

# **Division of Labor: A Democratic Approach towards Understanding Manual Asymmetries in Non-Human Primates**

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## Certificate

This is to certify that this dissertation entitled “Division of Labor: A Democratic Approach towards Understanding Manual Asymmetries in Non-Human Primates” towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents original research carried out by “Nisarg Desai, IISER Pune” under the supervision of “Mewa Singh, Professor, Biopsychology Department, University of Mysore ” during the academic year 2014-2015.



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## Declaration

I hereby declare that the matter embodied in the report entitled “Division of Labor: A Democratic Approach towards Understanding Manual Asymmetries in Non-Human Primates” are the results of the investigations carried out by me at the Biopsychology Department, University of Mysore, under the supervision of Mewa Singh and the same has not been submitted elsewhere for any other degree.



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## Abstract

Previously, through manipulative experiments we demonstrated the division of labor in hand usage in free-ranging bonnet macaques wherein we showed that unlike human handedness, the two hands in primates are specialized for different kinds of tasks (maneuvering in 3-d space versus physical strength). In an attempt to explore division of labor in other species, we reviewed the studies on handedness in capuchin monkeys, *Cebus* spp. and argued that the hand-usage patterns seen in those studies dovetail with the proposed idea of division of labor. Also, through our review we emphasized the need to consider forms and functions while studying laterality, proposed experimental designs that would facilitate studying manual asymmetries and qualified the scope of individual, population, or species comparisons. Further we speculated adaptive value of the division of labor and showed that it is associated with hand performance. Considering the problem of adaptive value in more detail, we mathematically modeled how an asymmetric element at lower level could instigate and govern asymmetries at the next higher level, then to other next higher level and so on; in the end lateralizing the whole system. We used the model to compare a symmetric (employing symmetric motor-action patterns) and an asymmetric (employing asymmetric motor-action patterns) system and showed that asymmetric system not only performed better as compared the symmetric system in terms of time optimization, but also provided greater advantage as the complexity of the task increased. Finally, we tested if the macaques were aware about the difference in maneuvering dexterity of their two hands using apparatus of the hand-performance differentiation task. However, the experimental setup could not provide sufficient evidence for the same.

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## Introduction

### Division of labor in hand-usage in primates

There is population-level right-hand bias in humans (around 90% humans are right handed) (Birkett, 1987; Raymond and Pontier, 2004). Thus, the origins of hand preference in humans and their closest relatives non-human primates are of great interest (Cashmore et al., 2008). Handedness in non-human primates might have evolved because of functional requirements viz. foraging in arboreal situations and it might also be a more primitive form of human handedness which might provide insights about the population-level bias in handedness in humans (Bradshaw and Rogers, 1993; MacNeilage et al., 1987; Papademetriou et al., 2005). Thus, behavioral asymmetries in non-human primates might provide understanding about the behavioral lateralities in humans. Primates generally show asymmetry in hand usage. It is generally referred to as handedness in literature (Andrew and Rogers, 2002; Bradshaw and Rogers, 1993; Fitch and Braccini, 2013). One can define handedness in terms of (i) hand used to solve a task or for a bimanual task, hand used to perform the most complex action: “hand preference,” or (ii) hand which is most efficient: “hand performance” (Barnsley and Rabinovitch, 1970).

Two notable theories look into the question of evolutionary origins of handedness in non-human primates: the task complexity theory (Fagot and Vauclair, 1991) and the postural origins theory (MacNeilage et al., 1987). According to postural origins theory, first the left hand was predominantly used for visually guided movements, and the right hand was predominantly used for postural support. Later, as some primates began adopting more terrestrial lifestyle, the right hand was predominantly used for physical manipulation and not for postural support as the opposable thumb developed and right hand was not required for supporting vertical posture. Nonetheless, the postural origins theory lacks an explanation for the initial dominance of the left-hand (as opposed to the right hand) for visually guided reaching, and above all, fails to explain the evolution of the population-level right-handedness during the progression from monkeys to humans (McGrew and Marchant, 1997).

Further, based on ideas proposed by MacNeilage et al., 1987, Fagot and Vauclair, 1991 proposed the task complexity theory. Fagot and Vauclair, 1991 acknowledge that hand preference might depend on the task and the situation, that is the novelty required in manual actions based on task demands as well as the time and space required by manual actions depending on situation might affect hand preference and thus, hand usage patterns. The task complexity theory separates tasks in the two broad domains viz. low-level tasks and high-level tasks. Low-level tasks comprise of manual actions that are cognitively less demanding and frequently employed (e.g. unimanual food reaching). They tend to show unbiased hand-usage patterns at the population-level that do not point towards hand specialization. On the other hand, high-level tasks comprise of manual actions that are highly cognitively demanding and thus not employed very frequently. They show biased hand-usage patterns at the population-level that point towards specialization of the two hands. Additionally, they speculate the lack of a particular (left or right) population-level bias in non-human primates and maintain that this inconsistency is because of the diversity of the tasks and differential cognitive processes that are employed while solving them. In a nutshell, they separate the tasks in the two domains viz. low-level and high-level, in order to give a distinction between two different types of manual asymmetries viz. hand preference and manual specialization. Many studies on different species confirm the task complexity theory: captive red-capped mangabeys, *Cercocebus torquatus* (Blois-Heulin et al., 2006; Laurence et al., 2011), captive Campbell's monkeys, *Cercopithecus campbelli* (Chapelain et al., 2006), captive tufted capuchins, *Cebus paella* (Lilak and Phillips, 2008; Spinozzi et al., 1998; Westergaard and Suomi, 1996), wild vervet monkeys, *Chlorocebus aethiops* (Harrison and Byrne, 2000), captive gorillas, *Gorilla gorilla berengei* (Byrne and Byrne, 1991), captive De Brazza's monkeys, *Cercopithecus neglectus* (Schweitzer et al., 2007; Trouillard and Blois-Heulin, 2005), wild Sichuan snub-nosed monkeys, *Rhinopithecus roxellana* (Zhao et al., 2010), and captive chimpanzees, *Pan troglodytes* (Colell et al., 1995). Nonetheless, in the task complexity theory, the description of a complex manual task is based on the spatiotemporal succession of the steps or the

number of steps involved in the task, which are largely contextual. Additionally, many other factors that might have played a role in the evolution of handedness are beyond the scope of these two theories.

Many other studies provide evidence for specialized usage of hands (in both natural as well as manipulative settings). In natural settings: captive chimpanzees (Hopkins, 1994) and captive gorillas (Meguerditchian et al., 2010) (for feeding), wild Sichuan snub-nosed monkeys (Zhao et al., 2010) and captive as well as wild chimpanzees (Hopkins et al., 2007) (for grooming), free-ranging Japanese macaques, *Macaca fuscata* (Leca et al., 2010) (for stone-play handling), captive sifakas, *Propithecus sp.* (Milliken et al., 2005) (for arboreal feeding). And in manipulative setting: red-capped mangabeys (Blois-Heulin et al., 2006), De Brazza's monkeys (Schweitzer et al., 2007), tufted capuchins, and rhesus macaques, *Macaca mulatta* (Westergaard and Suomi, 1996), olive baboons, *Papio anubis* (Vauclair et al., 2005), and chimpanzees (Hopkins, 1995).

In our previous study (Mangalam et al., 2014a) we claim that the observations from the aforementioned studies point towards the two hands being specialized for different tasks (requiring maneuvering in 3-d space or those requiring relatively higher physical strength). We substantiated the claim via observations from manipulative experiments as well as observations from spontaneous-routine activities like grooming, hitting or climbing, in natural setting. We further speculate the adaptive value of this division of labor in the following section.

