



Laterality in the wild: preferential hemifield use during predatory and sexual behaviour in the black-winged stilt

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(Received 29 March 2004; initial acceptance 5 May 2004;
final acceptance 7 September 2004; published online 17 February 2005; MS. number: 8061)

We recorded preferential use of the left and right monocular visual field in black-winged stilts, *Himantopus himantopus*, during predatory pecking and during courtship and mating behaviour in a naturalistic setting. The stilts had a population-level preference for using their right monocular visual field before predatory pecking; pecks that followed right-hemifield detection were more likely to be successful than pecks that followed left-hemifield detection, as evinced by the occurrence of swallowing and shaking head movements after pecking. In contrast, shaking behaviour, a component of courtship displays, and copulatory attempts by males were more likely to occur when females were seen with the left monocular visual field. Asymmetric hemifield use observed in natural conditions raises interesting issues as to the costs and benefits of population-level behavioural lateralization in wild animals.

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Traditionally, the study of cerebral lateralization, the different functional specialization of the left and right sides of the brain, has been the realm of neurology and neuropsychology. However, there are recent signs of interest in this topic among ethologists and evolutionary biologists (Raymond et al. 1996; Rogers & Andrew 2002; Vallortigara & Bisazza 2002; Ghirlanda & Vallortigara 2004). Such a change of attitude seems to have two reasons. First, there is increasing evidence that lateralization is not unique to the human species, but it is widespread among vertebrates (reviewed in Vallortigara et al. 1999; Rogers & Andrew 2002), thus raising the issue of its evolutionary origins and phylogenetic history. Second, there is an increasing understanding that perceptual asymmetries are not confined to the artificial conditions used in the laboratories of experimental psychologists (such as millisecond presentation of visual stimuli to the left or right hemifield), but they may occur in more natural conditions, particularly in animals with laterally placed eyes.

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Differential responsiveness to various forms of sensory stimulation according to whether the stimuli are on the left or right side of the animal's midline has been documented in a variety of species (reviewed in Vallortigara 2000; Rogers 2002). Examples include left-side perceptual biases in responding to predators in toads (*Bufo bufo*, *B. viridis* and *B. marinus*: Lippolis et al. 2002), domestic fowl, *Gallus gallus* (Andrew 1991; Rogers 2002) and teleost fish (Cantalupo et al. 1995; Bisazza et al. 2000); in aggressive responses towards conspecifics in lizards (*Anolis* sp.: Deckel 1995; Hews & Worthington 2001; Hews et al. 2004), toads (*B. bufo* and *B. marinus*: Robins et al. 1998; Vallortigara et al. 1998), domestic fowls (Rogers et al. 1985; Rogers 1991; Vallortigara et al. 2001) and gelada baboons, *Theropithecus gelada* (Casperd & Dunbar 1996); and rightward biases for responses requiring manipulation, such as feeding in chicks (Mench & Andrew 1986; Rogers 1991), pigeons, *Columba livia* (Güntürkün & Kesh 1987), quails, *Coturnix coturnix* (Valenti et al. 2003), and toads (*B. bufo* and *B. marinus*: Vallortigara et al. 1998), and in tool manufacture in crows, *Corvus moneduloides* (Hunt et al. 2001; and see also Andrew et al. 2000; Tommasi & Andrew 2002). Furthermore, preferential left-hemifield usage associated with social responses has been documented in several species of fish (Sovrano et al. 1999, 2001; De Santi et al. 2001; Sovrano, 2004), chicks

(Vallortigara & Andrew 1991, 1994; Vallortigara 1992), sheep, *Ovis aries* (Peirce et al. 2000), rhesus macaques, *Macaca mulatta*, and marmosets, *Callithrix jacchus* (Hook-Costigan & Rogers 1998; Vermeire et al. 1998; Weiss et al. 2002).

It is worth noting that these lateralized functions, which are manifested as side biases, may be disadvantageous for survival because relevant stimuli may happen to be located to the animal's left or right at random, and there is no a priori association between the meaning of a stimulus (e.g. its being a predator or a food item) and its being located to the animal's left or right. For instance, enhanced reactivity to predators approaching on the animal's left side (Lippolis et al. 2002) leaves prey more vulnerable to predators on their right side. Elevated agonistic responses directed at conspecifics on the animal's left side (e.g. Deckel 1995; Robins et al. 1998) might also be disadvantageous, as might also be the right-side preference for responding to prey (Vallortigara et al. 1998).

