bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Title

Asymmetries in the body, brain, and cognition: a systems-theory approach

Authors

M. Mangalam[1,*], N. Desai[2], M. Singh[3,4]

[1] Department of Psychology, University of Georgia, Psychology Building, 125 Baldwin Street, Athens, GA 30602, USA

[2] Indian Institute of Science Education and Research Pune, Dr. Homi Bhabha Road, Pashan, Pune 411 008, India

[3] Biopsychology Laboratory, and Institution of Excellence, University of Mysore, Manasagangotri, Mysore 570 006, India

[4] Jawaharlal Nehru Center for Advanced Scientific Research, Jakkur, Bangalore 560 064, India

(e-mail: madhur.mangalam@uga.edu; nisarg.p.desai@gmail.com; msingh@psychology.uni-mysore.ac.in)

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Abstract. Lateral asymmetries in body, brain, and cognition are ubiquitous among organisms. Asymmetries in motor-action patterns are a central theme of investigation, among others, as they are likely to have shaped primate evolution, and more specifically, their motor dexterity. Using an adaptationist approach one would argue that these asymmetries were evolutionarily selected because no bilateral organism can maneuver in three-dimensional space unless any one side becomes dominant and always takes the lead. However, which side becomes dominant is beyond the scope of this hypothesis as there is no apparent advantage or disadvantage associated with either the left or the right side. Both the evolutionary origin and adaptive significance of asymmetries in motor-action patterns remain largely unexplored. In the present study, we mathematically model how an asymmetry at a lower level could stimulate as well as govern asymmetries at the next higher level, and this process might reiterate; ultimately lateralizing the whole system. We then show by comparing two systems: one incorporating symmetric and the other incorporating asymmetric motor-action patterns, that (a) the asymmetric system performs better than the symmetric one in terms of time optimization, and (b) as the complexity of the task increases the advantage associated with asymmetries in the motor-action patterns increases. Our minimal model theoretically explains how lateral asymmetries could appear and evolve in a biological system using a systems theory approach.

Keywords: asymmetry; lateralization; motor-action pattern; specialization; systems theory.

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

1 Introduction

Lateral asymmetries in body, brain, and cognition are ubiquitous among organisms–they are prevalent among prokaryotes and eukaryotes, extending up to the highest life forms, that is, primates (Bradshaw and Rogers 1993). For example, bacterial colonies, such as *Proteus*, *Clostridium*, and *Bacillus* have a preferred direction of rotation (Hoeniger 1966); blue-green algae show differential left/right preferences while moving (Schmid 1918, 1919); the trajectory of propelling movements in *Amoeba* and *Infusoria* is asymmetric and the left/right distinction is species-specific (Bullington 1925, 1930; Grebecki and Micolajczyk 1968; Schaeffer 1931). Imagine any of these organisms moving in a three-dimensional space. Can they be entirely symmetrical? No, they can't be. Just the way a ship changes the direction of its propeller, these organisms have to create asymmetries in cilia, flagella, or the cytoplasm to initiate and continue the motion. Analogously, higher organisms are required to break environmental symmetry in various contexts (Bradshaw and Rogers 1993).

If lateral asymmetries are so persistent that they are ubiquitous among biological organisms, they must have been adaptive. From an adaptationist's perspective one would argue that lateral asymmetries were evolutionarily selected because no bilateral organism can maneuver in three-dimensional space unless any one side becomes dominant and always takes the lead. (Glezer (1987) strongly put forward this perspective in an open-peer commentary on MacNeilage (1987)). However, which side becomes dominant is beyond the scope of this hypothesis as there is no apparent advantage or disadvantage associated with either the left or the right side. It may be possible that asymmetries are not selected at each level independently, but at a particular level (perhaps, the lowest one) from which asymmetries at the higher levels consequently follow. Thus, the appearance and evolution of various forms of asymmetries in body, brain, and cognition can be formulated as a control and optimization problem.

The control and optimization problem related to lateral asymmetries in motor-action patterns can be approached using mathematical models. A working model is likely to explain the appearance and evolution of such asymmetries in biological organisms, and can address the engineering aspects of building them in artificial robotic systems. In the present study, we develop a minimal model to explain how lateral asymmetries could appear and evolve in a biological system using a systems theory approach. We mathematically model how an asymmetry at a lower level could stimulate as well as govern asymmetries at the next higher level, and this process might reiterate; ultimately lateralizing the whole system. We then compare two systems: one incorporating symmetric and the other incorporating asymmetric motor-action patterns, to examine whether (a) the asymmetric system performs better than the symmetric one in terms of time optimization, and (b) the advantage associated with asymmetries in the motor-action patterns increases with the complexity of the task.

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

2 The Model

We consider a hypothetical system, a humanoid robot: ROB. ROB works on an algorithm, which we can tweak depending on the context. We order ROB to pick up an object lying at some random position on its transverse plane (Fig. 1).

We make some assumptions that reduce the complexity of our calculations, but do not affect the validity of our model. We assume that:

(A1) ROB has a 178-degree field of vision, just like humans.

(A2) ROB lacks any lateral asymmetry in its body, brain, and cognition.

(A3) Since ROB lacks any asymmetry, it uses a random number generator to decide between the two laterally symmetrical elements (say, odd numbers corresponding to the right and even numbers corresponding to the left).

A1 allows us to mimic biological systems, wherein the perception is generally limited to about 100°, restricting the perception of the transverse axis. A2 allows us to analyze the dynamics of a few motor-action patterns in a perfectly symmetric system, and to build asymmetries in motor-actions patterns de novo. A3 provides us a mathematical tool to analyze the dynamics of a symmetrical system, and to compare it with that of an asymmetrical system, which we develop.

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

2.1 Symmetric motor-action patterns

Let ROB_S be the robot that employs completely symmetric motor-action patterns. Consider the transverse plane of $ROB_S's$ body. An object O can be variably placed in any of the four quadrants or on any of the four axis (Fig. 1). When prompted, ROB_S can reach for this object in one or more than one step depending on its position. These steps include: analyze the position of the object, turn rightwise or leftwise with equal probability; execute the terminal manual action using either the right or the left hand with equal probability. Let $t_t^s(R)$ be the time taken by ROB_S to turn 90° rightwise and $t_t^s(L)$ to turn 90° leftwise, $t_e^s(R|R)$ and $t_e^s(R|L)$ to pick up the object with the right hand when the object is lying towards the right and left sides of its midsagittal plane, respectively; $t_e^s(R|C)$ and$t_e^s(L|C)$ to pick up the object with the right hand and left hand, respectively, when the object is lying exactly on its midsagittal plane; $t_e^s(L|R)$ and $t_e^s(L|L)$ to pick up the object with the left hand when the object is lying towards the right and left sides of its midsagittal plane, respectively.

Then, when both hands are equally efficient, we can assume: $t_e^s(R|R) = t_e^s(L|L) = t_e^s \sim t_e^s(R|C) = t_e^s(L|C) < t_e^s(R|L) \sim t_e^s(L|R)$ and $t_t^s(R) = t_t^s(L) = t_t^s$.

We determine the total time required by ROB_S to pick up the object lying on position α: S_α, by calculating the expected value using probability distribution function. In order to calculate the expected value of the total time required by ROB_S to pick up the object, we sum over all the possible combinations of steps weighted by the probability of their occurrence. In few cases, this results in a convergent arithmetico-geometric infinite series, the sum of which can be obtained using standard procedures.

Position A:

When the object is lying towards the ventral side of its transverse axis and towards the right side of its midsagittal plane (Fig. 1), ROB_S can pick it up using its right or left hand with equal probability (Fig. 2a).

So,

$$S_A = 0.5(t_e^s(R|R)) + 0.5(t_e^s(L|R)).$$

Position B:

When the object is lying towards the ventral side of its transverse axis and exactly on its midsagittal plane (Fig. 1), ROB_S can pick it up using its right or left hand with equal probability (Fig. 2b).

So,

$$S_B = 0.5(t_e^s(R|C)) + 0.5(t_e^s(L|C)).$$

Position C:

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

When the object is lying towards the ventral side of its transverse axis and towards the right side of its midsagittal plane (Fig. 1), ROB_S can pick it up using its right or left hand with equal probability (Fig. 2c).

