

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

Madhur Mangalam<sup>1,\*</sup>, Nisarg Desai<sup>2,5</sup> and Mewa Singh<sup>3,4</sup>

<sup>1</sup>Department of Psychology, University of Georgia, Athens, GA 30602, USA

<sup>2</sup>Indian Institute of Science Education and Research, Pune 411 008, India

<sup>3</sup>Biopsychology Laboratory, and Institute of Excellence, University of Mysore, Mysore 570 006, India

<sup>4</sup>Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru 560 064, India

<sup>5</sup>Present address: Department of Anthropology, University of Minnesota, Minneapolis, MN 55455, USA

**A consequence of the ‘gold rush’-like hunch for human-like handedness in non-human primates has been that researchers have been continually analysing observations at the level of the population, ignoring the analysis at the level of an individual and, consequently, have potentially missed revelations on the forms and functions of manual asymmetries. Recently, consecutive studies on manual asymmetries in bonnet macaques, *Macaca radiata* revealed both the functional and adaptive significance of manual asymmetries respectively, and pointed towards the division of labour as being the general principle underlying the observed hand-usage patterns. We review the studies on manual asymmetries in capuchin monkeys, *Cebus* spp. and argue that the observed hand-usage patterns might reflect specialization of the two hands for accomplishing tasks that require different dexterity types (i.e. manoeuvring in three-dimensional space or physical strength). To this end, we do a step-by-step analysis of the various tasks used in the studies on manual asymmetries in capuchin monkeys. We then describe the division of labour as a general principle underlying manual asymmetries in non-human primates and propose experimental designs that would elaborate the forms and functions of manual asymmetries in non-human primates and the associated adaptive value.**

**Keywords:** Division of labour, hand performance and preference, laterality, manual asymmetry, non-human primates.

APPROXIMATELY 90% of humans preferentially use the right hand to perform complex manual actions<sup>1,2</sup>. In order to understand the adaptive value of this population-level right-handedness, which is peculiar to humans, it is important to understand the evolutionary origin of manual asymmetries in humans as well as in their phylogenetic relatives, the non-human primates. Manual asymmetries of some kind or the other are almost ubiquitous among

the non-human primates. However, for a long time the population-level lateral bias in hand usage in non-human primates remained equivocal. Considering that the exogenous factors, such as the initial position of a stimulus with respect to a subject, body posture of the subject, etc. might influence hand usage, researchers considered manual asymmetries in non-human primates to be analogous, and not homologous, to manual asymmetries in humans. Regardless of such an ambiguity, hand preference in non-human primates has been hypothesized to have evolved owing to functional and morphological adaptations to feeding in arboreal contexts<sup>3-5</sup>.

As opposed to the prevailing ideas on population-level right-hand preference in humans, MacNeilage *et al.*<sup>6</sup> argued that human-like population-level lateral bias in hand usage is evident in non-human primates, and proposed the postural origins theory. According to this theory, among non-human primates initially the left hand became specialized for visually guided movements and the right hand became specialized for postural support. Subsequently, in non-human primate species that adopted a relatively more terrestrial lifestyle, the right hand became more specialized for physical manipulation than for postural support, owing to the decreasing demands on the right hand to support vertical posture. However, the postural origins theory fails to describe why initially the left-hand (and not the right hand) became specialized for visually guided reaching and more importantly, how a population-level right-handedness evolved during the transition from monkeys to apes to humans<sup>7</sup>. Overall, the postural origins theory incorporates the physical constraints on hand usage imposed by the body posture, but does not explain the variations in hand-usage patterns, corresponding to the novelty and spatio-temporal scale of manual actions.

In the earlier studies on manual asymmetries in non-human primates, terms such as ‘task complexity’ and ‘task demands’ were used without ever being comprehensively defined. For example, complexity of a reaching-for-food task was measured in terms of the number of

\*For correspondence. (e-mail: madhur.mangalam@uga.edu)

steps preceding the terminal act of reaching for food, with almost no reference to the precision of movement in any of the manual actions. This made it difficult to draw any conclusions with regard to the forms and functions of manual asymmetries in non-human primates. Subsequently, based on the perspective put forward by MacNeilage *et al.*<sup>6</sup>, while simultaneously acknowledging the possibility that hand-usage patterns might vary with novelty and the spatio-temporal scale of the manual actions, as indicated by the previous studies on hand-usage patterns in non-human primates, Fagot and Vauclair<sup>8</sup> put forward the task complexity theory. This theory proposes the following: (a) Low-level tasks (i.e. those involving cognitively less demanding actions that are practised frequently) elicit symmetrical hand-usage patterns at the level of the population and manual preferences at the level of an individual, not necessarily indicative of any kind of specialization. (b) High-level tasks (i.e. those involving cognitively more demanding manual actions that are practised rarely) elicit asymmetrical hand-usage patterns at the level of the population, likely to be indicative of some kind of cognitive specialization. They also argued that inconsistencies in directional biases arise owing to the diversity in the tasks used to elicit manual asymmetries and the cognitive processes involved in solving them. Overall, these two types of tasks, low-level and high-level, elicit two different types of lateralization, hand preference and manual specialization.

During the course of a study on bonnet macaques, *Macaca radiata*<sup>9</sup>, we observed a peculiarity in the hand-usage patterns of the study individuals. The hand used for the terminal act of reaching remained almost consistent irrespective of the number of steps involved in the food extraction process. This, rather counter-intuitive observation provoked us to carry out a systematic study on manual asymmetries in bonnet macaques. Two consecutive studies revealed both the functional and adaptive significance of manual asymmetries respectively, and pointed towards the division of labour as being the principle underlying the observed hand-usage patterns<sup>1,2</sup>. In contrast to the conventional ideas on manual asymmetries in non-human primates, these observations demonstrated the specialization of the two hands for tasks requiring manoeuvring in three-dimensional space or those requiring physical strength, as inferred by their consistent usage across a variety of spontaneous and experimental tasks. Also, our task apparatus revealed some peculiarities in the form of manual asymmetries, which galvanized us to analyse the tasks used to elicit manual asymmetries in the other studies. In this article we summarize our analysis of these tasks and put forward our ideas on the division of labour in hand usage.