## **Division of labor in hand-usage associated with hand performance**

One way to understand the prevalence of asymmetries in body, brain, and cognition is to study their adaptive value i.e. advantages or disadvantages associated with them in terms of performance (time or energy optimization). Here, we examined if the division of labor in hand usage as

described by (Mangalam et al., 2014a), stating that one hand is specialized for tasks requiring maneuvering in 3-d space and the other is specialized for tasks requiring relatively higher physical strength, is related to improved hand performance in bonnet macaques. We used two experimental tasks (unimanual and bimanual) to quantify the laterality in hand usage, and used a hand-performance differentiation task to quantify hand performance and examined whether they are related. We quantified their association by showing negative relationships between (a) the latency in food extraction by the maneuvering hand in the hand-performance differentiation task (lower latency means higher performance) and the normalized difference between the performances of the two hands (a measure of difference in efficiencies of the two hands). Here, the maneuvering hand was decided based on the bimanual food-reaching task, and (b) the normalized difference between the performances of the two hands and the absolute difference between the laterality in hand usage in the unimanual and the bimanual food-reaching tasks (lesser difference means higher manual specialization). This difference in the laterality in hand usage (measured as Handedness Index, HI) between the unimanual and the bimanual food-reaching tasks gave us a measure of manual specialization, which is different from hand preference. Collectively, these negative correlations imply that the division of labor between the two hands is related with higher hand performance.

In the light of our findings from these studies (Mangalam et al., 2014a, 2015), we review studies on capuchin monkeys as described in the section below.

## **Division of labor: a democratic approach towards understanding manual asymmetries in non-human primates**

We analyze tasks used in various studies on handedness in capuchin monkeys, *Cebus spp.* and assert that the observations in these studies point towards specialization as described by Mangalam et al., 2014a (stating that one hand is specialized for tasks requiring maneuvering in 3-d space and the other is specialized for tasks requiring relatively higher physical strength)

(Mangalam et al., 2014b). For the tasks from these studies, we particularly do the following: (a) analyze them based on their attributes like the number of hands required to solve them viz. unimanual, pseudo unimanual, or bimanual; and the progression of manual actions in space and time viz. sequential or concurrent. (b) Determine how laterality in hand usage is manifested (in terms of forms and functions) from these tasks within the behavioral repertoire of an individual, a population, or a species. (c) Argue about the validity of the inter-individual, -population, or -species comparisons. From our analysis, we conclude that division of labor is a general principle underlying handedness in non-human primates, and also propose experimental paradigms that can facilitate observing the forms and functions of handedness in non-human primates, and also their adaptive value, in order to substantiate this possibility.

From our studies on bonnet macaques (Mangalam et al., 2014a, 2015) and our analysis of tasks used in handedness studies in capuchin monkeys (Mangalam et al., 2014b), we find the following: (a) Because of an inherent bias towards human-like handedness, studies on handedness in non-human primates have been only looking at patterns at the population level and thus failing to understand forms and functions of manual asymmetries which can be revealed by studying patterns at the individual level. (b) These studies don't properly define task complexity and task requirements in terms of the form (e.g., power or precision grip; see Napier, 1956) or function (e.g., maneuvering in 3-d space and providing physical strength) and so are largely contextual. (c) In tasks involving more than one steps, the step(s) before the final step might not be a part of the behavioral repertoire of an individual, a population, or a species. In such a situation, comparisons of hand-usage patterns between individuals, populations, or species might be misleading. So, in the review, we emphasised the need to consider forms and functions while studying laterality, and the associated adaptive value, proposed experimental designs that would facilitate studying manual asymmetries and qualified the scope of between individual, population, or species comparisons.

We further try to speculate the adaptive value of asymmetries and this time employ a mathematical modeling approach. We use systems theory

approach to model asymmetries in a humanoid robotic system as described in the section below.

## Exploring manual asymmetries using systems-theory approach

Asymmetries in body, brain, and cognition are very prevalent among organisms. They are observed from micro-organisms (prokaryotes and eukaryotes) to higher life forms like primates (Bradshaw and Rogers, 1993). For example, in bacteria like *Proteus*, *Clostridium*, and *Bacillus* asymmetry is observed in the direction of rotation (Hoeniger, 1966); in unicellular organisms like *Amoeba* and *Infusoria* there is asymmetry in the trajectory of propelling movements (Bullington, 1925, 1930; Schaeffer, 1931). One can anticipate that the first appearance of asymmetry could arise out of the very basic need of movement. A completely symmetric organism simply cannot move and thus symmetry has to be broken in order for movement to arise. Similarly, as there is asymmetry in the environment, asymmetries within organisms might appear in order to deal with environmental asymmetry.

This striking prevalence of asymmetries raises questions about what sustains such asymmetries. An adaptationist's perspective would be that these asymmetries are adaptive, that is to say that they provide some advantage to the organisms. As observed in Mangalam et al., 2015, one could hypothesize that the asymmetries provide a performance advantage and thus, we attempt to formulate the problem of asymmetries as a control and optimization problem wherein, asymmetries facilitate time or energy optimization.

We approach the control and optimization problem using a mathematical model. We use systems theory approach to develop a minimal mathematical model to address the problem of asymmetries. According to systems theory, an asymmetric element at lower level could stimulate as well as govern asymmetries at a next higher level, then to other next higher level and so on; in the end lateralizing the whole system (Thelen and Smith, 1996). We use the model to design and compare two systems (a completely symmetric and an asymmetric) in a humanoid robot attempting to solve a task

that requires solving a simple object-reaching task. We show that the asymmetric system performs better than the symmetric system in terms of time optimization and additionally it provides greater advantage as the complexity of the task increases.

## **Do monkeys know that they perform better with one hand?**

### **Experiment 1**

Building up on our past work wherein we showed that one hand is more efficient than the other (Mangalam et al., 2014a), we explored if monkeys have an understanding about this peculiarity of theirs i.e. whether they know that one of their hands is more efficient as compared to the other. This requires an experimental paradigm wherein only one hand can be used at a time and also should incorporate conditions that would elicit decision-making process to choose either of the hands depending on the external conditions; from which one can make inferences about the awareness of the macaques about the difference in the efficiency of the two hands. The need for forcing the usage of only one hand at a time is fulfilled by the apparatus of the hand performance differentiation task used in previous experiments (Mangalam et al., 2014a, 2015). And the need to elicit a decision-making process was addressed by introducing a threat in the form of a human approaching with eye contact, thus creating a sense of urgency to solve the task.

## **Methods**

### **Ethics Statement**

We adhered to the American Society of Primatologists (ASP) “Principles for the Ethical Treatment of Nonhuman Primates” and conducted the present study as a part of an ongoing research project that was approved by the Institutional Animal Ethics Committee (IAEC) at the University of Mysore (because we conducted our research on individuals which (a) did not belong to an endangered or a protected species, and (b) inhabited an unprotected land with an unrestricted public access, our research work did not require permission from any other authority).

### **Experiment 1**

#### **Subjects and Study Site**

We conducted the experiment on 7 bonnet macaques, 2 juvenile males, 1 juvenile female and 2 adult females from Chamundi Hill top and 2 adult females from Chamundi foothills in Mysore, India (2°14'41"N 76°40'55"E). We observed the hand usage patterns from a distance after placing the apparatus within ca. 1 m of the focal macaque when there was no conspecific within ca. 3 m from it.

#### **Experimental procedure**

We first determined the maneuvering hand of the macaques by presenting them three grapes, a number sufficient to motivate the macaques to perform the task, in an unlidded wire mesh box repeated seven times to control for external confounding factors that might effect the hand usage pattern. We observed the hand used to extract the grapes and labeled it as the maneuvering hand. Further, we designed a three-step experiment using the apparatus of the hand performance differentiation task. The apparatus of the hand-performance differentiation task consists of two unlidded wire mesh



boxes placed below wooden pieces which are fixed such that they ergonomically allow only one particular hand at a time and thus force the macaques to also use their non-preferred hand for food extraction tasks (Figure 1, Movie S1). This is possible because of the positioning of the board with respect to the restricted opening to the mesh box, which is much less wide as compared to a macaque's width, which ergonomically allows only the hand facing the board to reach the bottom of the mesh box.

