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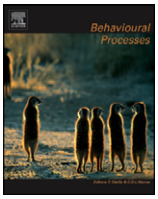

Short report

Evidence of population-level lateralized behaviour in giant water bugs, *Belostoma flumineum* Say (Heteroptera: Belostomatidae): T-maze turning is left biased

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ABSTRACT

Lateralized behaviour occurs in diverse animals, but relatively few studies examine the phenomenon in invertebrates. Here we report a population-level left turn bias in the giant water bug *Belostoma flumineum* Say (Heteroptera: Belostomatidae) in an underwater T-maze. Individuals made significantly more left turns than right turns, including when they were naïve and first introduced to the maze. Water bugs also showed significantly longer runs of consecutive left turns than right turns (i.e. LLLLL). The length of these runs, however, did not increase with experience in the maze, suggesting that the effect is not the result of learning. There were also no differences in turning bias between male and female water bugs. The proximate mechanism(s) underlying the left turn bias is unknown, but directional cues in the environment were eliminated by rotating the maze 180° between experiments, suggesting the mechanism(s) is endogenous. To our knowledge this is the first study of lateralized behaviour in the Heteroptera or in a swimming invertebrate animal.

1. Introduction

Humans are familiar with lateralized behaviour: approximately 90% of us exhibit preference for and better dexterity with our right hands (McManus, 2002; Corballis, 2003), a pattern that is probably associated with asymmetry in brain structure and function (Sun and Walsh, 2006) and appears to be ancient in our species (Coren and Porac, 1977). Other human behaviours are lateralized, such as a tendency to turn the head to the right rather than to the left when kissing (Güntürkün, 2003). Although other primates show “handedness”, it is unclear whether wild populations are biased toward the right or left. For example, McGrew and Marchant (1999) found that wild chimpanzees often showed a significant preference for one hand when breaking open fruits, but the number of individuals showing right- and left-hand bias was roughly equal. Although studies have found some evidence of population-level right-handedness in wild populations of chimpanzees (Hopkins and Cantalupo, 2005), most data are from studies of captive populations (McGrew and Marchant, 1997). Interestingly, “handedness” also occurs in non-primate animals that construct tools. Hunt et al. (2001) found that New Caledonian crows overwhelmingly manufacture tapered leaf tools from the left edge of the leaf.

Lateralized biases occur in diverse animals, and most studies focus on vertebrate animals (reviewed by Rogers, 2002; Rogers and Andrew, 2002) including reindeer (Espmark and Kinderas, 2002), prosimian and simian primates (Laska and Tutsch, 2000), and bottlenose dolphins (Marino and Stowe, 1997). A comparative study by Casey and Sleigh (2001) found lateralized behaviour in domestic chickens (*Gallus gallus*) and bobwhite quails (*Colinus virginianus*) but not in Japanese quails (*Coturnix japonica*), snapping turtles (*Chelydra serpentina*), or leopard geckos (*Eublepharis macularius*). Franklin and Lima (2001) found lateral biases in antipredatory scanning behaviour in dark-eyed juncos (*Junco hyemalis*), which tended to favor the right eye, as well as American tree sparrows (*Spizella arborea*), which tended to favor the left eye. In a study of prenatal motor behaviours in domestic chicks (Casey and Martino, 2000), asymmetrical hatching behaviours were involved in the development of lateralized turning biases. In fact, there may be differences between immature and adult animals in lateralization. Valenti et al. (2003) found that 2-week-old quail chicks, but not adults, showed lateralized responses to pecking an array of items when different eyes were occluded. In some anuran species, tadpoles preferentially approach conspecifics in their left visual field (Dadda et al., 2003). Also, the poeciliid fish *Girardinus falcatus* exhibits left biased detour avoidance when approaching a model of a predator (Bisazza et al., 2000) and breeding experiments demonstrate that this bias is heritable.

One common measure of behavioural lateralization is a bias in the direction an animal turns during orientation or navigation. In humans, turning biases tend to the right, but the effect is stronger in females than males (Mead and Hampson, 1996). In bobwhite quail chicks, prenatal visual experience influences population-level left

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turn biases (Casey and Lickliter, 1988). Male smooth newts, *Triturus vulgaris*, exhibit a population-level lateralized bias in turning during spermatophore transfer (Green, 1997). Wassersug et al. (1999) found that bullfrogs, *Rana catesbeiana,* and clawed frogs, *Xenopus laevis*, differ in turn bias when descending from the water surface: *Rana* exhibits a marked bias to the left, whereas *Xenopus* shows no bias at all. The authors note that *Rana* has only a single left spiracle through which water enters the mouth, whereas *Xenopus* has a spiracle on both sides of the body. Similar results were obtained from wood frog larvae, *Rana sylvatica* (Oseen et al., 2001). However, *Microhyla ornata* tadpoles are externally symmetrical, but develop a left turn bias (Yamashita et al., 2000).

Lateralized turn bias is also found in some invertebrate taxa, but invertebrate studies are rare relative to studies of vertebrate animals (Letzkus et al., 2006). Some of the earliest reports of invertebrate turn bias include annelids (Swartz, 1929), lice (Wigglesworth, 1941), and beetles (Putnam, 1962). Several species of honeybee exhibit a significant rotational bias during flower visits (Kells and Goulson, 2001). Formicid ants exhibit an intrinsic turn bias during search behaviour on arborial branches. Using artificial stick mazes, Jander (1990) found that ants show directional bias when choosing which branch to follow at a bifurcation.

