Journal of Theoretical Biology 390 (2016) 50–60

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Self-organization of laterally asymmetrical movements as a consequence of space–time optimization

Madhur Mangalam [a,*], Nisarg Desai [b,1], Mewa Singh [c,d]

[a] Department of Psychology, University of Georgia, Athens, GA 30602, USA
[b] Indian Institute of Science Education and Research Pune, Pune 411008, India
[c] Biopsychology Laboratory, Institute of Excellence, University of Mysore, Mysore 570006, India
[d] Jawaharlal Nehru Center for Advanced Scientific Research, Bangalore 560064, India

HIGHLIGHTS

- Asymmetrical systems outperform symmetrical systems by optimizing space and time.
- The space–time advantage increases with the increasing complexity of the task.
- Laterally asymmetrical movements can self-organize through space–time optimization.

ARTICLE INFO

Article history:
Received 23 May 2015
Received in revised form
15 September 2015
Accepted 30 October 2015
Available online 28 November 2015

Keywords:
Laterally asymmetrical movements
Functional asymmetry
Laterality
Self-organization
Space–time optimization

ABSTRACT

Laterally asymmetrical movements are ubiquitous among organisms. A bilaterally symmetrical organism cannot maneuver through a two- or three-dimensional space unless and until one side of its body leads, because the forces that cause the movements of the body are generated within the body. One question follows: are there any costs or benefits of laterally asymmetrical movements? We test whether directionally consistent laterally asymmetrical movements at different levels of organization of movements (at the individual, and not the population level) can work synergistically. We show—by means of a hypothetical system resembling a humanoid robot—that a laterally asymmetrical movement at a lower level of organization of movements can stimulate laterally asymmetrical movements that are directionally consistent at consecutive higher levels. We show—by comparing two hypothetical systems, incorporating laterally symmetrical and asymmetrical movements, respectively—that the asymmetrical system outperforms the symmetrical system by optimizing space and time and that this space–time advantage increases with the increasing complexity of the task. Together, these results suggest that laterally asymmetrical movements can self-organize as a consequence of space–time optimization.

1. Introduction

Functional asymmetries associated with behavior and cognition are ubiquitous among organisms (reviewed by Bradshaw and Rogers, 1993; Rogers et al., 2013, Rogers, 2002; Rogers and Andrew, 2002; Vallortigara and Rogers, 2005). For example, a poeciliid fish, *Girardinus falcatus* (Cantalupo et al., 1995) and Australian lungfish, *Neocaratodus fosteri* (Lippolis et al., 2009), toads of three different species, *Bufo* spp. (Lippolis et al., 2002), domestic chicks, *Galus galus domesticus* (Rogers, 2000), and striped-faced dunnart, *Sminthopis macroura* (Lippolis et al., 2005) react to predators on their left more vigorously compared to right, and during agoniztic encounters, cane toads, *Bufo marinus* (Robins and Rogers, 2004; Robins et al., 1998), tree lizards, *Urosaurus ornatus* (Hews and Worthington, 2001), domestic chicks (Vallortigara et al., 2001), gelada baboons, *Theropithecus gelada* (Casperd and Dunbar, 1996), and horses, *Equus caballus* (Austin and Rogers, 2012) direct more aggressive responses towards conspecifics on their left compared to right. Thus, different types of functionally relevant lateral asymmetries prevail across species and contexts.

Among different types of lateral asymmetries, laterally asymmetrical movements have been of special interest to researchers. Laterally asymmetrical movements are prevalent among the prokaryotes and eukaryotes and extend up to the cognitively most advanced primates. For example, *Proteus*, *Clostridium*, and *Bacillus* bacteria (Hoeniger, 1964) and blue-green algae rotate clockwise or anti-clockwise preferentially (Schmidt, 1919). Likewise, *Ameba* and

* Corresponding author.
E-mail address: madhur.mangalam@uga.edu (M. Mangalam).
[1] Present affiliation: Department of Anthropology, University of Minnesota, Minneapolis, MN 55455, USA.

http://dx.doi.org/10.1016/j.jtbi.2015.10.038
0022-5193/

Infusoria propel towards their right or left preferentially depending on the species (Bullington, 1925; 1930; Grebecki and Micolajczyk, 1968; Schaeffer, 1931). *Temnothorax albipennis* ants predominantly turn left when exploring unknown nest sites (Hunt et al., 2014). Domestic chicks predominantly use their right foot to initiate locomotion (Tommasi and Vallortigara, 1999). Capuchin monkeys, *Cebus apella* (Spinozzi et al., 1998), bonnet macaques, *Macaca radiata*, and several other species of monkeys (reviewed by Papademetriou et al., 2005), and chimpanzees, *Pan troglodytes* (Lonsdorf and Hopkins, 2005) and humans (McManus, 2002) predominantly use one of their hands over the other for several activities. Asymmetrical use of the limbs is widespread among vertebrates, even among the taxonomic groups that use the appendages only occasionally (reviewed by Rogers and Andrew, 2002).