We review the studies on manual asymmetries in capuchin monkeys, *Cebus* spp. (because they have been subjected to extensive study) and argue that the observed hand-usage patterns might reflect specialization of the two hands for accomplishing tasks that require different

dexterity types. To this end, we do a step-by-step analysis of the various tasks used in the studies on manual asymmetries in capuchin monkeys, as follows: (a) We analyse the different manual tasks that have been used to study manual asymmetries in non-human primates on the basis of attributes such as the number of hands required to solve a given task (i.e. unimanual, pseudo unimanual or bimanual) and the spatio-temporal progression of manual actions (i.e. sequential or concurrent). (b) We determine the forms and functions of manual asymmetries that these tasks can potentially elicit within the broader scope of the behavioural repertoire of an individual, a population, or a species. (c) We qualify the scope of the inter-individual, -population, or -species comparisons. We then describe the division of labour as a general principle underlying manual asymmetries in non-human primates and, in order to substantiate this possibility, propose experimental designs that would elaborate the forms and functions of manual asymmetries in non-human primates and the associated adaptive value.

### Manual asymmetry paradigms

In primates, manual asymmetries evolved subsequent to hemispheric specialization, that is, as a by-product of a more fundamental cerebral asymmetry affecting sensory motor functioning<sup>10</sup>. Accordingly, tasks that are likely to challenge the differential abilities of the two hemispheres are more likely to elicit manual asymmetries: hand preference, that is, the preferential usage of one hand to perform a unimanual task or to execute the most complex action while performing a bimanual task, or hand performance, that is, differential performance of the two hands in solving the same task<sup>8</sup>. In the manual preference paradigm, repetitive presentations of a given task produce individual scores of right- and left-hand uses. These scores are then used to derive the strength and bias of manual lateralization. The strength is obtained in several statistical ways, all of which basically calculate some index of the deviation from a random 50% hand usage regardless of the hand preferred, wherein bias refers to the direction of manual preference (left or right). In the manual performance paradigm, on the basis of the differential reaction time or accuracy of the two hands in solving the same task, individuals are classified as right- or left-handers when one hand performs better on average than the other. Studies on manual asymmetries in non-human primates make use of an array of spontaneous and experimental tasks to describe the two kinds of manual asymmetries, which we analyse below.

#### *Quadrupedal (pseudo) unimanual reaching-for-food tasks*

Typically, quadrupedal (pseudo) unimanual reaching-for-food tasks involve reaching for food placed on the

ground, on a platform, tray or in a vessel accessible directly<sup>11–19</sup>, or through a hole<sup>18,20</sup>, using one hand (here, we use the word ‘pseudo’ before unimanual because the whole process of obtaining food does involve both hands, as there just cannot be any unimanual reaching-for-food task for any quadrupedal individual).

An appropriate assessment of hand preference with regard to unimanual reaching-for-food tasks has several underlying assumptions: (a) A subject is equally likely to use any of its two hands, which is practically possible only when the subject is acquiring either sitting or bipedal posture, such that there are no ergonomic constraints on the usage of any of the two hands. (b) Food is located exactly on the sagittal plane of the body of the subject, so that its spatial arrangement does not influence hand preference (though this assumption is almost always met, as there is an equal probability of food being located towards the right and left of the sagittal plane).

Whereas quadrupedal (pseudo) unimanual reaching-for-food tasks are assumed to involve only one hand; they implicitly involve the other hand which is required to passively maintain tripodal posture. This hand faces an increase in physical load when the other hand is set free for prehension. Thus, one hand is used to maintain tripodal posture and the other hand is used to manoeuvre in three-dimensional space or to make precision grips, following the principle of division of labour. Also, under experimental conditions, ergonomic constraints imposed by the possible asymmetries in the body posture of an individual, together with or independent of the preferential use of one hand for maintaining tripodal posture, are likely to influence hand preference in quadrupedal (pseudo) unimanual reaching-for-food tasks. However, studies on hand preference in capuchins have drawn conclusions with regard to the effect of the complexity of the tasks on hand preference without ever deploying a purely unimanual task independent of these influences.

### *Bipedal (pseudo) unimanual reaching-for-food tasks*

Typically, bipedal (pseudo) unimanual reaching-for-food tasks involve obtaining a single piece of food placed on a high-rise platform, tray or in a vessel accessible directly<sup>14,15,18</sup> or through a hole<sup>16,18</sup>, using one hand (as in the case of the quadrupedal (pseudo) unimanual reaching-for-food tasks, we use the word ‘pseudo’ before unimanual).

Bipedal (pseudo) unimanual reaching-for-food tasks can only be solved using both hands and in no less than two or three steps: (P1) Two-step process – Step 1: setting one hand, hand-1 (i.e. either left or right hand), free from maintaining quadrupedal posture and using it to hold a high-rise structure (this action is physically demanding as the body is lifted/pulled upwards) while maintaining tripodal posture using the other hand, hand-2. Step 2: set-

ting the other hand, hand-2, free from tripodal posture and using it to reach for food while maintaining bipedal posture using the other hand, hand-1. (P2) Three-step process – Step 1: setting one hand, hand-1, free from maintaining quadrupedal posture and using it to hold a high-rise structure (as mentioned above, this action is physically demanding as the body is lifted/pulled upwards) while maintaining tripodal posture using the other hand, hand-2. Step 2: setting the other hand, hand-2, free from tripodal posture and using it to hold the high-rise structure. Step 3: using one hand, (P1a) hand-1 (in which case the sequence is functionally similar to the previous one) or (P2b) hand-2, to reach for food.