So,

$$S_C = 0.5(t_e^s(R|L)) + 0.5(t_e^s(L|L)).$$

Position D:

When the object is lying exactly on its transverse axis and the left side of its midsagittal plane (Fig. 1), ROB_S cannot see it; it has to turn 90° sideways. ROB_S can turn rightwise or leftwise with 0.5 probability each. Consider the following three possible combinations of steps (Fig. 2d):

If ROB_S turns leftwise the object is within its field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. As $t_e^s(R|C) = t_e^s(L|C) = t_e^s$, the time taken by ROB_S to pick up the object is given by:

$$0.5(t_t^s(L) + t_e^s)$$

If ROB_S turns rightwise the object is still out of its field of vision; it has to turn 90° sideways. Again, ROB_S can turn rightwise or leftwise with 0.25 probability each (Fig. 2d). Upon one more turn in the same direction, which has 0.125 probability, the object is within $ROB_S's$ field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. The time taken by ROB_S to pick up the object is given by:

$$0.125(t_t^s(R) + t_t^s(L)+t_t^s(L) + t_e^s)+0.125(t_t^s(R) + t_t^s(R)+t_t^s(R) + t_e^s)$$

Similarly, in the next case, the time taken by ROB_S to pick up the object is given by:

$$0.0625(t_t^s(R) + t_t^s(L)+t_t^s(R)+t_t^s(L)+t_t^s(L) + t_e^s)+0.0625(t_t^s(R) + t_t^s(R)+t_t^s(L) + t_t^s(R)+t_t^s(R) + t_e^s)$$

$$\ldots$$

As $t_t^s(R) = t_t^s(L) = t_t^s$, the above expressions can be written as:

$$0.5(t_t^s + t_e^s)$$

$$0.25(3t_t^s + t_e^s)$$

$$0.125(5t_t^s + t_e^s)$$

$$\ldots$$

Thus,

$$S_D = 0.5(t_t^s + t_e^s) + 0.25(3t_t^s + t_e^s) + 0.125(5t_t^s + t_e^s) + \cdots = 6t_t^s + t_e^s.$$

Position E:

When the object is lying on the dorsal side of its transverse axis and the left side of its midsagittal plane (Fig. 1), ROB_S cannot see it; it has to turn 90° sideways. ROB_S

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

can turn rightwise or leftwise with 0.5 probability each. Consider the following three possible combinations of steps (Fig. 2e):

If ROB_S turns leftwise the object is within its field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. As $t_e^s = t_e^s(L|L) < t_e^s(R|L)$, the minimum time taken by ROB_S to pick up the object is given by:

$$0.5(t_t^s(L) + t_e^s)$$

If ROB_S turns rightwise the object is still out of its field of vision; it has to turn 90° sideways. Again, ROB_S can turn rightwise or leftwise with 0.25 probability each (Fig. 2d). If ROB_S turns rightwise, the object is within $ROB_S's$ field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. The minimum time taken by ROB_S to pick up the object is given by:

$$0.25(t_t^s(R) + t_t^s(R) + t_e^s)$$

And, if ROB_S turns leftwise the object is still out of its field of vision; it has to turn 90° sideways. Again, ROB_S can turn rightwise or leftwise with 0.25 probability each (Fig. 2d). If ROB_S turns leftwise, the object is within $ROB_S's$ field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. The time taken by ROB_S to pick up the object is given by:

$$0.125(t_t^s(R) + t_t^s(L) + t_t^s(L) + t_e^s)$$

$$\ldots$$

As $t_t^s(R) = t_t^s(L) = t_t^s$, the above expressions can be written as:

$$0.5(t_t^s + t_e^s)$$

$$0.25(3t_t^s + t_e^s)$$

$$0.125(3t_t^s + t_e^s)$$

$$\ldots$$

Thus,

$$S_E = 0.5(t_t^s + t_e^s) + 0.25(2t_t^s + t_e^s) + 0.125(3t_t^s + t_e^s) + \cdots = 2t_t^s + t_e^s.$$

Position F:

When the object is lying on the ventral side of its transverse axis and exactly on the midsagittal plane (Fig. 1), ROB_S cannot see it; it has to turn 90° sideways. ROB_S can turn rightwise or leftwise with 0.5 probability each. Consider the following three possible combinations of steps (Fig. 2f):

If ROB_S turns rightwise the object is still out of its field of vision; it has to turn 90° sideways. Again, ROB_S can turn rightwise or leftwise with 0.25 probability each. If ROB_S turns rightwise the object is within its field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. As $t_e^s(R|C) = t_e^s(L|C) = t_e^s$, the time taken by ROB_S to pick up the object is given by:

$$0.25(t_t^s(R) + t_t^s(R) + t_e^s)$$

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

If ROB_S turns leftwise it is back to its initial orientation. Then, it can pick up the object turning rightwise consecutively twice with 0.125 probability. As $t_e^s(R|C) = t_e^s(L|C) = t_e^s$, the time taken by ROB_S to pick up the object is given by:

$$0.125(t_t^s(R) + t_t^s(L) + t_t^s(R) + t_t^s(R) + t_e^s)$$

Similarly, in the next case, the time taken by ROB_S to pick up the object is given by:

$$0.0625(t_t^s(R) + t_t^s(L) + t_t^s(R) + t_t^s(L) + t_t^s(R) + t_t^s(R) + t_e^s)$$

$$\ldots$$

A similar analysis follows when ROB_S turns leftwise with 0.5 probability, yielding the following terms:

$$0.25(t_t^s(L) + t_t^s(L) + t_e^s)$$

$$0.125(t_t^s(L) + t_t^s(R) + t_t^s(L) + t_t^s(L) + t_e^s)$$

$$0.0625(t_t^s(L) + t_t^s(R) + t_t^s(L) + t_t^s(R) + t_t^s(L) + t_t^s(L) + t_e^s)$$

$$\ldots$$

As $t_t^s(R) = t_t^s(L) = t_t^s$, the above expressions can be written as:

$$0.25(2t_t^s + t_e^s)$$

$$0.125(4t_t^s + t_e^s)$$

$$0.0625(6t_t^s + t_e^s)$$

$$\ldots$$

Thus,

$$S_F = 0.5(2t_t^s + t_e^s) + 0.25(4t_t^s + t_e^s) + 0.125(6t_t^s + t_e^s) + \cdots = 8t_t^s + t_e^s.$$

Position G:

When the object is lying on the dorsal side of its transverse axis and the right side of its midsagittal plane (Fig. 1), ROB_S cannot see it; it has to turn 90° sideways. ROB_S can turn rightwise or leftwise with 0.5 probability each. Consider the following three possible combinations of steps (Fig. 2g):

If ROB_S turns rightwise the object is within its field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. As $t_e^s = t_e^s(R|R) < t_e^s(L|R)$, the minimum time taken by ROB_S to pick up the object is given by:

$$0.5(t_t^s(R) + t_e^s)$$

If ROB_S turns leftwise the object is still out of its field of vision; it has to turn 90° sideways. Again, ROB_S can turn rightwise or leftwise with 0.25 probability each (Fig. 2d). If ROB_S turns leftwise, the object is within $ROB_S's$ field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. The minimum time taken by ROB_S to pick up the object is given by:

$$0.25(t_t^s(L) + t_t^s(L) + t_e^s)$$

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

And, if ROB_S turns rightwise the object is still out of its field of vision; it has to turn 90° sideways. Again, ROB_S can turn rightwise or leftwise with 0.25 probability each (Fig. 2d). If ROB_S turns rightwise, the object is within $ROB_S's$ field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. The minimum time taken by ROB_S to pick up the object is given by:

$$0.125(t_t^s(L) + t_t^s(R) + t_t^s(R) + t_e^s)$$

$$\ldots$$

As $t_t^s(R) = t_t^s(L) = t_t^s$, the above expressions can be written as:

$$0.5(t_t^s + t_e^s)$$

$$0.25(3t_t^s + t_e^s)$$

$$0.125(3t_t^s + t_e^s)$$

$$\ldots$$

Thus,

$$S_G = 0.5(t_t^s + t_e^s) + 0.25(2t_t^s + t_e^s) + 0.125(3t_t^s + t_e^s) + \cdots = 2t_t^s + t_e^s.$$