In the above examples, the laterally asymmetrical movements are present at two different levels of biological organization: (i) within individuals, following no particular common direction across individuals, within a group or population (that is, at the individual level), and (ii) within individuals, following a particular common direction across individuals, within a group or population (that is, at the population level). (i) Laterally asymmetrical movements at the individual level correspond to the optimization of neural processing of information; one hypothesis is that unilateral stimuli eliciting contralateral muscle responses are faster compared to ipsilateral responses (Young, 1962). In support of this hypothesis, empirical results indicate that lateral asymmetries may speed up responses to threat (Dadda et al., 2010) and increase neural capacity (Vallortigara, 2000) and parallel processing of sensory information (Rogers et al., 2004). (ii) Lateral asymmetries at the population level correspond to evolutionarily stable strategies—a concept that the evolutionary biologist John Maynard-Smith (1982) developed to study competition and cooperation among individuals. Initially, individuals develop lateral asymmetries to optimize their neurophysiological and/or neurocomputational resources; later, the interactions among the lateralized individuals lead to the alignment of their lateral asymmetries. Both mathematical models (Ghirlanda and Vallortigara, 2004; Ghirlanda et al., 2009; Vallortigara, 2006) and empirical results (Bisazza et al., 2000; Bisazza et al., 2002; Rogers and Vallortigara, 2008) support this hypothesis.

Given that laterally asymmetrical movements are ubiquitous among biological organisms, they are likely to have been adaptive and/or inevitable (Vallortigara and Rogers, 2005). It is impossible for a bilaterally symmetrical organism to maneuver through a two- or three-dimensional space until one side of the body leads, because the forces that cause the movements of the body are generated within the body (Glezer (1987) put forward this perspective as a comment on MacNeilage et al. (1987)). Although this hypothesis does not predict which side of the body would lead, as there is no apparent advantage or disadvantage of the right or left side, and whether the same side would always lead or not, it stresses a key point that organisms cannot maneuver while conserving their symmetry. It might be possible that evolutionary pressures would have selected laterally asymmetrical movements at different levels of organization of movements differently (based on the relevance of the environment to that level and/or movement), or, alternatively, would have selected laterally asymmetrical movements that are directionally consistent across different levels of organization of movements. One way to test these two hypotheses is to model mathematically laterally asymmetrical movements as an optimization problem.

In the present study, we test (theoretically) whether directionally consistent laterally asymmetrical movements at different levels of organization of movements (at the individual, and not the population level) can work synergistically. We test—by means of a hypothetical system resembling a humanoid robot—if a laterally asymmetrical movement at a lower level of organization of movements can stimulate laterally asymmetrical movements that are directionally consistent at consecutive higher levels. We test—by comparing two hypothetical systems, incorporating laterally symmetrical and asymmetrical movements, respectively—if the asymmetrical system outperforms the symmetrical system by optimizing space and time and that this space–time advantage increases with the increasing complexity of the task.

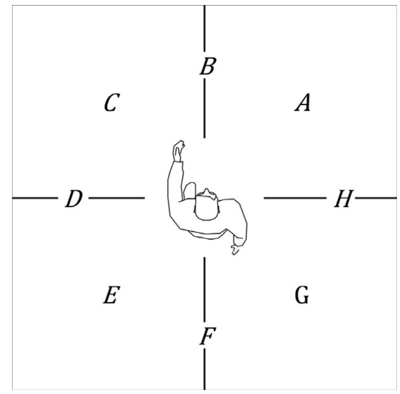

Fig. 1. Various positions of the object in the transverse plane of *ROB*'s body.

2. Model

We use a hypothetical system resembling a humanoid robot, *ROB*; *ROB* works on predetermined algorithms, which we can tweak as per the need. We instruct *ROB* to pick up an object, *O*, placed at some position on its transverse plane (Fig. 1). We assume the following to simplify calculations; these assumptions do not affect the validity of the present model:

1. *ROB* has a 178° forward-facing horizontal field of view.
2. *ROB* can turn only 90° at a time to the right and left.
3. *ROB* lacks any structural or functional asymmetries initially, but instead uses a random number generator to decide between the two laterally symmetrical counterparts of a movement (say, odd and even numbers corresponding to the right and left, respectively).

A1 mimics vertebrates that typically cannot see on or behind the transverse axis of their body without rotating their head. A2 reduces the analysis to the dynamics of only a few movements. A3 allows to develop laterally asymmetric movements de novo and to compare the efficiency of the movements of a perfectly symmetrical system with an asymmetrical system (which we develop).

2.1. Laterally symmetrical movements

Let ROB_S be a robot incorporating laterally symmetrical movements and *O* an object placed on any of the four quadrants or the four axes of its transverse plane (positions *A* to *H*; Fig. 1). ROB_S takes at least one of the following steps to pick up the object depending on the position of the object: analyze the position of the object, turn 90° either to the right or left with equal probability; execute the terminal manual action using either the right or left hand with equal probability. Let (a) $t_t^s(R)$ and $t_t^s(L)$ be the time that ROB_S takes to turn 90° to the right and left, respectively; (b) $t_e^s(R|R)$ and $t_e^s(R|L)$ be the time that ROB_S takes to pick up the object with its right hand when the object is on the right and left side of its midsagittal plane, respectively; (c) $t_e^s(R|C)$ and $t_e^s(L|C)$ be