However, most of the studies have been conducted so far in the laboratory. Exceptions concern studies on handedness in nonhuman primates (e.g. Boesch 1991; McGrew & Marchant 1997, 2001). However, there are presently controversies concerning the presence and nature of handedness in nonhuman primates in natural conditions (cf. McGrew & Marchant 1997; Hopkins 1999) making handedness a poor behavioural model of the phenomenon of cerebral lateralization (which has been recorded in nonhuman primates at the neural level, e.g. Poremba et al. 2004, and in tasks other than handedness, e.g. Hauser 1993; Hook-Costigan & Rogers 1998). Another exception is the naturalistic research on tool manufacture and use in New Caledonian crows, *Corvus moneduloides* (Hunt 2000; Hunt et al. 2001; Hunt & Gray 2004; Rutledge & Hunt 2004; Weir et al. 2004). Seminal studies on lateralization in birds have been done by Franklin & Lima (2001) for antipredator behaviour and by Workman & Andrew (1986) for courtship behaviour. We do need, however, more research on lateralization in natural conditions, because we do not know whether side biases caused by brain lateralization affect in any relevant way the behaviour of animals in natural conditions. We studied this issue by investigating the predatory and sexual behaviour of a bird species, the black-winged stilt, *Himantopus himantopus*, in natural conditions.

METHODS

We videorecorded black-winged stilts with a digital camera from bird-watching screens in an area of flooded pastures at the Foce Isonzo Natural Reserve on the northeastern Italy coastline. Data were gathered from three different samples, during spring and summer of 2001, 2002 and 2003. Individuals were identified from the mantle colour and head patterns.

Predatory Behaviour

Stilts nearly always use visual cues for prey detection and capture. The commonest feeding method is a direct

peck at visible prey in the water column or on the ground (Goriup 1982; Espin et al. 1983; Pierce 1996). Typically, birds scan the surface of the water moving their head and using their left and right monocular hemifields to scrutinize the environment (e.g. Martin & Katzir 1994). Detection of a potential prey results in orienting the head towards it and making a peck under control of binocular vision (Martin & Katzir 1994). We recorded the number of pecks at potential prey after initial detection by the left or right hemifield in 14 males and seven females in 2001 and 15 males and eight females in 2002. We used the following criteria to determine whether predatory attacks were made under initial detection by the left or right hemifield. When the individual in the videorecording was seen frontally or dorsally, we used the bill direction, head and neck rotation and which eye was visible to make a judgement. When the position was not exactly dorsal or frontal we used a series of cues: (1) an increase or decrease in light and shadow over the body; (2) an increase or decrease in the visible portion of the head; (3) the point of bill dipping with respect to the nearest leg. To minimize any potential observer's bias, two persons separately examined the videorecordings; concordance in their judgements was 98%. Predatory pecks were recorded at various times (0600–0900, 1000–1300, 1400–1700 and 1800–2100 hours), to check for biases associated with light reflection on the water surface.

We computed a laterality index to evaluate preferences in the use of the left and right hemifield during predatory behaviour: (number of prey attacks elicited under right-hemifield detection/total number of prey attacks) \times 100. Values significantly higher than 50% would thus indicate predominant right-hemifield use and values significantly lower than 50% would indicate predominant left-hemifield use. We calculated the index for each animal, and the group means \pm SEM with respect to sex and season of observation. After checking for the normality of the distribution and homogeneity of variances, we entered the data in an analysis of variance (ANOVA) with sex and season as main factors. Significant departures from chance level (50%) were estimated by one-sample two-tailed *t* tests.

Pecks could be scored as successful or not successful on the basis of whether the bird was observed to show swallowing and shaking head movements after the peck. We used this to estimate whether predatory attacks carried out after detection by the left or right hemifield were associated with different degrees of success. An index of success associated with the hemifield used was calculated as percentage of prey detected by the right hemifield. Values significantly higher than 50% would thus indicate higher predatory success under right-hemifield use and values significantly lower than 50% would indicate higher predatory success under left-hemifield use. We calculated an index for each animal, and group means \pm SEM with respect to sex and season of observation. After checking for the normality of the distribution and homogeneity of variances, we entered the data in an ANOVA with sex and season as main factors. Significant departures from chance level (50%) were estimated by one-sample two-tailed *t* tests. Statistics were computed using SPSS version 11 (SPSS Inc., Chicago, IL, U.S.A.).