Position H:

When the object is lying exactly on its transverse axis and the right side of its midsagittal plane (Fig. 1), ROB_S cannot see it; it has to turn 90° sideways. ROB_S can turn rightwise or leftwise with 0.5 probability each. Consider the following three possible combinations of steps (Fig. 2h):

If ROB_S turns rightwise the object is within its field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. As $t_e^s(R|C) = t_e^s(L|C) = t_e^s$, the time taken by ROB_S to pick up the object is given by:

$$0.5(t_t^s(R) + t_e^s)$$

If ROB_S turns leftwise the object is still out of its field of vision; it has to turn 90° sideways. Again, ROB_S can turn rightwise or leftwise with 0.25 probability each (Fig. 2d). Upon one more turn in the same direction, which has 0.125 probability, the object is within $ROB_S's$ field of vision. Then, it can pick up the object using its right or left hand with 0.5 probability each. The time taken by ROB_S to pick up the object is given by:

$$0.125(t_t^s(L) + t_t^s(R) + t_t^s(R) + t_e^s) + 0.125(t_t^s(L) + t_t^s(L) + t_t^s(L) + t_e^s)$$

Similarly, in the next case, the time taken by ROB_S to pick up the object is given by:

$$0.0625(t_t^s(L) + t_t^s(R) + t_t^s(L) + t_t^s(R) + t_t^s(R) + t_e^s) + 0.0625(t_t^s(L) + t_t^s(L) + t_t^s(R) + t_t^s(L) + t_t^s(L) + t_e^s)$$

As $t_t^s(R) = t_t^s(L) = t_t^s$, the above expressions can be written as:

$$0.5(t_t^s + t_e^s)$$

$$0.25(3t_t^s + t_e^s)$$

$$0.125(5t_t^s + t_e^s)$$

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

…

Thus,

$$S_H = 0.5(t_t^s + t_e^s) + 0.25(3t_t^s + t_e^s) + 0.125(5t_t^s + t_e^s) + \cdots = 6t_t^s + t_e^s.$$

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

The above expressions represent the time required by ROB_S to pick up the object lying variably on its transverse plane. Now, in the following section, we attempt to introduce lateral asymmetries in the motor-action patterns, making ROB_S asymmetric, that is, ROB_A.

2.2 Introducing asymmetries in motor-action patterns

A system is strictly symmetric prima facie, and so is the environment. To make use of the environment the system needs to break its symmetry. This can be done either through an asymmetric element in the environment or through an asymmetric element in the system itself. Environmental asymmetry is a transient solution because it is very likely to be spatiotemporally variable. Thus, the system needs to develop an asymmetric element within itself to break environmental symmetry. An asymmetric element thus introduced can pave the way for the appearance and evolution of asymmetric elements at next higher level, and so on; ultimately lateralizing the whole system.

We start with ROB_S, lets denote it for convenience as ROB. For simplifying our calculations, we program ROB to minimize the time required to execute various steps. With these simplifications, we start with ROB whose both hands are equally efficient, that is, $t_e(R|R) = t_e(L|L) = t_e < t_e(R|L) \sim t_e(L|R)$; $t_t(R) = t_t(L)$.

When the object is lying at:

Positions A and C

ROB takes time t_d ($t_d \ll t_e$) to determine the position of the object with respect to its midsagittal plane. I program ROB to pick it up with the corresponding hand in time t_e. Thus, ROB completes this task in time $t = t_d + t_e(R|R)$ when the object is lying at position A and $t = t_d + t_e(L|L)$ when the object is lying at position C. Alternatively, ROB can complete the task with its opposite hand in time $t = t_d + t_e(L|R)\ or\ t = t_d + t_e(R|L)$. However, as $t_e(R|R) = t_e(L|L) < t_e(R|L) \sim t_e(L|R)$; the former is more efficient. (Table 1)

Position B

ROB takes infinite time (i.e., $t_d \to \infty$), as it is unable to determine which hand to use. To resolve this problem, I program ROB to pick up this object with its right hand in such situations. ROB completes this task in time $t = t_d + t_e(R|C)$. ROB doesn't pick up the object with its left hand as it is programmed to always pick up the object with the right hand whenever the object is on midsagittal plane. (Table 1)

At positions D, E, F, G, and H, ROB has to turn around. ROB can turn around employing one of the following two algorithms: (a) to always turn around rightwise or leftwise in time t_t, or (b) to turn around either 90° rightwise or 90° leftwise in time t_t with equal probability using a random number generator (say, odd numbers corresponding to turning rightwise and even numbers corresponding to turning

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

leftwise). If a further turn is required, it will always be in the same direction as the previous one.

Position D

ROB can either turn 90° rightwise thrice and complete the task in time $t = 3t_t(R) + t_d + t_e(R|C)$, or turn 90° leftwise once and complete the task in time $t = t_t(L) + t_d + t_e(R|C)$. As $t_t(R) = t_t(L)$, the latter is more efficient. (Table 1)

Position E

ROB can either turn 90° rightwise twice and complete the task in time $t = 2t_t(R) + t_d + t_e(R|R)$, or turn 90° leftwise once and complete the task in time $t = t_t(L) + t_d + t_e(L|L)$. Alternatively, ROB can complete the task with opposite hand in time $t = 2t_t(R) + t_d + t_e(L|R)\ or\ t = t_t(L) + t_d + t_e(R|L)$. However, as $t_e(R|R) = t_e(L|L) < t_e(R|L) \sim t_e(L|R)$ the former cases are more efficient. (Table 1)

Position F

ROB can either turn 90° rightwise twice and complete the task in time $t = 2t_t(R) + t_d + t_e(R|C)$, or turn 90° leftwise twice and complete the task in time $t = 2t_t(L) + t_d + t_e(R|C)$. Both alternatives are equally efficient. (Table 1)

Position G

ROB can either turn 90° rightwise once and complete the task in time $t = t_t(R) + t_d + t_e(R|R)$, or turn 90° twice and complete the task in time $t = 2t_t(L) + t_d + t_e(L|L)$. Alternatively, ROB can complete the task with opposite hand in time $t = t_t(R) + t_d + t_e(L|R)\ or\ t = 2t_t(L) + t_d + t_e(R|L)$. However, as $t_e(R|R) = t_e(L|L) < t_e(R|L) \sim t_e(L|R)$ the former cases are more efficient. (Table 1)

Position H: ROB can either turn 90° rightwise once and complete the task in time $t = t_t(R) + t_d + t_e(R|C)$, or turn 90° thrice and complete the task in time $t = 3t_t(L) + t_d + t_e(R|C)$. As $t_t(R) = t_t(L)$, the former is more efficient. (Table 1)

Whereas when the object is lying on positions D or E, turning 90° leftwise is more efficient than turning 90° rightwise, when the object is lying on positions G and H, turning 90° rightwise is more efficient than turning 90^oleftwise. When the object is lying on position F, turning 90° rightwise or turning 90^oleftwise are equally efficient. As there are equal number of more or less efficient cases for turning rightwise or leftwise, there is no scope for turning bias. However, in the current setup, the right hand is preferentially used for the terminal act whenever the object is placed symmetrically with respect to the body; thus, a right-hand bias for terminal action has been introduced. Now, consider the case where ROB's one hand is more efficient than the other.

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Given the fact that in any system the resources are limited, there has to be an unequal distribution of these resources depending on the needs. ROB has limited cognitive capacity and thus, if one hand becomes more efficient another hand shows an equal reduction in efficiency. Without loss of generality, we can assume either hand to be more efficient. Here, we proceed with further analysis considering the right hand to be more efficient. Then, when the right hand is more efficient than the left hand, one would observe a small reduction in $t_e(R)$ and an equal increase in $t_e(L)$, that is, $t_e(R) = t_e(L) - dt$, which would pave way for right hand dominance under certain boundary conditions depending on the object position. The following situation arises at different object positions:

Positions A, B, and C

At positions A and B, ROB doesn't need to determine which hand to use, that is, $t_d = 0$; ROB always picks up the object with the right hand in time $t = t_e(R|R)$ or $t_e(R|C)$. At position C, ROB can pick up the object with either hand. However, if the right hand performs better than the left i.e. the boundary condition $t_e(R|L) < t_e(L|L)$ holds, right hand dominance evolves.