In first step in the experiment, both the wire mesh boxes will be filled with equal number of grapes. In this case, one would expect a macaque to choose the side of its maneuvering hand first. In second step, there will be more grapes in the mesh box corresponding to hand opposite to the maneuvering hand. In this case, one would expect the macaque to approach the mesh box with higher number of grapes first. In the final step, there will be greater number of grapes in the mesh box corresponding to hand opposite to the maneuvering hand. Additionally, there will be a threat in the form of a human approaching at a constant speed with eye contact to the macaque. Here, if the macaques shift to the wire mesh box on the maneuvering hand side, consisting of lower number of grapes, one can infer that the macaques have some understanding about one of their hands being more efficient. The final step can be valid only if the expectation in the second step is met i.e. if the macaques prefer the mesh box with greater number of grapes even if the mesh box corresponds to the hand opposite to its maneuvering hand.

We conducted five trials for each step while conducting the final step only if the expectation in the second step was met. The number of grapes was five in each mesh box for step one. For step two and three, the number of grapes in the mesh box corresponding to the maneuvering hand was four and the number of grapes corresponding to the supporting hand was seven.

**FIGURE 1.** Apparatus for the hand-performance-differentiation task



# Results and Discussion

## Experiment 1

Table 1 reports raw data for hand usage by the seven macaques. Task 1 is the food extraction task used to determine the maneuvering hand and the number of times (out of 7) the majorly used hand was used is mentioned as maneuvering hand in the table. Three (AF2, JF1 and JM2) out of the seven macaques did not respond to the unequal number of grapes in the second step and hence the final step was not carried out for them. Other three (AF3, AF4 and JM1) show expected patterns whereas AF1 showed expected patterns three out of five times.

**TABLE 1.** Raw data on hand usage for in five trials for each of the three steps (M=maneuvering hand, S=supporting hand)

	AF1		AF2		AF3		AF4		JF1		JM1		JM2	
	M	S	M	S	M	S	M	S	M	S	M	S	M	S
<b>Task 1</b>	5	2	7	0	7	0	7	0	7	0	7	0	7	0
<b>Step 1</b>	5	0	5	0	5	0	5	0	4	1	5	0	4	1
<b>Step 2</b>	0	5	5	0	1	4	0	5	4	1	0	5	5	0
<b>Step 3</b>	3	2	-	-	5	0	4	1	-	-	4	1	-	-

Step 1 consists of equal number of grapes in both the wire-mesh boxes and one would expect that in absence of any confounding variables, the macaques would prefer the mesh box corresponding to their maneuvering hand first and extract from the other box later. Consistency was observed for all the macaques over the five trials and they always used their maneuvering hand first. In step 2, the mesh box corresponding to the supporting hand has greater number of grapes and so if the macaques are going for greater quantity of food over quick extraction, they would prefer the mesh box with greater number of grapes first. This was observed for four out of the seven macaques. The next step was carried out only for these four macaques. In step 3, again there were greater number of grapes in the mesh box corresponding to the supporting hand, but there is a threat in the form of human approaching the macaque at constant speed and eye-contact, which creates a sense of urgency to extract the food. Thus, the macaques would be

expected to choose quick extraction over greater quantity in this case and since these are the same individuals who chose greater quantity over quick extraction in the absence of threat, one can infer that they realize that they can extract food faster with their maneuvering hand. Three (AF3, AF4 and JM1) out of four macaques showed a clear shift whereas one macaque (AF1) showed the expected pattern three out of five times.

Though expected results are seen for three of the macaques, the number is not sufficient for obtaining any reliable inference. Also, none of the other individuals from the two groups could be considered a valid sample as either they could not solve the task, or they did not attempt to solve at all. Few of the females who had previously participated in the hand-performance differentiation task did not participate this time. This might have been because either they were carrying newly born infants or they were pregnant and thus showed reluctance to participate in the experiment.

# Exploring manual asymmetries using systems-theory approach

## The Model

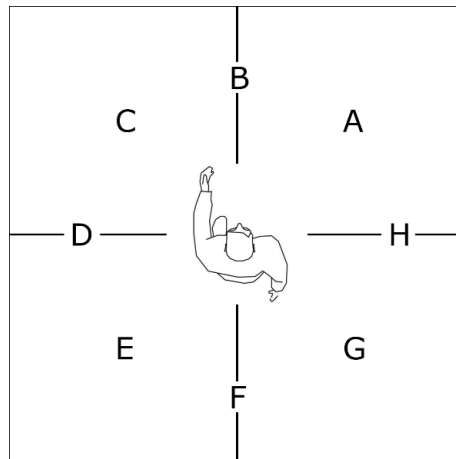
We aim to speculate the adaptive value of handedness by examining advantages associated with asymmetries in hand usage. We use systems theory approach to develop a minimal mathematical model to address the problem of asymmetries. According to systems theory, an asymmetric element at lower level could stimulate as well as govern asymmetries at a next higher level, then to other next higher level and so on; in the end lateralizing the whole system (Thelen and Smith, 1996). We aim to use the model to design and compare two systems (a completely symmetric and an asymmetric). Further, we aim to examine the difference between the two systems as the complexity of the task increases.

In order to do the above, we speculate the dynamics in case of a hypothetical humanoid robotic system (we name it *ROB*). *ROB* has to solve a simple task of reaching an object that might be lying anywhere on its transverse plane (Fig 2). We speculate how there might evolve situation wherein asymmetries appear and work out conditions under which the asymmetries would sustain once appeared. We start with a completely symmetric system that is not biased to use any of the hands predominantly. Also, for simplicity, without compromising the validity of the model, we assume the following:

- (A1) At a time, *ROB* can scan 178-degrees on its front side, like humans.
- (A2) Initially *ROB* is completely symmetric. We denote it as  $ROB_S$ .
- (A3) In absence of asymmetry,  $ROB_S$  makes decisions using a random number generator.

These assumptions let us mimic a biological system and provide us with a mathematical tool to proceed with our calculations.

**FIGURE 2.** The possible positions of an object in the transverse plane of ROB's body.



## Symmetric motor-action patterns

An object can lie anywhere on the transverse plane of  $ROB_S$ 's body (in any of the four quadrants, Fig. 2). In order to perform the object-reaching task,  $ROB_S$  has to scan the position of the object, if needed, turn either side with equal probability and finally pick the object with either hand with equal probability. The following notations will be used throughout:

$t_t^s(R)$  and  $t_t^s(L)$ : the time taken by  $ROB_S$  to turn  $90^\circ$  rightwise and leftwise respectively.

$t_e^s(R|R)$  and  $t_e^s(R|L)$ : the time taken by  $ROB_S$  to execute the action of picking up the object with its right hand given the object is lying on the right and on the left side of its midsagittal plane, respectively.