Courtship and Mating Behaviour

Stilts form pairs in early spring and mate repeatedly (Goriup 1982; Tinarelli 1992). During courtship, the female assumes a soliciting posture with the head lowered and the bill held more or less horizontally. The male strides from side to side of the female, pausing to alternate two behavioural sequences: (1) immerse bill in water and shake it; (2) preen breast and wings (Cramp & Simmons 1983; Pierce 1996). The amount of shaking and preening behaviour and the mean time spent by males courting a female on the female's left or right side (and thus having the female in their right or left hemifield) was computed from video recordings of courtship behaviour sequences of 30 pairs in 2002 and 23 pairs in 2003.

All these behaviours were expressed as laterality indexes (Fig. 1), e.g. (number of preening behaviours shown when observing the female with the right hemifield/total number of preening behaviours) \times 100. The hemifield used by males before mounting the female and the time taken to fly over her and back to water after cloacal contact were computed as a laterality index as above (i.e. (number of

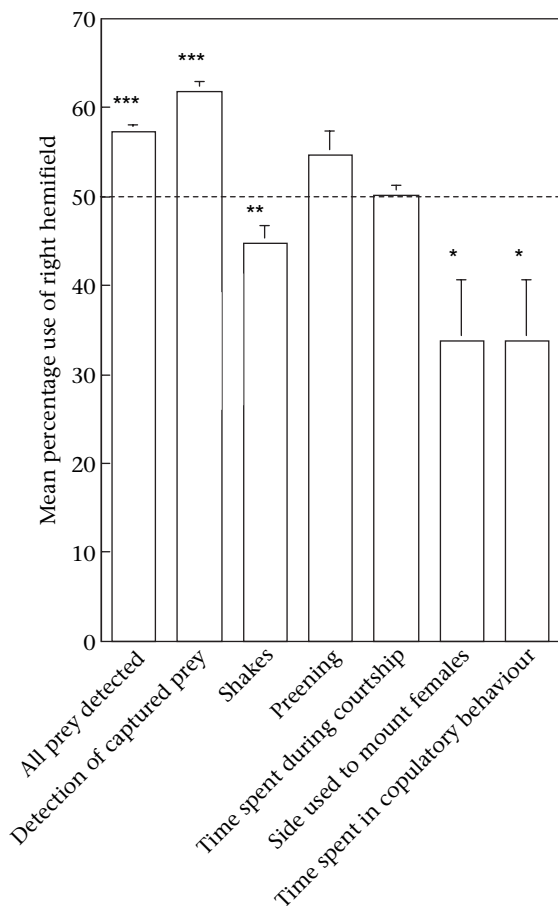


Figure 1. Mean \pm SEM percentages of use of the right hemifield for each behavioural category. Values higher (or lower) than 50% indicate preference for use of the right (left) hemifield. Significant departures from chance level (50%) are indicated by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, one-sample two-tailed t tests).

copulation attempts after right-hemifield approach/total number of copulation attempts) \times 100; (total time spent in copulatory behaviour after right-hemifield approach/total time spent in copulatory behaviour) \times 100). Mating attempts without cloacal contact were excluded. No extrapair copulations were observed.

RESULTS

Predatory Behaviour

Overall, we recorded a mean \pm SD of 220.82 ± 9.97 peck movements for the 44 adult individuals observed. The ANOVA on percentages of right-hemifield use in the 2001 and 2002 samples did not reveal any significant effect associated with sex ($F_{1,40} = 0.13$, $P = 0.72$), season ($F_{1,40} = 0.19$, $P = 0.67$) and sex \times season interaction ($F_{1,40} = 0.001$, $P = 0.98$). Prey attacks occurred preferentially under right-hemifield use (Fig. 1). This was confirmed by analysis carried out with nonparametric tests on the data for each individual bird (Table 1).

The ANOVA on percentages of success under right-hemifield use did not reveal any significant effect associated with sex ($F_{1,40} = 0.70$, $P = 0.41$), season ($F_{1,40} = 0.14$, $P = 0.71$) and sex \times season interaction ($F_{1,40} = 1.21$, $P = 0.28$). Higher predatory success under right-hemifield detection was observed (Fig. 1, Table 1).

There was no significant effect of time of day on the hemifield asymmetry (ANOVA: 2001: $F_{3,60} = 2.05$, $P = 0.14$; 2002: $F_{3,60} = 0.18$, $P = 0.91$). The same was true for the indexes of success (2001: $F_{3,60} = 2.60$, $P = 0.09$; 2002: $F_{3,60} = 0.01$, $P = 0.1$).

