Handedness in long-tailed macaque (*Macaca fascicularis*) and Human

Master thesis
Pauline Chatagny

Work conducted in the laboratory of Prof Eric M. Rouiller
Under the supervision of Prof Eric M. Rouiller
Department of Medicine
Unit of Physiology

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1. Abstract

The aim of this study was to determine the hand preference and the hand dominance in eight long-tailed macaques and in twenty humans.

Four behavioral tests have been executed by the monkeys: the modified Brinkman board, the reach and grasp drawer, the tube and the bimanual board tasks. Three behavioral tests, adapted versions from the monkeys tasks (modified Brinkman board, tube and bimanual board tasks), as well as a handedness questionnaire have been conducted in human subjects.

The results obtained in monkeys showed a large disparity across individuals. Nevertheless we can conclude that two monkeys are right-handers (dominance and preference), whereas two other animals show a different lateralized preference and dominance. Finally the last four monkeys have either a right preference and no dominance, or a left/right dominance and no preference. It is not possible to conclude for handedness at the population level. Indeed the number of subjects is too small, therefore the analysis remained at the individual level.

For human subjects, the results of the hand preference mostly follow the self estimation of lateralization given by the subjects. The left-handers are strongly left lateralized and the right-handers are strongly right lateralized. We have to attenuate this conclusion for the tube task, where the results were more contrasted. Indeed some subjects showed a different direction of lateralization for this task. The hand dominance is mostly coherent with the hand preference, although some subjects did not exhibit significant differences.

The present study provides preliminary evidence that hand dominance and hand preference are substantially different between macaques and human subjects, with a large disparity in the former and more consistency in the latter.
2. Introduction

Handedness. How could we define it? Commonly handedness is synonymous of hand preference. For most people the preferred hand is the hand we will use to write, or the hand which is most used, or else, the hand which is most efficient. For this work, we will distinguish two notions: hand preference and hand dominance. We define the hand of preference as the hand with which subjects prefer to work on a specific task, instinctively and without worrying if this hand is the most efficient one. For bimanual tasks, the preferred hand is the hand which executes the most complex action or the manipulative role, whereas the non-preferred hand acts as postural support. Hand dominance is the hand which shows the best efficiency to do a particular action (Serrien et al, 2006).

The aim of this experiment is to determine hand preference and hand dominance in eight crab-eating macaques and in twenty humans. The interest of this research lies in several points.

Firstly different research groups in Fribourg work on some aspects of the motor system. They use, as model, crab-eating macaques (Macaca fascicularis) to study the potential of recovery of the central nervous system (CNS) after cortical or spinal lesions, or to test new treatment for subjects with Parkinson’s disease. For all these cases, the hand dominance has been already studied since many years but as many studies have pointed it out (Fagot and Vauclair, 1991; Kastner-Koller et al, 2007; Derakhshan, 2005), distinction between hand dominance and hand preference raises new questions. As shown by Ettlinger and colleagues (1985), the relation between hand preference, hemispheric dominance and behavioral aspects is strong. For this reason and in a concern of improvement of our model it seems to be important to determine the hand dominance and preference. It is also important to study the same aspects in human to be able to do comparisons and therefore to have a better understanding of the motor system in primates.
Secondly, once the handedness will be determined, the way will be opened for a lot of new fundamental and detailed questions as the precise link between handedness and hemispheric dominance, handedness and many neurological deficits, researches on evolution... For all these questions, the starting point stays the assessment, the evaluation of handedness.

This work is organized in two main parts. The first one deals with the theoretical topics. I will explain the main concepts to allow a better approach of the topic. The second part will focus on the behavioral study, with description of the different tasks, the results and a final survey on the evaluation of handedness in monkeys and humans.

2.1 Motor system

Voluntary and involuntary movements are controlled by specific regions of the CNS, called together the motor system. This system can be defined by three hierarchical levels and is also organized in parallel.

The first level includes the associative areas of the neocortex and basal ganglia. Their main function is to prepare the “motor strategies” in order to reach the target of a movement in the best conditions. The second level includes the motor cortex and the cerebellum. It has to elaborate the “parameters of the movement”. Finally, the third level involves the spinal cord and the brain stem which have to perform the action. They activate the motoneurones and the interneurones which create the movement and all actions implicated for this movement (postural stabilization...). These three levels are modulated by inputs of the somatosensory system. Only the cerebral cortex and the brain stem have a direct access to the spinal cord. The other structures have only an indirect access via the cortex or the brain stem (Bear et al, 2006).
The motor cortex is particularly important in the motor system [Fig.1]. It is subdivided in several areas (in the large sense). The primary motor cortex (M1) corresponds to the Brodmann’s area 4, the premotor (PM) and the supplementary motor areas (SMA) altogether correspond to the Brodmann’s area 6 whereas the cingulate motor area (CMA), comprises the areas 23 and 24 of Brodmann.

Each cortical motor area plays a defined role in the movement. M1 is responsible of the execution of the movement and has a determinant role for simple motor tasks. PM and SMA are more implicated in complex motor tasks and in the planning of movements.

Figure 1: Organization and somatotopy of the motor cortex in human and macaque monkey (Kandel et al, 2000).

The link between the motor cortex and the spinal cord is provided by the descending pathways [Fig.2]. There are two main systems: the ventromedial pathway and the lateral pathway. The first one is composed of three different tracts: reticulospinal, tectospinal and vestibulospinal tracts. The second one comprises two tracts: the rubrospinal and the corticospinal tracts. The ventromedial pathway plays a role for the locomotion, the stability and the posture of the body just as the rubrospinal tract, whereas the corticospinal tract has a predominant function during voluntary movements. It is therefore this system which interests us for the present study (Lemon, 1993 and 2008; Brinkman, 1984; Brinkman and Kuypers, 1972; Nudo et al, 2001).
Figure 2: On the left, in blue, the corticospinal fibers: some fibers terminate in the ventromedial intermediate zone (bilaterally), shown in green, whereas the most part terminate contralaterally in the dorsolateral intermediate zone (in red) and directly on motoneurones which innervate arm and hand (in blue with black circles). On the right side, the reticulospinal, tectospinal and vestibulospinal fibers are in green and the rubrospinal fibers are in red. The black arrows represent cortical projections. (Lemon, 2008).

2.1.1 Corticospinal tract (CST)

The CST takes mainly its origin from the frontal lobe: M1, PM, SMA and CMA. It comes also from the postcentral gyrus of the parietal lobe, but to a lesser extent. It is composed of large pyramidal neurons in the layer V (Catsman-Berrevoets and Kuypers, 1976; Jones and Wise, 1977).

