Cerebral and behavioural asymmetries in animal social recognition

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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 same-sex individuals and (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; Lugout 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, Bluthé, 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.

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, etc. (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).

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 fasciatus; previous experience with individuals individually reared) 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 (Karavitch and Atema, 1998; Gherardi, Cenni, Parisi and Aquilotti, 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 laterali zed 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, rainbow trout (Oncorhynchus mykiss) demonstrated the ability 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. Parent 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 fish species with parental care (Corophiescrease haematopterus, Sagae, 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 (Sagae, 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 costs of territorial defence (Dale, 2000). Similarly, ruff's (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, Speed 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 (Merch and Keeling, 2001; Nicol, 2004; Rogers and Astonishing, 1991; Schjelderp-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., Beaugrad, Hogue and Lague, 1997; Rosa Salva, Daisley, Regolin and Vallortigara, 2009). The young chick’s ability to recognize conspecifics and social signals is critical in identifying conspecifics and social signals in general, and social partners in particular, for the first days after hatching. Chicks’ early social interactions are thus guided by a set of experience-independent predispositions that determine preference to attend to conspecifics, 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 photorealistic face-like stimuli (Rosa Salva, Regolin and Val
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In line with the precocious development of social behaviour in this species, IR has also been demonstrated in mammals other than sheep, revealing some remarkable similarities with data obtained in this species. Helfers (*Bo et al*). For example, 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, Depueit, Heyman and Baudoin, 2009*). Moreover, cattle can only quite among familiar conspecifics (*Hagen and Broom, 2003*), even using only visual cues from 2D images of conspecifics' heads (*Coulon, Baudoin, Heyman and Depueit, 2011*). Dogs (*Canis familiaris*) are capable of distinguishing their own faces from faces of other species (from birds to other canids) (*Racca et al.*, 2010). Similarly, dolphins (*Tursiops truncates*) clearly discriminate between familiar and unfamiliar humans (*Thielges, 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*) and orangutans (*Pongo pygmaeus*) have been demonstrated to be able to recognize a certain individual (*Coulon et al.*, 2007), even using only visual cues from 2D images of conspecifics' heads (*Coulon, Baudoin, Heyman and Depueit, 2011*). Dogs (*Canis familiaris*) are capable of distinguishing their own faces from faces of other species (from birds to other canids) (*Racca et al.*, 2010). Similarly, dolphins (*Tursiops truncates*) clearly discriminate between familiar and unfamiliar humans (*Thielges, Lemasson, Kuczaj, Boye and Blois-Heulin, 2011*).

Laterality in social recognition

It is now well established that brain asymmetries occur throughout the animal kingdom (*Rogers and Andrews, 2002; Vallortigara and Rogers, 2005, MacNeilage, Rogers and Vallortigara, 2007; Vallortigara and Dejod, 2008, 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, Mochorro and Hopkins, 2002a,b; Forrestier et al., 2003; Vallortigara, 2011*), birds (*e.g.*, *Rogers, 1997; Rugani, Kelly, Szldest, Regolin and Vallortigara, 2010; Vallortigara, 2000*) and even amphibians (*Vallortigara, Rogers, Bisazza, Lippolis and Roberts, 1998*, *fish (e.g.*, *Andrew et al.*, 2009; *Soriano, Rainoldi, Bisazza and Vallortigara, 1999*; *Soriano and Andrew*, 2006* and invertebrates (*e.g.*, *Ades and Ramiere, 2002; Byrne, Kuba and Griebel, 2002; Cooper, Nudo, Gonzalez, Vinson and Liang, 2011*; *Division et al.*, 2009; *Franszelli, Vallortigara and Rogers, 2010*; *Hobert, Kintz*, 2002; *Kihig, Steenhof, Cou, Lucente and Castillo, 2008*; *Letteke, Boeddeker, Wood, Zhang and Srinivasan, 2007*; *Rogers and Vallortigara, 2008; Pascual, Huang, Neve and Preat, 2004*).

Lateralization at the individual level (*i.e.*, not necessarily characterized by a consistent pattern within the population) is associated with clear computational advantages, such as the possibility to avoid a costly reduplication of functions and slow interhemispheric interactions, 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 stronger lateralized individuals could be more fit to deal with predators (*Brown, Western and Brainthwaite*, 2007), possibly also due to their facilitated social coordination. However, as a consequence of the increasing evidence of population level lateralization (*e.g.*, *Vallortigara, Chappell*, 2010) and the fact that non-human primates and other lateralized 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 in naïve monkeys showed a spontaneous interest toward both types of faces (other 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.
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 (Daisy, 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 chicks). Transitive inference, in fact, allows chicks 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, like humans, apes exhibit a left visual field (LVF) advantage for the recognition of facial emotional expressions (Morris and Hopkins, 1993; see also Fernandez-Duque and Vallortigara, 1992a). 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, Hausser and Akre, 2001).

