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## Hemispheric differences in the recognition of partly occluded objects by newly hatched domestic chicks (*Gallus gallus*)

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**Abstract** Domestic chicks are capable of perceiving as a whole objects partly concealed by occluders (“amodal completion”). In previous studies chicks were imprinted on a certain configuration and at test they were required to choose between two alternative versions of it. Using the same paradigm we now investigated the presence of hemispheric differences in amodal completion by testing newborn chicks with one eye temporarily patched. Separate groups of newly hatched chicks were imprinted binocularly: (1) on a square partly occluded by a superimposed bar, (2) on a whole or (3) on an amputated version of the square. At test, in monocular conditions, each chick was presented with a free choice between a complete and an amputated square. In the crucial condition 1, chicks tested with only their left eye in use chose the complete square (like binocular chicks would do); right-eyed chicks, in contrast, tended to choose the amputated square. Similar results were obtained in another group of chicks imprinted binocularly onto a cross (either occluded or amputated in its central part) and required to choose between a complete or an amputated cross. Left-eyed and binocular chicks chose the complete cross, whereas right-eyed chicks did not choose the amputated cross significantly more often. These findings suggest that neural structures fed by the left eye (mainly located in the right hemisphere) are, in the chick, more inclined to a “global” analysis of visual scenes, whereas those fed by the right eye seem to be more inclined to a “featural” analysis of visual scenes.

**Keywords** Lateralisation · Hemispheric difference · Amodal completion · Domestic chick

### Introduction

Visually guided behaviour needs to constantly deal with “incompleteness”, due to the fact that the natural environment is mostly made of opaque objects that may well overlap and partly hide each other. Nevertheless, human perception allows for this, because the directly visible parts appear to continue behind the occluders. This process of “amodal completion” has been pointed out and extensively investigated in our species by perceptual psychologists (Grossberg and Mingolla 1985; Kanizsa 1979; Michotte 1963; Michotte et al. 1964).

Studies on animals indicate that mammals (chimpanzees, Sato et al. 1997; rhesus monkeys, Osada and Schiller 1994; baboons, Deruelle et al. 2000; mice, Kanizsa et al. 1993) do seem to experience completion of partly occluded objects. In birds, evidence is more contradictory. Using the naturalistic setting made available by filial imprinting, Regolin and Vallortigara (1995) and Lea et al. (1996) showed that newly hatched domestic chicks (*Gallus gallus*) behaved as if they could experience amodal completion. Evidence has been obtained for completion in adult hens using conditioning procedures (Forkman 1998; Forkman and Vallortigara 1999). Also psittacine birds, such as parrots and parakeets (Funk 1996; Pepperberg and Funk 1990), mynahs (Plowright et al. 1998) and magpies (Pollok et al. 2000) pass without difficulty standardised tests of object permanence in which the subject has to respond to partly occluded objects. In contrast, pigeons (*Columba livia*) seem to respond on the basis of local, visible, features (Cerella 1980) and fail to complete (Sekuler et al. 1996) or even to perceive (Fujita 2001) continuation of the figure behind the occluder. It seems that pigeons would be most prone to perceive complex stimuli as an assembly of local features, responding to partly occluded objects on the basis of the visual information remaining after fragmentation of the stimulus. However, it has been

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shown (Watanabe and Ito 1991) that using naturalistic stimuli (colour slides of conspecifics rather than artificial figures) pigeons do not respond only to local features. Also, recent work (Di Pietro et al. 2002) shows how pigeons are capable of recognising two-dimensional partly occluded objects, but only if special training is provided.

Investigating the perception of subjective contours, a phenomenon closely linked to amodal completion (Shipley and Kellman 1992), Prior and Güntürkün (1999) showed that a minority (4 out of 14) of the pigeons in their study reacted as if they were seeing subjective contours. Control experiments indicated that pigeons responding to subjective contours were attending to the “global” pattern of the stimuli, whereas pigeons not responding to subjective contours were attending to single elements. These results seem to suggest that pigeons can actually perceive and discriminate complex stimuli on the basis of either the local parts or the global configuration, switching, with some effort, from a featural to a global style of analysis. The fact that only pigeons attending to the more “global” aspects of the stimulation respond to subjective contours suggests that such individual variability in attending “globally” or “locally” to visual scenes can explain why pigeons fail in amodal completion tests effective in other species (see Sekuler et al. 1996).

An interesting mechanism which could underlie the above-mentioned differences in performance between bird species might concern the fact that in pigeons the frontal binocular visual field (needed, for example, for enacting a successful pecking response) is mainly represented within the tectofugal pathway (Güntürkün and Hahmann 1999; Hellmann and Güntürkün 1999), whereas in chicks it seems to be represented within the thalamofugal system. In fact, in chicks (and not in pigeons; Hodos et al. 1984), lesions to the thalamofugal visual system affect tasks which rely on frontal viewing to a marked degree (Deng and Rogers 1997, 1998a, b). These differences could be also associated with brain asymmetry (Rogers 1980, 1996, 2002; Rogers and Deng 1999). Research using temporary occlusion of one eye, which takes advantage of complete decussation of optic nerve fibres and of large segregation of function between the two hemispheres in the avian brain (see Andrew 1991; Rogers 1995; Vallortigara et al. 1999, 2001) has revealed that the right eye (largely sending input to the left hemisphere) is dominant in pigeons’ visual discrimination learning (Güntürkün 1997) and presumably favours a featural strategy of analysis of visual scenes. Chicks, in contrast, have shown a more balanced and complementary use of the two eye systems, with the left eye (and right hemisphere) being dominant when more global strategies of analysis are needed (such as in spatial analyses, see Rashid and Andrew 1989; Tommasi et al. 2000; Vallortigara 2000; and individual social recognition, see Deng and Rogers 2002a; Vallortigara 1992; Vallortigara and Andrew 1994). Although the pattern emerging in monocular left and right stimulation in the study by Prior and Güntürkün (1999) on perception of subjective contours was similar, suggesting that in pigeons that responded to subjective contours both

the left and the right hemispheres were capable of “filling in” processes, it could be that a basic asymmetry between the two hemispheres is revealed by the difference between pigeons responding and not responding to subjective contours. For instance, it could be that dominance by one or other hemisphere favours a “global” or “local” strategy of analysis of visual stimuli. In the present study, we tested these ideas in the domestic chick, using the imprinting paradigm applied to recognition of partly occluded objects in monocularly tested birds.