The fibers go through the internal capsule, then through the cerebral peduncle in the midbrain, then the pons and at this moment, they project through the medulla. At the junction between the medulla and the spinal cord, 80-90% of the axons decussates and moves on in the lateral zone of the spinal cord (in the dorsolateral funiculus), to finally terminates on distal muscles, on the contralateral side. The 10-20% of the non-crossed axons terminate mainly on proximal and axial muscles (Courtine et al, 2007). The final connection can be indirect on interneurons or direct on motoneurons. This last direct connection is a special feature of primates (the cortico-motoneuronal system: CM). Contrary to the indirect CS tract, the CM projection derives mostly from M1.
As said before, the CM is a new feature in primates, in comparison to other mammals which do not have direct connection on motoneurons. Another special feature is the increasing dominant role played by the CST to the detriment of the other descending pathways. The CM allows better control of movements of the cortical regions on the hand and the arm. It ensures partly to fractionate the muscular activity, therefore, some independent movements of digits are possible under voluntary control, such as the “performance of relatively independent finger movements (RIFM)”. Among other things, the RIFM comprises the precision grip (Lemon, 1993).

The precision grip concept was introduced by Hepp-Reymond and Wiesendanger (1972) and is considered as a highly difficult movement, required when grasping small objects between two fingers, the thumb and generally the index finger (Liu and Rouiller, 1999). The difficulty comes from the fact that, to execute this movement, the cooperation of several muscles of hand and arm, tendons, ligaments is involved. In the same way, it needs to stabilize the upper limb to ensure a better effectiveness (Porter and Lemon, 1993).

### 2.1.2 Comparisons between human and nonhuman primates

The differences between human and the various nonhuman primates lie mainly in the complexity of cortical and spinal systems involved in motor behavior. Indeed during primates evolution, the subtleties and refinement in organization of these systems have little-by-little increased through species, from New World Monkeys and Old World Monkeys to apes and humans (Courtine et al, 2007).
From an anatomical point of view, despite similarity of the hand in terms of number and disposition of digits, the arrangement of joints, tendons and muscles are quite different, as well as their motor capacities. In the same way, the number of direct CM connection is directly linked with the dexterity [Fig.3]. Therefore, New World Monkeys have a pseudo-opposition of the thumb and the index finger whereas there is a true opposition in Old World Monkeys (e.g. Macaca), which allows, as previously explained, to grasp and manipulate small objects skillfully. This capacity is still more efficient in apes and humans (Lemon, 1993 and 2008). So macaques and humans can execute manual grasping tasks in a very similar efficiency and with similar behavior.

Figure 3: “Relationship between the development of the CST and the emergence of fine motor control abilities. In rodents, there are no direct connections between CS neurons and the cervical motoneurons that innervate forelimb muscles – interneurons relay cortical input to motor neurons. In the evolution of the CST in nonhuman primates and humans, direct CS connections with motoneurons have emerged, together with an increase in the size and number of the CS fibers. Accordingly, the size of the excitatory postsynaptic potential (EPSP) elicited by cortical neurons on motoneurons has increased during primate evolution. Furthermore, most of the CST fibers in rodents travel in the dorsal column. In contrast, the primate CST is mostly located in the lateral columns, and a significant proportion of CS fibers (10%-20%), descend ipsilaterally (…).” (Courtine et al., 2007).

Macaques monkeys show also very equivalent metabolic and pharmacodynamic system, as well as same properties in the blood-brain barrier in comparison to human. They have the capacity to learn tasks as human would execute them (Courtine et al, 2007). For all these reasons, macaque monkeys are often used as a model in biomedical research (see Weatherall report, 2006).
2.2 Lateralization

Most of organisms belong to the Phylum of bilateria [Fig.4]. The main feature of this phylum is to show a bilateral symmetry. Despite this feature, most organisms exhibit some left-right asymmetries. The explanation for these asymmetries lies in the adaptation. For instance, the internal organs are organized in an asymmetrical manner, probably for function’s efficiency and for a profit of space. Other systems show an asymmetry, such as the CNS and the behavior (Corballis, 2009).

Figure 4: Phylum Bilateria in which we can find the Vertebrates to the Arthropoda. (Lichtneckert and Reichert, 2005)

The brain is divided into two hemispheres. Although these hemispheres seems to be identical from an anatomical point of view (except for the planum temporale), their functions can be different. So there is a lateralization of some functions, such as language, perception, spatial treatment, emotion or else handedness. Commonly, the functional asymmetry is not complete, which means that both hemispheres can act in every functions (except for language), but not in the same manner and with the same efficiency. They have their respective abilities and these abilities complement themselves (Hellige, 2002).
2.2.1 Handedness

Handedness in humans has been well studied in the last years. About 90% of humans are right-handers and have a left hemisphere specialization for manual function (e.g. Broca, 1865; Oldfield, 1971; Kimura, 1977; Springer and Deutsch, 1989).

It was commonly assumed that handedness was a feature of humans. This assumption is more and more refuted by the evidence of behavioral asymmetries in nonhuman primates (Hopkins, 2007). It is however difficult to find a motor functional lateralization at the population level in macaques (Schmidt et al, 2008).

2.2.2 Definition

Handedness is more defined as a continuum and not as a marked difference between left-/right-handers. Indeed, it ranges from strong left-handers to strong right-handers (Annett, 1998). As already described, we distinguish two notions under this term: the hand preference and the hand dominance (Porac and Coren, 1981). The hand dominance is defined as the hand which exhibits the best performance to execute a specific task whereas the preferred hand is the hand which is instinctively chosen to perform a task or, in the case of bimanual task, the hand which plays the manipulative role or the more complex action (in contrast to the postural role) (Serrien et al, 2006; Kastner-Koller et al, 2007).

From an anatomical point of view, left and right-handers seem to show morphological differences in cortical representations and corpus callosum. In this last structure, the differences seem to be due to the degree of laterality rather than its direction. So subjects with less lateralized functions appear to have a bigger corpus callosum. These morphological differences are translated into physiological differences: M1 is asymmetrically activated in more lateralized subjects (in the dominant hemisphere) whereas the activation is more bilateral in less lateralized subjects (Bernard et al, 2011). Kim et colleagues (1993), as well as Siebner et al (2002) have shown that right-handers have more asymmetrical activation in this area, whereas the activation in left-handers is more bilateral.
The view of Derakhshan (2005) is a little bit different. For him, the callosal traffic between the two hemisphere seems to be unidirectional and dependant on the laterality. Indeed, the dominant ("executive") hemisphere has direct control on contralateral side of the body ("dominant side"), whereas the "minor" hemisphere does not have this direct control, but has to act via the corpus callosum. Thus, moving the non-dominant side of the body need a bi-hemispherical activation.

2.2.3 Origins

There are several theories to explain the development, the apparition of handedness, but none of them have been really verified. In the following section, we will give a general view of the most common theories.