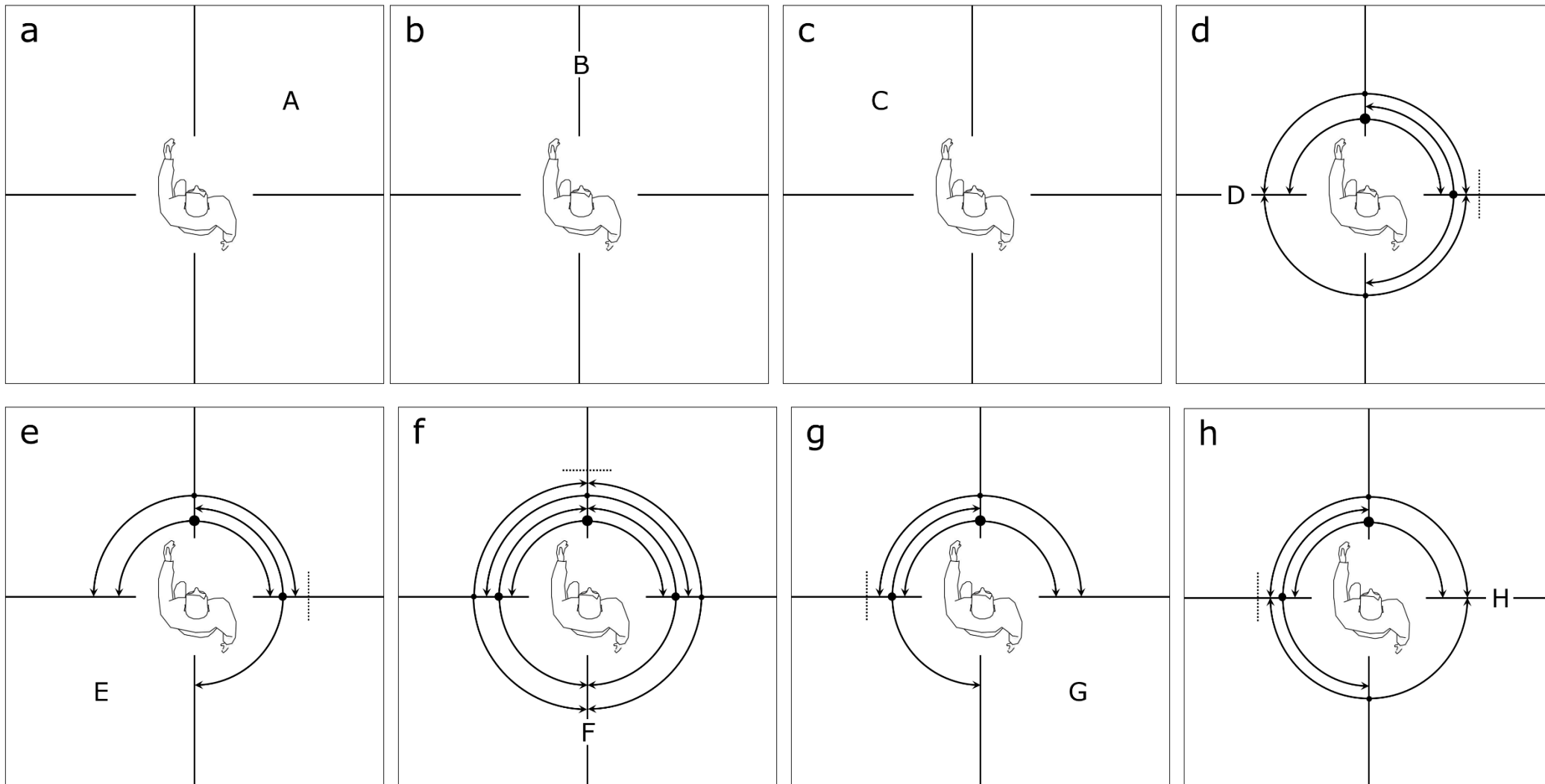
$t_e^s(R|C)$  and  $t_e^s(L|C)$ : the time taken to execute the action of picking up the object with the right and left hand respectively, when the object is lying exactly on the center.

$t_e^s(L|R)$  and  $t_e^s(L|L)$ : the time taken by  $ROB_S$  to execute the action of picking up the object with its left hand given the object is lying on the right and on the left side of its midsagittal plane, respectively.

For  $ROB_S$ , as both hands are equally efficient:  $t_e^s(R|R) = t_e^s(L|L) = t_e^s(R|C) = t_e^s(L|C) < t_e^s(R|L) \sim t_e^s(L|R)$  and  $t_t^s(R) = t_t^s(L) = t_t^s$  can be assumed.

To calculate the average time required by  $ROB_S$  to pick up the object from different position  $\alpha$  (denoted by  $S_\alpha$ ), we calculate the expected value using probability distribution function. This results in a weighted sum for all steps, weighted by the probability of the occurrence of each step. For some positions, it is a convergent arithmetico-geometric infinite series whose sum can be calculated using standard formula.

**FIGURE 3 a-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.





The following values can be calculated for  $S_\alpha$  for different positions:

*Position A:* Here,  $ROB_S$  can pick up the object using its either hand with equal (0.5) probability (Fig. 3a). So,

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

Similarly,

$$\textit{Position B: } S_B = 0.5(t_e^s(R|C)) + 0.5(t_e^s(L|C)).$$

$$\textit{Position C: } S_C = 0.5(t_e^s(R|L)) + 0.5(t_e^s(L|L)).$$

*Position D:* Here, the object is not visible in first scan, so a need to turn arises.  $ROB_S$  can turn either side with equal probability till the object is found in its 178-degree field of vision. Three possible combinations of steps are shown in Fig. 3d. The time required for each combination to reach the object can be calculated as follows:

Combination 1: Turn left with 0.5 probability and pick up the object with left/right hand with 0.5 probability. So, time taken is:

$$0.5(t_t^s(L) + t_e^s), \text{ As } t_e^s(R|C) = t_e^s(L|C) = t_e^s$$

Combination 2: Turn right with 0.5 probability, turn left/right with 0.25 probability, again turn left/right with 0.125 probability and finally pick up the object with left/right hand with 0.5 probability. So, the time taken is:

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

Combination 3: With similar calculations the next case would be:

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

...

One can write the above expressions as (since  $t_t^s(R) = t_t^s(L) = t_t^s$ ):

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

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

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

...

Thus,

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

*Position E:* With similar analysis as in the previous case, we get (Fig. 3e):

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

*Position F:* (Fig. 3f)

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

*Position G:* (Fig. 3g)

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

*Position H:* (Fig. 3h)

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

These are the values of  $S_\alpha$  for  $ROB_S$ . In the following section, we introduce lateral asymmetries in the motor-action patterns of  $ROB_S$  giving rise to  $ROB_A$ .

## Introducing asymmetries in motor-action patterns

As mentioned earlier, one of the very basic needs of an organism viz. movement requires symmetry breaking. Thus, the need for movement might be a cause for the first asymmetric element to evolve. On the other hand, asymmetry might be required in order to deal with environmental asymmetry. an asymmetric element at lower level could instigate and govern asymmetries at the next higher level, then to other next higher level and so on; in the end lateralizing the whole system.

For convenience, we denote  $ROB_S$  as  $ROB$ . As we are looking at this problem as a time optimization problem, we program  $ROB$  such that it minimizes the time for various steps.

We start with  $ROB$ , whose both hands are equally efficient i.e.  $t_e(R|R) = t_e(L|L) = t_e < t_e(R|L) \sim t_e(L|R)$ ;  $t_t(R) = t_t(L)$ .

For different positions we calculate the time required with the new programming.

### *Positions A and C*

$t_d$  ( $t_d \ll t_e$ ), is the time taken by  $ROB$  to scan and determine where the object lies with respect to its midsagittal plane.  $ROB$  is programmed to pick up the object with its corresponding hand in time  $t_e$ . So the time taken at the two positions will be:  $t = t_d + t_e(R|R)$  for position A and  $t = t_d + t_e(L|L)$  for position C. On the other hand, using opposite hand, the task can be completed in time  $t = t_d + t_e(L|R)$  or  $t = t_d + t_e(R|L)$ .

Nonetheless, since  $t_e(R|R) = t_e(L|L) < t_e(R|L) \sim t_e(L|R)$ ; the former is more efficient. (Table 2)

### *Position B*

With the current programming,  $ROB$  is unable to decide which hand to use. So we do additional programming and introduce the first symmetric element i.e. programmed to use right hand in such situations. So, time taken is  $t = t_d + t_e(R|C)$ . The alternative (pick up the object with left hand) doesn't hold because of the programming. (Table 2)

Other positions: D, E, F, G, and H, require turning. *ROB* is programmed to take the first turn with equal probability and take other turns if required in the direction of the previous turn.

