, Schier and Wilson, 2000). In the frequent *situs inversus (fsi)* line of zebrafish, the reversal of visceral and neuroanatomical asymmetries (in the epithalamus) is coupled with the reversal of some behavioural lateralization effects, including those revealed by the mirror test (Barth et al., 2005). Future studies should be devoted to the integration of the two lines of research described above by developing domestic chicks displaying *situs inversus*. This animal model could be then used to test the presence and direction of the functional asymmetries normally observed in IR. Another most interesting possibility would be to study the interaction of environmental factors (e.g., light exposure) and genetic determinants of such asymmetries.

Conclusive remarks

Evidence reviewed in this paper shows that phylogenetically distant animal species demonstrate forms of visual social recognition (either IR, familiarity-based recognition or conspecific recognition), a sophisticated cognitive ability of great adaptive value for most types of social interaction. Even more relevant, the majority of studies revealed a consistent lateralization pattern for this kind of task, pointing toward a right-hemispheric dominance. However, the picture emerging from the reviewed research is more complex than that, suggesting that the two cerebral hemispheres contribute in different ways to different aspects of social recognition. In particular, the right hemisphere is likely to play a dominant role in IR (or in familiarity-based recognition), whereas the left hemisphere could have an important role when animals are required to perform category-based distinctions, such as those employed for recognizing conspecifics versus heterospecifics (or to recognize faces from non-face objects) (see Figure 3 for a schematic representation of the different functions enacted by the two cerebral hemispheres). Evidence on the response latency of face-cells in the right versus left hemisphere of sheep brain is a good example on this regard, since it shows that the temporal advantage of the right hemisphere is limited to face recognition and does not affect simple face detection (Peirce and Kendrick, 2002). Moreover, analyzing response latencies of these face-cells it is possible to observe another interesting aspect of lateralization in social recognition. In fact, neurons in the left hemisphere respond after the time necessary to identify a face is elapsed and are likely to be involved in processing-stages occurring after IR has already been performed, such as processing of behavioural responses appropriate to the recognized face. Also in domestic chicks the left hemispheric dominance for social recognition has been observed in contexts in which the control of behavioural responses was a crucial aspect of the task, such as in the detour test, in which the right-hemisphere dominance re-emerged only when the animals reacted to the presence of a certain degree of novelty in the social stimuli (Vallortigara et al., 1999). Similarly, chicks tend to predominantly use the left hemisphere when inspecting a potential social companion for the first time. In this circumstance chicks have to refrain from approaching this attractive object until it is categorized as a potential social companion (again a left-hemisphere function) (Dharmaretnam and Andrew, 1994; McKenzie et al., 1998).

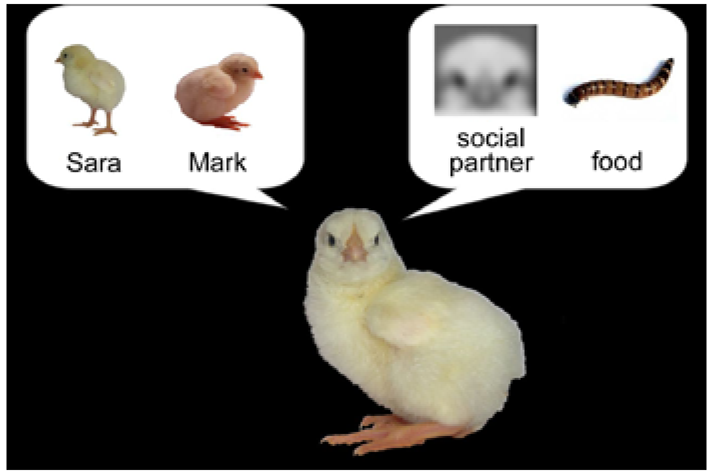

Figure 3. *Illustrative representation of the functions that we hypothesise to be enacted by the two cerebral hemispheres, according to the general differences in their processing styles.*

Overall, lateralization observed in social recognition seems to derive from more general differences in the processing styles of the two hemispheres, rather than being a domain specific phenomenon emerging only in this context. The right hemisphere's specialization for discrimination of social companions is likely to be a consequence of its dominant role in the assessment of novelty and of its configural (global) processing stile, associated with its ability to encode the peculiar and distinctive features of individual objects. Both these specializations could be aspects of a wider predisposition of the right hemisphere for developing a detailed and contextual representation of objects. A complementary specialization of the left hemisphere for rapid assignment of a stimulus to a category, for processing releaser stimuli and consequently for control of responses, can account for most cases of left-hemispheric involvement in social recognition, as discussed above.