Several researchers are more supporters for a genetic explanation, although the classical Mendelian approach with a recessive allele for the left bias has to be rejected. Indeed, left-handers’parents can have right-handed children (Rife, 1940; McManus and Bryden, 1992). For instance, Annett (1998) with her right-shift theory and McManus (1999) propose models with alleles for right-handedness and for handedness becoming left- or right-lateralized by chance. On the other hand, some studies conclude that handedness has a genetic component, but that single-gene models are not verified and that a multifactorial model would be more appropriate (Franks et al, 2002; Van Agtmael et al, 2003). These models will not be discussed further in this work. Hopkins (2001, 2006) has exhibited some evidence for a genetic influence on the expression of handedness in apes, in the way that hand preference is heritable, even in related individuals living in different environments. However this heritability could also be dependent on external factors such as offspring parities.

Some other studies have shown the influence of environmental factors, either before or after birth. For instance, the concentration of cortisol in the plasma, which informs us about the stress’s state, measured in infant monkeys, seems to have an influence on manual laterality (Westergaard et al, 2000). Birth orders, age of the mother and in fact all factors affecting the development in utero seem to have implications too in the development and the apparition of handedness (Hopkins and Dahl, 2000; Hopkins et al, 2000; Annett, 1998).
Finally we can conclude that, with our modern theories of developmental biology, genetic and environmental factors are probably both necessary for the development of handedness and are inseparable. They both influence the development of this phenotype (Schaafsma et al, 2009).
3. Materiel and methods

For the aim of this study, four behavioral tests have been executed by the monkeys. They have taken place during about seven months, but not at the same frequency. Humans have had three corresponding tests, and had to respond to a handedness questionnaire. In this section we will describe in details the different behavioral methods, as well as the procedures to analyze the data.

3.1 Behavioral study on monkeys

The experiments were conducted on eight young female monkeys (Macaca fascicularis), aged between 6 and 7 years old at the beginning of the tests [Table 1]. None of the subjects have executed the different tasks before this study, so they were totally naïve. Every behavioral task has been approved by the ethical committee and was in accordance with the Guidelines for the Care and Use of Laboratory Animals (ISBN 0-309-05377-3; 1996) and authorized by local (Swiss) veterinary authorities. Experimental procedures were designed to minimize pain and suffering for the animals.

Table 1: summary table of behavioral parameters.

<table>
<thead>
<tr>
<th></th>
<th>Mk-AN</th>
<th>Mk-AT</th>
<th>Mk-CA</th>
<th>Mk-DI</th>
<th>Mk-LO</th>
<th>Mk-MA</th>
<th>Mk-MI</th>
<th>Mk-TH</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Age (at the beginning of the experiments)</strong></td>
<td>6 years old</td>
<td>7 years old</td>
<td>7 years old</td>
<td>7 years old</td>
<td>7 years old</td>
<td>7 years old</td>
<td>7 years old</td>
<td>6 years old</td>
</tr>
<tr>
<td><strong>Weigh (at the beginning of the experiments)</strong></td>
<td>3.2kg</td>
<td>3.4kg</td>
<td>3.7kg</td>
<td>3.4kg</td>
<td>3kg</td>
<td>3.2kg</td>
<td>3.1kg</td>
<td>3.9kg</td>
</tr>
<tr>
<td><strong>Brinkman board task</strong></td>
<td>103 sessions</td>
<td>100 sessions</td>
<td>89 sessions</td>
<td>121 sessions</td>
<td>100 sessions</td>
<td>123 sessions</td>
<td>91 sessions</td>
<td>100 sessions</td>
</tr>
<tr>
<td><strong>Drawer task</strong></td>
<td>12 sessions 151 trials</td>
<td>17 sessions 230 trials</td>
<td>15 sessions 190 trials</td>
<td>14 sessions 159 trials</td>
<td>18 sessions 335 trials</td>
<td>16 sessions 152 trials</td>
<td>16 sessions 183 trials</td>
<td>17 sessions 360 trials</td>
</tr>
<tr>
<td><strong>Tube task</strong></td>
<td>18 sessions 163 trials</td>
<td>20 sessions 287 trials</td>
<td>10 sessions 104 trials</td>
<td>18 sessions 189 trials</td>
<td>10 sessions 108 trials</td>
<td>30 sessions 308 trials</td>
<td>8 sessions 54 trials</td>
<td>16 sessions 175 trials</td>
</tr>
<tr>
<td><strong>Bimanual board task</strong></td>
<td>18 sessions 371 trials</td>
<td>19 sessions 331 trials</td>
<td>13 sessions 269 trials</td>
<td>14 sessions 309 trials</td>
<td>12 sessions 324 trials</td>
<td>36 sessions 489 trials</td>
<td>7 sessions 53 trials</td>
<td>17 sessions 466 trials</td>
</tr>
</tbody>
</table>
During each behavioral test, the monkey was seated in a primate chair [Fig.5]. The primate chair is in Plexiglas®, with adjustable opening allowing free head movements although the monkey is restrained. The animal is sitting on horizontal bars of which the height can be modified in function of the size of the monkey. So it ensures an adapted and comfortable position. The chair is also provided with two independent sliding doors at the front which allow working during a specific task with both hands separately or simultaneously.

Each experimental session was filmed with one or three digital video camera recorders, depending on the task (Drawer, tube and bimanual board task with one camera; Brinkman board task with three cameras).

The length of a daily session was about sixty minutes and the experiments were conducted with background music to drown out possible, external noises. At the end of the session the animals received their daily ration of food, composed of cereals, fruits and vegetables.

3.1.1 Modified Brinkman board task

The modified Brinkman board and its different adapted versions from the original test of Brinkman and Kuypers (1973) have often been used for behavioral and motor studies (Brinkman, 1983; Rouiller et al, 1998; Liu and Rouiller, 1999; Freund et al, 2009). In the present study we have used the modified Brinkman board [Fig.6]. It is made up of a rectangular board of Perspex® with 50 slots: 25 horizontal and 25 vertical. Each slot measures 6mm deep, 14mm long and 7mm wide. The board itself measures 22cm length, 12cm wide and 1.2cm thick. Each slot is filled with banana or sugar flavored pellet. The size of slots permits the monkeys just to grasp the pellets with the precision grip, generally using the thumb and the index finger (or another finger, with a flexion of the distal phalanx).

Figure 5: Monkey in the primate chair. Both sliding doors are opened.
The horizontal slots represent a bigger difficulty in comparison to the vertical ones, because they involve a rotation of the wrist. The board is positioned in front of the monkey with 40 degree of inclination.

**Figure 6: Modified Brinkman board. The slots are filled with banana flavored pellets.**

During each session, the animal has used firstly both hands, then the right and the left one separately and alternatively (for instance: both hands, then left and then right; the next day, both hands, then right and then left...). The monkey was placed either in a middle position, or at the left, or else at the right with respect to the board, in such manner that the hand with which she worked was aligned to the setup.

Videos illustrating this task can be visualized on the website: http://www.unifr.ch/neuro/rouiller/research/motorcontcadre.php.