These sequences of manual actions involve both hands, following the principle of division of labour, that is, one hand is used to perform the actions demanding relatively more physical strength (e.g. lifting/pulling the body), and the other hand is used to perform the actions demanding more sophistication (e.g. making precision grips or manoeuvring in three-dimensional space). However, studies on hand preference in capuchins have almost never reported the stepwise usage of the two hands for solving bipedal (pseudo) unimanual reaching-for-food tasks as described above, restricting their data collection and analysis only to manual actions that are directly associated with prehension. Comparative assessment of hand preference in the quadrupedal and bipedal (pseudo) unimanual reaching-for-food tasks, as reported in the literature<sup>14,21,22</sup> demonstrates that capuchins consistently use one hand for prehension in both types of tasks, which is possible only while following either the two-step process (i.e. P1) or the second of the three-step process (i.e. P2b) for solving bipedal (pseudo) unimanual reaching-for-food tasks.

### *Quadrupedal/bipedal coordinated bimanual tasks*

Typically, solving a coordinated bimanual task involves obtaining food from ~10–15 cm long and ~3–5 cm wide transparent/opaque tube<sup>12–14,22,23</sup>. An individual that is assuming a quadrupedal position can solve the task in two or three steps – (P1) Step 1: picking up the tube with one hand, hand-1, while maintaining tripodal posture with the other hand, hand-2. Step 2: attaining bipedal posture by freeing hand-2 and extracting the food from the tube with the same hand. (P2) Step 1: picking up the tube with one hand, hand-1, while maintaining tripodal posture with the other hand, hand-2. Step 2: attaining bipedal posture by freeing hand-2 and shifting the tube from hand-1 to hand-2. Step 3: extracting the food with hand-1. Thus, it needs to be determined whether an individual continues holding the tube with the same hand or shifts it to the other hand. In case of a shift, the observed hand-usage pattern can be explained using the principle of the division of labour<sup>2</sup>, and in the other case as well as when an individual is

assuming a bipedal posture while picking up the tube, sequential planning of motor actions. However, studies do not analyse manual asymmetries in solving coordinated bimanual tube task from this perspective and, therefore, present only a partial picture.

### *Sequential unimanual/bimanual versus concurrent - bimanual tasks*

Typically, solving a box task involves obtaining a single piece of food placed on a tray inside a clear plexiglass box. The box can be opened by lifting its lid that is hinged to one of its walls. There are two different versions of the box task. In one version, the lid may remain open once it is lifted beyond a point<sup>12,24</sup>, in which case the task can be solved in either two steps: lifting the lid and reaching for food, in a sequential unimanual/bimanual manner (L-L/R-R, L-R/R-L, B-L/B-R); or three steps: lifting the lid, holding the lid up and reaching for food, in a concurrent bimanual manner (L-RL/R-LR, L-LR/R-RL, B-LR/B-RL). In another version, the box includes a stop screw on the back of the lid which causes the lid to fall shut if it is not held open<sup>12,24</sup>, in which case the task can be solved only in three steps: lifting the lid, holding the lid up and reaching for food, in a concurrent bimanual manner (L-RL/R-LR, L-LR/R-RL, B-LR/B-RL; in the latter two cases, the sequence is functionally similar to the previous one).

Spinozzi and Truppa<sup>24</sup> assessed hand preference in 23 tufted capuchins using the box tasks. While solving the sequential unimanual/bimanual box task, the capuchins indiscriminately (in 48.8% and 36.9% trials) used the strategies involving no differentiation (L-L/R-R, i.e. lifting the lid and reaching for food with the same hand) and differentiation of roles for the two hands (L-R/R-L, i.e. lifting the lid with one hand and reaching for food with the other hand). While solving the concurrent bimanual version of the task, the capuchins predominantly (in 73.4% trials) used the strategy involving complete differentiation of roles for the two hands (L-LR/R-RL, i.e. lifting the lid and holding it up with the same hand, while simultaneously reaching for food with the other hand) more often than the other two possible strategies (L-RL/R-LR and B-LR/B-RL). In a nutshell, the capuchins did not show any difference in the direction and strength of hand preference for prehension between the sequential unimanual/bimanual and concurrent bimanual versions of the box task, demonstrating the similarity between them.

This example demonstrates that sequential unimanual/bimanual and concurrent bimanual box tasks elicit similar direction and strength of hand preference. This also holds true for several other tasks as described above. In fact, a general principle involving partial/complete differentiation of roles for the two hands is likely to underlie manual asymmetries and, therefore, sequential unimanual/bimanual and concurrent bimanual tasks should not be treated differently.

### *Haptic search tasks*

Typically, solving a haptic search task involves obtaining food mixed with some non-edible material<sup>16,25</sup>, or placed in the crevices on the surface of variably shaped objects<sup>26–28</sup> from the inside of an opaque box (~15–30 cm × 15–30 cm × 15–30 cm) through a small opening (diameter <5 cm; these dimensions allow inserting only one hand at a time). Haptic discrimination has been found to be more difficult than visual discrimination in non-human primates (see for example, Wilson<sup>29</sup> in rhesus macaques), perhaps because haptic perception without visual guidance is uncommon in natural settings. Thus, haptic judgments are likely to be novel and consequently, cognitively more demanding compared to visually guided judgments. Studies on manual asymmetries therefore make use of haptic search tasks to differentially challenge the perceptual motor abilities of the hands, which are likely to be affected by functional differences between the left and right hemispheres. However, studies do not compare hand-usage patterns between haptic and visually guided reaching (though studies by Spinozzi and Cacchiarelli<sup>25</sup>, and Lacreuse<sup>28</sup> stand out as exceptions); rather they just describe manual asymmetries in haptic search tasks. This hardly reveals something substantial as studying haptic judgments in isolation from visually guided judgments, fails to resolve manual asymmetries stemming from the absence of the visual cues alone.