We believe that, in order to appropriately interpret the existing literature as well as the results of future studies investigating asymmetries in social recognition, we shall need to avoid unprofitable oversimplifications. This can be done by taking into account that both hemispheres crucially contribute to the processing of social stimuli and to IR. The dominant role enacted by one or the other hemisphere is strongly dependent on task requirements as well as on current motivational and emotional factors (e.g., sexual motivation versus motivation to gregarious behaviour, see Bisazza et al., 1998). The study of sex differences in the strength and direction of lateralization represents a means to investigate the effect of such factors, and this aspect should never be overlooked in studies on lateralization of social recognition. Research conducted in fish also provided beautiful examples of how it is possible to study the contribution of early experience and of inheritable adaptations in determining the current motivational-emotional state and the differential involvement of the two cerebral hemispheres (Brown et al., 2007).

A clear example of complementary specialization of the two hemispheres was recently provided by a study on pigeons' categorization ability, using visual stimuli that should not elicit social responses in the species tested (Yamazaki et al., 2007). Pigeons were trained to discriminate pictures containing versus not containing human beings, followed by a generalization test on novel exemplars of the same trained categories (human present and human absent). Manipulating the familiarity of different parts of the stimuli and distorting (scrambling) them according to various criteria the authors demonstrated that LE-pigeons were prone to respond on the basis of the familiarity of the individual stimulus they were facing (i.e., they appeared to operate on an exemplar-based mode). Also, the right hemisphere showed a superior performance over the left one in recognizing familiar positive stimuli, but not when transfer to novel images was tested. Thus, hemispheric dominance shifted according to the cognitive strategy employed in different phases (recognition of individual familiar stimuli or category assignment of novel ones). Moreover, subjects having the right hemisphere in use were severely disturbed by manipulations altering the overall stimulus configuration. Thus, when deciding whether a stimulus belongs to the reinforced category, the left-eye system tends to base its judgment on configural, relational information. On the contrary, subjects having the left hemisphere in use were not affected by stimulus familiarity and tended to base their choice on local category-defining cues (performance of the RE-subjects was not significantly impaired when scrambled stimuli were used). The results obtained by Yamazaki and colleagues (2007) are particularly relevant not only because they are such a clear-cut instance of complementary specialization, but also because they stress once again the generality of the observed lateralization pattern, extending it to a categorization task different from those employed in most of the studies reviewed in the present paper. Other notable examples of this complementary specialization, outside the field of social cognition, derive from the tendency of the left-eye-system to use global-geometrical cues in spatial orientation tasks, as opposed to the local-featural cues used by the left hemisphere (e.g., see Vallortigara, Pagni and Sovrano, 2004 for evidence in chicks, Clayton and Krebs, 1994 for other birds, Cowell, Waters and Denenber, 1997; Crowne, Novotny, Maier and Vitols, 1992, for mammals). Also, the right hemisphere's superiority for amodal completion in chicks could derive from its' ability to analyze the overall stimulus configuration thanks to a global processing stile that takes into account visual relations between different objects (or objects' parts) (Regolin, Marconato and Vallortigara, 2004). See Vallortigara, Rogers and Bisazza (1999), for a partial review of similar evidence. On the other hand, the advantage of the right-eye-system for local processing has been demonstrated in primates employing Navon-tasks and hierarchical stimuli (e.g., Hopkins, 1997, chimpanzees; Martin 1979, humans; see Deruelle and de Schonen, 1995, for similar evidence in infants). Moreover, in chicks, the propensity of the left-hemisphere to treat equally stimuli that differ on one single parameter has also been demonstrated in tasks involving feeding responses rather than social-affiliative ones. Two notable examples are the pebble floor task, in which only the left hemisphere is able to categorize different pebbles as non food items (see Rogers, 2008 for a review), and the pecking-habituation test. This habituation test exploits a spontaneous decrease in chicks' pecking rate toward an object (a coloured glass bead) after repeated exposure to it. In this task, chicks with their right-eye-system in use do not show recovery from habituation even after conspicuous changes in the appearance of the habituated object (Andrew, 1991). The functional lateralization pattern observed for social recognition is based on hemispheric-specific processing styles that may generally characterize the vertebrate brain. These divergent processing styles predispose the cerebral hemispheres to adopt specific functions whenever a specific mode of analysis is superior. Thus, it is not the function itself but the way in which relevant information is processed that determines the pattern of functional lateralization. The evidence reviewed here suggests that the principle of organization is common between distant species and adds to the growing literature indicating the evolutionary continuum of cerebral lateralizations between human and non-human species.

The generality of the pattern of differential hemispheric specializations described above, observed in different species and tasks, is consistent with the hypothesis that it could reflect a fundamental property in the organization of the central nervous system, evolved as a solution to the problem of functional incompatibility of the operations required for category assignment versus for IR of different members of the category (Vallortigara et al., 1999). In fact, circuits specialized for registering the idiosyncratic features necessary to discriminate individual members of a category cannot efficiently extract invariant category-defining properties, making it profitable to devote equivalent structures in the two hemispheres to only one of the two functions. The lateralization effects observed in social recognition represent another instance of this general incompatibility of specializations of the two hemispheres.

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