### 3.1.2 Reach and grasp drawer task

For this task, the primate chair was placed in front of the drawer with both sliding doors opened, so the animal had to use both hands. Because of a spring mechanism, once opened, the drawer had to be maintained with one hand to avoid that it closed again, while the monkey used the other hand to grasp the pellet, which was placed in a hole inside the drawer. The dimensions of the object are mentioned on the figure 7.
During one session, the animal executed about 5 to 15 trials. One trial was achieved when the monkey opened the drawer with one hand, kept it open and grasped the pellet with the other hand.

**Figure 7: Drawer in a front view (left panel) and from top (right panel).**

### 3.1.3 Tube task

This task was inspired by the Tube Task of Hopkins (1995), who wanted to determine handedness in chimpanzees. Our tube, in transparent acrylic glass (PPMA or Plexiglas®), is so transformed for Macaques with the following dimensions: the handle measures 4cm long and 2cm diameter, the tube itself is 9cm long with a depth of 7cm, an external diameter of 6cm and an internal diameter of 5cm. At the bottom of the tube, there is a slot with a diameter of 0.5cm and a depth of 0.7cm [Fig.9; left panel]. This slot allows placing a sticky reward like sultana or little pieces of apple.

Our tube was attached to a rope by the handle and hung, in the way that it was placed in front of the primate chair, aligned with the central bar between the sliding doors. The base of the tube was at the level of the base of the doors.

The two sliding doors were opened and the animal had to hold the suspended tube with one hand while he reached the reward with the other hand and brought it to the mouth.

A daily session comprised ten to twenty trials.
3.1.4 Bimanual board task

This task was adapted from the bimanual coordinated task of Mark and Sperry (1968). Our bimanual board is made of transparent acrylic glass (PMMA or Plexiglas®). It measures 15.8cm long, 13.1cm breadth and has a thickness of 2cm. It comprises nine holes (Fig.10, left panel). Each hole has an upper diameter of 9.5mm and a lower diameter of 7mm and contains a sticky reward, like sultana or a little piece of apple. The board is fixed with about 20 to 30 degrees of inclination.

The primate chair was placed in the front of the board and both sliding doors were opened. The monkey had two possibilities to retrieve the reward: push the reward with the one hand above the board and collect it below the board with the other hand or push the reward with the hand positioned below the board and retrieve it above the board with the other hand.

One daily session included three to five repetition of the whole board, with retrieval of each reward. Each hole represented a trial.

3.2 Study on humans

The subjects for this study were twenty persons aged between 18 and 30 years old. They presented themselves as left- or right-handers and it corresponded to the hand they used to write. We had ten left-handers (6 men and four women) and ten right-handers (4 men and 6 women) (Appendix 1). Each subject came one time and executed three behavioral tasks before responding to the questionnaire. The three tasks were positioned on a table and every session was filmed with a digital video camera recorder. The subjects began with the modified Brinkman board task, then with the bimanual board task and finally with the tube task. The handedness questionnaire came at the end.

Before the beginning of the tests, the subjects sat on a chair in the middle and in front of the experiment table. They had to adjust the height of the chair to feel comfortable.
3.2.1 Modified Brinkman board task

For this part of the experiment, we have used an adapted model of the previously presented (see section: 2.1.1) modified Brinkman board. This board was already used for test with human being (Badoud, 2009) within the framework of study on handedness in humans.

This board is made of a wooden board of 58cm long and 28.5cm wide. It comprises fifty slots of 4.3cm long, 2.2cm wide and 1.8cm deep. It is tilted with a 30 degree angle. Before the beginning of a session, each slot is filled with a bolt (external diameter: 1.8cm, internal diameter: 1cm) [Fig.8]. The bolts replace the food pellets which are used for the tests with monkeys. The slots are done in a manner that subjects have to use the precision grip to retrieve the bolts. Their disposition is identical to the classical modified Brinkman board.

![Modified Brinkman board adapted for human being. The slots are filled with a bolt.](image)

Before the test started, the experimenter informed the subjects about the rules of the task. They had to execute it as fast as possible, taking one bolt each time, putting it into a plastic box which was maintained in the middle and in the front of the board. They were not allowed throw the bolt into the box. These rules allowed normalizing the test. When the rules were clear, the test started. The subject had to use alternatively ten times the right hand and ten times the left hand (left, right, left....). The experimenter determined with which hand the subject had to begin.
3.2.2 Tube task

This task is a human being adapted model from the tube used with monkeys. It is also an acrylic glass tube (PPMA or Plexiglas®) with the following dimensions: the tube itself measures 14.7cm long, 12.8cm depth, with an external diameter of 12cm and an internal diameter of 11cm. The handle is 9.5cm long and has a diameter of 3cm. The slot positioned in the bottom of the tube has a diameter of 2.2cm and is 0.9cm depth [Fig.9, right panel]. The reward is a candy (Yupi strawberry kiss or Yupi MarschMallows). A second tube was available when the subject had smaller hands. Every dimension is the same except for the diameters of the tube (external diameter: 9cm, internal diameter: 8cm).

Figure 9: Tube for monkeys (left panel) and for humans (right panel).

The tube was positioned with its base on the table and the handle upwards. The subject placed his hands on each side of the tube. The experimenter gave him the instructions. He had to take the reward and to use both hand to execute the task. He had the possibility to eat the reward or to give it to the experimenter. Then he had to put the tube back on the table at its initial location. He had to do the task twenty times.

One trial was achieved when the subject grabbed the tube with one hand when, simultaneously he took the reward with the other. Therefore a complete session comprised twenty trials.
3.2.3 Bimanual board

This task is a human being adapted model of the bimanual board for monkeys. It is a transparent acrylic glass board of 13cm wide, 16cm long, 2cm depth and pierced with 9 holes with a diameter of 2.2cm [Fig.10, right panel]. The board is fixed with 30 degree of inclination.

Before the test started, each hole was filled with a pellet in modeling clay. The experimenter gave the instructions to the subjects. He had to empty the board using both hands. He had to take only one pellet each time and to put it into a plastic box placed in the front of the board. One session corresponded to empty the board twenty times. Each hole represented one trial.

3.2.4 Handedness questionnaire

At the end of the experiments the subject had to answer to a questionnaire about handedness [Appendix 2]. This questionnaire was elaborated by Chris McManus (2009). It was chosen because it fills several pertinent criteria to assess handedness (Oldfield, 1971). The questions which were asked dealt with actions of daily life such as: with which hand do you write, you hold a potato while you are peeling it, you throw a ball...
3.3 Analysis of data

This section concerns every data, those derived from human beings and from monkeys.

The data of the behavioral tasks have been manually analyzed from the recorded video sequences. The program named VirtualDubMpeg2® allowed to visualize the film frame per frame making it possible to have very precise measurements (frame rate: 25/s). The data were then collected into worksheet Excel® and then they were analyzed with the program Sigmastat® and plotted with the programs Sigmaplot® or Excel®. Details about the statistical tests will be given in a following section (Statistical analysis).