Another most prominent phenomenon associated with right hemispheric dominance in face perception is the Left Gaze Bias (LGB) (Gao, 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.

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; Lah, Rueckert and Levy, 1981; Hellige et al., 1994; Burt and Perret, 1997; for neuroimaging studies see Kanwisher, Chun, McDermott and Ledden, 1996; Kanwisher, Tong and Nakayama, 1998; for evidence on brain-damaged patients see De Renzi, Perani, Carliesimo, 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 humans. For example, like animals, apes exhibit a left visual field (LVF) advantage for the recognition of facial emotional expressions (Morris and Hopkins, 1993; see also Fernandez-Duque and Vallortigara, 1992a). 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, Hausser and Akre, 2001).

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<table>
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<td>Broad et al., 2000</td>
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<td>Du Costa et al., 2004</td>
<td>Sheep (O. aries)</td>
<td>Brain activation (f-os and zif/268 mRNA expression) during exposure to conspecific faces</td>
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Table 1. Summary of the principal studies on laterality and social recognition.

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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 LG, which extended to non-face objects (Guo et al., 2009). The LG has also been found in pet dogs (Canis familiaris) (Guo et al., 2009). Even thinning testing studies were equally well socialized to both people and other dogs, a LG 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 LG. It is conceivable that the emergence of the LG could be associated with different underlying mechanisms in primates and in domestic dogs. In dogs the LG may have evolved during domestication as a specific adaptation to facilitate interactions with human beings (e.g., the LG facilitates processing of the owner’s face that is more effective in expressing anger and whose emotional expressions can be more easily recognized, Indersmidt and Gur, 2003). According to this argument, the LG can be considered limited to primates or to species that need to socialize with primates or primates-like human beings. Further, studies should test the presence of the LG 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 technical aspects of the experiments, from those usually employed in humans (Pinsk, D’Simone, Moore, Gross and Kastner, 2005). Similar results favouring the right hemisphere in face recognition have also been obtained in testing tasks with non-human primates (Hampton and Vermeire, 1988; Vermeire, Hampton and Erdmann, 1988; Vermeire and Hamilton, 1998).

Somehow surprisingly, studies conducted in sheep revealed an even clearer right-lateralization specialization for face processing, compared to research on non-human primates. Behavioural studies employing mirrored hemifaces and chimeric faces as stimuli demonstrated a LHV advantage for IR of faces of familiar conspecifics, but not for human faces (Kendrick, 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, Aukst, Huber, Hausmann and Güntürkün (2007) found evidence of an overall right hemisphere advantage but in a limited number of 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 that have 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 LHV advantage when the familiar sheep so 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 groups of about 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 delayed shift of the hemispheric specialization for 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 the rhesus macaque condition, it is possible to be a specific rhesus macaque per se, but simply a most common object of expertise (e.g., Diamond and Carey, 1986; Nelson, 2001; Pascalis et al., 2002; see but Farah, Rabinowitz, Quinn and Liu, 2000 for an example of evidence supporting the opposite view). It has been hypothesized that face perception might be a consequence of extensive exposure to this sort of stimulus during a critical period of the early postnatal development (Johnson, 2005; Johnson, Grossman and Faronni, 2008). The lack of LHV advantage for the processing of human faces in sheep could thus be due to the 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 (whether the hemisphere charges the focus 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, genetic 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 (Kendrick and Kendrick, 2003). 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 exposure to goat faces. This effect appeared to be associated both with face processing and with emotional reaction to the 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-hemispheres 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 in sheep 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 organized on the basis of animal species, as same species recognition is 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 chicks are able to recognize conspecific faces, for example, 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-hemisphere responses to familiar social stimuli 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 only highlight some 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 nest (the imprinted object). The imprinting process 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 retain 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
When discussing the sex difference, we mainly consider the right hemisphere. RE-chicks use their right hemisphere, while LE-chicks rely on their left one. RE-chicks approach the two social objects (either natural or artificial imprinting object) and, in a binocular approach, choose the stranger and females the companion (Vallortigara and Andrew, 1991). In general, chicks’ behaviour in this kind of task 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).

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, in BIN-chicks, the 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 amount of information conveyed to the right hemisphere). For example, 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, this white stripe-specific preference changed 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 LE-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 stimula 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 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). For example, 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 left hemisphere. However, only in the right hemisphere, there is also evidence that a smaller number of neurons are responsive to imprinting (result not used in the present testing). 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 lateralization in normal (i.e., not deprived of social partners) and in chicks reared in a complete isolation. In particular, these authors showed a significant choice of the imprinting object in imprinted chicks compared to non-imprinted chicks. This effect is evident in both the right and left hemisphere. However, only in the right hemisphere, there is also evidence that a smaller number of neurons are responsive to imprinting (result not used in the present testing). 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.