Courtship and Mating Behaviour

The ANOVA on the mean percentages of right-hemifield use for courtship behaviour did not reveal any significant effect associated with the season of observation (shaking: $F_{1,51} = 0.17$, $P = 0.90$; preening: $F_{1,51} = 2.72$, $P = 0.11$; time: $F_{1,51} = 0.88$, $P = 0.35$). Significant departures from chance level were observed only for shaking behaviour: males made significantly more shakes while watching the female with their left than with their right hemifield (Fig. 1). No significant biases were observed for preening behaviour and for the time spent to the left or to the right of the female during courtship (Fig. 1). A significant left-hemifield bias for time spent during courtship was, however, revealed by nonparametric tests (Table 1).

Significant asymmetries were observed for the side males used to mount females and for the time spent in copulatory behaviour on each of the two sides. The ANOVA did not reveal any significant effect of season (side: $F_{1,51} = 0.18$, $P = 0.67$; total time: $F_{1,51} = 0.19$, $P = 0.67$). Most copulation attempts were carried out after left-hemifield approach and the time spent in copulatory behaviour was significantly longer after left-hemifield approach (Fig. 1). The latter asymmetry was also confirmed by nonparametric tests on the data for each individual bird (Table 1).

Table 1. Individual data of the use of left and right hemifield for each behavioural category

Season	Sex	All prey detected		Detection of captured prey		Shakes		Preening		Time spent on courtship		Side used to mount females		Time spent in copulatory behaviour		Season
		Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	
2001	M	96	148	49	84	17.8	14.2	3.8	6.5	5.8	5.9	4	0	5.3	0	2002
2001	M	106	110	60	56	17.5	6.5	9.0	2.0	9.7	7.5	2	0	4.8	0	2002
2001	F	282	360	161	244	15.7	9.7	2.3	2.0	5.6	4.7	0	4	0	4.5	2002
2001	M	90	120	55	5	9.7	5.3	5.0	6.6	5.7	7.7	3	0	6.0	0	2002
2001	M	125	142	89	111	10.3	5.8	4.4	5.8	8.4	12.7	6	0	4.5	0	2002
2001	M	99	117	50	67	8.5	16.0	5.0	6.0	6.3	6.7	0	2	0	4.1	2002
2001	F	90	119	53	80	7.3	12.3	3.0	6.5	5.6	7.8	0	3	0	4.5	2002
2001	F	87	124	50	84	9.3	1.5	2.0	3.0	6.9	6.6	4	0	6.4	0	2002
2001	M	76	133	46	85	11.3	5.0	5.5	4.8	8.1	4.9	4	0	4.3	0	2002
2001	M	93	119	73	104	9.0	5.0	5.0	5.0	5.7	6.5	2	0	4.4	0	2002
2001	M	99	112	54	60	10.3	6.3	1.3	4.6	4.9	5.7	4	0	5.8	0	2002
2001	M	89	123	43	86	5.3	5.2	1.8	3.6	4.9	5.5	0	4	0	5	2002
2001	M	108	100	53	50	8.7	12.0	2.0	1.7	5.1	3.9	0	2	0	3.8	2002
2001	F	97	113	50	71	8.0	5.3	2.7	1.7	5.1	4.1	3	0	3.7	0	2002
2001	M	81	131	48	84	4.5	5.2	2.5	5.7	6.4	3.9	0	4	0	4.2	2002
2001	F	75	121	22	56	17.0	5.0	7.0	11.0	7.1	6.2	1	0	7.6	0	2002
2001	M	59	116	23	60	10.0	18.0	13.0	12.0	9.4	10.1	1	0	4.0	0	2002
2001	M	90	124	63	101	7.0	4.0	3.0	2.0	4.1	5.4	1	0	3.7	0	2002
2001	F	101	108	53	69	19.0	11.0	2.0	4.0	7.1	6.3	0	1	0	3.1	2002
2001	M	88	111	39	62	6.0	16.0	5.0	11.0	7.7	10.8	0	1	0	4.0	2002
2001	F	92	117	26	71	10.0	18.0	11.0	8.0	7.9	7.4	1	0	3.9	0	2002
2002	M	96	120	48	86	11.0	8.0	4.0	2.0	4.3	5.1	1	0	4.7	0	2002
2002	M	82	130	40	96	9.0	7.0	9.0	10.0	7.3	6.8	1	0	6	0	2002
2002	M	86	123	50	83	2.0	9.0	3.0	3.0	5.7	4.8	0	1	0	5.2	2002
2002	M	97	113	52	67	10.0	10.0	3.0	5.0	6.3	6.3	1	0	3.2	0	2002
2002	M	79	120	49	86	9.0	3.0	3.0	5.0	6.0	6.6	1	0	3.6	0	2002
2002	M	92	118	62	86	13.0	8.0	4.0	5.0	5.0	5.3	1	0	4.9	0	2002
2002	M	99	112	58	71	3.0	3.0	0	2.0	4.9	2.9	1	0	4.1	0	2002
2002	M	90	119	44	74	3.0	4.0	1.0	0	5.1	5.3	0	1	0	5	2002
2002	M	80	129	40	92	4.0	2.0	0	6.0	4.6	3.3	1	0	3.9	0	2002
2002	M	86	123	47	83	11.8	6.6	6.4	8.6	6.4	6.5	5	0	5.4	0	2003
2002	M	80	130	31	86	5.0	7.0	10.0	14.0	7.5	5.5	0	2	0	7	2003
2002	M	99	117	53	68	10.0	8.0	3.5	6.0	5.8	5.5	2	0	7.1	0	2003
2002	M	91	121	43	72	10.7	5.3	6.0	6.3	5.6	5.6	3	0	5.3	0	2003
2002	M	102	109	53	54	14.0	15.2	12.5	7.0	8.4	5.8	0	5	0	5.2	2003
2002	M	81	128	45	90	8.0	10.0	5.0	8.0	3.8	9.5	1	0	5.2	0	2003
2002	F	80	129	42	90	10.0	6.5	9.8	6.0	4.9	6.5	4	0	3.2	0	2003
2002	F	90	120	59	71	8.0	2.0	8.0	7.0	5.7	4.3	3	0	4.2	0	2003
2002	F	96	114	50	73	11.0	3.0	2.0	4.0	4.9	4.5	1	0	6.6	0	2003
2002	F	91	118	39	70	10.6	8.6	7.8	8.0	7.6	7.8	0	10	0	4.0	2003
2002	F	91	121	43	69	8.8	9.0	10.3	6.3	6.2	6.6	0	4	0	4.5	2003
2002	F	82	127	40	82	9.0	12.0	8.0	4.0	3.5	7.8	0	1	0	4.1	2003
2002	F	89	110	47	83	10.0	6.0	3.0	3.0	5.4	3.7	1	0	5.8	0	2003
2002	F	98	112	56	71	3.0	3.0	5.0	8.0	5.4	8.7	0	2	0	5	2003
						4.7	7.0	5.3	5.3	5.2	5.8	0	3	0	5.8	2003
						7.8	8.1	5.6	6.0	5.4	6.0	0	10	0	3.9	2003
						11.0	13.0	7.0	1.5	6.0	3.7	2	0	8.4	0	2003
						6.5	4.5	0	1.6	5.4	5.9	3	0	5.8	0	2003