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## Experiment 1

In the first experiment we aimed to investigate the presence of lateralisation for amodal completion in chicks. We therefore replicated the experiment by Regolin and Vallortigara (1995) with chicks imprinted in the binocular condition but then tested with only their left or right eye in use.

### Methods










#### *Subjects and rearing conditions*

Subjects were 160 female Hybro *Gallus gallus* chicks (a local variety derived from the White Leghorn breed) obtained weekly from a local commercial hatchery [Avicola Berlanda Edio and C. Snc, Carmignano di Brenta (PD), Italy] where they had been incubated and hatched in identical and standard conditions (including prehatching exposure to the incubator light due to routine controls of the eggs). Once hatched and sexed by the hatchery personnel, chicks were placed in closed dark boxes and transported to the laboratory. At their arrival, chicks were immediately housed singly in standard metal home cages (22×30 cm large, 40 cm high) constantly lit by 30 W fluorescent lamps (placed 45 cm above the cages). Each chick was placed together with its own imprinting stimulus pasted onto one of the shorter walls of the cage, at about chick’s head height (about 5 cm from the floor), and kept in standard rearing conditions (28–31°C temperature and 68% humidity) with food and water available ad libitum.

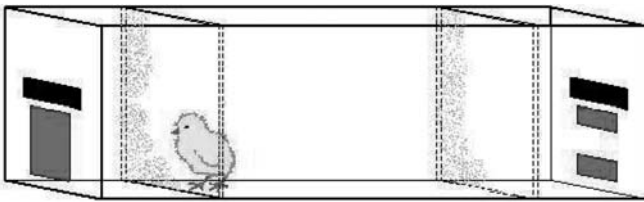
Chicks were randomly assigned to three experimental groups, and all chicks of one group were exposed, in their home cages, to copies of a same object. The three different imprinting stimuli used (Fig. 1) were: (a) a red cardboard square (4.5×4.5 cm), partly occluded by a black rectangular cardboard bar (10×1.5 cm) superimposed on it, (b) a whole red square identical to that used for condition a but without any occluder present and (c) an “amputated square” made only by the two visible parts of stimulus a (1.5×4.5 cm each) separated by a central gap (1.5 cm).

#### *Procedure*

In the early morning of day 3, chicks from each imprinting group were randomly assigned to one of two testing

	CONDITION <i>a</i>	CONDITION <i>b</i>	CONDITION <i>c</i>
IMPRINTING			
TEST	 	 	 

**Fig. 1** The stimuli employed for the three imprinting conditions of experiment 1 and, for each of such conditions, the two stimuli used in the free-choice test administered on day 3. In the critical condition (condition *a*) if amodal completion is perceived the whole square should be chosen. Note that the black bar was present at test only for those chicks that had been imprinted onto the occluded square



**Fig. 2** The apparatus employed for the 6-min free-choice test which chicks underwent on day 3. The most crucial condition is represented (condition *a*): monocular chicks that had been imprinted onto the occluded square could now choose between an amputated version of it (physically identical to the visible parts of the imprinting object itself) and a complete, not occluded square

conditions: left eye in use (LE) and right eye in use (RE). Overall,  $n=79$  chicks (of which  $n=23$  imprinted in condition *a*,  $n=33$  in condition *b* and  $n=23$  in condition *c*) were temporarily patched on their left eye (RE), and  $n=81$  chicks (of which  $n=25$  imprinted in condition *a*,  $n=33$  in condition *b* and  $n=23$  in condition *c*) were temporarily patched on their right eye (LE). The patching procedure is a minimally disturbing procedure for the animal, requiring handling for only a few seconds; it consists in gently placing a special removable tape onto one eye (the tape is cup-shaped and does not prevent the normal movements of the chick's eye lid). Following patching, all chicks were allowed a 30-min acquainting time in their own home cages to become accustomed to the new monocular condition.

The test situation is represented in Fig. 2, in which the test apparatus (see Vallortigara and Andrew 1991 for a detailed description) is also shown. It consisted of a runway 45 cm long, 20 cm wide and 30 cm high divided, by two fine lines drawn on the floor, into three virtual compartments: one central and two side compartments (length 15 cm each). On top of the apparatus a removable unidirectional screen made it possible for the experimenter to insert and remove the chick from the apparatus, and to observe its behaviour from above without being seen. At each end of the runway was a fine sheet of transparent glass through which one of the test stimuli (pasted onto the end wall 14 cm away) could be seen.

The test consisted for all chicks of a choice between a whole square (of 4.5×4.5 cm, i.e. identical to imprinting stimulus *b*) placed on one end of the test apparatus, and an "amputated" version of the square (identical to imprinting stimulus *c*) on the other end of the apparatus. In order to keep the test situation as similar as possible to the rearing condition, chicks imprinted onto the square occluded by the black bar (*a*), had an identical black bar also present at test, pasted 1 cm above each of the two test stimuli.

Each chick was in turn placed in the central portion of the test corridor and its behaviour was thereafter observed for six consecutive minutes. A computer-driven event recorder was operated every time the chick exited from the central compartment and stepped into one of the side compartments or moved from one compartment to another. In this way the number of seconds spent, minute by minute, in each of the three compartments was recorded.