3.3.1 Hand dominance

The hand dominance was determined with one task: the modified Brinkman board for which, in this section, we only consider data when the use of one hand was imposed.

Two types of data were analyzed for the monkeys: the score, that is the number of pellets taken in 30 seconds and the contact time (CT) which is defined as the time interval between the moment when the subject enters with a finger (often the index finger) into the slot and the moment when his fingers go out the slot with the reward. The figure 11 illustrates this measurement.

The CT is a pertinent additional parameter, because the score can be sometimes biased. Indeed the animal can be disturbed with noises, or have a lack of motivation or concentration and in these cases, he can stop to work. Moreover, the CT truly measures the manipulation of the objects.

Figure 11: Illustration of the contact time. On the picture 1, the monkey enters with his index finger in the slots. On picture 2, he uses the precision grip to take a pellet. On the third picture, he goes out of the slot with the pellet.
The CT was measured on the first five horizontal and first five vertical slots in the twenty last sessions of the task, when most monkeys reached a plateau, whereas the score was measured for every session. The onset of the plateau was fixed when a value in the flat curve of the score was not exceeded by the five following values.

For human beings we just measured the score in 30 seconds.

### 3.3.2 Hand preference

For monkeys, four tests allowed us to determine the hand preference: the modified Brinkman board when the animal used both hands, the drawer task, the tube task and the bimanual board task.

For humans, two tests, the tube task and the bimanual board task, and the questionnaire indicated their hand preference.

For the tube task we defined the preferred hand as the hand which took the reward into the tube. Indeed this hand had the manipulative role whereas the other hand, that held the tube, had the postural role.

For the bimanual task, we saw that the subjects used two different methods to retrieve the reward. In the first one, the hand above the board pushed the reward while the other hand collected it below the board. In the second one, the hand positioned below the board pushed the reward and the other hand grasped it above the board. In the first method, the preferred hand is the one which pushes the reward. Indeed its role is manipulative, whereas the role of the other hand is postural. For the second method, the preferred hand is the one which retrieves the reward. This action is more manipulative and more difficult in comparison to the role of the other hand. In fact, to retrieve the pellet in this case involves the precision grip movement. Additionally the board has an inclination which makes this movement still more difficult.
For the drawer task, the preferred hand was the hand which took the reward (manipulative role) while the other hand, the postural one, held the drawer.

For these three tasks, we measured the handedness index (HI) (Westergaard et al, 1997; Spinozzi et al, 1998; Hopkins et al, 2004; Schmidt et al, 2008), calculated as the number of times the right hand (R) was used as preferred hand minus the number of times the left hand (L) was used as preferred hand, divided by the total.

\[
HI = \frac{R-L}{R+L}
\]

Therefore, a minus HI reflects a left bias and a positive HI reflects a right bias. It gives an index of lateralization between +1 (strongly right-handed) and -1 (strongly left-handed).

For the modified Brinkman board task, we measured the score in 30 seconds when the animal had free hands. Therefore we counted the number of pellets grasped with each hand during the first 30 seconds.

For the questionnaire, we calculated the score by using the criteria of Chris McManus (2009):

“Laterality scores (laterality indices):

Score all the items as -1 = Always left, -.5 = Usually left, 0 = Either, +.5 = Usually right and +1 = Always right. For items 4 (dish), 6 (jar) and 9 (potato) a strong right-hander would answer left. These three items should therefore be reverse scored by changing the sign on the values given previously (i.e. +1=Always left, etc.). Having done this then one can obtain several measures:

Overall laterality score. The average of all eleven items

Cultural pressure score. Items on which there is strong social/cultural pressure to use the right hand. i.e. 5 (clock), 8 (knife).”

The score was then transformed in percentage (-100% indicating strongly left-handed and +100%, strongly right-handed).
3.3.3 Statistical analysis

For the tube, drawer and the bimanual board tasks we used the chi-square test.

For the scores of the Brinkman board, we used either the paired t-test or the Wilcoxon signed-rank test.

For the CT of the modified Brinkman board, we used either the t-test or the Mann-Whitney U test.
4. Results

This section is divided in two parts: the first one concerns the results obtained from the monkeys and, the second one, the results obtained from the human beings.

4.1 Monkeys

In this section, the results of each monkey are mostly treated separately because of their variability among individuals. The hand dominance and the hand preference are separately treated.

4.1.1 Hand dominance

As reminder, the hand dominance was determined based on the total score in 30 seconds (vertical and horizontal slots) and the CT (first five horizontal and first five vertical slots of the twenty last recorded sessions) of the modified Brinkman board, when the animal had to use one of his hands, either the left one, or the right one. The dominant hand is the hand with a higher score, or shorter CT, than the other hand.

We did a distinction among the scores. Indeed, we decided to separate the scores obtained during the learning curve from the scores obtained at the plateau in order to see if there were differences between these two states and if some dominance appeared already during the learning phase. As previously described, the onset of the plateau was fixed when a value in the flat curve of the score was not exceeded by one of the five following values. The scores (left/right hand for total, vertical and horizontal slots) for each monkey are available for more detail in the appendices 3 to 10. On these graphs the plateau is also represented (the black line).
The figure 12 represents the score for the left and the right hand for each monkey during the learning curve. Firstly we can observe great differences among individuals, the fastest monkey being Mk-DI (highest score) and the slowest, Mk-AN (lowest score). Then four monkeys (Mk-DI, Mk-LO, Mk-MA and Mk-MI) showed a significant difference for the manual dexterity between the right and the left hand. Indeed, Mk-DI and Mk-LO were faster with the right hand (p<0.001), whereas Mk-MA and Mk-MI performed better with their left hand (p=0.018 and p=0.003, respectively). The other monkeys (Mk-AN, Mk-AT, Mk-CA and Mk-TH) did not show any difference of manual dexterity between one and the other hand (n.s., meaning non-significant).

Figure 12: Total score (horizontal and vertical slots) for each monkey during the learning curve, when the use of one hand was imposed.
The figure 13 shows the score of the left and the right hand for each monkey during the plateau. The first thing we can highlight is the presence of two plateaux for Mk-DI (see also Appendix 6). After the learning phase, Mk-DI showed a decrease of the numbers of grasped pellets, corresponding to a first plateau, followed by a second higher plateau. This situation may eventually be explained by a diminution of the motivation. At first plateau, this monkey showed a significant difference between his right and his left hand, with a better score with the right hand (p<0.001), whereas there was no significant difference between both hand in the second plateau. For the other monkeys, three of them had a significant difference of dexterity between the hands, Mk-AN, Mk-CA and Mk-MA. The first one was better with his left hand (p=0.036), whereas Mk-CA and Mk-MA were more dextrous with their right hand (p=0.002 and p<0.001, respectively). Mk-AT, Mk-LO, Mk-MI and Mk-TH did not show any significant difference of the manual dexterity between their hands at plateau.