Positions D, E, F, G, and H: ROB follows the same sequences of steps as in the previous setup, but always uses its right hand for the terminal act (Table 1; expressions highlighted in bold represent the most efficient solutions).

As described above, an asymmetric element introduced at a lower level can pave the way for the appearance and evolution of asymmetric elements at next higher level, and so on. However, this can happen only when the motor-action pattern at the next higher level lies with the boundary conditions determined by the asymmetry at the lower level. In the present setup, ROB will develop a rightwise turning bias under certain boundary conditions, because it has its right hand more dominant as well as more efficient. In that case, the motor action-patterns that involve turning rightwise are more efficient than those that involve turning leftwise. With all the asymmetries combined, ROB becomes ROB_A. The boundary conditions for rightwise turning bias are derived below:

Positions A, B, and C

ROB_A follows a sequence identical to the previous case and the most efficient cases are highlighted in bold.

Positions D, E, F, G, and H: ROB_A follows the same sequences of steps as in the previous setup, but always uses its right hand for the terminal act. Also, the rightwise turn would be more efficient as compared to leftwise turn, if the boundary conditions derived below hold. They are as follows:

Position D:

At position D, the solution involving rightwise turning would be more efficient if:

$$3t_t(R) + t_e(R|C) < t_t(L) + t_e(R|C)$$

So, we get

$$t_t(R) < t_t(L)/3$$

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Position E:

At position E, the solution involving rightwise turning would be more efficient if:

$$2t_t(R) + t_e(R|R) < t_t(L) + t_e(R|L)$$

So, we get

$$t_t(R) < t_t(L)/2 + (t_e(R|L) - t_e(R|R))/2$$

As, $t_e(R|L) \sim t_e(R|R)$,

$$t_t(R) < t_t(L)/2$$

Position F:

At position F, the solution involving rightwise turning would be more efficient if:

$$2t_t(R) + t_e(R|C) < 2t_t(L) + t_e(R|C)$$

So, we get

$$t_t(R) < t_t(L)$$

Position G:

At position G, the solution involving rightwise turning would be more efficient if:

$$t_t(R) + t_e(R|R) < 2t_t(L) + t_e(R|L)$$

So, we get

$$t_t(R) < 2t_t(L) + t_e(R|L) - t_e(R|R)$$

As, $t_e(R|L) \sim t_e(R|R)$,

$$t_t(R) < 2t_t(L)$$

Position H:

At position D, the solution involving rightwise turning would be more efficient if:

$$t_t(R) + t_e(R|C) < 3t_t(L) + t_e(R|C)$$

So, we get

$$t_t(R) < 3t_t(L)$$

Thus, if the boundary conditions as derived above hold, ROB_A will always turn rightwise yielding the most efficient solutions at particular positions. The boundary condition inducing an overall rightwise turning bias i.e. at all positions, is the one which is the most constrained i.e. $t_t(R) < t_t(L)/3$.

So if the boundary conditions $t_e(R|L) < t_e(L|L)$ and $t_t(R) < t_t(L)/3$ hold, the asymmetric system ROB_A evolves. A schematic representation of the evolution of asymmetries in motor-action patterns is presented in Figure 3. The flowcharts for

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

algorithms for ROB_A and ROB_B for the most efficient solutions given the boundary conditions are satisfied are shown in Figure 4.

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

2.3 Are asymmetries advantageous?

We compare the above two models: ROB_S, which incorporates symmetric motor-action patterns, and ROB_A, which incorporates asymmetric motor-action patterns, to examine whether (a) the asymmetric system performs better than the symmetric one in terms of time optimization, and (b) the advantage associated with the asymmetries in the motor-action patterns increases with the complexity of the task.

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

2.3.1 Symmetric versus asymmetric systems

Let the average time required by ROB_S to complete the task at position α be denoted by S_α and that by ROB_A be denoted by A_α. We determined (a) the expected values of S_α based on a probability distribution, and (b) used the minimum values of A_α as derived in the previous section. Then, for each position (i.e., A through H), we compare the time required by ROB_S and ROB_A to pick up the object, the difference between the two denoted by $(S-A)_\alpha$. When the object is lying at the:

Position A:

$$S_A = 0.5(t_e^s(R|R)) + 0.5(t_e^s(L|R)).$$

$$A_A = t_e^a(R|R).$$

Then,

$$(S-A)_A = 0.5(t_e^s(R|R)) + 0.5(t_e^s(L|R)) - t_e^a(R|R).$$

As $t_e^s(R|R) < t_e^s(L|R)$,

$$(S-A)_A > t_e^s(R|R) - t_e^a(R|R) > 0.$$

Let $t_e^s(R|R) - t_e^a(R|R) = \delta t$, then

$$(S-A)_A > \delta t.$$

Position B:

$$S_B = 0.5(t_e^s(R|C)) + 0.5(t_e^s(L|C)).$$

As derived above (see Table 1), for ROB_A:

$$A_B = t_e^a(R|C).$$

Then,

$$(S-A)_B = 0.5(t_e^s(R|C)) + 0.5(t_e^s(L|C)) - t_e^a(R|C).$$

As $t_e^s(R|C) = t_e^s(L|C)$,

$$(S-A)_B = t_e^s(R|C) - t_e^a(R|C).$$

As $t_e^s(R|C) = t_e^s(R|R)$, $t_e^a(R|C) = t_e^a(R|R)$, and $t_e^s(R|C) > t_e^a(R|C)$,

$$(S-A)_B = t_e^s(R|R) - t_e^a(R|R) > 0.$$

And, as $t_e^s(R|R) - t_e^a(R|R) = \delta t$,

$$(S-A)_B = \delta t.$$

Position C:

$$S_C = 0.5(t_e^s(R|L)) + 0.5(t_e^s L|L)).$$

$$A_C = t_e^a(R|L).$$

Then,

$$(S-A)_C = 0.5(t_e^s(R|L)) + 0.5(t_e^s L|L)) - t_e^a(R|L).$$

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

As $t_e^s(R|L) > t_e^s(L|L)$,

$$(S-A)_C > t_e^s(L|L) - t_e^a(R|L) > 0.$$

As the boundary condition: $t_e^a(R|L) < t_e^a(L|L)$, applies to ROB_A,

$$(S-A)_C > t_e^s(L|L) - t_e^a(L|L) > 0.$$

As $t_e^s(L|L) = t_e^s(R|R)$ and $t_e^a(R|R) < t_e^a(L|L)$,

$$0 < (S-A)_C < t_e^s(R|R) - t_e^a(R|R).$$

And, as $t_e^s(R|R) - t_e^a(R|R) = \delta t$,

$$0 < (S-A)_C < \delta t.$$

Position D:

$$S_D = 0.5(t_t^s + t_e^s) + 0.25(3t_t^s + t_e^s) + 0.125(5t_t^s + t_e^s) + \cdots = 6t_t^s + t_e^s.$$

$$A_D = 3t_t^a(R) + t_e^a(R|C).$$

Then,

$$(S-A)_D = (6t_t^s + t_e^s) - \left(3t_t^a(R) + t_e^a(R|C)\right).$$

As $t_t^s(R) > t_t^a(R)$,

$$(S-A)_D > 3t_t^a(R) + t_e^s - t_e^a(R|C).$$

As $t_e^s = t_e^s(R|C) = t_e^s(L|C)$,

$$(S-A)_D > 3t_t^a(R) + t_e^s(R|C) - t_e^a(R|C).$$

As $t_e^s(R|C) = t_e^s(R|R)$ and $t_e^a(R|C) = t_e^a(R|R)$,

$$(S-A)_D > 3t_t^a(R) + t_e^s(R|R) - t_e^a(R|R).$$

And, as $t_e^s(R|R) - t_e^a(R|R) = \delta t$,

$$(S-A)_D > 3t_t^a(R) + \delta t.$$

Position E:

$$S_E = 0.5(t_t^s + t_e^s) + 0.25(2t_t^s + t_e^s) + 0.125(3t_t^s + t_e^s) + \cdots = 4t_t^s + t_e^s.$$