There is indeed evidence that lateralization may increase foraging success in primates (McGrew & Marchant 1999; Hopkins et al. 2002; Hopkins & Russell 2004) and pigeons (Güntürkün et al. 2000).

More direct experimental evidence for an advantage of lateralization has been obtained recently in the domestic chick. In this species the embryo is oriented so that the right eye is exposed to light (and the left eye is occluded), and this puts the left hemisphere in charge of certain visually guided patterns of behaviour. Chicks from eggs exposed to light thus show normal lateralization in these behaviours, whereas chicks from eggs reared in darkness are not lateralized (although they are lateralized in other behaviours, reviewed in Rogers & Andrew 2002). Lateralized chicks (from eggs exposed to light) perform the simultaneous tasks of finding food and watching out for predators more efficiently than nonlateralized (from eggs maintained in darkness) chicks (Rogers et al. 2004).

However, it is worth stressing that behavioural and brain lateralization represents an instance of a population-level (i.e. 'directional'), not individual-level asymmetry (Denenberg 1981). Although the departure from an equiprobable distribution is small, the fact that a similar direction of bias is observed in more than 50% of the individuals of the population casts doubt on the simple idea that the advantages provided by lateralization in terms of brain efficiency may counteract the ecological disadvantages of responding differently to stimuli located to the left or right side of an animal's midline. Enhanced brain efficiency could be obtained even with individual lateralization (i.e. with half of the animals showing a leftward bias and the other half showing a rightward bias). Ghirlanda & Vallortigara (2004) observed that the alignment of the direction of asymmetry at the population level may even be disadvantageous, because it makes individual behaviour more predictable to other organisms. This makes it unlikely that directional asymmetry is the mere by-product of genetic expression: in mice, *Mus musculus*, artificial selection for the strength of paw preference, without affecting the direction of this preference, has been proved possible (Collins 1985). Ghirlanda & Vallortigara (2004) suggested that alignment of the direction of behavioural asymmetries in a population can arise as an evolutionarily stable strategy (Maynard Smith 1982), when individually asymmetrical organisms must coordinate their behaviour with that of other asymmetrical organisms. Alignment in the direction of lateralization would be not required for predatory behaviour as we observed in black-winged stilts (apart from the possibility that prey themselves are lateralized), but it could be the by-product of a more basic alignment that has occurred for other, more interactive activities, such as those involved in courtship, mating and other forms of social behaviour.