#### *Position D*

The two alternatives are: (a) to turn rightwise thrice in which case time required is  $t = 3t_t(R) + t_d + t_e(R|C)$  or (b) to turn leftwise once in which case, time required is  $t = t_t(L) + t_d + t_e(R|C)$ . Since  $t_t(R) = t_t(L)$ , the latter is more efficient. (Table 2)

#### *Position E*

The two alternatives involving picking the object with the corresponding hand yield times:  $t = 2t_t(R) + t_d + t_e(R|R)$  or  $t = t_t(L) + t_d + t_e(L|L)$ . And the alternatives involving picking the object with opposite hands yield times:  $t = 2t_t(R) + t_d + t_e(L|R)$  or  $t = t_t(L) + t_d + t_e(R|L)$ . Nonetheless, since  $t_e(R|R) = t_e(L|L) < t_e(R|L) \sim t_e(L|R)$  the former cases are more efficient. (Table 2)

#### *Position F*

The two equally efficient alternatives yield  $t = 2t_t(R) + t_d + t_e(R|C)$  or  $t = 2t_t(L) + t_d + t_e(R|C)$ . (Table 2)

#### *Position G*

The two alternatives involving picking the object with the corresponding hand yield times:  $t = t_t(R) + t_d + t_e(R|R)$  or  $t = 2t_t(L) + t_d + t_e(L|L)$ . And the alternatives involving picking the object with opposite hands yield times:  $t = t_t(R) + t_d + t_e(L|R)$  or  $t = 2t_t(L) + t_d + t_e(R|L)$ . Nonetheless, since  $t_e(R|R) = t_e(L|L) < t_e(R|L) \sim t_e(L|R)$  the former cases are more efficient. (Table 2)

*Position H:* The two alternatives yield times  $t = t_t(R) + t_d + t_e(R|C)$  or  $t = 3t_t(L) + t_d + t_e(R|C)$ . Since  $t_t(R) = t_t(L)$ , the former is more efficient. (Table 2)

**TABLE 2.** 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	$t_d$	$t_e(R R)$ $t_e(L R)$	<b><math>t_d + t_e(R R)</math></b> $t_d + t_e(L R)$	N/A	$t_e(R R)$	N/A	<b><math>t_e(R R)</math></b>
B	0	$t_d$	$t_e(R C)$	<b><math>t_d + t_e(R C)</math></b>	N/A	$t_e(R C)$	N/A	<b><math>t_e(R C)</math></b>
C	0	$t_d$	$t_e(L L)$ $t_e(R L)$	$t_d + t_e(R L)$ <b><math>t_d + t_e(L L)</math></b>	$t_e(R L) < t_e(L L)$	<b><math>t_e(R L)</math></b> $t_e(L L)$	N/A	<b><math>t_e(R L)</math></b> $t_e(L L)$
D	$3t_t(R)$ $t_t(L)$	$t_d$ $t_d$	$t_e(R C)$ $t_e(R C)$	$3t_t(R) + t_d + t_e(R C)$ --- <b><math>t_t(L) + t_d + t_e(R C)</math></b>	N/A	$3t_t(R) + t_e(R C)$ --- <b><math>t_t(L) + t_e(R C)</math></b>	$t_t(R) < t_t(L)/3$	<b><math>3t_t(R) + t_e(R C)</math></b> --- $t_t(L) + t_e(R C)$
E	$2t_t(R)$ $t_t(L)$	$t_d$ $t_d$	$t_e(R R)$ $t_e(L L)$	<b><math>2t_t(R) + t_d + t_e(R R)</math></b> $2t_t(R) + t_d + t_e(L R)$ --- $t_t(L) + t_d + t_e(R L)$ <b><math>t_t(L) + t_d + t_e(L L)</math></b>	$t_e(R L) < t_e(L L)$	<b><math>2t_t(R) + t_e(R R)</math></b> $2t_t(R) + t_e(L R)$ --- <b><math>t_t(L) + t_e(R L)</math></b> $t_t(L) + t_e(L L)$	$t_t(R) < t_t(L)/2$	<b><math>2t_t(R) + t_e(R R)</math></b> $2t_t(R) + t_e(L R)$ --- $t_t(L) + t_e(R L)$ $t_t(L) + t_e(L L)$
F	$2t_t(R)$ $2t_t(L)$	$t_d$ $t_d$	$t_e(R C)$ $t_e(R C)$	<b><math>2t_t(R) + t_d + t_e(R C)</math></b> --- <b><math>2t_t(L) + t_d + t_e(R C)</math></b>	N/A	<b><math>2t_t(R) + t_e(R C)</math></b> --- <b><math>2t_t(L) + t_e(R C)</math></b>	$t_t(R) < t_t(L)$	<b><math>2t_t(R) + t_e(R C)</math></b> --- $2t_t(L) + t_e(R C)$
G	$t_t(R)$ $2t_t(L)$	$t_d$ $t_d$	$t_e(R R)$ $t_e(L L)$	<b><math>t_t(R) + t_d + t_e(R R)</math></b> $t_t(R) + t_d + t_e(L R)$ --- $2t_t(L) + t_d + t_e(R L)$ <b><math>2t_t(L) + t_d + t_e(L L)</math></b>	$t_e(R L) < t_e(L L)$	<b><math>t_t(R) + t_e(R R)</math></b> $t_t(R) + t_e(L R)$ --- <b><math>2t_t(L) + t_e(R L)</math></b> $2t_t(L) + t_e(L L)$	$t_t(R) < 2t_t(L)$	<b><math>t_t(R) + t_e(R R)</math></b> $t_t(R) + t_e(L R)$ --- $2t_t(L) + t_e(R L)$ $2t_t(L) + t_e(L L)$
H	$t_t(R)$ $3t_t(L)$	$t_d$ $t_d$	$t_e(R)$ $t_e(R)$	<b><math>t_t(R) + t_d + t_e(R C)</math></b> --- $3t_t(L) + t_d + t_e(R C)$	N/A	<b><math>t_t(R) + t_e(R C)</math></b> --- $3t_t(L) + t_e(R C)$	$t_t(R) < 3t_t(L)$	<b><math>t_t(R) + t_e(R C)</math></b> --- $3t_t(L) + t_e(R C)$

Here, because of an equal number of more efficient cases for either right or left side, there is no bias introduced. Only in the case when the object is exactly on the center, a right hand bias is introduced. We continue our analysis by making one of the hands more efficient than the other.

Since every system faces the problem of limited resources, the resources have to be unequally distributed in order to cater the needs of the system. *ROB*'s cognitive capacity is also limited and so it has to be distributed between the two hands such that one hand is more efficient and the other is equally less efficient. Here, we assume without loss of generality that the right hand is more efficient. So, we will have  $t_e(R) = t_e(L) - dt$ . This difference would give rise to certain boundary conditions, which can be calculated as follows for each position:

*Positions A, B, and C*

At A and B, we will have  $t_d = 0$  as there is no decision making required for choosing the hand. So time taken will be:  $t = t_e(R|R)$  or  $t_e(R|C)$ . At C, *ROB* can use any hand, but in order for right hand dominance to evolve we would need the boundary condition  $t_e(R|L) < t_e(L|L)$ .

*Positions D, E, F, G, and H:* Here, the addition to the previous algorithm lies in the terminal step wherein *ROB* always uses its right hand. (Table 1; most efficient solutions are in boldface).

So these boundary conditions determine how the asymmetry at a lower level is sustained. We further work out the boundary conditions for rightwise turning bias (rightwise because there is right hand dominance) to evolve. With all the biases, *ROB* becomes *ROB<sub>A</sub>*.

*Positions A, B, and C*

*ROB<sub>A</sub>* works the same way as *ROB*. (Table 1; most efficient solutions are in boldface).