$$A_E = 2t_t^a(R) + t_e^a(R|R).$$

Then,

$$(S-A)_E = (4t_t^s + t_e^s) - (2t_t^a(R) + t_e^a(R|R)).$$

As $t_t^s(R) > t_t^a(R)$,

$$(S-A)_E > 2t_t^a(R) + t_e^s - t_e^a(R|R).$$

As $t_e^s = t_e^s(R|R)$,

$$(S-A)_E > 2t_t^a(R) + t_e^s(R|R) - t_e^a(R|R).$$

And, as $t_e^s(R|R) - t_e^a(R|R) = \delta t$,

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

$$(S-A)_E > 2t_t^a(R) + \delta t.$$

Position F:

$$S_F = 0.5(2t_t^s + t_e^s) + 0.25(4t_t^s + t_e^s) + 0.125(6t_t^s + t_e^s) + \cdots = 8t_t^s + t_e^s.$$

$$A_F = t_t^a(R) + t_e^a(R|C).$$

Then,

$$(S-A)_F = (8t_t^s + t_e^s) - (2t_t^a(R) + t_e^a(R|C)).$$

As $t_t^s(R) > t_t^a(R)$,

$$(S-A)_F > 6t_t^a(R) + t_e^s - t_e^a(R|C).$$

As $t_e^s = t_e^s(R|C)$,

$$(S-A)_F > 6t_t^a(R) + t_e^s(R|C) - t_e^a(R|C).$$

As $t_e^s(R|C) = t_e^s(R|R)$ and $t_e^a(R|C) = t_e^a(R|R)$,

$$(S-A)_F > 6t_t^a(R) + t_e^s(R|C) - t_e^a(R|C).$$

And, as $t_e^s(R|R) - t_e^a(R|R) = \delta t$,

$$(S-A)_F > 6t_t^a(R) + \delta t.$$

Position G:

$$S_F = 0.5(t_t^s + t_e^s) + 0.25(2t_t^s + t_e^s) + 0.125(3t_t^s + t_e^s) + \cdots = 4t_t^s + t_e^s.$$

$$A_G = t_t^a(R) + t_t^a(R|R).$$

Then,

$$(S-A)_G = (4t_t^s + t_e^s) - (t_t^a(R) + t_e^a(R|R)).$$

As $t_t^s(R) > t_t^a(R)$,

$$(S-A)_G > 3t_t^a(R) + t_e^s - t_e^a(R|R).$$

As $t_e^s = t_e^s(R|R)$,

$$(S-A)_G > 3t_t^a(R) + t_e^s(R|R) - t_e^a(R|R).$$

And, as $t_e^s(R|R) - t_e^a(R|R) = \delta t$,

$$(S-A)_G > 3t_t^a(R) + \delta t.$$

Position H:

$$S_F = 0.5(t_t^s + t_e^s) + 0.25(3t_t^s + t_e^s) + 0.125(5t_t^s + t_e^s) + \cdots = 6t_t^s + t_e^s.$$

$$A_H = 6t_t^a(R) + t_t^a(R|C).$$

Then,

$$(S-A)_H = (6t_t^s + t_e^s) - (t_t^a(R) + t_e^a(R|C)).$$

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

As $t_t^s(R) > t_t^a(R)$,

$$(S-A)_H > 5t_t^a(R) + t_e^s - t_e^a(R|C).$$

As $t_e^s = t_e^s(R|C)$,

$$(S-A)_H > 5t_t^a(R) + t_e^s(R|C) - t_e^a(R|C).$$

As $t_e^s(R|C) = t_e^s(R|R)$ and $t_e^a(R|C) = t_e^a(R|R)$,

$$(S-A)_H > 5t_t^a(R) + t_e^s(R|R) - t_e^a(R|R).$$

And, as $t_e^s(R|R) - t_e^a(R|R) = \delta t$,

$$(S-A)_H > 5t_t^a(R) + \delta t.$$

Thus, $(S-A)_\alpha > 0 \; \forall \; \alpha$. This implies that ROB_A, which incorporates asymmetric motor-action patterns, performs better in terms of time optimization than ROB_S, which incorporates symmetric motor-action patterns.

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

2.3.2 Task complexity and the advantage associated with asymmetry

It is easier for ROB_S, as well as for ROB_A, to pick up the object when it is lying at the position B than at the positions A and C, which are equally cognitively demanding, followed by the positions D, E, F, G, and H since these tasks have additional requirements in terms of turning sidewise and locating the object again. Let the complexity of the task α be denoted by C_α. Without careful consideration one would infer the order of the complexity of the tasks as:

$$C_B < C_A = C_C < C_D = C_E = C_F = C_G = C_H.$$

Assuming that the motor-action patterns are symmetric, the steps required to pick up the object lying at the positions A and C, D and H, and E and G would be similar. Then, while also considering the spatial relationship between these positions (Fig. 1) one would modify the inferred order of complexity of the tasks. The new order would be:

$$C_B < C_A = C_C < C_D = C_H < C_E = C_G < C_F.$$

But, given the fact that ROB cannot perceive objects lying on its transverse axis as it is assumed that, just like humans, ROB has a 178-degree field of vision, when ROB takes the first turn in the direction opposite to that of the object, it needs to turn sidewise once or more, so that the object lies within its field of vision. For example, when the object is lying at the position D, ROB would require to turn sidewise at least once more as compared to when the object is lying at the position E, when ROB turns rightwise first. Also, the lateral symmetry of the position F makes it the lengthiest task for both ROB_S and ROB_A. Thus, carefully considering several factors that might affect the complexity of these tasks, one would infer the order of complexity as:

$$C_B < C_A = C_C < C_E = C_G < C_D = C_H < C_F.$$

The values of $(S-A)_\alpha$ also follow a similar order (Table 2; see Fig. 5):

$$min(S-A)_B < min(S-A)_{A\ or\ C} < min(S-A)_{E\ or\ G} < min(S-A)_{D\ or\ H} < (S-A)_F.$$

This suggests that as the complexity of the task increases the advantage associated with asymmetries in the motor-action patterns in terms of time optimization increases. Though without asymmetries in the motor-action patterns it might seem that tasks E and G should have the same value of $min(S-A)$, and so should the tasks D and H, the introduction of the asymmetries alters the values of $min(S-A)$. The rightwise turning bias combined with right-hand dominance in ROB_A provides an overall advantage in terms of time optimization, altering these values.

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

3 Discussion

In the present study, we develop a minimal model to explain how lateral asymmetries could appear and evolve in a biological system using a systems theory approach. Our model demonstrates that a lower level could stimulate as well as govern asymmetries at the next higher level, and this process might reiterate; ultimately lateralizing the whole system (though we incorporated only two broad levels of asymmetries; see Fig 3). In a comparison of two systems: one incorporating symmetric and the other incorporating asymmetric motor-action patterns, the asymmetric system performs better than the symmetric one in terms of time optimization, and as the complexity of the task increases the advantage associated with asymmetries in the motor-action patterns increases. Thus, asymmetry at any particular level might not be a representative of patterns in a multi-level system. For example, manual asymmetry might be an outcome of a cascade at various levels and may not provide complete information.

In our model, the first asymmetry (i.e., using the right hand for the terminal act when the object is lying towards the ventral side of the transverse plane and exactly on the midsagittal plane) arises out of the conflict between environmental symmetry and the symmetry of the system, which inhibited any motor action. The system could overcome this conflict either by modifying the environment, or by introducing an asymmetry in itself. Breaking the environmental symmetry is a temporary solution because the environment is spatiotemporally variable. So, asymmetry in introduced in the system itself. In biological organisms this can be stochastic. This is then followed by the difference in the efficiency of the two hands, and one-hand dominance, which is sustained if the boundary conditions are satisfied (here, boundary conditions are nothing more than a threshold difference in time efficiency between the two laterally symmetric motor-action patterns. With further complication, when movements require more degrees of freedom (i.e., the object is lying towards the dorsal side of the transverse plane), one-hand dominance stimulates asymmetry in turning; which is sustained when another set of boundary conditions are satisfied. Finally, this highly asymmetric system becomes much more efficient as compared to its initial symmetric state. The increase in efficiency between the two systems becomes more pronounced as the complexity of the task increases.