Figure 13: Total score (horizontal and vertical slots) for each monkey at plateau, when the use of one hand was imposed. The star represents the first plateau and the triangle, the second plateau (see text).
The data for the CT are plotted in two graphics: the first one concerns the vertical slots and the second one, the horizontal slots. Moreover, two graphs per monkey (one for the left hand, the other for the right hand) with detailed data are available from the appendices 11 to 18. Overall, and as expected the CT for the vertical slots has a tendency to be shorter (better dexterity) than the CT for the horizontal slots.

The figure 14 shows the CT for the first five vertical slots for every monkey. It is important to recall that the smallest the CT, the best the performance. Overall we can notice that the CT is more or less constant in all monkeys (except Mk-LO and to some extent Mk-AN and Mk-MA). The CT was significantly shorter for the left hand for Mk-AN and Mk-DI (p=0.002 and p=0.005, respectively), whereas it was significantly shorter for the right hand for Mk-CA and Mk-LO (p<0.001 for both). For the other monkeys (Mk-AT, Mk-MA, Mk-MI and Mk-TH) there was no significant difference of CT between the two hands.

Figure 14: CT for the vertical slots during the twenty last recorded sessions at plateau (imposed use of one hand), for every monkey.
The figure 15 concerns the CT for the horizontal slots during the twenty last analyzed sessions at plateau. Generally the CT in the horizontal slots has a tendency to be less regular than the CT in the vertical slots (length of the boxes). Most monkeys have a significant difference between the CT of the left and right hand, except Mk-AN (n.s). Mk-AT, Mk-CA, Mk-DI and Mk-MA have a better CT for their right hand (p=0.029 for Mk-AT and p<0.001 for the three other monkeys), whereas Mk-LO, Mk-MI and Mk-TH show a better CT for their left hand (p<0.001 for the first two and p=0.007 for the last one).

*Figure 15: CT for the horizontal slots during the twenty last recorded sessions (imposed use of one hand), for every monkey.*
4.1.2 Hand preference

As reminder, the hand preference in monkeys is determined by using the results of the modified Brinkman board, when the use of the two hands was free and the results of the three other tasks: the bimanual board, the tube and the drawer tasks.

For the modified Brinkman board, we did a distinction among the scores. Indeed, we decided to separate the scores obtained during several phases. These phases were easy to separate because there were distinct differences between them. The monkeys evolved in their manner to execute the task and in the choice of one hand to the detriment of the other along the sessions [e.g. Fig.16].

Figure 16: Score for the horizontal slots for Mk-AN. The vertical dotted line separates two phases: the phase I in which the right hand (in red) was hardly ever used and the phase II during which both hands were used more or less at the same frequency (see the following statistical tests). The difference between the two phases is obvious.

The scores for vertical and horizontal slots for each monkey are available for detailed information in the appendices 19 to 26. The dotted lines separate the distinct phases.
The figure 17 shows the scores during the phase I for the vertical slots. Four monkeys exhibited a significant preference to use one of their hands (Mk-AN, Mk-DI, Mk-LO and Mk-TH), whereas the four other monkeys showed no significant preference (Mk-AT, Mk-CA, Mk-MA and Mk-MI). Mk-AN and Mk-TH have a left-handed preference (p<0.001 and p=0.002, respectively), while Mk-DI and Mk-LO have a right-handed preference (p<0.001 for both).

Figure 17: Score for vertical slots during the phase I, for each monkey (free use of either hand).
The figure 18 concerns the score during the phase I, but for the horizontal slots. Here, most monkeys showed a significant hand preference, except Mk-MA which did not exhibit a hand preference in the phase I [see also fig. 17]. Mk-AN, Mk-AT, Mk-MI and Mk-TH used preferably more their left hand (p=0.019 for Mk-AT and p<0.001 for the three other monkeys), whereas Mk-CA, Mk-DI and Mk-LO use more often their right hand (p=0.026, p<0.001 and p=0.006, respectively).

Figure 18: Score for horizontal slots during the phase I, for each monkey (free use of either hand).
The figures 19 and 20 show the scores for the vertical slots and the horizontal slots, respectively, but this time, during the phase II. Mk-DI has the particularity to have three phases [see also appendix 22], so here phases II and III were plotted on the same graphs.

Most scores for the vertical slots [Fig.19] do not exhibit a significant difference between both hands, except for Mk-LO and Mk-MA, which show a significant preference for their right hand (p<0.001 for both).

Figure 19: Score for vertical slots during the phase II (III), for each monkey (free use of either hand). The star represents the first plateau and the triangle, the second plateau (see text).
On the contrary, six on eight monkeys show a preference for one or the other hand in the phase II for the horizontal slots [Fig.20]. Indeed, Mk-AT and Mk-MI have a left-handed preference (p<0.001 for both), whereas Mk-CA, Mk-DI, Mk-LO and Mk-MA exhibit a right-handed preference (p<0.001 for the four monkeys). Mk-DI does not show a significant difference in the phase III.

Figure 20: Score for horizontal slots during the phase II (III), for each monkey (free use of either hand). The star represents the first plateau and the triangle, the second plateau (see text).

The spell out HI for the bimanual board, the tube and the drawer tasks are plotted on a same bar graph [Fig. 21]. The first thing we notice is the absence of systematic consistency in seven of 8 monkeys and across tasks. That is why we analyzed separately the results of each monkey for each task. Secondly, we see that these tasks are very lateralized (confirmed later with the statistical results).
Mk-AN has an HI of 0.6, 0.99 and -1 for the bimanual board, the tube and the drawer task, respectively. So these results indicate that the preferred hand for the first two tests was the right hand (p<0.001 for both) and for the drawer task it was the left hand (p<0.001).

Mk-AT has an HI of 0.77, -0.6 and -0.7 for the bimanual board, the tube and the drawer task, respectively. These results show a preference for the right hand for the bimanual board (p<0.001), whereas a left-handed preference was exhibited for the tube and the drawer task (p<0.001 for both).

Mk-CA has an HI of 0.41, 0.12 and -0.3 for the bimanual board, the tube and the drawer task, respectively. The bimanual board task shows a right-handed preference (p<0.001), whereas the drawer task exhibited a left-hand preference (p<0.001). There was no significant preference for the tube task (n.s).

Mk-DI has an HI of 1, 0.69 and -0.7 for the bimanual board, the tube and the drawer task, respectively. So this monkey has a right-hand preference for the first two tasks (p<0.001 for both) and a left-hand preference for the latter task (p<0.001).