*Positions D, E, F, G, and H:* *ROB<sub>A</sub>* works the same way as *ROB*, but in addition to that, the right turn will be more efficient than the left if the following boundary conditions hold.

*Position D:* For rightwise turn to be more efficient, we want:

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

So, we get

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

*Position E:* Similarly,

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

So,

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

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

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

*Position F:*

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

So,

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

*Position G:*

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

So,

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

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

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

*Position H:*

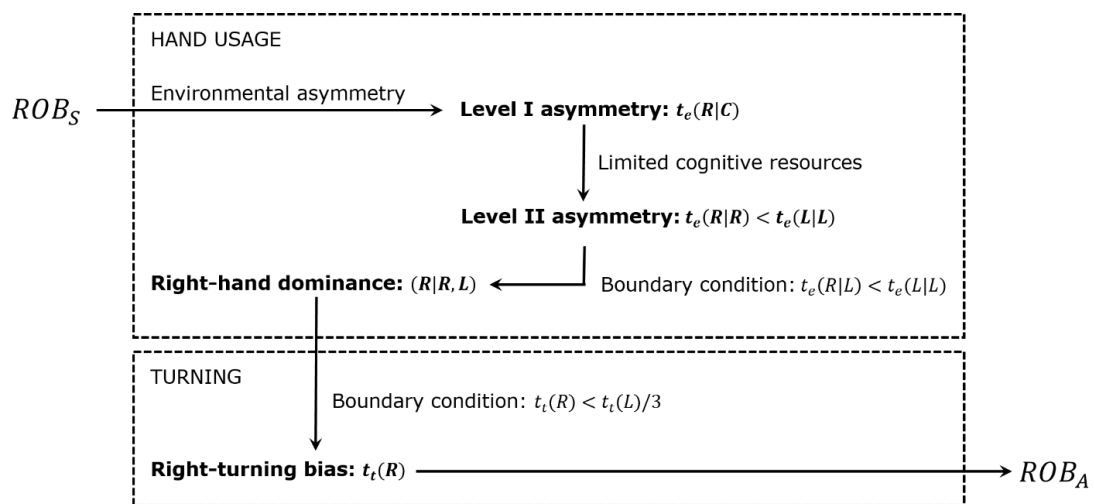
$$t_t(R) + t_e(R|C) < 3t_t(L) + t_e(R|C)$$

So,

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

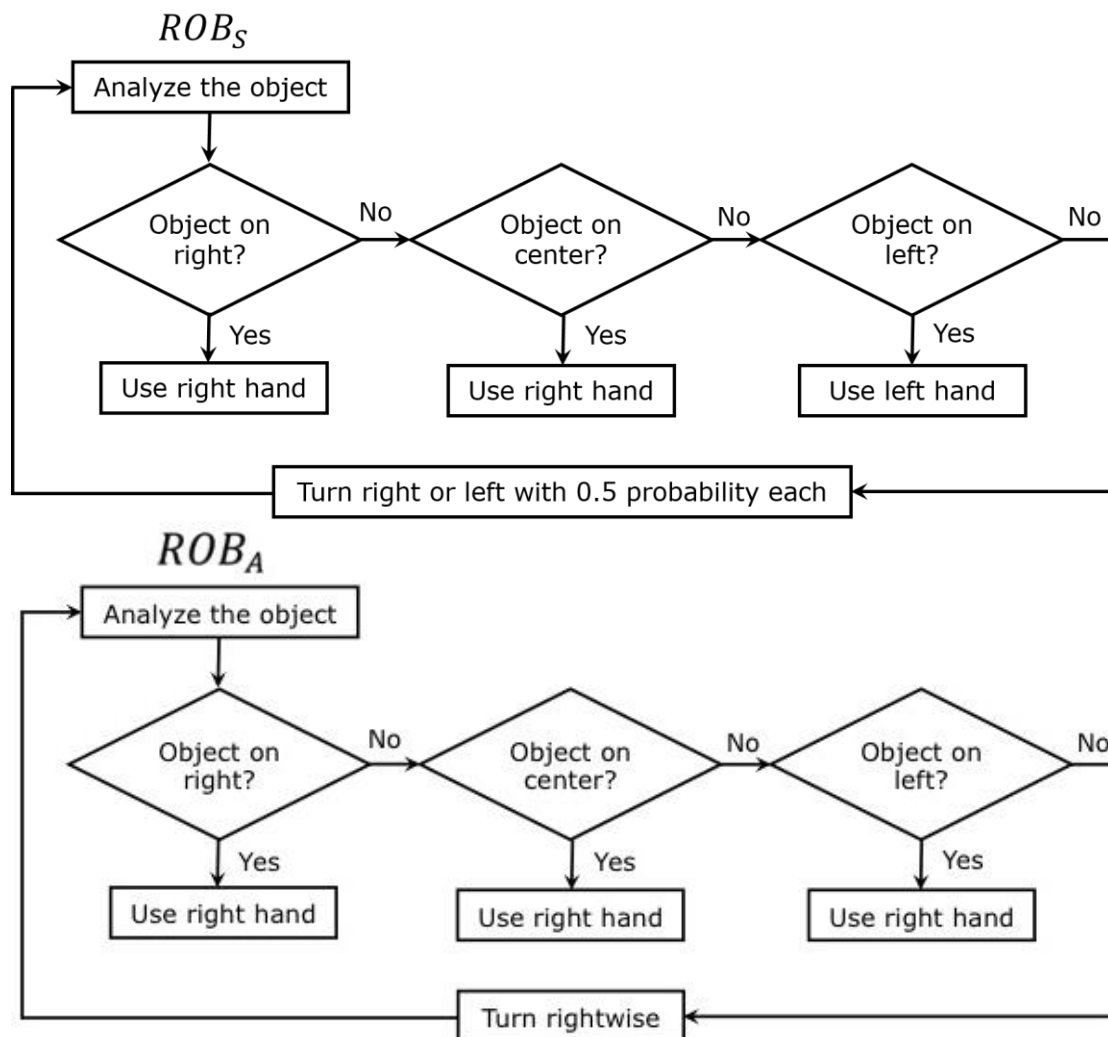
So the boundary conditions above make  $ROB_A$  turn right always for highest efficiency. The most constrained boundary condition of all is  $t_t(R) < t_t(L)/3$ , and so for  $ROB_A$  to evolve, the two boundary conditions  $t_e(R|L) < t_e(L|L)$  and  $t_t(R) < t_t(L)/3$  need to hold. The entire process is schematically represented in Figure 4 and the flowcharts showing algorithms for  $ROB_A$  and  $ROB_S$  are shown in Figure 5.

**FIGURE 4.** Progression of lateral asymmetries in motor-action patterns in a system.





**FIGURE 5.** The flowcharts for  $ROB_S$  and  $ROB_A$  for the most efficient alternative.



## Are asymmetries advantageous?

We compare the aforementioned two systems: the symmetric  $ROB_S$  and the asymmetric  $ROB_A$ . We check whether  $ROB_A$  performs better than  $ROB_S$  in terms of time optimization and whether asymmetries in  $ROB_A$  provide more advantage as the task-complexity increases.

### *Symmetric versus asymmetric systems*

We denote the average time taken by  $ROB_S$  at different positions  $\alpha$  by  $S_\alpha$  and that by  $ROB_A$  by  $A_\alpha$ , the values of which have been calculated in the previous sections. We now see the difference between the two  $(S - A)_\alpha$  in order to compare them.

*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 in above sections (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,

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

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:*

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

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

Then,

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

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:*

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

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

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

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

*Position F:*

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

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

Then,

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

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  $t_e^a(R|C) = t_e^a(R|R)$ ,

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

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:*

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

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

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:*

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

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

Then,

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

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

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

So,  $(S - A)_\alpha > 0 \forall \alpha$ . Thus,  $ROB_A$  performs better than  $ROB_S$ .