### *Probing/tool-using tasks*

Typically, solving a (pseudo) unimanual probing task involves manipulating a wooden dowel inserted into a small hole in a clear plexiglass box in order to displace a food reward off a shelf where it could be retrieved manually<sup>17</sup>, using a stick to obtain food material present inside a vessel with a narrow opening while maintaining a tripod posture<sup>18,30–33</sup> (another version may involve using a sponge<sup>19</sup>) or a bipedal posture<sup>12,18,34</sup>. Another tool-using task is nut-cracking that involves coordinated bimanual handling of stones to crack nuts<sup>35,36</sup>. It is important to note here that the above probing/tool-using tasks are similar in terms of the number of hands required to solve the task (i.e. unimanual, pseudo unimanual or bimanual), and the spatio-temporal progression of manual actions (i.e. sequential or concurrent), except for the fact that they involve an extension of the body, controlling which requires finer finger adjustments through response-produced feedback. Thus, functionally similar to simple reaching-for-food tasks, probing/tool-using tasks are likely to prove helpful only if the form of manual asymmetries (i.e. with respect to grip type) is considered.

### *Spontaneous tasks*

Hand-usage patterns in tasks such as grooming<sup>11</sup>, maternal cradling and infant positioning<sup>37–39</sup> are more likely to

be influenced by the specialization of the two hands for more common activities such as feeding than these tasks themselves. For example, a female capuchin which has its left hand specialized for fine finger adjustments or manoeuvring in three-dimensional space and its right hand specialized for physical support, is more likely to use its right hand for maternal cradling and infant positioning just to keep its left hand free for the usual feeding activities (as they require more sophisticated manual actions). However, studies merely describe the hand used for these activities without considering the forms and functions of the associated manual asymmetries.

#### *Forms and functions of manual asymmetries*

The corticomotoneuronal connections innervating the hands regulate the timing and precision of the muscular forces required for fine finger adjustments through response-produced feedback (see, for example, Porter<sup>40</sup>). It follows from this fact that actions with finer sequential finger movements are more likely to elicit manual asymmetries than simpler actions, as Elliott and Chua<sup>41</sup> proposed in humans (also see refs 42–44). There exists a possibility that lateral asymmetry in the number of corticomotoneuronal connections innervating the hands governs the forms and functions of manual asymmetries: the hand with lesser corticomotoneuronal connections is specialized for manual operations that primarily involve physical strength, or those that require power grips, and the hand with greater corticomotoneuronal connections is specialized for manual actions that involve manoeuvring in three-dimensional space, or those that require precision grips (see ref. 1). The above step-by-step analysis of different manual tasks reveals sequential or concurrent fundamental manual actions. These actions can be then classified in terms of the form into either the power or precision grip, or in terms of the function into either manoeuvring in three-dimensional space or providing physical strength.

#### *Inter-individual, -population or -species comparisons*

Some intermediate step(s) involved in solving a multi-step task might not be a part of the behavioural repertoire of an individual, a population, or a species. Consequently, the perceived complexity of a task might vary across individuals, populations or species, making inter-individual, -population or -species comparisons of hand preferences across complex tasks erroneous. Diversity in factors causing spatio-temporal inter-individual, -population, or -species variations in manual actions may also influence hand-usage patterns at multiple levels of organization. For example, Sfar *et al.*<sup>45</sup> did a comparative assessment of hand preference in red howlers, *Alouatta seniculus* and yellow-breasted capuchins, *Sapajus xan-*

*thosternos*. The red howlers, which habitually use the mouth to obtain food, selectively took part in the reaching-for-food tasks and also exhibited stronger hand preferences than the yellow-breasted capuchins in the tasks that were relatively simple to solve. However, differences in the strength of hand preference diminished with the increasing complexity of the reaching-for-food tasks, that is, the relatively more complex tasks were perceived as equally complex by both the red howlers and the yellow-breasted capuchins. Both these observations demonstrate that different species may perceive a task less or more complex owing to differences in their feeding ecology and niche structure. Thus, manual asymmetries in non-human primates should be studied not just in isolation, but within the broader scope of the behavioural repertoire of an individual, a population or a species.

Thus, we found that: (a) a consequence of the ‘gold rush’ like hunch for human-like handedness in non-human primates has been that researchers have been continually analysing observations at the level of the population, ignoring analysis at the level of an individual and, consequently, have potentially missed revelations on the forms and functions of manual asymmetries. (b) These studies lack an a priori description of a cognitively demanding and/or less-demanding manual action and the requirements of the task in terms of the form (e.g. power or precision grip; see Napier<sup>46</sup>) or function (e.g. manoeuvring in three-dimensional space and providing physical strength) and, therefore, remain largely contextual. (c) In multi-step tasks, even when requiring less precision, step(s) preceding the terminal act might not be a part of the behavioural repertoire of an individual, a population or a species, in which case, inter-individual, -population or -species comparisons of hand-usage patterns are likely to be erroneous.

#### *Division of labour as a general principle*

On the basis of our studies on manual asymmetries in bonnet macaques<sup>1,2</sup>, our review of studies on manual asymmetries in capuchin monkeys, *Cebus* spp. and our analysis of the various tasks used in these studies, collectively suggest that ‘division of labour’ is a general principle underlying manual asymmetries in non-human primates. In order to substantiate this possibility, we propose the following:

#### *Division of labour in hand usage is likely to be prominently visible in transitions between tasks with variable requirements*

Individuals may have to make transitions between tasks with variable requirements and depending on these, vary hand usage. Suppose, for example, an individual that preferentially uses the left hand to make power grips and the right hand to make precision grips is solving a

reaching-for-food task that involves obtaining food items from a portable container (e.g. a water bottle), the individual holds the container in the left hand and retrieves the food items with the right hand. A conspecific then approaches this focal individual and so it moves with the bottle to some other location, say to a nearby high-rise platform, or to a distant branch. There can be two ways an individual can do so: (a) by holding the bottle in the left hand and climbing with the right hand, or (b) by shifting the bottle to the right hand, setting the left hand free and climbing with the left hand. If one hand is specialized for manual operations that require power grips and the other hand is specialized for manual operations that require precision grips, or alternatively for manoeuvring in three-dimensional space and providing physical strength, the second way seems more plausible (see Mangalam *et al.*<sup>1</sup> for another such example). So, if the transition involves tasks with variable requirements, division of labour becomes evident. In order to observe the division of labour in hand usage based on task demands, an experimental design should examine hand preference across situations synonymous to that in the above example. Stringent changes in hand-usage patterns while shifting contexts would demonstrate division of labour in hand usage.