Although we restricted our focus to a few asymmetries in motor-action patterns (i.e., hand performance and hand preference, turning bias), the analytical method that we developed herein can be generalized to any form of lateral asymmetry, which transcends several degrees of freedom. Our model is not just restricted to the asymmetries favoring the right over the left, but is also generalizable to those that favor the left over the right. Also, whereas we developed our model by meeting the most limiting boundary condition for the appearance of both one-hand dominance and turning bias), the system may develop differential asymmetries depending on the extent to which the required boundary conditions are met.

However, there are several limitations of our model:

(L1) Our minimal model does not incorporate the energy variable. It provides the control solution only in terms of time optimization. A sophisticated model explaining

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

lateral asymmetries should incorporate both the time and the energy variables, simultaneously optimizing them.

(L4) Our minimal model explains the prevalence of lateral asymmetries in motor-action patterns, but only qualitatively. It does not incorporate the extent to which these asymmetries are advantageous in terms of time optimization. A more sophisticated model should quantify each variable incorporated, and their limits.

(L3) Our model considers that stochastic events introduce asymmetric elements in a system, that is, it does not explain how they are introduced, but explains how they are sustained once introduced. Also, it is linear in nature, whereas in biological organisms, random events and stochastic processes may affect the outcomes slightly differently. However, the effects may not be that significant.

(L4) Our model assumes that ROB has a 178-degree field of vision, in order to mimic human-like organisms with comparable fields of vision. This is likely to affect the sequence of steps required to solve a task and consequently, the total time. However, since this constraint is common to both the symmetric and asymmetric systems in the present study, it does not affect the validity of our model.

(L5) Our model assumes that ROB can turn exactly 90° at a time, which may not happen in reality. Depending on the position of the object a partial turn (i.e., $< 90^o$) may be enough for ROB to locate the object within its 178-degree field of vision and execute the next step. However, this simplification does not affect the validity of the model given that while executing a rapid motor action, it becomes increasingly difficult to process afferent information (see Schmidt and Lee 2005).

More sophisticated models, extending the theme of the present one, are required to explain the structure of lateral asymmetries. Other than addressing the aforementioned limitations, future models should incorporate additional variables, such as the stochasticity in decision making, for a more robust cost-benefit analysis. Such models can be evaluated and tested by incorporating them into intelligent robotic systems.

Acknowledgements. We thank Werner Kaumanns for that fruitful discussion which led to this manuscript.

References

Bradshaw J, Rogers LJ (1993) The Evolution of Lateral Asymmetries, Language, Tool Use and Intellect. Academic Press, San Diego

Bullington WE (1925) A study of spiral movement in the ciliate *Infusoria*. Achieve fur Protisten 50: 219–275

Bullington WE (1930) A further study of spiraling in the ciliate *Paramecium* with a note on morphology and taxonomy. J Exp Zool 56: 423–429

Grebecki A, Micolajczyk E (1968) Ciliary reversal and re-normalization in *Paramecium caudatum*. Acta Protozoologica 5: 297–303

Hoeniger J (1966) Cellular changes accompanying the swarming of *Proteus mirabilis*. Can J Microbiol 12:113–123

Glezer II (1987) The riddle of Carlyle: the unsolved problem of the origin of handedness. Behav Brain Sci 10: 273–275

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

MacNeilage PF, Studdert-Kennedy MG, Lindblom B (1987) Primate handedness reconsidered. Behav Brain Sci 10: 247–263

Schaeffer AA (1931) On molecular organization in Ameban protoplasm. Science 74: 47–51

Schmid G (1918) Zur Kenntnis der Oscillatorienbewegung. Flora 111: 327–379

Schmid G (1919) Ein Hilfsmittel zum Unterscheiden verschiedener Oscillatoria- und Phormidiumarten. Berliner deutsche botanische Ges. 37: 473–376

Schmidt, RA, Lee, TD (2005). Motor Control and Learning: A Behavioral Emphasis. Human Kinetics, Champaign, Illinois

Table 1. Time taken by ROB to pick up an object lying in various positions in the transverse plane of its body and the boundary conditions under which lateral asymmetries could appear and evolve.

Constraints				Both hands are equally efficient ($t_e(R\|R) = t_e(R\|C) = t_e(L\|L) = t_e < t_e(R\|L) \sim t_e(L\|R)$).	Right hand is more efficient ($t_e(R\|R) \sim t_e(R\|C) < t_e(L\|L)$); Rightwise and leftwise turning are equally efficient ($t_t(R) = t_t(L)$); Right-hand dominance would evolve.		Right hand is more efficient ($t_e(R\|R) \sim t_e(R\|C) < t_e(L\|L)$); Rightwise turning bias would evolve.	
Position of the object	**Time to turn (t_t)**	**Time to decide (t_d)**	**Time to execute the terminal action (t_e)**	**Total time (t)** (expressions in bold represent the more efficient alternative)	**Boundary condition for right-hand dominance**	**Total time (t)** (expressions in bold represent the more efficient alternative)	**Boundary condition for rightwise turning bias**	**Total time (t)** (expressions in bold represent the more efficient alternative)
A	0 0	t_d t_d	$t_e(R\|R)$ $t_e(L\|R)$	$\boldsymbol{t_d + t_e(R\|R)}$ $t_d + t_e(L\|R)$	N/A	$t_e(R\|R)$	N/A	$\boldsymbol{t_e(R\|R)}$
B	0	t_d	$t_e(R\|C)$	$\boldsymbol{t_d + t_e(R\|C)}$	N/A	$t_e(R\|C)$	N/A	$\boldsymbol{t_e(R\|C)}$
C	0 0	t_d t_d	$t_e(L\|L)$ $t_e(R\|L)$	$t_d + t_e(R\|L)$ $\boldsymbol{t_d + t_e(L\|L)}$	$t_e(R\|L) < t_e(L\|L)$	$\boldsymbol{t_e(R\|L)}$ $t_e(L\|L)$	N/A	$\boldsymbol{t_e(R\|L)}$ $t_e(L\|L)$
D	$3t_t(R)$ $t_t(L)$	t_d t_d	$t_e(R\|C)$ $t_e(R\|C)$	$3t_t(R) + t_d + t_e(R\|C)$ --- $\boldsymbol{t_t(L) + t_d + t_e(R\|C)}$	N/A	$3t_t(R) + t_e(R\|C)$ --- $\boldsymbol{t_t(L) + t_e(R\|C)}$	$t_t(R) < t_t(L)/3$	$\boldsymbol{3t_t(R) + t_e(R\|C)}$ --- $t_t(L) + t_e(R\|C)$
E	$2t_t(R)$ $t_t(L)$	t_d t_d	$t_e(R\|R)$ $t_e(L\|L)$	$\boldsymbol{2t_t(R) + t_d + t_e(R\|R)}$ $2t_t(R) + t_d + t_e(L\|R)$ --- $t_t(L) + t_d + t_e(R\|L)$ $\boldsymbol{t_t(L) + t_d + t_e(L\|L)}$	$t_e(R\|L) < t_e(L\|L)$	$\boldsymbol{2t_t(R) + t_e(R\|R)}$ $2t_t(R) + t_e(L\|R)$ --- $\boldsymbol{t_t(L) + t_e(R\|L)}$ $t_t(L) + t_e(L\|L)$	$t_t(R) < t_t(L)/2$	$\boldsymbol{2t_t(R) + t_e(R\|R)}$ $2t_t(R) + t_e(L\|R)$ --- $t_t(L) + t_e(R\|L)$ $t_t(L) + t_e(L\|L)$
F	$2t_t(R)$ $2t_t(L)$	t_d t_d	$t_e(R\|C)$ $t_e(R\|C)$	$\boldsymbol{2t_t(R) + t_d + t_e(R\|C)}$ **---** $\boldsymbol{2t_t(L) + t_d + t_e(R\|C)}$	N/A	$\boldsymbol{2t_t(R) + t_e(R\|C)}$ **---** $\boldsymbol{2t_t(L) + t_e(R\|C)}$	$t_t(R) < t_t(L)$	$\boldsymbol{2t_t(R) + t_e(R\|C)}$ **---** $2t_t(L) + t_e(R\|C)$
G	$t_t(R)$ $2t_t(L)$	t_d t_d	$t_e(R\|R)$ $t_e(L\|L)$	$\boldsymbol{t_t(R) + t_d + t_e(R\|R)}$ $t_t(R) + t_d + t_e(L\|R)$ --- $2t_t(L) + t_d + t_e(R\|L)$ $\boldsymbol{2t_t(L) + t_d + t_e(L\|L)}$	$t_e(R\|L) < t_e(L\|L)$	$\boldsymbol{t_t(R) + t_e(R\|R)}$ $t_t(R) + t_e(L\|R)$ --- $\boldsymbol{2t_t(L) + t_e(R\|L)}$ $2t_t(L) + t_e(L\|L)$	$t_t(R) < 2t_t(L)$	$\boldsymbol{t_t(R) + t_e(R\|R)}$ $t_t(R) + t_e(L\|R)$ --- $2t_t(L) + t_e(R\|L)$ $2t_t(L) + t_e(L\|L)$
H	$t_t(R)$ $3t_t(L)$	t_d t_d	$t_e(R)$ $t_e(R)$	$\boldsymbol{t_t(R) + t_d + t_e(R\|C)}$ **---** $3t_t(L) + t_d + t_e(R\|C)$	N/A	$\boldsymbol{t_t(R) + t_e(R\|C)}$ --- $3t_t(L) + t_e(R\|C)$	$t_t(R) < 3t_t(L)$	$\boldsymbol{t_t(R) + t_e(R\|C)}$ --- $3t_t(L) + t_e(R\|C)$

