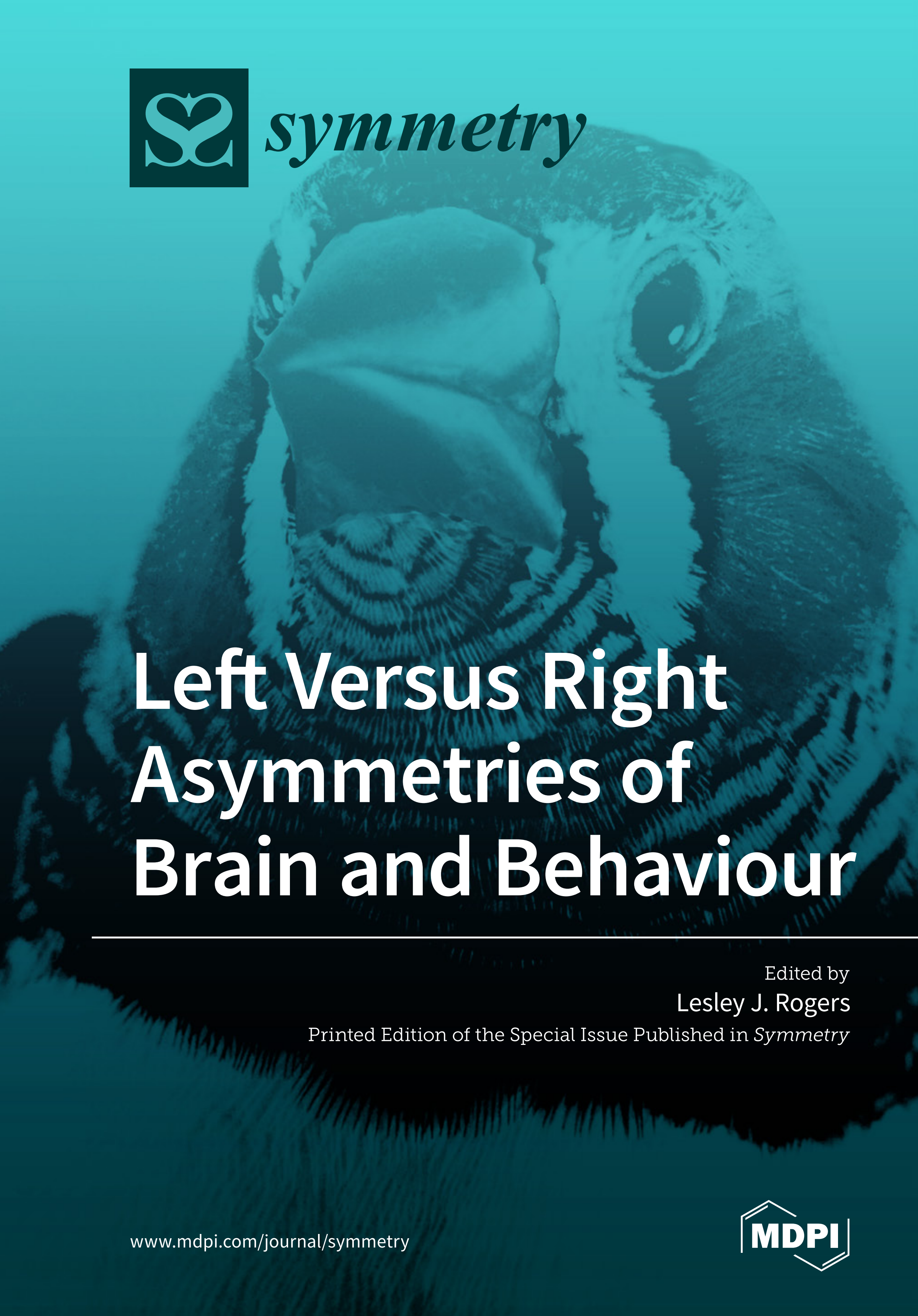

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Left Versus Right Asymmetries of Brain and Behaviour

Edited by
Lesley J. Rogers

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Special Issue Editor

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About the Special Issue Editor

Lesley J. Rogers is a Fellow of the Australian Academy of Science and Emeritus Professor at the University of New England, Australia. After being awarded a First-Class Honours degree by the University of Adelaide, she studied at Harvard University in USA and then the University of Sussex, UK. She was awarded a Doctor of Philosophy and, later, a Doctor of Science from the University of Sussex, UK. After returning to Australia, she held academic positions at Monash University and the University of New England. Her publications, numbering over 500, include 18 books and over 280 scientific papers and book chapters, mainly on brain and behaviour. In the 1970s, her discovery of lateralized behaviour in chicks was one of three initial findings that established the field of brain lateralization in non-human animals, now a very active field of research. Initially, her research was concerned with the development of lateralization in the chick as a model species, and the importance of light stimulation before hatching, which she investigated at the neural and behavioural levels. She then compared lateralized behaviour in different species spanning from bees to primates and, more recently, has focused on the advantages of brain asymmetry and the link between social behaviour and population-level asymmetry. Her other roles include Editor of the journal *Laterality* and Academic Editor of numerous other scientific journals.

Preface to "Left Versus Right Asymmetries of Brain and Behaviour"

Asymmetry of the brain and of behaviour is a characteristic of a wide range of vertebrate species, as shown by an increasing number of studies testing animals in the laboratory and in the natural environment. Some asymmetries of behaviour have also been found in invertebrate species. Given its ubiquity, lateralization must confer an advantage for survival, despite the apparent disadvantages of side biases in perception and response. A disadvantage of lateralized responding is evidenced by the fact that many species are more likely to respond to a predator when it is seen on their left side and to their prey when it is seen on their right side. How do different species deal with these asymmetries? The topics covered in this book address this question and report further evidence of lateralized brain and behaviour in non-human species. In addition, the brain function involved in lateralized processing and control of response is discussed, and also the relationship between lateralized behaviour and animal welfare.