Mk-LO shows an HI of 0.96, -0.9 and 0.83 for the bimanual board, the tube and the drawer task, respectively. There was a right-hand preference for the bimanual board and the drawer tasks (p<0.001), whereas the preference was for the left hand for the tube task (p<0.001).
Mk-MA has an HI of -0.3, -1 and 0.17 for the bimanual board, the tube and the drawer task, respectively. This monkey has a left-hand preference for the first two tasks (p<0.001 for both), whereas he showed a right-hand preference for the drawer task (p=0.004).

Mk-MI has an HI of 0.7, -1 and 0.53 for the bimanual board, the tube and the drawer task, respectively. These results indicate a preference for the right hand for the bimanual board and the drawer tasks (p<0.001 for both) and a left-hand preference for the tube task (p<0.001).

Mk-TH has an HI of 0.95, 0.69 and 0.79 for the bimanual board, the tube and the drawer task, respectively. This monkey has therefore a right-hand preference for the three tasks (p<0.001 for the three tasks).

4.1.3 Summary of hand dominance and hand preference data

The table 2 gives a summary of all results for every monkey.

Table 2: Summary of all results for the 8 monkeys. V.S and H.S mean vertical and horizontal slots, respectively. L.C, 1st Pl and 2nd Pl refer to for learning curve, first plateau and second plateau, respectively. In the same way, P.I/II/III means phases I/II/III. The letter L indicates a left-hand dominance/preference and the letter R, a right-hand dominance/preference, whereas n.s means a non significant difference.
4.2 Human

4.2.1 Hand dominance

As reminder, the hand dominance is determined by the total score (vertical and horizontal slots) of each hand during the modified Brinkman board task.

Graphs for each human subject are available in appendices 27 (left-handed subjects) and 28 (right-handed subjects). Generally we can observe a training effect along the session. Indeed most subjects increased their performance [see appendices 27-28]. Moreover, most subjects developed strategies to still increase their performance: for instance, they begun to grasp each bolts of the vertical slots and then the bolts of the horizontal one, or they begun each trial in the left/right side... Additionally, in this sample of subjects, the right-handers were better than the left-handers (p<0.001, Mann-Whitney Rank sum test) and the women were better than the men (p=0.009, Mann-Whitney Rank sum test).

Concerning the dominance we compared the total score in 30 seconds of the left and the right hand for each subject [Fig.22]. Generally, the scores reached values between 15 and 40. Out of twenty subjects, only nine showed a significant hand dominance. In left-handed subjects (references in blue in Fig.22), five persons had a left-hand dominance: AB, AH, AP, MF and VC (p=0.038, p=0.002, p<0.001, p=0.045 and p<0.001, respectively) and one had a right-hand dominance (SB with p=0.015). For the right-handed subjects (references in red in Fig.22), three of them showed a right-hand dominance (AG, JG and MS, with p=0.025, p=0.004 and p=0.005, respectively).
Figure 22: Score (total slots) during 30 seconds with left/right hand, for each human subject. The identification initials of the subjects are in blue vs red, when the subjects presented themselves as left- vs right-handers, respectively.
4.2.2 Hand preference

As reminder, two tasks, namely the tube and the bimanual board task, as well as the handedness questionnaire were used to assess the hand preference.

The spell out HI for the bimanual board and for the tube tasks was plotted on the same graph for all subjects [Fig.23].

Most subjects exhibited an HI near to -1 or to 1. The p-value for each test, for each subject is less than 0.001, except for the tube task of FL (n.s). The results show that most left-handers (i.d. in blue in Fig.23) used their left hand as the preferred hand (HI is negative), whereas the right-handers (i.d. in red in Fig.23) used their right hand as the preferred hand (HI is positive). Only three left-handers exhibited a preference for the right hand for the bimanual board task (AP, CC and MB). One left-handed subject (CC) showed also a preference for the right hand for the bimanual board.

In the same way, only four right-handers (AC, GS, JG and NF) showed a preference for their left hand for the tube task and one right-handed subject exhibited a preference for the left hand for the bimanual board.

![Figure 23: HI for the bimanual board and for the tube task. The i.d. initials of the subjects are in blue vs red, when the subjects presented themselves as left- vs right-handers, respectively.](image-url)
The score derived from the handedness questionnaire was calculated with and without the items on which there is strong social and cultural pressure to use the right hand (see appendix 2: items 5 and 8). The score were then transformed in percentage and plotted on two graphs [Fig.24 and 25 for the overall score and for the score without social and cultural pressure, respectively].

Figure 24: Overall laterality score in percentage for each subject. The references of the subjects are in blue vs red for the self announced left-handers vs right-handers.

The overall score [Fig.24] for the self announced right-handers (i.d. initiales in red in Fig.24) is positive, ranging between 53.85% and 100%, whereas the score for the self announced left-handers (i.d. initiales in blue in Fig.24) is mostly negative, ranging between -30.77% and -73.08%, except for one subject, AB, who shows a positive score (26.92%).

The laterality score without social and cultural pressure is similar to the overall score. Indeed the directions of the lateralization are the same for each subject, whereas the strength of the lateralization changes a little. Therefore, the score for the self announced right-handers (i.d. initiales in red in Fig.25) is positive, ranging between 46.15% and 84.62%, whereas the score for the self announced left-handers (i.d. initiales in blue in Fig.25) is mostly negative, ranging between -42.31% and -80%, except for the subject AB, exhibiting a score of 11.53%.
4.2.3 Summary of hand dominance and hand preference data

The tables 3 (left-handed subjects) and 4 (right-handed subjects) give an overview of all results for each human subject.

Table 3: Overview of all results for left-handers. The letter L indicates a left-handed dominance/preference and the letter R, a right-handed dominance/preference, whereas n.s means a non significant difference.
Table 4: Overview of all results for right-handers. The letter L indicates a left-handed dominance/preference and the letter R, a right-handed dominance/preference, whereas n.s means a non significant difference.

<table>
<thead>
<tr>
<th>Hand preference and dominance</th>
<th>AC</th>
<th>AG</th>
<th>FL</th>
<th>GS</th>
<th>JG</th>
<th>JS</th>
<th>MEB</th>
<th>MS</th>
<th>NF</th>
<th>VB</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vatert 3rinkman board task</td>
<td>n.s</td>
<td>R</td>
<td>n.s</td>
<td>R</td>
<td>n.s</td>
<td>R</td>
<td>n.s</td>
<td>R</td>
<td>n.s</td>
<td>n.s</td>
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<tr>
<td>Biml. Board task</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>L</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td>Tube task</td>
<td>L</td>
<td>R</td>
<td>n.s</td>
<td>L</td>
<td>L</td>
<td>R</td>
<td>R</td>
<td>L</td>
<td>R</td>
<td>R</td>
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<tr>
<td>Handedness questionnaire</td>
<td>R</td>
<td>R</td>
<td>R</td>
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</table>
5. Discussion

The first observation we can highlight is the great variability among the monkeys. Indeed, each monkey shows very different results for which, at first appearance, it is difficult to see a direct link. However when we analyze these results in depth we can draw the following observations.