Table 2. Time taken by the perfectly symmetric (ROB_S) and asymmetric (ROB_A) systems to pick up an object lying in various positions in the transverse plane of their body.

Position of the object	ROB_S ($t_t^s(R) = t_t^s(L) = t_t^s$; $t_e^s(R\|R) = t_e^s(L\|L) = t_e^s(R\|C) = t_e^s(L\|C) = t_e^s$)	ROB_A (see Table 1)	$S - A$ ($\delta t = t_e^s(R\|R) - t_e^a(R\|R)$) (see derivations in the text)
A	$0.5(t_e^s(R\|R)) + 0.5(t_e^s(L\|R))$	$t_e^a(R\|R)$	$> \delta t$
B	$0.5(t_e^s(R\|C)) + 0.5(t_e^s(L\|C)) = t_e^s(R\|C)$	$t_e^a(R\|C)$	$= \delta t$
C	$0.5(t_e^s(R\|L)) + 0.5(t_e^s L\|L))$	$t_e^a(R\|L)$	$> \delta t$
D	$0.5(t_t^s + t_e^s) + 0.25(3t_t^s + t_e^s) + 0.125(5t_t^s + t_e^s) + \cdots = 6t_t^s + t_e^s$	$3t_t^a(R) + t_e^a(R\|C)$	$> 3t_t^a(R) + \delta t$
E	$0.5(t_t^s + t_e^s) + 0.25(2t_t^s + t_e^s) + 0.125(3t_t^s + t_e^s) + \cdots = 4t_t^s + t_e^s$	$2t_t^a(R) + t_e^a(R\|R)$	$> 2t_t^a(R) + \delta t$
F	$0.5(2t_t^s + t_e^s) + 0.25(4t_t^s + t_e^s) + 0.125(6t_t^s + t_e^s) + \cdots = 8t_t^s + t_e^s$	$2t_t^a(R) + t_e^a(R\|C)$	$> 6t_t^a(R) + \delta t$
G	$0.5(t_t^s + t_e^s) + 0.25(2t_t^s + t_e^s) + 0.125(3t_t^s + t_e^s) + \cdots = 4t_t^s + t_e^s$	$t_t^a(R) + t_e^a(R\|R)$	$> 3t_t^a(R) + \delta t$
H	$0.5(t_t^s + t_e^s) + 0.25(3t_t^s + t_e^s) + 0.125(5t_t^s + t_e^s) + \cdots = 6t_t^s + t_e^s$	$t_t^a(R) + t_e^a(R\|C)$	$> 5t_t^a(R) + \delta t$

bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Fig. 1. The possible positions of an object in the transverse plane of ROB's body.

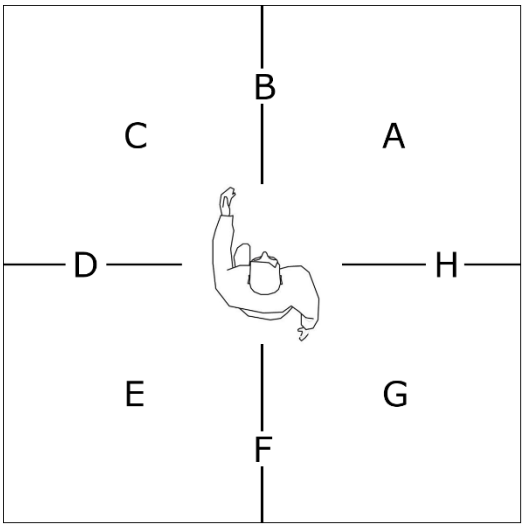
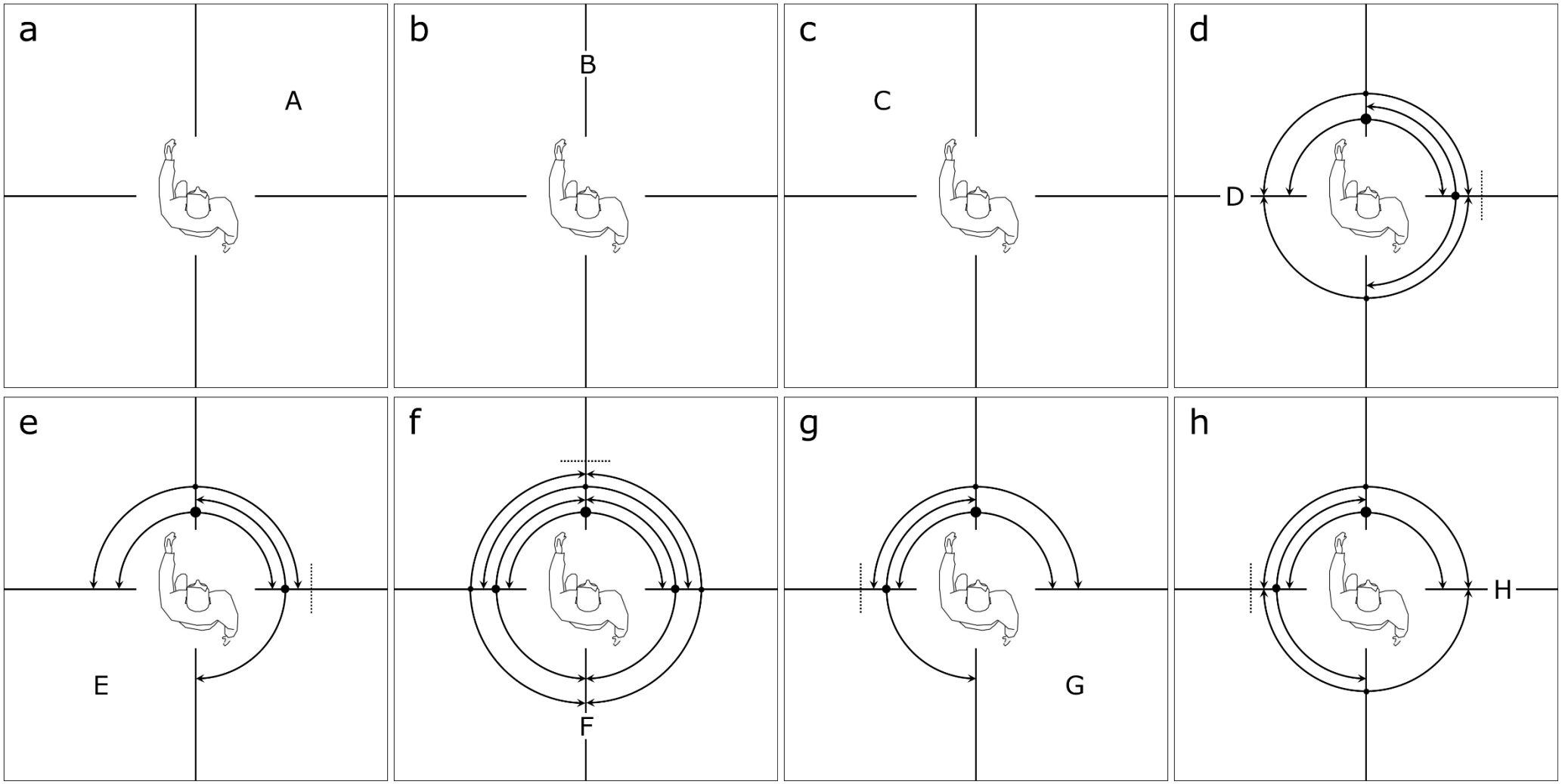
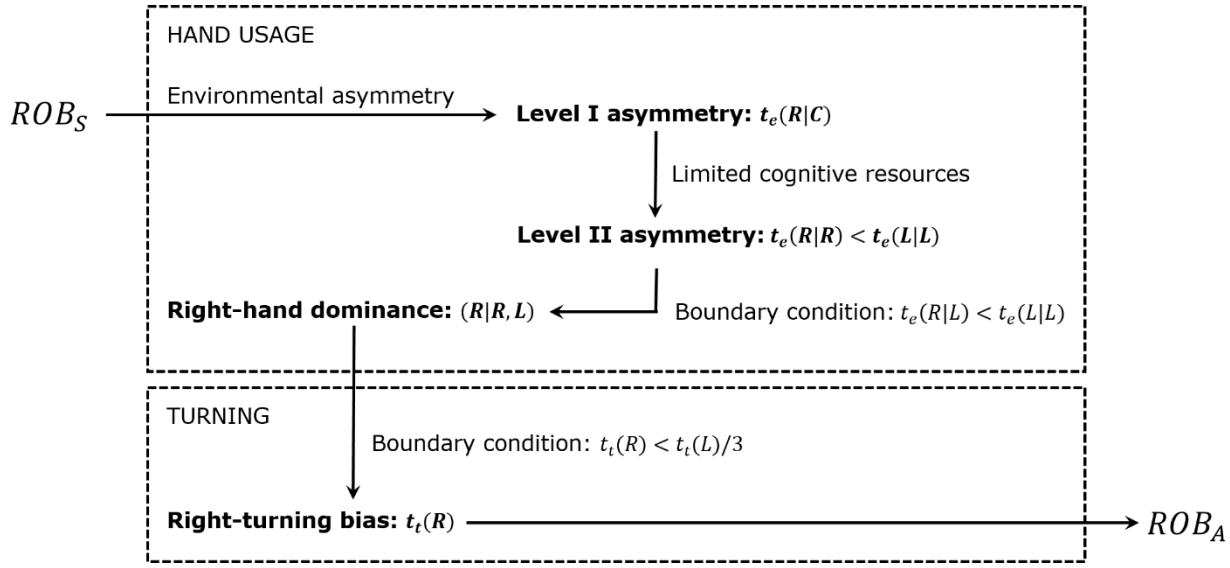