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 approach to a 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 and are more likely to choose a novel object (e.g., visual experience of a group of conspecifics; different from that previously employed by Vallortigara and Andrew, 1994) and will approach stimuli that are not too different from their imprinting object. This may seem a disadvantageous feature in a young animal, regardless of its sex, but it is likely to be an advantage for chicks reared in a small space (e.g., nest box). 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 memo- rized aspect of the familiar social companion may be different enough to be noticed by the chicken (e.g., the visual experience of a group of conspecifics provided before the subjects start to be reared in pairs). This result can improve the discriminative performance of BIN- and RE-subjects, which become able to express a choice between familiar and unfamiliar chicks, at least at an 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 this 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 al- tricial 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 different studies. In fact human infants suffering from congenital cataracts do not experience any form of visual input during the first months of life. On the contrary, in the study of Deng and Rogers (2002b) all chicks had unrestricted visual experience in their rearing environment and of at least one cage-mate; the deprived subjects only lacked visual experience of a group of conspecifics.
for the potential risks associated with their stronger exploratory tendency. Moreover, in 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 identity 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 metaccontrol, i.e., the mechanism by which one hemisphere takes charge of behaviour involving conflicting responses from the contralateral side of the brain. Until a recent study in pigeons (Adam and Gümütürkün, 2009), which demonstrated that this process occurs also in avian species, metaccontrol had been directly investigated only in primates (Hollis and Marshall, 1969; Michimata, 1988; Urges, Bricolo and Aglioti, 2005; for evidence from macaques see Kavic et al., 2009). However, indirect evidence of metaccontrol in avian species was already available in the literature (e.g., see the above reviewed research on the lateralization of cognitive processes more relevant for animals, like birds, with laterally placed eyes). The lateralization of the frontal visual fields (McKenzie, Andrew and Vallortigara, 2001) seems to be associated with differences in lateralization, rather than in motivational word. It has been argued that being more prepared 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 age, females being more likely to use 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 hypothesize that, in males experiencing progressively very kind of left hemisphere, a 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 either the ipsilateral (Vallortigara et al., 2005) or the contralateral (Dharmaretnam and Andrew, 1994) eye (left hemisphere) (Dharmaretnam and Andrew, 1994; 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 become less evident as they age 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 only instead 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 (males 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 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 (the detour test; Monocular-unihemispheric sleep). The discrimination 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 or newly hatched chick the use of the left hemisphere to monitor the stimulus would be deleterious. The left hemisphere (fed by the right eye) 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 a similar specialization for social object discrimination. This result should be interpreted considering the task employed in this study and the problems that it poses to an 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 target 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 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 exploration. 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 objects is related to the assessment of novelty, rather than to the assessment of familiarity.
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- playing preferential use of one eye only when the target was a group of females, a sexual stimulus (Biasaza, Pignatti and Vallortigara, 1997a; 1997b; Biasaza 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 nigricaudata, G. julaceus, Poecilia reticulata) when tested in a novel environment. Sexual motivation was associated with right eye use and higher affective 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 (Biasaza et al., 1998).

- An interesting set of studies conducted by Brown and his collaborators investigated how early experience and emotional context control the detour test (Brown et al., 2007). Brown et al. (2007) investigated the detour behaviour of wild-caught fish (Brachyrhaphis episcopi) obtained either from high- or 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 in 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 (male or female) represents a remarkably diverse stimulus to the group of conspecifics. An isolated conspecific could, in fact, elicit a lower degree of gregarious behaviour, since 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 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 the conspecific stimulus was much more similar 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 conspecics, even though this was evident only for the highly-predated subjects. The 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 manner, whereas 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 explored 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 the characteristic slow wave deep sleep. Episodes of monocular sleep in one hemisphere seem to be associated 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 Mascalzi, 2006a). Interestingly, experiencing changes in the appearance of the imprinting object caused a bias for left hemisphere monocular unilateral sleep (Bobbo, Vallortigara and Mascalzi, 2006b). The interpretation of this last result is less clear, since it could be explained either as an attempt 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 imprinting on a given stimulus. In his original theorization Lorenz (1935) claimed that imprinting was a primary process, and that the very next day the first imprinting object was 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) (Kemp 1984). Both 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)? Limb and electrophysiological studies demonstrated that potential memory traces for a single object are not evenly distributed between hemispheres: the right 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 object or its binocular visual field, 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 stimulus 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 release stimuli. According to this, the left hemisphere responds to a single 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 Mascalzi, 2006a). The activity of the right hemisphere 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 or in the left versus the right visual field (LVF). LVF asymmetries 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 is involved, but the right IMM is also crucial in establishing 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 older males when in the LNF (Hews and Worthington, 2001), see also Deckel, 1995, for evidence on male 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, lateralization may be aversive (e.g., because they are bigger than their opponent, see Hews and Worthington, 2001) could decide to use the LNF 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 left-eye bias during aggressive or courtship behaviour in an American toad (Bufo americanus) (De Santi, Sovrano, Bisazza, 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 cand Hays, 1998) and that, in these animals, right-hand 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 Limnolia, 1981, with a consequent impairment in right hemisphere’s cognitive functions other than social cognition (e.g., spatial abilities in rats, Blanchard, Riley and Hanigan, 1987).