The reciprocal position of the two test stimuli in the apparatus and the starting position of each chick at test (i.e. which eye faced which test stimulus) were fully balanced across individuals. For the analysis, the number of seconds spent in each of the two side compartments (i.e. choices for one or the other test stimulus) was computed for each chick and for each minute of the test, as follows:

$$\frac{\text{Time (s) spent by the whole square}}{\text{Total Time (s) spent by the two test stimuli}} \times 100$$

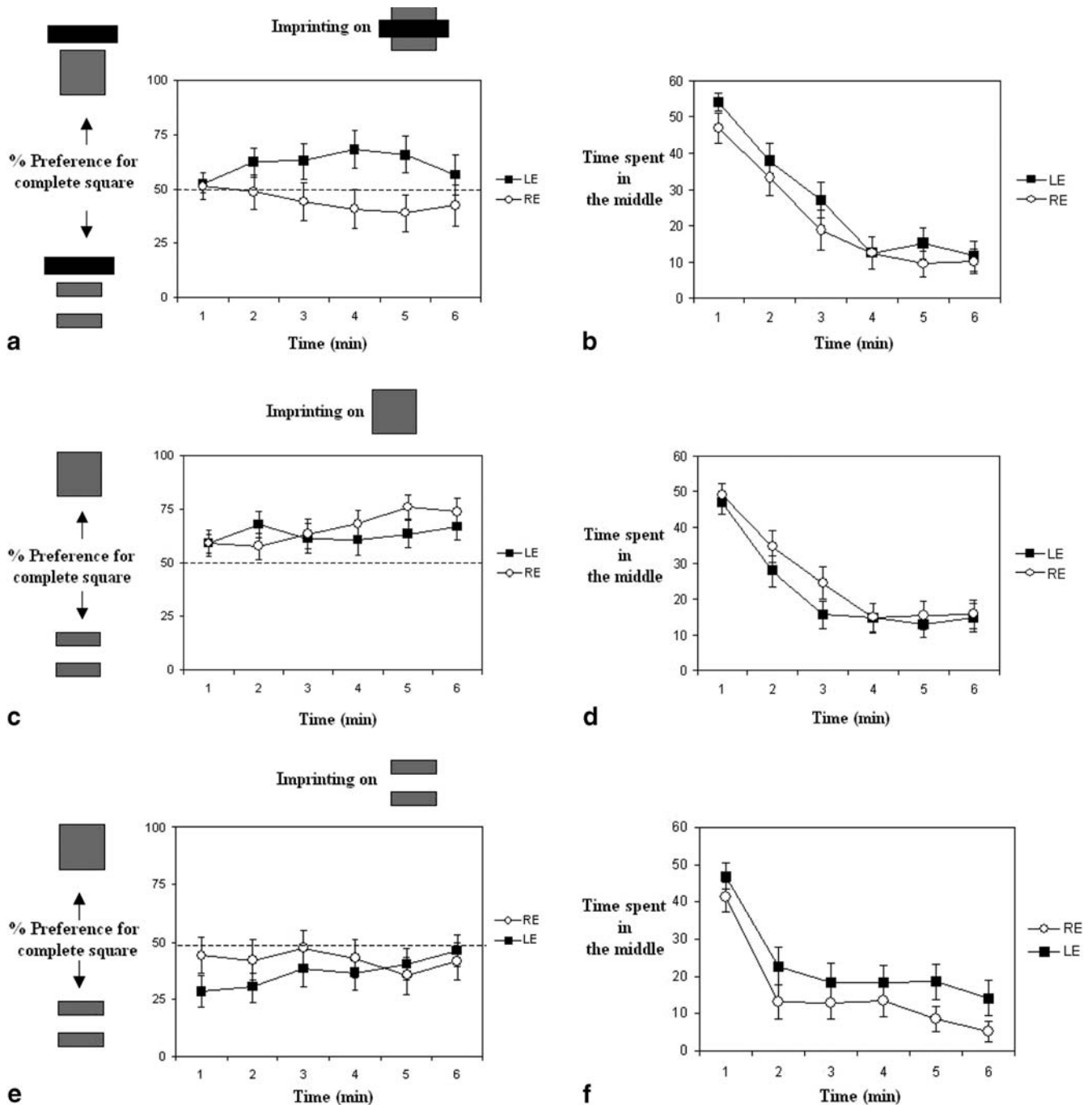
Departures from chance level (50%) indicated either a preference for the whole square (>50%) or for the "amputated" square (<50%), and were estimated by a two-tailed, one-sample *t*-test. An ANOVA was performed on these data, with Eye as a between-subject factor and Time (from the first to the sixth minute) as a within-subject factor.

A separate analysis was run for the time spent in the central compartment, expressed as amount of time (seconds) spent, minute by minute, by each chick in the middle part of the testing apparatus.

## Results

Results for chicks imprinted on the partly occluded square (stimulus *a*) are shown in Fig. 3a. The ANOVA revealed a significant main effect of Eye [ $F_{(1,46)}=4.482$ ,  $P=0.0397$ ]. The effects of Time and the Eye × Time interaction were not significant [ $F_{(5,230)}=0.23$ ,  $P>0.1$  and  $F_{(5,230)}=1.176$ ,  $P=0.32$ , respectively]. On average, chicks using their left eye (LE) preferred the complete square [mean±SEM: 61.2±3.1; two-tailed, one-sample *t*-test:  $t_{(24)}=3.61$ ,  $P<0.01$ ]. Chicks using their right eye (RE), on the other hand, did not show a clear choice, though they seemed to prefer the amputated square [mean±SEM: 44.3±3.4; two-tailed, one-sample *t*-test:  $t_{(22)}=1.676$ ,  $P>0.1$ ].

Data for the time spent in the middle are shown in Fig. 3b. The ANOVA revealed a significant main effect of Time [ $F_{(5,230)}=48.677$ ,  $P=0.0001$ ]: there was in general a progressive decrease in the time spent in the central compartment during the testing time and this effect, expected



**Fig. 3** **a** Choices (means with SEM are shown) displayed at test by the chicks imprinted onto the occluded square, expressed as preference for the whole square. As it can be seen, left-eyed chicks, differently from right-eyed chicks, prefer the whole square in spite of the fact that the amputated one is physically more similar to the imprinting object itself. **b** Time spent, minute by minute, by the chicks in the centre of the apparatus (means with SEM are shown). **c** Choices (means with SEM are shown) displayed at test by the chicks imprinted onto the whole square, expressed as preference for the whole square itself, which is, in this case, the famil-

iar object, and, as it can be seen, is preferentially chosen by both left- and right-eyed chicks. **d** Time spent, minute by minute, by the chicks in the centre of the apparatus (means with SEM are shown). **e** Choices (means with SEM are shown) displayed at test by the chicks imprinted onto the amputated square, expressed as preference for the whole square, i.e. the novel object. As it can be seen, both left- and right-eyed chicks preferred the familiar object. **f** Time spent, minute by minute, by the chicks in the centre of the apparatus (means with SEM are shown)

in this sort of test (see Vallortigara and Andrew 1991), most probably reflects the chicks' habituation to the novel environment and will not be further discussed. There were

no significant effects of Eye and of Eye  $\times$  Time interaction [ $F_{(1,46)}=1.008$ ,  $P=0.32$  and  $F_{(5,230)}=0.474$ ,  $P>0.1$ , respectively].