It is clear that we have moved a long way from the view that behavioural asymmetries are a sort of laboratory trick, observed only in the artificial conditions of the laboratory of the experimental psychologist; left-right asymmetries in the behaviour of wild animals in their natural environment seem to be ubiquitous and need to be taken into account by behavioural biologists.

Acknowledgments

We thank the management of Foce Isonzo Natural Reserve and SBIC for granting access and logistic support. Special thanks to Barbara Cimador for her help, Silvano Candotto for his help and pictures, Federico Gasparo for transfers and Gabriella Stefani for video recordings.

References

- Andrew, R. J. 1991. The nature of behavioural lateralization in the chick. In: *Neural and Behavioural Plasticity. The Use of the Chick as a Model* (Ed. by R. J. Andrew), pp. 536–554. Oxford: Oxford University Press.
- Andrew, R. J., Tommasi, L. & Ford, N. 2000. Motor control by vision and the evolution of cerebral lateralization. *Brain Language*, **73**, 220–235.
- Bisazza, A., Cantalupo, C., Capocchiano, M. & Vallortigara, G. 2000. Population lateralization and social behaviour: a study with sixteen species of fish. *Laterality*, **3**, 269–284.
- Boesch, C. 1991. Handedness in wild chimpanzees. *International Journal of Primatology*, **6**, 541–558.
- Cantalupo, C., Bisazza, A. & Vallortigara, G. 1995. Lateralization of predator-evasion response in a teleost fish (*Girardinus falcatus*). *Neuropsychologia*, **33**, 1637–1646.
- Casperd, L. M. & Dunbar, R. I. M. 1996. Asymmetries in the visual processing of emotional cues during agonistic interactions by gelada baboons. *Behavioural Processes*, **37**, 57–65.
- Collins, R. L. 1985. On the inheritance of direction and degree of asymmetry. In: *Cerebral Lateralization in Nonhuman Species* (Ed. by S. D. Glick), pp. 41–71. New York: Academic Press.
- Cramp, S. & Simmons, K. E. L. 1983. Family Recurvirostridae. In: *The Birds of the Western Palearctic*. Vol. 3 (Ed. by K. E. L. Simmons), pp. 36–47. Oxford: Oxford University Press.
- De Santi, A., Sovrano, V. A., Bisazza, A. & Vallortigara, G. 2001. Mosquitofish display differential left- and right-eye use during mirror-image scrutiny and predator-inspection responses. *Animal Behaviour*, **61**, 305–310.
- Deckel, A. W. 1995. Lateralization of aggressive responses in *Anolis*. *Journal of Experimental Zoology*, **272**, 194–200.
- Denenberg, V. H. 1981. Hemispheric lateralization in animals and the effects of early experience. *Behavioural and Brain Sciences*, **4**, 1–49.
- Espin, P. M. J., Mather, R. M. & Adams, J. 1983. Age and foraging success in black-winged stilts *Himantopus himantopus*. *Ardea*, **71**, 225–228.
- Franklin, W. E. & Lima, S. L. 2001. Laterality in avian vigilance: do sparrows have a favourite eye? *Animal Behaviour*, **62**, 879–885.
- Ghirlanda, S. & Vallortigara, G. 2004. The evolution of brain lateralization: a game theoretical analysis of population structure. *Proceedings of the Royal Society of London, Series B*, **271**, 853–857.
- Goriup, P. D. 1982. Behaviour of black-winged stilts. *British Birds*, **75**, 12–24.
- Güntürkün, O. & Kesh, S. 1987. Visual lateralization during feeding in pigeons. *Behavioral Neuroscience*, **101**, 433–435.
- Güntürkün, O., Diekamp, B., Manns, M., Nottelmann, F., Prior, H., Schwarz, A. & Skiba, M. 2000. Asymmetry pays: visual lateralization improves discrimination success in pigeons. *Current Biology*, **10**, 1079–1081.
- Hauser, M. D. 1993. Right hemisphere dominance for the production of facial expression in monkeys. *Science*, **261**, 475–477.
- Hews, D. K. & Worthington, R. A. 2001. Fighting from the right side of the brain: left visual field preference during aggression in