### *Task complexity and the advantage associated with asymmetry*

We now consider the complexity when the object is located at different positions. We denote the complexity at position  $\alpha$  by  $C_\alpha$ . It is easy to speculate that position B is the least complex involving no decision-making followed by A and C that have one component of decision making and are equally cognitively demanding. Other positions viz. D, E, F, G and H have a component of turning involved and thus are more complex. One can immediately infer the complexity order as:

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

With further consideration, assuming symmetric motor-action patterns, one can infer that the number of steps for positions A and C, D and H, and E and G would be similar. Additionally, considering the spatial orientation (Fig. 2) one can modify the previous order as:

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

Finally, knowing that *ROB* has 178-degree field of vision, the best solution for positions on the transverse axis (D and H) would involve one more step as compared to positions E and G when *ROB* turns on the opposite side first i.e. when *ROB* turns right first, position D would require one more turning step as compared to position E and similarly for positions H and G. Also, because of the symmetry of position F, it is the most complex for both  $ROB_S$  and  $ROB_A$ . So, the order of complexity after considering all factors is as follows:

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

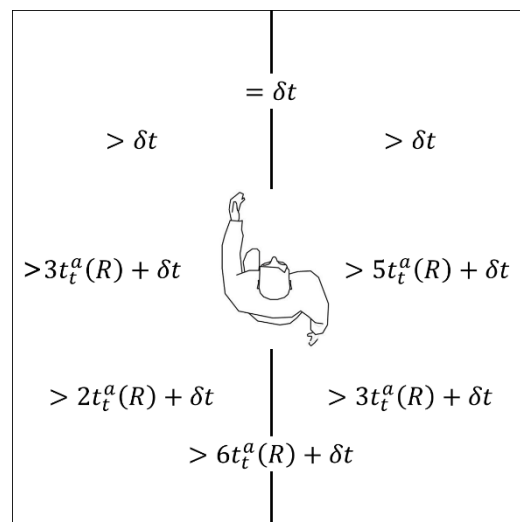
The minimum values of  $(S - A)_\alpha$  obtained in the previous section show a similar order (Table 3; see Fig. 6):

$$\begin{aligned} \min(S - A)_C < \min(S - A)_B < \min(S - A)_A < \min(S - A)_{E \text{ or } G} < \\ & \min(S - A)_{D \text{ or } H} < (S - A)_F. \end{aligned}$$

From this we can conclude that asymmetries provide a greater advantage with complex tasks. In absence of asymmetries, one might think that the values of  $\min(S - A)$  should be the same for positions E and G, or for

positions D and H, the presence of the asymmetries (the right turning bias and right hand dominance) gives an overall performance advantage and changes these values. Also the advantage is less significant for less complex tasks (A, B and C).

**FIGURE 6.** The minimum values of  $S - A$  for the different positions of the object ( $\delta t = t_e^s(R|R) - t_e^a(R|R)$ ).





**TABLE 3.** 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 5)	$S - A$ ( $\delta t = t_e^s(R R) - t_e^a(R R)$ ) (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	$0.5(t_e^s(R L)) + 0.5(t_e^s(L L))$	$t_e^a(R L)$	$> 0$
D	$0.5(t_f^s + t_e^s) + 0.25(3t_f^s + t_e^s) + 0.125(5t_f^s + t_e^s) + \dots = 6t_f^s + t_e^s$	$3t_f^a(R) + t_e^a(R C)$	$> 3t_f^a(R) + \delta t$
E	$0.5(t_f^s + t_e^s) + 0.25(2t_f^s + t_e^s) + 0.125(3t_f^s + t_e^s) + \dots = 4t_f^s + t_e^s$	$2t_f^a(R) + t_e^a(R R)$	$> 2t_f^a(R) + \delta t$
F	$0.5(2t_f^s + t_e^s) + 0.25(4t_f^s + t_e^s) + 0.125(6t_f^s + t_e^s) + \dots = 8t_f^s + t_e^s$	$2t_f^a(R) + t_e^a(R C)$	$> 6t_f^a(R) + \delta t$
G	$0.5(t_f^s + t_e^s) + 0.25(2t_f^s + t_e^s) + 0.125(3t_f^s + t_e^s) + \dots = 4t_f^s + t_e^s$	$t_f^a(R) + t_e^a(R R)$	$> 3t_f^a(R) + \delta t$
H	$0.5(t_f^s + t_e^s) + 0.25(3t_f^s + t_e^s) + 0.125(5t_f^s + t_e^s) + \dots = 6t_f^s + t_e^s$	$t_f^a(R) + t_e^a(R C)$	$> 5t_f^a(R) + \delta t$

## Discussion

In this study, the appearance and sustenance of asymmetries in a biological system have been explained using a minimal model developed by system theory approach. The model exhibits that a lower level could promote and control the next higher level and through reiteration the entire system maybe lateralized. We considered two levels of asymmetries: one considering symmetric motor-action patterns and other considering asymmetric motor-action patterns. We observed that the asymmetric system performed better in terms on time optimization, and increasing task complexity showed an increase in the advantage associated with the asymmetries. Hence in a multi-level system, asymmetry at any level does not represent patterns throughout the system like a manual asymmetry may not provide complete information and might be because of cascade at different levels.

The first asymmetry in our model was introduced when the object was lying exactly on ROB's midsagittal plane. The need for asymmetry arose because of the conflict between symmetry in the system and symmetry in the environment. This can be addressed by breaking either of the two symmetries but breaking environmental symmetry will only be a temporary solution as the environment is variable over space and time. Thus, ROB breaks the symmetry within itself. This might happen stochastically in a biological system. The next level of asymmetry is the differential efficiency of the two hands after which one hand dominance evolves. This asymmetry is sustained under the boundary conditions, which are a measure of the difference in the efficiency of two symmetric motor action patterns. Later with additional degrees of freedom viz. turning, the previous asymmetry i.e. one hand dominance stimulates the asymmetry in turning which is again sustained under boundary conditions. This asymmetric system in the end performs better than the symmetric system and is thus sustained. Also, it provides more advantage with increasing task complexity, which might explain greater prevalence of manual laterality in non-human primates for more complex tasks as suggested by the task complexity theory. Task complexity theory states that more complex tasks would elicit greater handedness. Here, the

model shows a greater advantage associated with asymmetries as the complexity of the task increases and thus greater handedness can be observed. As the model does not incorporate postures and associated hand preference patterns resulting from them, the postural origins theory stays out of scope of the model.

Though our model focuses only on certain asymmetries in motor actions (i.e., hand preference and turning bias), our analysis can be extended to any form of asymmetry over many degrees of freedom. Our model remains interchangeable for left and right sides and does not explain dominance of either one of them, though the analysis may be extended to explain that, considering the ecological factors (for example, factors like feeding ecology viz. arboreal or terrestrial or both, might elicit adaptations that result in biased hand usage, see Sfar et al., 2014) and social factors (for example, it has been suggested that population level right handedness might be an outcome of balance of costs and benefits between cooperation and competition, see Abrams and Panaggio, 2012). Further, as there are different boundary conditions for different states, a system may use these differential boundary conditions to develop differential asymmetric elements.

Nonetheless, like every model, there are limitations in our model described as follows:

(L1) Our minimal model is designed to provide solution in terms of time optimization. In the current formulation time and energy are interchangeable and the same dynamics would hold for energy optimization. However, a more sophisticated model should study time and energy optimization simultaneously using dynamical systems.

(L2) Our minimal model can only provide a qualitative explanation. Though this makes the model more general, a sophisticated model should explain the dynamics quantitatively.

(L3) Our model cannot explain how the asymmetries are introduced, it only explains how the asymmetries are sustained under certain boundary conditions once they are introduced. Also, the model takes a linear approach whereas in biological systems, many non-linear stochastic events might play

a role in bring about the patterns that we observe. Nonetheless, their effects may not be significant.