Results for chicks imprinted on the complete square (stimulus *b*) are shown in Fig. 3c. The ANOVA did not reveal any significant effect related to the Eye in use [ $F_{(1,64)}=0.198$ ,  $P>0.1$ ]. The effect of time was either not significant [ $F_{(5,320)}=2.163$ ,  $P=0.058$ ], nor was the interaction Eye  $\times$  Time [ $F_{(5,320)}=1.636$ ,  $P=0.15$ ]. Overall, there was a significant preference by all chicks for choosing the complete square over the amputated square [two-tailed, one-sample  $t$ -test:  $t_{(65)}=4.26$ ,  $P<0.001$ ; mean $\pm$ SEM: 64.5 $\pm$ 3.4].

Time spent in the middle is shown in Fig. 3d. The ANOVA revealed a significant main effect of Time [ $F_{(5,320)}=50.072$ ,  $P=0.0001$ ]. No other statistically significant effects were observed [Eye:  $F_{(1,64)}=0.696$ ,  $P>0.1$ ; Eye  $\times$  Time:  $F_{(5,320)}=0.805$ ,  $P>0.1$ ].

Results for chicks imprinted on the amputated square (stimulus *c*) are shown in Fig. 3e. The ANOVA did not reveal any significant effect [Eye:  $F_{(1,44)}=0.780$ ,  $P>0.1$ ; Time:  $F_{(5,220)}=0.465$ ,  $P>0.1$ ; Eye  $\times$  Time:  $F_{(5,220)}=0.789$ ,  $P>0.1$ ]. Overall, there was a significant preference for the amputated square over the complete square [two-tailed, one-sample  $t$ -test:  $t_{(45)}=6.238$ ,  $P<0.0001$ ; mean $\pm$ SEM: 39.3 $\pm$ 1.7].

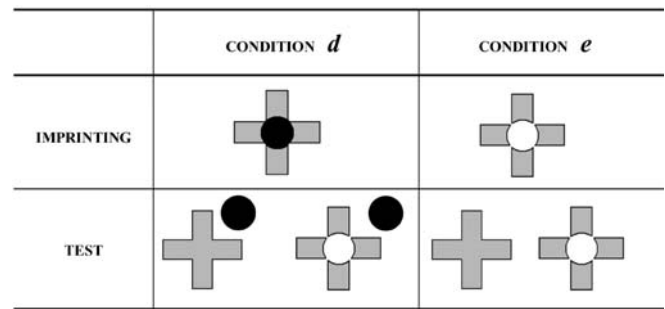
Time spent in the central compartment is shown in Fig. 3f. The ANOVA revealed a significant main effect of Time [ $F_{(5,220)}=37.430$ ,  $P=0.0001$ ]; the effect of Eye and the interaction Eye  $\times$  Time were not significant [ $F_{(1,44)}=2.378$ ,  $P=1.30$  and  $F_{(5,220)}=0.338$ ,  $P>0.1$ , respectively].

Overall, chicks imprinted on the complete square (*b*) preferred the complete square to the amputated one; on the contrary, chicks imprinted on the amputated square (*c*) preferred the amputated square to the complete one. Chicks' choice hence depends on previous imprinting on a certain configuration, and not on preferences for novelty and/or larger coloured area. Chicks imprinted on the partly occluded square (*a*) and tested with their left eye in use preferred the complete square to its amputated version, this in spite of the fact that they have been actually exposed to an imprinting stimulus physically identical to the amputated square as for the shape and extension of the red surface. Thus, left-eyed chicks seem to "complete" partly occluded objects as binocular chicks do (Lea et al. 1996; Regolin and Vallortigara 1995). Right-eyed chicks, in contrast, did not show any clear evidence of amodal completion, quite in contrast they exhibited a trend to choose the amputated square, as if they had been imprinted to stimulus *c* rather than *a*.

These results suggest that, in the domestic chick, the hemisphere in charge of completing a partly occluded object would be, for tasks of this kind, the right hemisphere (fed by the left eye), or at least that left-eyed chicks tend to focus their attention onto the characteristics of the global configuration, whereas right-eyed chicks would pay attention also, and maybe more so, to the local features of the stimulus.

## Experiment 2

Results of experiment 1 show that left-eyed chicks are capable of amodal completion, confirming what has been



**Fig. 4** The stimuli employed for the two imprinting conditions of experiment 2, and, for each of such conditions, the two stimuli used in the free-choice test administered on day 3. In the critical condition (condition *d*), if amodal completion is perceived then the whole cross should be chosen. Note that the black patch was present at test only for those chicks that had been imprinted onto the patched cross

obtained for the same species in previous experiments on binocular chicks (Lea et al. 1996; Regolin and Vallortigara 1995).

The square stimuli used for the first experiment were, once occluded by the rectangular bar, symmetrical only along the horizontal axis. In order to control for any effect due to stimulus symmetry and orientation, especially after occlusion, a cross was employed instead of a square in a new series of experiments as this shape remains symmetrical along both the horizontal and vertical axis after occlusion by a round black patch.