*Division of labour in hand usage is likely to be visible and understood in tasks with differential requirements*

Napier<sup>46</sup> described prehensile functions of the human hand, such as grasping and gripping: an object can be grasped/gripped by either holding it in a clamp formed by partly flexed fingers and palm, while applying a counter pressure by the thumb lying more or less in plane of the palm – the ‘power’ grip, or pinching it between the flexor aspects of the fingers and the opposing thumb – the ‘precision’ grip. Performing certain manual operations primarily requires power and precision plays a secondary role, whereas performing certain other manual operations primarily requires precision and power plays a secondary role. And this task-specific requirement of power and precision grip is likely to influence hand-usage patterns in a given manual operation. In New World monkey species, the typical hinge-shaped joint of the thumb at the base of the palm allows abduction/adduction and flexion/extension movements, but not rotational movement, the key factor in opposability<sup>47</sup>. For a long time it was thus held that no New World monkey species could grasp objects with precision<sup>47–49</sup>. However, comparative behavioural studies demonstrated that capuchins stand out from other platyrrhine species because of their (a) high degree of manual dexterity<sup>27,50,51</sup>, (b) frequent use of precision grips that mainly involve lateral aspects of digits for picking up small objects<sup>20,52,53</sup>, and (c) capacity to perform relatively independent movements of the digits<sup>52,53</sup>.

Anatomical and physiological features of the neural substrate that control manual actions might explain the high manual dexterity in capuchins. The capuchins can act out highly fractionated movements of the fingers/digits owing to the large number and extension of the corticomotoneuronal connections that innervate the hand<sup>54–57</sup>, as observed in humans and chimpanzees<sup>58</sup>. Moreover, studies reported that the individuals that preferentially used the right hand to reach for food in a concurrent bimanual tube task, exhibited a greater leftward bias of the anterior cerebellum<sup>59</sup> and had a shallower central sulcus<sup>60</sup>, as well as a smaller overall corpus callosum in the contralateral hemisphere<sup>61</sup>, compared to those that preferentially used the left hand or did not show hand preference; although there was no difference in the size of the left-frontal petalia between the two<sup>62</sup>.

A few studies investigated manual asymmetries with respect to the control and movement of the fingers/digits in capuchins. Christel and Frigaszy<sup>53</sup> reported that the individuals did not exhibit considerable patterns in hand preference or hand performance with respect to the power or precision grips used to grasp currants and grapes lying on a tray. Spinozzi *et al.*<sup>20</sup> reported that the individuals preferentially used one hand to grasp a food item fixed on a tray and did not show any difference in performance with respect to the power or precision grips, but extracted the food faster with the preferred hand than the non-preferred hand with respect to the precision grips (and not with respect to the power grips). Spinozzi *et al.*<sup>23</sup> reported that the individuals preferentially used one hand to retrieve a raisin from a transparent hollow tube fixed horizontally to the upper end of a vertical metal bar and extracted the food faster with the preferred hand than the other hand. Whereas these findings indicate that precise control/movement of the fingers/digits is more likely to elicit manual asymmetries than the imprecise ones, there are problems with the experimental set-ups.

If, suppose, one hand is specialized for manual operations that primarily involve physical strength and, therefore, require power grips, and the other hand is specialized for those that involve manoeuvring in three-dimensional space and, therefore, require precision grips, a manual operation that primarily requires either one or the other of the two forms and functions of the hand is likely to influence hand-usage patterns with respect to a particular type of grip as well as grip-formation patterns with respect to a particular hand. The three studies – Christel and Frigaszy<sup>53</sup>, Spinozzi *et al.*<sup>20</sup> and Spinozzi *et al.*<sup>23</sup> – employ reaching-for-food tasks that primarily involve manoeuvring in three-dimensional space and, therefore, require precision grip. This is likely to be the reason why Christel and Frigaszy<sup>53</sup> did not find manual asymmetries with respect to the types of grips, and Spinozzi *et al.*<sup>20</sup> did not find a difference in performance between the two hands with respect to the power grips, presenting a distorted and partial picture of manual asymmetries.

We propose an experimental design to unambiguously determine the forms and functions of manual asymmetries in non-human primates. One should examine hand preference in a concurrent, bimanual reaching-for-food task. In one scenario, the manual operations should require a power grip followed by a precision grip; in another scenario, the manual operations should require a precision grip followed by a power grip. Contrasting hand-usage patterns in these two scenarios would indicate that the individuals preferentially used the two hands depending on the requirements of the tasks, that is, one hand to perform the manual operations involving manoeuvring in three-dimensional space and the other hand to perform those involving physical strength. One should then examine hand performance with regard to the requirements of the tasks in a concurrent, bimanual hand-performance-differentiation task. In one scenario, this task should ergonomically force the usage of either the left or the right hand to perform a manual operation requiring either a power grip or a precision grip. In another scenario, this task should ergonomically force the usage of either the left or the right hand to perform a manual operation requiring a precision grip and the other hand to perform the one requiring a power grip. A more effective and/or efficient power grip in one scenario and a precision grip in the other scenario would indicate that the individuals used the two hands depending on the specializations, that is, difference in the manual dexterity of the two hands.