- free-ranging male tree lizards (*Urosaurus ornatus*). *Brain Behavior and Evolution*, **58**, 356–361.
- Hews, D. K., Castellano, M. & Hara, E. 2004. Aggression in females is also lateralized: left-eye bias during aggressive courtship rejection in lizards. *Animal Behaviour*.
- Hook-Costigan, M. A. & Rogers, L. J. 1998. Lateralized use of the mouth in production of vocalizations by marmosets. *Neuropsychologia*, **36**, 1265–1273.
- Hopkins, W. D. 1999. On the other hand: statistical issues in the assessment and interpretation of hand preference data in non-human primates. *International Journal of Primatology*, **20**, 851–866.
- Hopkins, W. D. & Russell, J. L. 2004. Further evidence of a right hand advantage in motor skill by chimpanzees (*Pan troglodytes*). *Neuropsychologia*, **42**, 990–996.
- Hopkins, W. D., Cantalupo, C., Wesley, M. J., Hostetter, A. & Pilcher, D. 2002. Grip morphology and hand use in chimpanzees (*Pan troglodytes*): evidence of a left hemisphere specialization in motor skill. *Journal of Experimental Psychology: General*, **131**, 412–423.
- Hunt, G. R. 2000. Human-like, population level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proceedings of the Royal Society of London, Series B*, **267**, 403–413.
- Hunt, G. R. & Gray, R. D. 2004. The crafting of hook tools by wild New Caledonian crows. *Proceedings of the Royal Society of London, Series B*, **271**, S88–S90.
- Hunt, G. R., Corballis, M. C. & Gray, R. D. 2001. Laterality in tool manufacture by crows. *Nature*, **414**, 707.
- King, A. S. 1981. Cloaca. In: *Form and Function in Birds*. Vol. 2 (Ed. by A. S. King & J. McLelland), pp. 107–148. New York: Academic Press.
- Lippolis, G., Bisazza, A., Rogers, L. J. & Vallortigara, G. 2002. Lateralization of predator avoidance responses in three species of toads. *Laterality*, **7**, 163–183.
- McGrew, W. C. & Marchant, L. F. 1997. On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in non-human primates. *Yearbook of Physical Anthropology*, **40**, 201–232.
- McGrew, W. C. & Marchant, L. F. 1999. Laterality of hand use pays off in foraging success for wild chimpanzees. *Primates*, **40**, 509–513.
- McGrew, W. C. & Marchant, L. F. 2001. Ethological study of manual laterality in the chimpanzees of the Mahale mountains, Tanzania. *Behaviour*, **138**, 329–358.
- Martin, G. R. & Katzir, G. 1994. Visual fields and eye movements in herons (Ardeidae). *Brain Behavior and Evolution*, **44**, 74–85.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Mench, J. A. & Andrew, R. J. 1986. Lateralization of a food search task in the domestic chick. *Behavior Neural Biology*, **46**, 107–114.
- Nyland, K. B., Lombardo, M. P. & Thorpe, P. A. 2003. Left-sided directional bias of cloacal contacts during house sparrow copulations. *Wilson Bulletin*, **115**, 470–473.
- Peirce, J. W., Leigh, A. E. & Kendrick, K. M. 2000. Configurational coding, familiarity and the right hemisphere advantage for face recognition in sheep. *Neuropsychologia*, **38**, 475–483.
- Petersen, A. D., Lombardo, M. P. & Power, H. W. 2001. Left-sided directional bias of cloacal contacts during tree swallow copulations. *Animal Behaviour*, **62**, 739–741.
- Pierce, R. J. 1996. Family Recurvirostridae (stilts and avocets). In: *Handbook of the Birds of the World*. Vol. 3 (Ed. by J. Hoyo, A. Elliott & J. Sargatal), pp. 332–347. Barcelona: Lynx.
- Poremba, A., Malloy, M., Saunders, R. C., Carson, R. E., Herschovitch, P. & Mishkin, M. 2004. Species-specific calls evoke asymmetric activity in the monkey's temporal lobe. *Nature*, **427**, 448–451.
- Raymond, M., Pontier, D., Dufour, A. & Møller, A. P. 1996. Frequency-dependent maintenance of left handedness in humans. *Proceedings of the Royal Society of London, Series B*, **263**, 1627–1633.
- Robins, A., Lippolis, G., Bisazza, A., Vallortigara, G. & Rogers, L. J. 1998. Lateralization of agonistic responses and hind-limb use in toads. *Animal Behaviour*, **56**, 875–881.
- Rogers, L. J. 1991. Development of lateralization. In: *Neural and Behavioral Plasticity: The Use of the Domestic Chick as a Model* (Ed. by R. J. Andrew), pp. 507–535. Oxford: Oxford University Press.
- Rogers, L. J. 2000. Evolution of hemispheric specialisation: advantages and disadvantages. *Brain Language*, **73**, 236–253.
- Rogers, L. J. 2002. Lateralization in vertebrates: its early evolution, general pattern, and development. *Advances in the Study of Behaviour*, **31**, 107–161.
- Rogers, L. J. & Andrew, R. J. 2002. *Comparative Vertebrate Lateralization*. Cambridge: Cambridge University Press.
- Rogers, L. J., Zappia, J. V. & Bullock, S. P. 1985. Testosterone and eye-brain asymmetry for copulation in chickens. *Experientia*, **41**, 1447–1449.
- Rogers, L. J., Zuppa, P. & Vallortigara, G. 2004. Advantages of having a lateralized brain. *Proceedings of the Royal Society of London, Series B, Biology Letters*, **271**, 420–422.
- Rutledge, R. & Hunt, G. R. 2004. Lateralized tool use in wild New Caledonian crows. *Animal Behaviour*, **67**, 327–332.
- Sovrano, V. A. 2004. Visual lateralization in response to familiar and unfamiliar stimuli in fish. *Behavioural Brain Research*, **152**, 385–391.
- Sovrano, V., Rainoldi, C., Bisazza, A. & Vallortigara, G. 1999. Roots of brain specializations: preferential left-eye use during mirror-image inspection in six species of teleost fish. *Behavioural Brain Research*, **106**, 175–180.
- Sovrano, V. A., Bisazza, A. & Vallortigara, G. 2001. Lateralization of response to social stimuli in fishes: a comparison between different methods and species. *Physiology and Behavior*, **74**, 237–244.
- Tinarelli, R. 1992. Risultati dell'indagine nazionale sul cavaliere d'Italia (*Himantopus himantopus*). *Ricerche di Biologia della Selvaggina*, **87**, 34–38.
- Tommasi, L. & Andrew, R. J. 2002. The use of viewing posture to control visual processing by lateralised mechanisms. *Journal of Experimental Biology*, **205**, 1451–1457.
- Valenti, A., Sovrano, V. A., Zucca, P. & Vallortigara, G. 2003. Visual lateralization in quails. *Laterality*, **8**, 67–78.
- 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 and Language*, **73**, 189–219.
- Vallortigara, G. & Andrew, R. J. 1991. Lateralization of response to change in a model partner by chicks. *Animal Behaviour*, **41**, 187–194.
- Vallortigara, G. & Andrew, R. J. 1994. Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behavioural Processes*, **33**, 41–58.
- Vallortigara, G. & Bisazza, A. 2002. How ancient is brain lateralization? In: *Comparative Vertebrate Lateralization* (Ed. by L. J. Rogers & R. J. Andrew), pp. 9–69. Cambridge: Cambridge University Press.
- Vallortigara, G. & Rogers, L. J. In press. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*.