## Methods

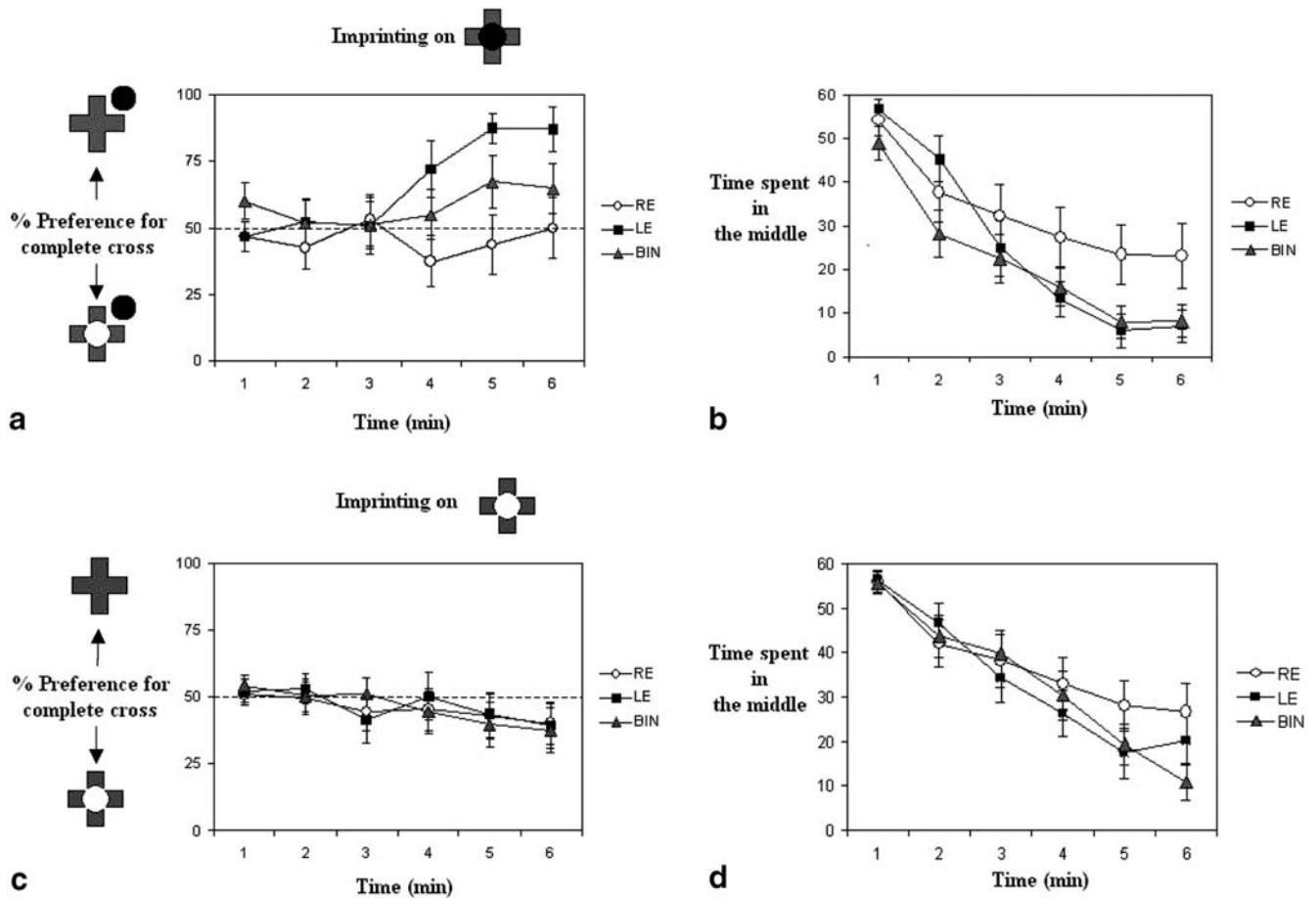
### Subjects and rearing conditions

Subjects were a novel group of 123 female Hybro chicks obtained from the same commercial hatchery and kept in standard rearing conditions identical to those described for experiment 1.

Imprinting stimuli used in experiment 2 can be seen in Fig. 4. Some of the chicks ( $n=52$ ) were imprinted on a red cardboard cross (made of two orthogonal rectangles of 1.5 $\times$ 5 cm), partly occluded by black round cardboard patch (2.7 cm in diameter) (condition *d*). The remaining chicks ( $n=71$ ) were imprinted onto an "amputated" version of the same cross (condition *e*) in which a central gap took the place of the area occupied by the black patch.

### Procedure

The testing procedure and apparatus were identical to those described for experiment 1. At test (see Fig. 4) each chick was in turn presented with a choice between a whole red cardboard cross identical to that of imprinting stimulus *d* (but with no occluder superimposed), and, on the other end of the runway, the amputated version of the



**Fig. 5** **a** Choices (means with SEM are shown) displayed at test by the chicks imprinted onto the occluded cross, expressed as preference for the whole cross. As it can be seen, left-eyed chicks preferred the whole cross to its amputated version, particularly in the last minutes of test. **b** Time spent, minute by minute, by the chicks in the centre of the apparatus (means with SEM are shown). **c** Choices (means with SEM are shown) displayed at test by the chicks imprinted onto the amputated cross, expressed as preference for the whole cross, i.e. the novel object. As it can be seen, chicks tended to prefer the familiar object in the last minutes of the test. **d** Time spent, minute by minute, by the chicks in the centre of the apparatus (means with SEM are shown)

same cross (i.e. imprinting stimulus *e*). Only for those chicks that had been exposed to stimulus *d* during imprinting, was the black patch also present at test, pasted near the cross (about 0.5 cm on its upper right side, as shown in Fig. 4), to keep the testing condition as homogeneous as possible to rearing conditions.

At test, chicks belonging to each of the two imprinting conditions were assigned to three separate groups: binocular chicks (BIN,  $n=45$  overall, of which  $n=20$  were imprinted in condition *d* and  $n=25$  in condition *e*), left-eyed chicks (LE, chicks eye patched on their right eye,  $n=39$  overall, of which  $n=16$  were imprinted in condition *d* and  $n=23$  in condition *e*), and right-eyed chicks (RE, patched on their left eye,  $n=39$  overall, of which  $n=16$  were imprinted in condition *d* and  $n=23$  in condition *e*).

Time spent by each chick in the side compartments, i.e. near one or the other test stimuli was analysed as:

$$\frac{\text{Time (s) spent by the whole cross}}{\text{Total Time (s) spent by the two test stimuli}} \times 100$$

The unoccluded cross was arbitrarily chosen as a reference stimulus. Thus, significant departures from chance level (50%) indicated either choice for the whole cross (>50%) or the other stimulus (<50%).

Data have been analysed by ANOVA with Eye as a between-subject factor and Time (from the first to the sixth minute) as a within-subject factor.

