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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.

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.

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

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(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). Seminatural 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) × 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 ± 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 ± 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.).