*Division of labour in hand usage is likely to improve hand performance in terms of efficiency of the power and precision grips*

Manual asymmetries might have ecological disadvantages as they can potentially make an individual vulnerable to attack/defend appropriately only when the prey/predator is present on a particular side. Also, as the stimuli are randomly located with respect to the sagittal plane of an individual, i.e. towards left or right, it might make it difficult to solve a particular task. However, manual asymmetries are likely to help increasing manual specialization, the benefits of which surpass the associated ecological disadvantages (reviewed by Vallortigara and Rogers<sup>63</sup>). Trehub<sup>64</sup> drew a distinction between mere hand preference and manual specialization by exemplifying human infants who exhibit manual specialization and not hand preference (this idea was carried forward by Fagot and Vauclair<sup>8</sup> in non-human primates). According to Trehub<sup>64</sup>, hand preference refers to the consistent usage of one hand to solve familiar, relatively simple and highly practised tasks, and may not be necessarily accompanied by an improvement in hand performance; whereas manual specialization refers to the consistent usage of one hand to solve novel, relatively complex and not-practised tasks that require peculiar action patterns and is necessarily accompanied by an improvement in

hand performance. Trehub<sup>64</sup> also described that individuals generally exhibit manual specialization only in the context of tasks that involve cognitively demanding manual actions (see, for example, Mangalam *et al.*<sup>1</sup> showing that manual specialization in bonnet macaques in tasks requiring peculiar action patterns, viz. in terms of tasks that require either higher manoeuvring dexterity or higher physical strength). Thus, there exists a marked difference between hand preference and manual specialization in terms of the resulting difference in performance of the two hands, evidently visible while considering the forms and functions of manual asymmetries, as described in the previous section.

Only one study examined the relationship between strength of hand preference and the corresponding hand performance in capuchins. Fragaszy and Mitchell<sup>11</sup> reported that the individuals exhibited a weak, but statistically non-significant, positive relationship between strength of hand preference and the corresponding hand performance in the (pseudo) unimanual and bimanual versions of the box task. However, they acknowledged that the strength of hand preference could have affected the timing of the hand movements, thereby affecting the relationship between strength of hand preference and the corresponding hand performance. A similar study in another non-human primate species – the bonnet macaque, Mangalam<sup>2</sup>, reported a negative relationship between (a) hand performance of the preferred hand, and the difference in hand performance between the two hands, in a hand-performance-differentiation task, and (b) difference in hand performance between the two hands and the difference in the strength of hand preference in another (pseudo) unimanual and bimanual versions of the box task in bonnet macaques. These findings indicate that a greater strength of hand preference is associated with a higher difference in the performance of the two hands. However, research lacks sufficient evidence supporting the hypothesis that hand preference, or better yet, division of labour in hand usage improves hand performance in terms of the time and/or energy required to perform a given task.

We propose an experimental design to determine the adaptive value of hand preference. One should examine hand preference in a (pseudo) unimanual reaching-for-food task (wherein, the manual operation should require either a power grip or a precision grip), and a concurrent, bimanual reaching-for-food task (wherein the manual operations should require a power grip with one hand followed by a precision grip with the other hand, or a precision grip with one hand followed by a power grip with the other hand). One should then examine hand performance in a hand-performance-differentiation task that should ergonomically force the usage of either the left or the right hand to perform a manual operation requiring either a power grip or a precision grip, thus allowing to measure hand performance independent of ceiling effects as this task is unlikely to elicit, or better yet, prime any

motor actions associated with the opposite hand. A positive relationship between (a) hand performance of the hand with higher performance in the hand-performance-differentiation task and normalized difference in hand performance for the two hands, and (b) difference in hand performance for the two hands in the hand-performance-differentiation task and difference in strength of hand preference in the (pseudo) unimanual and bimanual reaching-for-food tasks, with respect to the power grips, precision grips, or both, would indicate that the division of labour in hand usage improves hand performance.

## Conclusion

Studies have investigated the evolutionary origin of hand-preference in non-human primates. Based on our analysis, we propose the division of labour as being a general principle underlying manual asymmetries. This principle is based on the difference in the intrinsic requirements of the tasks, which can be broadly divided into manoeuvring in three-dimensional space and providing physical support, acquiring power and precision grips respectively. Our review of studies on hand-usage patterns in non-human primates reveals conceptual and logistic problems with the spontaneous and experimental tasks used to determine hand-usage patterns. Moreover, methodology differs and confounding variables are often not appropriately addressed. We suggest that studies on manual asymmetries in non-human primates should design experiments that do not undermine this possibility. As far as the adaptive value of manual asymmetries is concerned, we suggest that, to obtain more unambiguous answers, studies should be conducted with experimental designs that allow comparing hand-usage patterns across species that vary in their phylogenetic relatedness and/or ecology, over a range of spontaneous activities and experimental tasks. It might be useful to study manual preferences not just in isolation, but within the broader scope of the behavioural repertoire of the species. Also, it might be advantageous to study the ontogeny of manual preferences. Studies of these kinds may help understand the forms and functions of manual asymmetries and the potential selection pressures under which manual asymmetries are likely to appear and evolve.

1. Mangalam, M., Desai, N. and Singh, M., Division of labor in hand usage in free-ranging bonnet macaques, *Macaca radiata*. *Am. J. Primatol.*, 2014, **76**, 576–585.
2. Mangalam, M., Desai, N. and Singh, M., Division of labor in hand usage is associated with higher hand performance in free-ranging bonnet macaques, *Macaca radiata*. *PLoS ONE*, 2015, **10**, e0119337.
3. Bradshaw, J. and Rogers, L. J., *The Evolution of Lateral Asymmetries, Language, Tool Use and Intellect*, Academic Press, San Diego, 1993.
4. Papademetriou, E., Sheu, C. F. and Michel, G. F., A meta-analysis of primate hand preferences, particularly for reaching. *J. Comp. Psychol.*, 2005, **119**, 33–38.