## Results

Results for chicks imprinted on the partly occluded cross (stimulus *d*) are shown in Fig. 5a. The ANOVA revealed a significant main effect of Time [ $F_{(5,245)}=3.425$ ,  $P=0.0052$ ] and Eye  $\times$  Time interaction [ $F_{(10,245)}=1.932$ ,  $P=0.0416$ ]. The effect of the eye in use was not significant [ $F_{(2,245)}=2.865$ ,  $P=0.066$ ]. Overall, BIN and LE chicks showed a significant preference for the complete rather than the amputated cross [two-tailed, one-sample *t*-test:  $t_{(35)}=2.97$ ,  $P<0.01$ ; mean $\pm$ SEM:  $61.78\pm 3.96$ ] and the pattern became clearer in the last 2 min [ $t_{(35)}=4.18$ ,  $P<0.001$ ; mean $\pm$ SEM:  $75.47\pm 6.09$ ], whereas RE chicks did not show any clear

choice [two-tailed, one-sample  $t$ -test:  $t_{(15)}=0.681$ ,  $P>0.1$ ; mean $\pm$ SEM: 45.61 $\pm$ 6.45; for the last 2 min  $t_{(15)}=0.299$ ,  $P>0.1$ ; mean $\pm$ SEM: 46.88 $\pm$ 10.43].

Time spent in the middle is shown in Fig. 5b. The ANOVA revealed a significant effect of Time [ $F_{(5,245)}=48.904$ ,  $P=0.0001$ ] and Eye  $\times$  Time [ $F_{(10,245)}=1.873$ ,  $P=0.0495$ ]. The main effect of Eye was not significant [ $F_{(2,49)}=2.223$ ,  $P=0.12$ ]. The interaction seemed to reflect the fact that right-eyed chicks spent longer times in the middle than the other two groups. It is unlikely that this was due to some emotional effect produced by the change in the imprinting stimulus, because such an effect was not observed in the previous experiment. Considering the chicks' choice, we are inclined to think that longer times in the middle in the RE group reflected indecision as to which stimulus to approach.

Results for chicks imprinted on the amputated cross (stimulus *e*) are shown in Fig. 5c. The ANOVA did not reveal any statistically significant main effect [Eye:  $F_{(2,68)}=0.095$ ,  $P>0.1$ ; Time:  $F_{(5,340)}=1.456$ ,  $P=0.20$ ]. Overall chicks did not seem to choose between the two stimuli [one-tailed, one-sample  $t$ -test – predicted results –  $t_{(70)}=1.667$ ,  $P>0.1$ ; mean $\pm$ SEM: 45.51 $\pm$ 2.74]. However, when only the last 2 min of test were considered, a preference emerged for the amputated cross [one-tailed, one-sample  $t$ -test – predicted results –  $t_{(70)}=1.918$ ,  $P<0.05$ ; mean $\pm$ SEM: 41.54 $\pm$ 4.41].

Time spent in the middle is shown in Fig. 5d. The ANOVA revealed a significant main effect of Time [ $F_{(5,340)}=54.977$ ,  $P=0.0001$ ]; there were no other significant effects [Eye:  $F_{(2,68)}=0.331$ ,  $P>0.1$ ; Eye  $\times$  Time:  $F_{(10,340)}=1.691$ ,  $P=0.081$ ], though even in this case RE chicks spent more time in the middle.

In experiment 2, chicks' choices emerged later, i.e. in the last 2 min of the test. When considering this time window, for chicks imprinted onto the amputated cross the preference goes overall to the amputated cross, in spite of the larger amount of red area present in the comparison stimulus (the whole cross), confirming the results obtained in experiment 1. In the more crucial condition of chicks imprinted onto the patched cross, on the other hand, a choice for the complete, amodally completed, cross emerges in the last 2 min only for binocular and left-eyed chicks. Right-eyed chicks do not show a clear preference, i.e. they do not prefer significantly more often the amputated stimulus.

In conclusion, a difference between eye conditions similar to that observed in experiment 1 seems to be present in this experiment, but only in the last minutes of test, and certainly less clear-cut than for experiment 1. Perhaps the process of completion in the stimuli used for experiment 2 is more difficult due to the relatively larger amount of occluded area in the cross as compared to the square: the occluded area, in the case of the patched cross, corresponds to 43% of its surface, i.e. about 10% more than what happens in the case of the occluded square, where only 33% of its surface is covered by the bar. It is possible that part of the difference in choice is in this case masked by differences in the time spent in the middle

compartment: in both testing conditions, but significantly only in the more crucial one involving amodal completion, right-eyed chicks showed longer times spent in the middle, possibly reflecting difficulty in choosing between the two stimuli.

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## General discussion

The results of the first experiment seem to suggest that the right hemisphere (LE) would be mainly responsible for the process of amodal completion of partly occluded objects. In order to amodally complete an object, the spatial relationships between the parts of a visual scene must be taken into account, a task at which the right hemisphere is known to be very good (Tommasi and Vallortigara 2001; Vallortigara 2000; Vallortigara and Andrew 1991).

Besides this, data from the second experiment show that chicks with only their left eye in use behave similarly to binocular chicks. It seems therefore that the right hemisphere could be more specialised at detecting the global structure of visual objects, while the left hemisphere might be more inclined at detecting local features. Moreover, the right hemisphere seems to be the hemisphere in charge of control of behaviour in these tasks (as evinced by the fact that binocular chicks behaved similarly to left-eyed chicks). Which hemisphere is in charge of control of overt behaviour can obviously change depending on several variables, such as the nature of the task and the motivational/emotional overtones associated with the task. There could be species differences as well. This is particularly intriguing with regards to the data collected in the pigeon, a species with a different organisation of the visual pathways as compared to the chick (Deng and Rogers 2002b). If, as it seems well documented (review in Güntürkün 1997), pigeons show a left hemisphere dominance during visual discrimination tasks in binocular conditions, this may well predispose this species towards a featural (rather than a global) style of analyses of visual scenes, making amodal completion difficult to observe.