(L4) The assumption of 178-degree field of vision to mimic humans affects the sequence of steps to solve the task, which affects the total time. But this does not undermine the validity of our model as the process remains the same even without this assumption we assume it for both, symmetric and asymmetric systems.

(L5) The assumption of  $90^\circ$  turns may be violated in real life, as sometimes only a partial turn (i.e.,  $< 90^\circ$ ) might be sufficient to locate the object within its field of vision. But this does not demean the validity of our model as it is more difficult to process surrounding information when rapid motor-actions are executed.

The current model has scope for extensions. Sophisticated models should not only address the above limitations but also include more variables like randomness in in decision making, for a more reliable cost-benefit analysis. Such a model might be incorporated in robotic systems and tested further.

# **Appendix**

## **Experiment 2**

### **Introduction**

The macaques at Chamundi hill top snatch the polythene carried by the pilgrims coming from the temple. These polythenes contain exactly two bananas. If a pilgrim resists and tries to get rid of the monkey by giving one banana from the polythene, the monkey would not leave unless the second banana is given. This means that they do know that there are two bananas in the polythene. Inspired from this observation, an experiment was designed in order to test for their counting ability.

Instead of being conditioned for two bananas, if the macaques have learned the number of bananas in the polythene through repeated iterations, they should be able to learn in case of a different number of food items inside the polythene. That is to say that the macaques should be able to count the number of food items inside the polythene. This requires an experimental paradigm that includes an article to carry food (other than polythene) that the macaques could associate with food and a food item (bananas or other items comparable in size) that can be varied in numbers to test for counting ability. Here, we used a box to carry food and small size tomatoes as food items kept inside the box.

### **Methods**

#### ***Subjects and Study Site***

We conducted the experiment on 4 bonnet macaques, 2 adult females, 1 adult male and 1 juvenile female from Chamundi Hill top in Mysore, India (2°14'41"N 76°40'55"E). We observed from a distance if the macaques attempted to explore the box placed within ca. 1 m of the focal macaque when there was no conspecific within ca. 3 m from it.

## *Experimental procedure*

We present each macaque with a closed box containing one tomato and allow the macaque to explore the box. After three sets of 7 trials each, instead of letting them explore the box, each macaque was given the tomato from the box and the box was put at a distance from the macaque. This was repeated everyday over the span of two weeks. If the macaque knows that there is only one tomato in the box, it would be expected that the macaque would not attempt to explore the box lying at a considerable distance. This process could be repeated with increasing number of the tomatoes every step, and putting the box away after giving them  $n-1$  tomatoes and seeing if they explore the box

## **Results and Discussion**

We observed that the adult female AF2 from the group did not explore the box in case of one tomato after repeating the three sets of seven trials each for two days. Thus, on the third day, the number was increased to two tomatoes and she was presented with both tomatoes for three sets of seven trials each. For the next set of observations, she was presented with one tomato from the box and the box was placed at a distance from her. But it was observed that she never attempted to explore the box. Further the experiment was done on three other individuals with one and two tomatoes inside the box, all of whom always explored the box regardless of number of tomatoes in the box. Thus, because of failure to obtain the expected results, the experiment was discontinued.

There could be various reasons for the failure of the experiment. Firstly, the number of trials that was fixed (three sets of seven trials each) might not have been sufficient for the macaques to train. The number of trials had been chosen considering that the macaques should not be fed too much at a time, as that might tend to reduce motivation for further trials. Also, the experiment would require a sufficiently big food item like a banana or tomato. A small food item like a grape may not deserve as much attention so as to get the macaques count, if at all they do; just like we would never count how

many grapes we ate, but we would count how many bananas we ate. Thus, a reasonably small number of trials (seven) are done in one set, which is repeated three times a day. A greater number of trials, in addition to the problem of satiation as stated above, might tend to make the macaques 'associate' a particular number of food items with the box, that is to say that they might tend to have a representation or a mental picture of food items associated with the box and not the number of food items per se. This is a problem only for a small number (say one, two or three) of food items inside the box, which can be perceived without number representation, and not as the number of items inside the box is increased. One cannot certainly say whether they would associate before or after three sets of seven trials, but increasing the number of trials has this risk. Also, the training process could not be controlled for external factors like presence of conspecifics, presence of humans etc. that could hinder the training process. Further, while the box was placed keeping in mind the presence of conspecifics in the vicinity, it could have played a role in biasing the results. This experiment might work if carried out in captivity where the experimenter would have greater control over the external confounding factors.

## Experiment 3

### Introduction

This experiment was designed to test if monkeys 'bully'. In order for a dominant individual to sustain its dominance, there can be two strategies. First, work for the betterment of oneself, i.e. improvise on characteristics that provide an advantage over other individuals, which in turn would engender greater dominance. In case of macaques, such characteristics might be size, aggression etc. that could be improvised by greater access to food resources. Or second, one can inhibit other individuals from improvising such skills, for example inhibit access of resources for other individuals or in other words, 'bully'. Here, we define bullying as forbidding a subordinate from accessing a resource that is not of interest to the dominant one. This experiment requires

a food item that is of interest to the subordinate individual, but not of interest to the dominant individual.

## Methods

### *Subjects and Study Site*

We conducted the experiment on 3 bonnet macaques, 3 juvenile males, from Chamundi foothills in Mysore, India (2°14'41"N 76°40'55"E). We observed the dynamics from a distance when we placed the groundnuts (a food item which was of interest to the 3 subordinate juveniles but was not of interest to the dominant adult male) within ca. 2 m of the dominant macaque macaque when the subordinate macaque was within ca. 2 m from it.

### *Experimental procedure*

Previously, for a separate experiment a fellow experimenter presented the dominant individual with groundnuts on various occasions i.e. various times of the day, to observe the extraction patterns. From his data, we know that the dominant adult male (AM1) never consumed the groundnuts, nor showed any exploratory behavior in most occasions. Also from his data we knew 3 juvenile males (often found in the vicinity of the dominant AM1) who consumed groundnuts. The dominance was determined by noting dyadic dominant or submissive interactions between the adult male and the 3 juvenile males in question. Dominant interactions comprise of threat, chase, attack, displacement and mounting (placing hand on hindquarters). Subordinate interactions comprise of fear-grimace, run away, submit/crouch, move away and screech. Thus, we could find the exact experimental conditions that we needed in order to carry out our experiment viz. a food item of interest to dominant individual, but not of interest to subordinate individual.

We present a subordinate individual with a food item (here, groundnut) that was of interest to the subordinate individual but not of interest to the dominant individual. We place the groundnut within ca. 2 m of the dominant macaque when the subordinate macaque was within ca. 2 m from it. We observed if the dominant macaque inhibited the subordinate individuals from



reaching the groundnut. This was repeated several times at different occasions (various times of day) to control for confounding factors viz. hunger, temperament etc.

## Results and Discussion

We observed that the on all occasions, the subordinate individuals never approached the groundnut in the presence of the dominant individual. Though one might argue this observation to be an evidence of indirect bullying, it is not necessarily the case for primarily the following two reasons: (a) one cannot know if the subordinate individual knows that the dominant individual is not interested in the food item, which is required in order to infer the observation as bullying, and (b) no dominance gestures were observed from the dominant individual which are again a necessity in order to infer if the observation can be called bullying. We could not find any other set of individuals that would include both dominant and subordinate individuals with a food item that is of interest to subordinate but not the dominant. This experiment can be carried out in controlled situations (like, captivity) wherein one can design food items and train the dominant individuals to not prefer certain food items and subordinate ones to prefer the same. For example, favorable food items can be packaged inside certain packaging and presented to subordinate individuals and unfavorable food items can be packed inside the same packaging and presented to the dominant individuals.

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## **Supplementary material**

Movie S1: The video shows an adult female performing food extraction using the apparatus of the hand performance differentiation task.