The paper by Frasnelli and Vallortigara addresses the question of why the majority of individuals in a population are lateralized in the same direction (population-level lateralization). They show that, although the cognitive advantage of having a lateralized brain places no constraints on the direction of lateralization, population-level lateralization develops as an evolutionary stable strategy when lateralized organisms must co-ordinate their behaviour with other lateralized organisms. This explains why population-level lateralization is a characteristic of social species. In this paper, the authors affirm that population-level asymmetry is also an advantage in so-called "solitary" species when individuals have to interact, as in aggressive and mating behaviour. They clarify an important point about inter-individual interaction and the evolution of lateralization as an evolutionary stable strategy.

The paper by Boeving and Nelson considers the link between social and affiliative behaviour from another perspective; by relating research showing that lateralization influences social structure in spider monkeys. Previous research had shown that social affiliative behaviour—embrace and face-embrace—in spider monkeys is left-side biased. In this paper, the authors apply social network analysis and find that laterality of affiliative behaviour influences social structure. Network patterns that are left-lateralized for affiliative behaviour are more cohesive than those that are right lateralized.

The paper by Üver, Xiao and Güntürkün reports research on the mechanism by which the brain deals with the conflicting responses elicited by each hemisphere's differing reaction to the same stimulus. In short, they reveal how one hemisphere achieves dominance (meta-control) over the other. Experiments addressing this issue involved sectioning the anterior commissure of pigeons, the largest commissure connecting the left and right sides of the avian brain. The results showed that meta-control is modified by interhemispheric transmission via this commissure, although it does not seem to depend entirely on it. The results suggest that the two hemispheres compete to take control of a particular behaviour and they do so on the basis of their processing speed. Since the hemisphere specialised to respond to a particular stimulus processes information faster than the other hemisphere, it takes control of the response.

From early research on lateralization of song production in the zebra finch, there has been speculation about the possibility that lateralization in this species differs from the general pattern found in other avian species and generally in vertebrates. The chapter by Rogers, Koboroff and Kaplan discusses more recent evidence refuting this idea and reports experimental evidence showing that population-level lateralization is present in preferred-eye use by zebra finches when they view a predator. Since zebra finches often alternate looking with the monocular field of one eye and then the other eye, a new method had to be developed in order to score eye preferences. The experiments showed that the birds have a significant preference to view a monitor lizard with their left-eye (using their right hemisphere). This result is discussed together with evidence of other asymmetries in zebra finches, for visual searching and courtship behaviour and for processing, producing and learning of song. The authors conclude that, contrary to earlier suggestions, the zebra finch brain is lateralized with the same pattern as that of that found in other vertebrate species.

Hausberger and colleagues consider lateralization of auditory processing. Auditory stimuli of differing salience (e.g., familiar versus novel sounds) were presented to Campbell's monkeys and only novel sounds elicited laterality. The monkeys had a significant right-hemisphere preference to attend to novel sounds but no preference to attend to familiar sounds. The authors also considered auditory lateralization in starlings. In starlings, the right hemisphere was found to process sounds of individual identity, whereas the left hemisphere was more involved in processing socially meaningless stimuli. The authors suggest an attention-based explanation to reconcile the different hypotheses about right-hemisphere specialisation.

Although many behavioural responses have a directional bias within the population, some types of laterality occur with equal numbers of left and right biased individuals in the population. Laterality in scale-eating cichlid fishes is such an example, discussed in the chapter by Hori and colleagues. These fish have asymmetry of the body, in the direction of the mouth opening either to the left or right side. The distribution of laterality within a population is bimodal (anti-symmetry). The authors have investigated the relationship between behavioural laterality and morphological asymmetry in two species studied over three decades. They found that the dimorphism is maintained dynamically with a cycle of four years oscillating between more left and more right individuals. This cycling is caused by frequency-dependent selection (the minority type having an advantage) between predator and prey species. Since both predator and prey fish are lateralized, the authors examine cross-predation versus parallel-predation in terms of the physical and sensory abilities of fishes.

The development of lateralization in Port Jackson sharks is dependent on temperature of the sea, as Pouca et al. report. They found that, under water temperatures predicted for the end of the century, development of sharks is affected, as seen by measuring preferences of direction taken during a detour test. Sharks incubated at the higher temperature had stronger lateralization (biased to detour to the right) than did sharks incubated at current sea temperature. The authors suggest that this change in lateralization might be a way by which the species could cope with deleterious effects of climate change.

Two papers deal with different aspects of laterality in dogs and its relationship to behaviour and welfare. The paper by Siniscalchi and colleagues reports on turning behaviour in sheepdogs. The dogs showed significantly more aggressive behaviour toward the sheep when they were circling the herd in an anticlockwise direction and so could see the sheep in their left visual field and process the information in their right hemisphere. Dominance of the right hemisphere in aggressive behaviour has been found also in a number of other vertebrate species. As the authors say, this relationship between motor lateralization and aggressive behaviour has practical implications for training sheepdogs.

The paper by Wells and colleagues relates laterality to the welfare of dogs. The subjects were rescued dogs and they were tested during the first week after they had been placed in a rescue shelter.

Paw preference measured in a food-retrieval task was linked to stress-related behaviour. The results showed that stronger left-paw preference was associated with higher stress-related behaviour, such as frequent change of state, vocalisations and lower body posture. This finding is in keeping with other findings of the association between left-limb preference and vulnerability to stress. The authors suggest that testing paw preference may be a useful tool for detecting different coping strategies in dogs entering a kennel environment and for targeting individuals at risk of experiencing reduced welfare.

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Special Issue Editor