One can wonder whether other explanations can be provided for this pattern of differences between eye conditions. Of course, there are several other features, such as stimulus size and contour continuity, that might account for the differences between the groups, besides the notion of "amodal completion". The aim of this paper was not to provide further evidence that chicks show amodal completion. Previous independent work has investigated these issues in depth, and has taken into account possible alternative explanations to amodal completion, such as differences in size and contour continuity (see Lea et al. 1996; Regolin and Vallortigara 1995; Vallortigara 2004). It is somewhat unavoidable that several physical parameters change in the stimuli from exposure to test. The point is to check whether any of these changes, other than amodal completion, can account for the results. Consider the change in size (which has already been considered in previous literature, see Regolin and Vallortigara 1995). It is clear from the results that binocular and left-eyed chicks do not

respond to larger (or smaller) red areas, because they prefer the stimulus with reduced area in condition *e* and the one with enlarged area in condition *d* (Fig. 4). Consider also the results of experiment 1. Conditions *b* and *c* are the usual conditions (with the expected outcomes) of a standard imprinting experiment: chicks simply go to the stimulus which is the same as to the one to which they have been exposed, irrespective of its having a larger (*b*) or a smaller (*c*) red area (see Fig. 1). The crucial condition is that of amodal completion (*a* in Fig. 1): here no physical similarity with the training stimulus can be predicted a priori. However, the behaviour of the chicks can tell us what stimulus they judge to more resemble the training (exposure) stimulus. Binocular and left-eyed chicks behave similarly in a way which is consistent with perceptual completion. Right-eyed chicks behave differently. We argue that a reasonable explanation for this outcome could be that they do not complete and respond to the stimulus “literally”.

It is also apparent from the data that imprinting seems to occur slightly better on the complete rather than on the broken stimulus (for example, compare Fig. 3c and Fig. 3e). However, it is very unlikely that stimulus size may contaminate any conclusion regarding amodal completion. In fact it is possible that there are preferences for certain aspects of the stimulus (such as size) and that this can partly affect the results in the “control conditions”, i.e. when completion is not involved. But, again, the point is that if in the condition with partial occlusion (*a* in Fig. 1 or *d* in Fig. 4) the chicks’ choices were dependent on a preference for the stimulus with the larger area, then the same should have occurred in condition *c* in Fig. 1 and condition *e* in Fig. 4. However, in all these cases the chicks did exactly the opposite, choosing the stimulus with the smaller area.

Another important issue concerns the type of hemispheric differences we are arguing for with regards to “global” and “local” processing. We are not arguing that the left-eye (right hemisphere) is “binding together” pieces of stimuli in every occasion. There is no reason to expect that, except when “the pieces” are the accidental by-product of occlusion. In condition *c* (Fig. 1), for instance, left-eyed chicks do not come to prefer the complete square, as perhaps would have been expected as a result of a generic “global processing”. The completion process is related to the evidence for occlusion, and there is no evidence that the stimulus configuration used as imprinting stimulus during exposure is “broken” as a result of occlusion in this case. In contrast, in condition *a* (Fig. 1) the binocular and left-eyed chicks choose the complete stimulus because, when the effect of occlusion is taken into account, the complete stimulus is the same as the imprinting (exposure) stimulus.

We believe that these hemispheric differences (as well as the possibly associated species differences) are mostly a matter of degree rather than of kind. Amodal completion is such a crucial mechanism that it is unlikely that it is simply not available to the animal at times. In the natural condition, when birds can use both hemifields freely, the two strategies of holistic and analytic visual analysis should

reciprocally support each other rather than compete. Thus, we are inclined to think that hemispheric differences can modulate, probably by attentional mechanisms, the type of analysis to be carried out on visual stimuli. Evidence suggests that birds are able to bring into action the hemisphere most appropriate to particular conditions and to particular stimuli by using lateral fixation with the contralateral eye (Dharmaretnam and Andrew 1994; Vallortigara et al. 1996). Such a mechanism may appear to be very unusual to us, because we are, as mammals, accustomed to using obligatory conjugate eye movements to fixate binocularly any stimulus of interest. However, lateralised mechanisms somewhat similar to those available to birds have been described in the human neuropsychology literature, for instance in the form of lateralised direction of gaze or voluntary eye movements to the left or to the right associated with the type of hemispheric strategies to bring into play (see, for example, Gross et al. 1978).

Interestingly, even in humans the right hemisphere seems to play a more important part in amodal completion. In a case study on two split-brain patients, Corballis et al. (1999) suggested that amodal completion seems to reflect a high-level lateralised process located in the right hemisphere. It remains, however, to establish whether this would reflect different abilities of each hemisphere in early visual processing or, rather, in attentional mechanisms as we have proposed here for birds’ lateralisation.

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## References

- Andrew RJ (1991) The chick in experiment: techniques and tests. General. In: Andrew RJ (ed) Neural and behavioural plasticity. Oxford University Press, Oxford, pp 6–11
- Cerella J (1980) The pigeon’s analysis of pictures. *Pattern Recogn* 12:1–6
- Corballis PM, Fendrich R, Shapley RM, Gazzaniga M (1999) Illusory contour perception and amodal boundary completion: evidence of a dissociation following callosotomy. *J Cogn Neurosci* 11:459–466
- Deng C, Rogers LJ (1997) Differential contributions of the two visual pathways to functional lateralization in chicks. *Behav Brain Res* 87:173–182
- Deng C, Rogers LJ (1998a) Organisation of the tectorotundal and SP/IPS-rotundal projections in the chick. *J Comp Neurol* 394:171–185
- Deng C, Rogers LJ (1998b) Bilaterally projecting neurons in the two visual pathways of chicks. *Brain Res* 794:281–290
- Deng C, Rogers LJ (2002a) Social recognition and approach in the chick: lateralization and effect of visual experience. *Anim Behav* 63:697–706
- Deng C, Rogers LJ (2002b) Factors affecting the development of lateralization in chicks. In: Rogers LJ, Andrew RJ (eds) Comparative vertebrate lateralization. Cambridge University Press, Cambridge, pp 206–246
- Deruelle C, Barbet I, Dépy D, Fagot J (2000) Perception of partly occluded figures by baboons (*Papio papio*). *Perception* 39: 1483–1497
- Dharmaretnam M, Andrew RJ (1994) Age- and stimulus-specific effects on the use of right and left eyes by the domestic chick. *Anim Behav* 48:1395–1406