5. Ward, J. P. and Hopkins, W. D., *Primate Laterality: Current Behavioral Evidence of Primate Asymmetries*, Springer-Verlag, New York, NY, 1993.
6. MacNeilage, P. F., Studdert-Kennedy, M. J. and Lindblom, B., Primate handedness reconsidered. *Behav. Brain Sci.*, 1987, **10**, 247–263.
7. McGrew, W. C. and Marchant, L. F., On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Yearb. Phys. Anthropol.*, 1997, **40**, 201–232.
8. Fagot, J. and Vauclair, J., Manual laterality in nonhuman primates: a distinction between handedness and manual specialization. *Psychol. Bull.*, 1991, **109**, 76–89.
9. Mangalam, M. and Singh, M., Flexibility in food extraction techniques in urban free-ranging bonnet macaques, *Macaca radiata*. *PLoS ONE*, 2013, **8**, e85497.
10. Witelson, S. F., Hand preference: basis or reflection of hemispheric specialization? *Behav. Brain Sci.*, 1988, **11**, 735–736.
11. Frigaszy, D. M. and Mitchell, S. R., Hand preference and performance on unimanual and bimanual tasks in capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.*, 1990, **104**, 275–282.
12. Lilak, A. L. and Phillips, K. A., Consistency of hand preference across low-level and high-level tasks in Capuchin monkeys (*Cebus apella*). *Am. J. Primatol.*, 2008, **70**, 254–260.
13. Meunier, H. and Vauclair, J., Hand preferences on unimanual and bimanual tasks in white-faced capuchins (*Cebus capucinus*). *Am. J. Primatol.*, 2007, **69**, 1064–1069.
14. Spinozzi, G., Castorina, M. G. and Truppa, V., Hand preferences in unimanual and coordinated-bimanual tasks by tufted capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.*, 1998, **112**, 183–191.
15. Westergaard, G. C., Kuhn, H. E., Lundquist, A. L. and Suomi, S. J., Posture and reaching in tufted capuchins (*Cebus apella*). *Laterality*, 1997, **2**, 65–74.
16. Parr, L. A., Hopkins, W. D. and de Waal, F. B. M., Haptic discrimination in capuchin monkeys (*Cebus apella*): evidence of manual specialization. *Neuropsychologia*, 1996, **35**, 143–152.
17. Garber, P. A., Gomes, D. F. and Bicca-Marques, J. C., Experimental field study of hand preference in wild black-horned (*Cebus nigritus*) and white-faced (*Cebus capucinus*) capuchins: evidence for individual and species differences. *Anim. Cogn.*, 2008, **11**, 401–411.
18. Westergaard, G. C., Kuhn, H. E. and Suomi, S. J., Effects of upright posture on hand preference for reaching vs the use of probing tools by tufted capuchins (*Cebus apella*). *Am. J. Primatol.*, 1998, **44**, 147–153.
19. Westergaard, G. C. and Suomi, S. J., Hand preference in capuchin monkeys varies with age. *Primates*, 1993, **34**, 295–299.
20. Spinozzi, G., Truppa, V. and Lagana, T., Grasping behavior in tufted capuchin monkeys (*Cebus apella*): grip types and manual laterality for picking up a small food item. *Am. J. Phys. Anthropol.*, 2004, **125**, 30–41.
21. Westergaard, G. C. and Suomi, S. J., Capuchin monkey (*Cebus apella*) grips for the use of stone tools. *Am. J. Phys. Anthropol.*, 1997, **103**, 131–135.
22. Westergaard, G. C. and Suomi, S. J., Hand preference for a bimanual task in tufted capuchins (*Cebus apella*) and rhesus macaques (*Macaca mulatta*). *J. Comp. Psychol.*, 1998, **110**, 406–411.
23. Spinozzi, G., Lagana, T. and Truppa, V., Hand use by tufted capuchins (*Cebus apella*) to extract a small food item from a tube: digit movements, hand preference, and performance. *Am. J. Primatol.*, 2007, **69**, 336–352.
24. Spinozzi, G. and Truppa, V., Problem-solving strategies and hand preferences for a multicomponent task by tufted capuchins (*Cebus apella*). *Int. J. Primatol.*, 2002, **23**, 621–638.
25. Spinozzi, G. and Cacchiarelli, B., Manual laterality in haptic and visual reaching tasks by tufted capuchin monkeys (*Cebus apella*): an association between hand preference and hand accuracy for food discrimination. *Neuropsychologia*, 2000, **38**, 1685–1692.



