



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

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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.

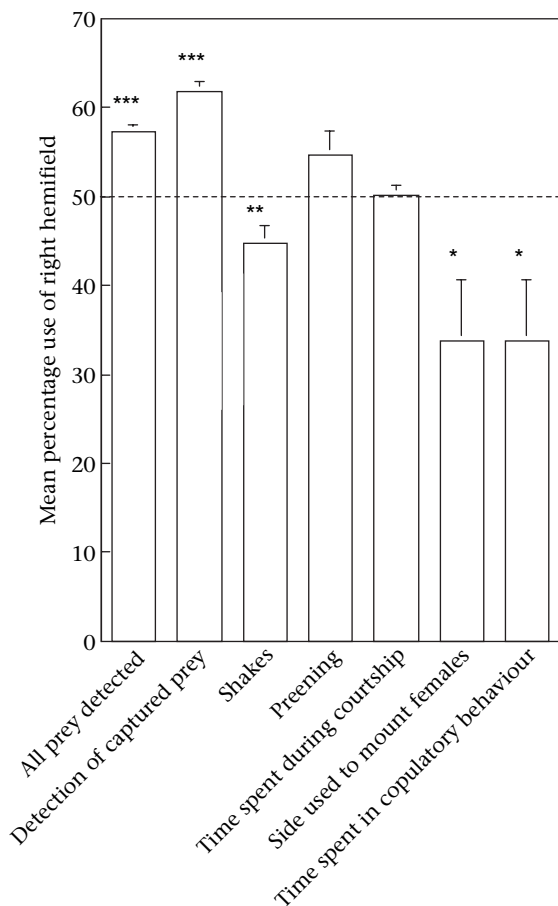
We computed a laterality index to evaluate preferences in the use of the left and right hemifield during predatory behaviour: (number of prey attacks elicited under right-hemifield detection/total number of prey attacks)  $\times$  100. Values significantly higher than 50% would thus indicate predominant 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  $220.82 \pm 9.97$  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

DISCUSSION

Our results revealed complementary visual lateralization in black-winged stilts, with preferential right-hemifield use during predatory behaviour and preferential left-hemifield use during courtship and copulatory behaviour. This, together with the fact that asymmetries were manifested at the population (group) level, makes it unlikely that the lateral biases would reflect peripheral asymmetries in sensory organs. Asymmetries in the morphology of the reproductive system of females also cannot account for these results. Female birds usually have only a left ovary and associated oviduct (King 1981). Thus, most cloacal contacts would be expected to start from the left side of the female (Petersen et al. 2001; Nyland et al. 2003), which is exactly the opposite of what we observed here. Unfortunately, it is unknown whether stilts have a left ovary and oviduct, and it is thus unclear whether asymmetries in sperm transfer (Petersen et al. 2001) can be linked to the opposite specialization of the right and left hemifield for predatory and copulatory behaviour.

Complementary visual hemifield preferences have been documented in other species. Toads, for instance, preferentially strike at prey seen in the right hemifield and at competing conspecifics during agonistic interactions when seen in the left hemifield (Vallortigara et al. 1998). Overall, the pattern shown here for black-winged stilts seems to be confirmed for other vertebrates: the left hemisphere (right hemifield) appears to be dominant in feeding behaviour and the right hemisphere (left hemifield) for several forms of interactions with conspecifics (reviewed in Rogers 2002 and see also Introduction). This is strongly suggestive of basic homology. Although exceptions to this basic pattern have been described (reviewed in Vallortigara & Bisazza 2002), it is difficult to establish whether variations between species in the direction of laterality reflect basic differences in laterality per se or differences in the behavioural strategies. It is possible that, for example, two species have the same general pattern of lateralization of brain function (say, right hemisphere for spatial functions and rapid, species-typical responses versus the left hemisphere for considered responses: see Rogers & Andrew 2002), but show opposite directions of lateralization in a particular behaviour because they process the available inputs differently as a result of experiencing different degrees of arousal/emotionality in the same context (see Vallortigara & Rogers, in press for a discussion).

What is interesting here is that these lateral biases appear in animals in the wild, in entirely unconstrained conditions of vision. This may appear in some way incongruous from a biological point of view, because any asymmetry of responding to visual stimuli located to the left or right of an animal's midline could cause serious problems in several circumstances. Predators and prey, for instance, should be detected and avoided with identical probability regardless of whether they are detected in one or the other monocular visual field. Clearly, there should be specific advantages for the functioning of the brain that counteract ecological disadvantages associated with lateral biases in behaviour (Rogers 2000; Vallortigara & Rogers, in press).

	95	125.7	51.2	81	9.3	7.8	4.8	5.3	6.0	5.6	5.3	1	0	5.9	0	2003
Mean	4.6	5.6	3.1	4.3	0.5	0.6	0.4	0.4	0.2	0.2	0.2	0.2	0.3	0.4	0.3	0.3
SEM	5.73	5.72	5.72	2.39	1.83	2.91	0.004	0.017	NS	NS	1.42	NS	2.43	0.015	0.015	0.015
Z																
P	0.0001	0.0001	0.0001	0.017	NS	0.004	0.004	0.017	NS	0.004	0.004	0.004	0.004	0.004	0.004	0.004

The leftmost columns show the season of observation and sex for predatory behaviour (M: male; F: female), the rightmost column shows the season of observation for courtship and copulatory behaviour (of males). Mean ± SEM left- and right-hemifield use are given and compared with the two-tailed Wilcoxon signed-ranks test.

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.

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