- Vallortigara, G., Rogers, L. J., Bisazza, A., Lippolis, G. & Robins, A.** 1998. Complementary right and left hemifield use for predatory and agonistic behaviour in toads. *NeuroReport*, **9**, 3341–3344.
- Vallortigara, G., Rogers, L. J. & Bisazza, A.** 1999. Possible evolutionary origins of cognitive brain lateralization. *Brain Research Reviews*, **30**, 164–175.
- Vallortigara, G., Cozzutti, C., Tommasi, L. & Rogers, L. J.** 2001. How birds use their eyes: opposite left-right specialisation for the lateral and frontal visual hemifield in the domestic chick. *Current Biology*, **11**, 29–33.
- Vermeire, B. A., Hamilton, C. R. & Erdmann, A. L.** 1998. Right-hemispheric superiority in split-brain monkeys for learning and remembering facial discriminations. *Behavioral Neuroscience*, **112**, 1048–1061.
- Weir, A. A. S., Kerward, B., Chappell, J. & Kacelnik, A.** 2004. Lateralization of tool use in New Caledonian crows (*Corvus moneduloides*). *Proceedings of the Royal Society of London, Series B*, **271**, 344–346.
- Weiss, D. J., Ghazanfar, A. A., Miller, C. T. & Hauser, M. D.** 2002. Specialized processing of primate facial and vocal expressions: evidence for cerebral asymmetries. In: *Comparative Vertebrate Lateralization* (Ed. by L. J. Rogers & R. J. Andrew), pp. 480–530. Cambridge: Cambridge University Press.
- Workman, L. & Andrew, R. J.** 1986. Asymmetries of eye use in birds. *Animal Behaviour*, **34**, 1583–1584.