26. Lacreuse, A. and Frigaszy, D. M., Manual exploratory procedures and asymmetries for a haptic search task: a comparison between capuchin monkeys (*Cebus apella*) and humans. *Laterality*, 1997, **2**, 247–266.
27. Lacreuse, A. and Frigaszy, D. M., Hand preferences for a haptic searching task by tufted capuchins (*Cebus apella*). *Int. J. Primatol.*, 1996, **17**, 613–632.
28. Lacreuse, A., Left hand preferences in capuchins (*Cebus apella*): role of spatial demands in manual activity. *Laterality*, 1999, **4**, 65–78.
29. Wilson, M., Tactual discrimination learning in monkeys. *Neuropsychologia*, 1965, **3**, 353–361.
30. Westergaard, G. C. and Suomi, S. J., The use of probing tools by tufted capuchins (*Cebus apella*): evidence for increased right-hand preference with age. *Int. J. Primatol.*, 1994, **15**, 521–529.
31. Westergaard, G. C., Kuhn, H. E. and Suomi, S. J., Laterality of hand function in tufted capuchin monkeys (*Cebus apella*): comparison between tool use actions and spontaneous non-tool actions. *Ethology*, 1998, **104**, 119–125.
32. Westergaard, G. C. and Suomi, S. J., Asymmetrical manipulation in the use of tools by tufted capuchin monkeys (*Cebus apella*). *Folia Primatol.*, 1994, **63**, 96–98.
33. Anderson, J. R., Degiorgio, C., Lamarque, C. and Fagot, J., A multi-task assessment of hand lateralization in capuchins (*Cebus apella*). *Primates*, 1996, **37**, 97–103.
34. Westergaard, G. C., Hand preference in the use and manufacture of tools by tufted capuchin (*Cebus apella*) and lion-tailed macaque (*Macaca silenus*) monkeys. *J. Comp. Psychol.*, 1991, **105**, 172–176.
35. Westergaard, G. C. and Suomi, S. J., Hand preference in the use of nut-cracking tools by tufted capuchin monkeys (*Cebus apella*). *Folia Primatol.*, 1993, **61**, 38–42.
36. Westergaard, G. C. and Suomi, S. J., Hand preference for stone artefact production and tool-use by monkeys: possible implications for the evolution of right-handedness in hominids. *J. Hum. Evol.*, 1996, **30**, 291–298.
37. Panger, M. A. and Wolfe, L. D., Carrying and hand-use patterns in Panamanian white-faced capuchins (*Cebus capucinus*). *Primates*, 2000, **41**, 407–411.
38. Westergaard, G. C., Haynie, M. K., Lundquist, A. L. and Suomi, S. J., Carrying, sharing, and hand preference in tufted capuchins (*Cebus apella*). *Int. J. Primatol.*, 1999, **20**, 153–162.
39. Hopkins, W. D., Laterality in maternal cradling and infant positional biases: implications for the development and evolution of hand preferences in nonhuman primates. *Int. J. Primatol.*, 2004, **25**, 1243–1265.
40. Porter, R., The corticomotoneuronal component of the pyramidal tract: corticomotoneuronal connections and functions in primates. *Brain Res.*, 1985, **1**, 1–26.
41. Elliott, D. and Chua, R., Manual asymmetries in goal-directed movement. In *Manual Asymmetries in Motor Performance* (eds Elliott, D. and Roy, E. A.), CRC Press, New York, NY, 1996, pp. 143–157.
42. Healey, J. M., Liederman, J. and Geschwind, N., Handedness is not a unidimensional trait. *Cortex*, 1986, **22**, 33–53.
43. Steenhuis, R. E., Hand preference and performance in skilled and unskilled activities. In *Manual Asymmetries in Motor Performance* (eds Elliott, D. and Roy, E. A.), CRC Press, New York, NY, 1996, pp. 123–142.
44. Steenhuis, R. E. and Bryden, M. P., Different dimensions of hand preference that relate to skilled and unskilled activities. *Cortex*, 1989, **25**, 289–304.
45. Sfar, N., Mangalam, M., Kaumanns, W. and Singh, M., A comparative assessment of hand preference in captive red howler monkeys, *Alouatta seniculus* and yellow-breasted capuchin monkeys, *Sapajus xanthosternos*. *PLoS ONE*, 2014, **9**, e107838.
46. Napier, J. R., The prehensile movements of the human hand. *J. Bone Joint Surg.*, 1956, **38**, 902–913.
47. Napier, J. R. and Napier, P. H., *A Handbook of Living Primates*, Academic Press, London, UK, 1967.
48. Bishop, A., Use of the hand in lower primates. In *Evolutionary and Genetic Biology of the Primates* (ed. Buettner, J. J.), Academic Press, New York, NY, 1964, pp. 133–225.
49. Napier, J. R., *Hands*, Princeton University Press, Princeton, New Jersey, 1993.
50. Frigaszy, D. M., Time budgets and foraging behavior in wedge-capped capuchins (*Cebus olivaceus*): age and sex differences. In *Current Perspectives in Primate Social Dynamics* (eds Taub, D. and King, F.), van Rostrand Reinhold, New York, NY, 1990, pp. 159–174.
51. Panger, M. A., Object-use in free-ranging white-faced capuchins (*Cebus capucinus*) in Costa Rica. *Am. J. Phys. Anthropol.*, 1988, **106**, 311–321.
52. Costello, M. B. and Frigaszy, D. M., Prehension in *Cebus* and *Saimiri*: I. Grip type and hand preference. *Am. J. Primatol.*, 1988, **15**, 235–245.
53. Christel, M. I. and Frigaszy, D. M., Manual function in *Cebus apella*. Digital mobility, preshaping, and endurance in repetitive grasping. *Int. J. Primatol.*, 2000, **21**, 697–719.
54. Muir, R. B. and Lemon, R. N., Corticospinal neurons with a special role in precision grip. *Brain Res.*, 1983, **261**, 312–316.
55. Kuypers, H. G. J. M., Anatomy of the descending pathways. In *Handbook of Physiology, Section 1: The Nervous System II* (eds Brookhart, V. B. V. and Mountcastle, J. M.), American Physiology Society, Bethesda, MD, 1981, pp. 597–666.
56. Lemon, R. N., Cortical control of the primate hand. *Exp. Physiol.*, 1993, **78**, 263–301.
57. Shinoda, Y., Yokota, J. L. and Futami, T., Divergent projection of individual corticospinal axons to motoneurons of multiple muscles in the monkey. *Neurosci. Lett.*, 1981, **23**, 7–21.
58. Bortoff, G. A. and Strick, P. L., Corticospinal terminations in two New-World primates: further evidence that corticoneuronal connections provide part of the neural substrate for manual dexterity. *J. Neurosci.*, 1993, **13**, 5105–5118.
59. Phillips, K. A. and Hopkins, W. D., Exploring the relationship between cerebellar asymmetry and handedness in chimpanzees (*Pan troglodytes*) and capuchins (*Cebus apella*). *Neuropsychologia*, 2007, **45**, 2333–2339.
60. Phillips, K. A. and Sherwood, C. C., Primary motor cortex asymmetry is correlated with handedness in capuchin monkeys (*Cebus apella*). *Behav. Neurosci.*, 2005, **119**, 1701–1704.
61. Phillips, K. A., Sherwood, C. C. and Lilak, A. L., Corpus callosum morphology in capuchin monkeys is influenced by sex and handedness. *PLoS ONE*, 2007, **2**, e792.
62. Phillips, K. A. and Sherwood, C. C., Cerebral petalias and their relationship to handedness in capuchin monkeys (*Cebus apella*). *Neuropsychologia*, 2007, **45**, 2398–2401.
63. Vallortigara, G. and Rogers, L. J., Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behav. Brain Sci.*, 2005, **28**, 575–588.
64. Trehub, S. E., Manual specialization and the developing brain: an overview. In *Manual Specialization and the Developing Brain* (eds Young, G. et al.), Academic Press, New York, NY, 1983, pp. 257–274.

Received 12 September 2015; revised accepted 5 February 2016

doi: 10.18520/cs/v110/i9/1630-1638