Fig. 2a-h. Schematic representation describing the possible sequences of steps that could be taken by ROB_S to pick up the object lying in various positions in the transverse plane of its body.



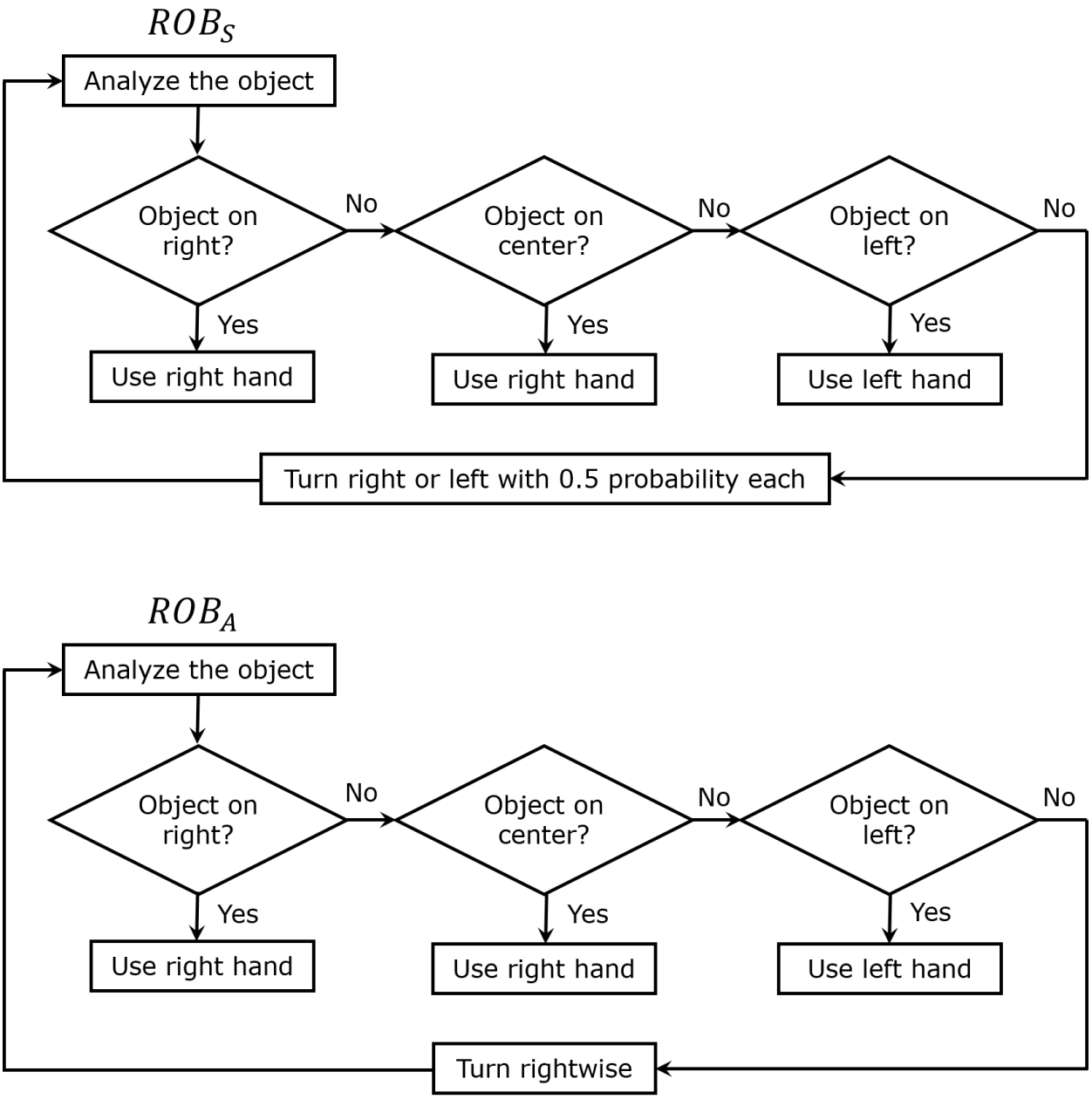
bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Fig. 3. Progression of lateral asymmetries in motor-action patterns in a system.



bioRxiv preprint doi: https://doi.org/10.1101/013268; this version posted December 26, 2014. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Fig. 4. The flowcharts for ROB_S and ROB_A for the most efficient alternative.



bioRxiv preprint doi: https://doi.org/10.1101/618268; this version posted December 26, 2024. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

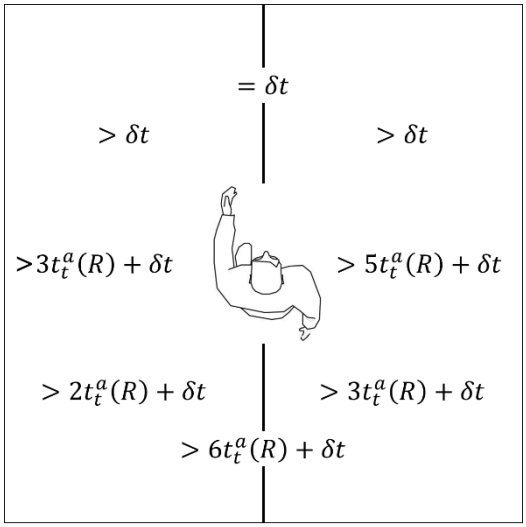



Fig. 5. The minimum values of $S - A$ for the different positions of the object ($\delta t = t_e^s(R|R) - t_e^a(R|R)$).