- Di Pietro NT, Wasserman EA, Young ME (2002) Effects of occlusion on pigeon's visual object recognition. *Perception* 31:1299–1312
- Forkman B (1998) Hens use occlusion to judge depth in a two-dimensional picture. *Perception* 27:861–867
- Forkman B, Vallortigara G (1999) Minimization of modal contours: an essential cross-species strategy in disambiguating relative depth. *Anim Cogn* 2:181–185
- Fujita K (2001) Perceptual completion in rhesus monkey (*Macaca mulatta*) and pigeons (*Columba livia*). *Percept Psychophys* 63:115–125
- Funk MS (1996) Development of object permanence in the New Zealand parakeet (*Cyanoramphus auriceps*). *Anim Learn Behav* 24:375–383
- Gross Y, Franko I, Lewin L (1978) Effects of voluntary eye movements on hemispheric activity and choice of cognitive mode. *Neuropsychologia* 17:653–657
- Grossberg S, Mingolla E (1985) Neural dynamics of form perception: boundary completion, illusory figures, and neon colour spreading. *Psychol Rev* 92:173–211
- Güntürkün O (1997) Avian visual lateralization: a review. *Neuroreport* 8:3–11
- Güntürkün O, Hahmann U (1999) Functional subdivisions of the ascending visual pathways in the pigeon. *Behav Brain Res* 98:193–201
- Hellmann B, Güntürkün O (1999) Visual field specific heterogeneity within the tectofugal projection of the pigeon. *Eur J Neurosci* 11:1–18
- Hodos W, Macko KA, Bessette BB (1984) Near-field acuity changes after visual system lesions in pigeons. II. Telen-cephalon. *Behav Brain Res* 13:15–30
- Kanizsa G (1979) *Organization in vision*. Praeger, New York
- Kanizsa G, Renzi P, Conte S, Compostela C, Guerani L (1993) Amodal completion in mouse vision. *Perception* 22:713–721
- Lea SEG, Slater AM, Ryan CME (1996) Perception of object unity in chicks: a comparison with human infant. *Infant Behav Dev* 19:501–504
- Michotte A (1963) *The perception of causality*. Basic Books, New York
- Michotte A, Thinés G, Crabbé G (1964) *Les compléments amodaux des structures perceptives*. Publications Universitaires de Louvain, Louvain
- Osada Y, Schiller PH (1994) Can monkeys see objects under condition of transparency and occlusion? *Invest Ophthalmol Vis Sci* 35:1664
- Pepperberg IM, Funk MS (1990) Object permanence in four species of psittacine birds: an African Grey parrot (*Psittacus erithacus*), an Illiger mini macaw (*Ara maracana*), a parakeet (*Melopsittacus undulatus*), and a cockatiel (*Nymphicus hollandicus*). *Anim Learn Behav* 18:97–108
- Plowright CMS, Reid S, Kilian T (1998) Finding hidden food: behavior on visible displacement tasks by mynahs (*Gracula religiosa*) and pigeons (*Columba livia*). *J Comp Psychol* 112:13–25
- Pollok B, Prior H, Güntürkün O (2000) Development of object permanence in food-storing magpies (*Pica pica*). *J Comp Psychol* 114:148–157
- Prior H, Güntürkün O (1999) Patterns of visual lateralization in pigeons: seeing what is there and beyond. *Perception Suppl* 28:22
- Rashid N, Andrew RJ (1989) Right hemisphere advantages for topographical orientation in the domestic chick. *Neuropsychologia* 27:937–948
- Regolin L, Vallortigara G (1995) Perception of partly occluded objects by young chicks. *Percept Psychophys* 57:971–976
- Rogers LJ (1980) Lateralization in the avian brain. *Bird Behav* 2:1–12
- Rogers LJ (1995) *The development of brain and behaviour in the chicken*. CAB International, Wallingford
- Rogers LJ (1996) Behavioral, structural and neurochemical asymmetries in the avian brain: a model system for studying visual development and processing. *Neurosci Biobehav Rev* 20:487–503
- Rogers LJ (2002) Advantages and disadvantages of lateralization. In: Rogers LJ, Andrew RJ (eds) *Comparative vertebrate lateralization*. Cambridge University Press, Cambridge, pp 126–153
- Rogers LJ, Deng C (1999) Light experience and lateralization of the two visual pathways in the chick. *Behav Brain Res* 98:277–287
- Sato A, Kanazawa S, Fujita K (1997) Perception of objects unity in chimpanzees (*Pan troglodytes*). *Jpn Psychol Res* 39:191–199
- Sekuler AB, Lee JAJ, Shettleworth SJ (1996) Pigeons do not complete partly occluded figures. *Perception* 25:1109–1120
- Shiple TF, Kellman PJ (1992) Strength of visual interpolation depends on the ratio of physically specified to total edge length. *Percept Psychophys* 52:97–106
- Tommasi L, Vallortigara G (2001) Encoding of geometric and landmark information in the left and right hemispheres of the avian brain. *Behav Neurosci* 115:602–613
- Tommasi L, Andrew RJ, Vallortigara G (2000) Eye use in search is determined by the nature of the task in the domestic chick. *Behav Brain Res* 112:119–126
- Vallortigara G (1992) Right hemisphere advantage for social recognition in the chick. *Neuropsychologia* 30:761–768
- Vallortigara G (2000) Comparative neuropsychology of the dual brain: a stroll through left and right animals' perceptual worlds. *Brain Lang* 73:189–219
- Vallortigara G (2004) Comparative vertebrate cognition: are primates superior to non-primates. In: Rogers LJ, Kaplan G (eds) *Vertebrate comparative cognition: are primates special?* Plenum, New York, (in press)
- Vallortigara G, Andrew RJ (1991) Lateralization of response by chicks to change a model partner. *Anim Behav* 41:187–194
- Vallortigara G, Andrew RJ (1994) Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behav Process* 33:41–58
- Vallortigara G, Regolin L, Bortolomio G, Tommasi L (1996) Lateral asymmetries due to preference in eye use during visual discrimination learning in chicks. *Behav Brain Res* 74:135–143
- Vallortigara G, Rogers LJ, Bisazza A (1999) Possible evolutionary origins of cognitive brain lateralization. *Brain Res Rev* 30:164–175
- Vallortigara G, Cozzutti C, Tommasi L, Rogers LJ (2001) How birds use their eyes: opposite left-right specialisation for the lateral and frontal visual hemifield in the domestic chick. *Curr Biol* 11:29–33
- Watanabe S, Ito Y (1991) Discrimination of individuals in pigeons. *Bird Behav* 9:20–29