A left-eye bias during aggressive or courtship behaviour has been demonstrated in toads (Bufo marinus, Robins, Lipolpis, 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 (e.g. Dadda, Sovrano and Bisazza, 2001). This laterality effect seems to strongly depend on the presence of gregarious behaviour and affiliative motivation, so that fishes differ strongly between males and females, with males being gregarious only when at risk of predation or in a novel environment (in anurans species gregariousness is shown by juvenile subjects, mainly on the basis of kinship 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 et al., 1997a; Zappia and Bullock, 1985). Other evidence consistent with this idea comes from 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-hemisphere bias on 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 Go. holcoides, and goby species) show a right-eye bias during a forced swimming test (against an unfamiliar stimulus) in a tank (Bisazza and Vallortigara, 2001; Bisazza, De Santi, Sovrano, and Vallortigara, 2001; De Santi et al., 1999; 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 a tank with a partner the risk of predation is increased (Sovrano et al., 1999), 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).

A similar 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, so that fishes differ strongly between males and females, with males being gregarious only when at risk of predation or in a novel environment (in anurans species gregariousness is shown by juvenile subjects, mainly on the basis of kinship familiarity recognition). See the paragraph (The detour test) for a discussion of motivational and experiential factors influencing the expression of laterality in fish species.

In addition to these studies, 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, so that fishes differ strongly between males and females, with males being gregarious only when at risk of predation or in a novel environment (in anurans species gregariousness is shown by juvenile subjects, mainly on the basis of kinship familiarity recognition). See the paragraph (The detour test) for a discussion of motivational and experiential factors influencing the expression of laterality in fish species.

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, and provides the right hemisphere with visual input. 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 from the right eye is less developed than the left (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 opposite side (from the left eye) (Schreyer and Kibbitt, 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

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ed 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 arises from the results mentioned 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 left-eye side of the thalamus to the contralateral hemisphere, determining increased integration between information in the frontal visual fields) 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 modulating communicative 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 sitas. These genes, along with others, regulate not only the heart asymmetry but also the asymmetry of viscer (viscera) 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 (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 behaviors 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 (and developmental) is still an open question and is likely to provide 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 dienencephalic forebrain regions, regulated by the expression of the eye positioning geneeya (Schier and Wilson, 2000). In the frequent situs inversus (fis) 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 asymmetry 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 reviewed a consistent lateralization pattern for this kind of task, pointing to 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 behavior is 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 (a left-hemisphere function) (Dharmaret- nam and Andrew, 1994; McKenzie et al., 1998).

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 stimuli is a consequence of its unique 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 basic 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 pike’s categorization ability, using visual stimuli that should not elicit social responses in the species tested (Yamazaki

![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.](Image 925 to 1187x744)
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 stimuli 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 stimuli familiarity and tended to base their choice on local-category-defining cues (performance of the RE-subjects was not significantly im- paired when scrambled stimuli were used). The results ob- tained by Yamaazaki and colleagues (2007) are particularly relevant not only for each single instance of complementary specialization, but also because they stress once again the generality of the observed laterali- zation pattern, extending it to a categorization task different from those employed in most of the studies reviewed in the present paper. All these aspects highlight the evolutionary continuity of cerebral lateralizations between human and non-human species.

The generality of the pattern of differential hemispheric specializations described above, observed in different spe- cies 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 IR of different members of the category (Vallortigara et al., 1999). In fact, circuits special- ized for registering the idiosyncratic features necessary to discriminate individual members of a category cannot ef- ficiently extract invariant category-defining properties, mak- ing it profitable to devote equivalent structures in the two hemispheres to only one of the two functions. The lateraliza- tion effects observed in social recognition represent another instance of this general incompatibility of specializations of the two hemispheres.

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