Here we report a population-level lateralized bias in the turning behaviour of giant water bugs *Belostoma flumineum* Say in a T-maze. Giant water bugs are relatively large aquatic insects (Heteroptera: Belostomatidae) inhabiting the margins of freshwater ponds and lakes across much of North America (Lauck and Menke, 1961) where they perch underwater in dense patches of submerged vegetation. Giant water bugs are predators of other aquatic invertebrates and small fish, and are themselves prey for larger predators such as fish or birds (Crowl and Alexander, 1989; Kight et al., 1995). Males have the unusual habit of providing exclusive post-copulatory care for eggs, which are cemented to the back by females (Smith, 1976; Kight and Kruse, 1992). The large surface area to volume ratio of eggs requires males to remain at the water surface to ensure that eggs receive sufficient oxygen for embryonic development (Smith, 1997). Hence water bugs, particularly males, must navigate through aquatic habitats of varied complexity and depth.

We were initially interested in training water bugs to swim left or right in a T-maze using different kinds of ecologically relevant reinforcers. However, an experimental complication arose during preliminary trials: water bugs tended to turn left when there were no reinforcers in either arm of the T-maze. We therefore conducted systematic observations to determine whether this left turn bias was a real phenomenon and whether it was intrinsic or driven by directional cues in the environment.

2. Materials and methods

Giant water bugs were collected as adults from ponds in Sussex County, New Jersey, in August 2003. Water bugs were transported from the collection sites in plastic coolers containing pond water and aquatic vegetation and thereafter housed in environmental chambers (15L:9D at 25C) in 40 L glass aquaria each containing mixed-sex groups of approximately 30 individuals. Each aquarium contained dechlorinated tap water and plastic vegetation substrata, and water bugs were fed crickets daily *ad libitum*. Principles of laboratory animal care (NIH publication no. 86-23, revised 1985) were followed, as well as specific laws of the United States of America and the State of New Jersey where applicable.

Independent groups of 10 males and 10 females were randomly selected from the stock aquaria for each experiment. Each water bug was released into the entrance of a translucent plastic cylindrical T-maze (entrance arm: 20 cm × 7 cm, left/right arms 10 cm × 7 cm each) submerged in 25 °C tap water in the center of a white plastic container (80 cm × 40 cm × 40 cm). After swimming forward 20 cm, a water bug reached the intersection of the maze, where it swam either left or right for a distance of approximately 10 cm until it reached the terminus of the chosen arm. At the end of each maze arm was a 2 cm depression containing aquarium gravel to which water bugs invariably clung upon reaching the end of the maze. Ten seconds later, subjects were removed from the maze and immediately replaced at its entrance. This process was repeated 20 times per individual, and the apparatus was cleaned and water changed between each experiment.

To control for environmental cues that might bias the turning direction of water bugs in the maze, we ran two separate reciprocal experiments on independent groups of 20 water bugs. Both experiments were identical with the exception that after the first group of 20 water bugs was tested the maze apparatus was rotated 180° in the laboratory room. This presumably reversed the polarity of all directional environmental cues such as lighting or electromagnetic fields. After the position of the apparatus was reversed, a second group of 10 males and 10 females was tested. Each experiment therefore served as a control for the other.

Data were statistically analyzed with non-parametric procedures following Siegel and Castellan (1988) with $\alpha = 0.05$. For each reciprocal experiment, we used the Wilcoxon matched-pairs signed-ranks test to compare the total number of left and right turns made by individuals. We also used the Chi-square test for equality of distributions to compare overall patterns of consecutive turns to the left or right. For example, any sequence of R would be a pattern of one run of one right turn whereas any sequence of RRR would be a pattern of one run of three right turns. Unequal distributions would indicate that water bugs made more turns in one direction without alternating to the other direction. We also used the two-sample Wilcoxon test to test for differences in the number of left turns made by males and females. Finally, we used the binomial test to determine whether water bugs were more likely to turn left or right when first introduced to the maze, as well as the Wilcoxon matched-pairs signed-ranks test to compare the first 10 and last 10 observations for each water bug. The former analysis tested whether any overall biases could be due to experience within the maze because during the initial trial each water bug was naïve about the maze. The latter analysis tested whether there were any training effects due to repeated exposure to the same maze.

3. Results

Water bugs exhibited a statistically significant bias for left turns in both experiments (Fig. 1). In the first experiment ($N = 20$), subjects entered the left arm significantly more often than the right arm (Fig. 1, Wilcoxon matched-pairs signed-ranks test, W-left = 140, W-right = 31, $p = 0.01593$). Individuals in the second experiment ($N = 20$), in which the apparatus was rotated 180°, also entered the left arm significantly more often (Wilcoxon matched-pairs signed-ranks test, W-left = 139, W-right = 32, $p = 0.01823$). This left turn bias was evident from the first trial for each subject: 26 turned left and 14 turned right when first introduced to the maze (binomial test, $p = 0.0403$). However, there appeared to be no training effects due to repeated exposure to the maze, with no difference between the number of left turns in the first 10 and last 10 exposures to the maze (Wilcoxon matched-pairs signed-ranks test, W-left = 140, W-right = 211, $p = 0.374$). There were also no differences in the number of left turns made by male and female water bugs (two sample Wilcoxon test, $W = 362.5$, $p = 0.6329$).

Because both experiments found a left turn bias, we pooled both groups to examine the frequencies of runs of consecutive left or right turns of different lengths. The distributions of left runs to right runs were significantly different from equal (Chi-square test