The first one has general significance: the difficulty of a task has an influence on the lateralization concerning the dominance as well as the preference. Indeed, the results coming from the bimanual tasks, involving a coordination of the hands show a lateral bias for every monkey (except for Mk-CA in the tube task, see table 2). In the same way, the results derived from the horizontal slots, which represent an additional difficulty due to the rotation of the wrist, show a greater lateralization than the results derived from the vertical slots in the modified Brinkman board. These observations are in line with the conclusions of Spinozzi et al (1998): the task complexity has a significant effect on the amplitude of laterality. The same conclusion applies to humans. The two bimanual tasks show for each human subject a strong bias of lateralization (except for one subject, FL, for the tube task, see Table 4).

Back to the monkeys, the second conclusion directly concerns the hand dominance of each subject. First, we observe differences between the learning phase and the plateau phase. The execution of a new task and the execution of a known task can take different neuronal circuits (Paillard, 1986), and therefore could explain these differences. For this study, we decided to take into account for the determination of the dominance only the plateau phase. This phase, when it was reached, remained stable along the time and therefore, provides a stable dominance. Moreover, it has more sense to take this plateau phase because, for future studies (spinal cord lesion, cortical lesions,...), we will compare this pre-lesion plateau phase with the post-lesion recovery plateau phase. So, taking the plateau phase and the contact time (for reminder, the CT is derived from the twenty last sessions in the plateau too), we can conclude that Mk-CA shows a marked right hand dominance. Mk-DI, Mk-AT and Mk-MA also have a tendency for a dominance of the right hand, whereas Mk-AN, Mk-MI and Mk-TH show a tendency for a left-hand dominance. It is difficult to find any hand dominance for Mk-LO. Indeed, this animal does not show any dominance for the score,
whereas the CT is right lateralized for the vertical slots and left lateralized for the horizontal slots. As the horizontal slots represent a greater difficulty, we may propose a left-hand dominance but with reservation.

The third conclusion concerns the hand preference. Firstly, we observe different hand preference depending on the tasks. This concurs with the idea that handedness is not one-dimensional but more specific to a task. The subjects are not completely right- or left-handers but are situated on along a continuum of handedness (Annett, 1998; Hopkins, 2006). For each monkey seven measurements have been done, except for Mk-DI for which we have done nine measurements: four concerning the modified Brinkman board (six for Mk-DI) and three concerning the three other tasks (Bimanual board, Tube and Drawer tasks: see Table 2). With regard to these results we can draw the following conclusions: Mk-DI, Mk-CA, Mk-TH and Mk-LO show a tendency towards a the right-hand preference, whereas Mk-AT shows a tendency toward a the left-hand preference. Mk-AN, Mk-MA and Mk-MI have a right hand preference for two tasks and a left hand preference for the two other tasks, therefore it is difficult to define for them a global hand preference (Table 5).

Now if we observe in more detail the results of the modified Brinkman board task for the preference, we can firstly underline a consistancy in the results. Indeed, if a hand preference appears, its direction (left or right) stays the same throughout the test for one animal. We can secondly observe differences in the strategy. Some monkeys showed an hand preference at beginning of the task (Phase I), whereas they did not exhibit any preference in Phase II (Mk-AN and Mk-TH and to some extent Mk-DI). Some other monkeys only showed a

Table 5: Overview of the hand preference for the eight monkeys. The letter L indicates a left-hand preference and the letter R, a right-hand preference, whereas n.s means a non-significant difference.
preference concerning the horizontal slots (Mk-AT, Mk-MI and Mk-CA). Mk-LO had a right-hand preference throughout the task. Finally Mk-MA, unlike Mk-AN, Mk-DI and Mk-TH, showed a preference in phase II and not in phase I. These behavioral differences could be explained by the hypothesis of Serrien et al. (2006), which proposed that the manner to perform a task is not only dependant on the task itself, but also on the performer-related characteristics. So “the skill level, the CNS status and the attentional focus of the performer” have also their influences. Another reason could be that the monkeys develop new strategies throughout the test; the training can modify the manner to perform the task. Indeed, the constraint of imposing the use of one hand at each session can habituate the animal to better use their non-preferred hand and then, during the trials with the free use of the hand, they use more and more their non-preferred hand (results became non-significant during the Phase II). This can explain the results of Mk-AN, Mk-TH and Mk-DI. The fact that some monkeys only exhibit a preference concerning the horizontal slots is explained by the greater difficulty that the latter task represents as compared to the vertical slots.

Finally, if we compare the hand dominance and the hand preference, Mk-CA and Mk-DI are right-handers (dominance and preference), whereas Mk-AT and Mk-TH show different hand dominance/preference (right dominance, left preference and left dominance, right preference, respectively). Mk-LO, which exhibits a right hand preference, does not really show any hand dominance, whereas Mk-AN, Mk-MA and Mk-MI, which exhibit left or right dominance, do not show any hand preference. The inter-individual variability of these results leads us to the following conclusion: the number of animals is probably too small to allow a general overview and it would be interesting to increase it in order to derived better comparisons, groupings and to get similar strategies among the subjects and therefore to have a better understanding of this phenomenon.

The results concerning the human subjects are less disparate and allow general conclusions. Firstly the results of the handedness questionnaire mostly follow the self estimation given by the subjects (except for one left-handed subject, AB). Indeed, the left-handers are strongly left lateralized and the right-handers are strongly right lateralized.

The score without social and cultural pressure gives a more natural and instinctive laterality, however we can see that the general direction of the score does not differ from the overall
score. This conclusion is also true for the bimanual board. Indeed the self estimation is also respected and most left-handers showed a left-handed preference for this task, whereas most right-handers exhibited a right-hand preference. It is not the case for the tube task, where four out of ten right-handers showed a left-hand preference and, one, no significant difference. Three out of ten left-handers exhibited a right-handed preference for the tube task. We can wonder about the pertinence of this task for the assessment of the hand preference. It would be interesting to test it on more subjects. Despite this open question, the hand preference is well established for each subject with our three tests and follows their self estimation.

The hand dominance given by the modified Brinkman board task is coherent with the hand preference in human subjects. Indeed right-handers who showed a hand dominance are right-hand dominant and it is the same for the left-handers (except for one). In general, even if the differences are not significant, we can observe better score with the left hand for the left-handers. It is not the case in the results of some right-handers, where sometimes the left-hand seemed to have performed better (Score of AC, FL, JS and VB in Fig.22). These particular results could be explained by the theory of Derakhsh (2005), arguing that 15%-20% of people do not show the same behavior and neuronal handedness.

Now if we compare humans and monkeys, as already highlighted, the main difference is the vast disparity of the monkeys results. Although the monkeys are as much laterialized as humans, the direction of the lateralization is not constant, contrary to humans. An explanation could be that the world in which humans live is much more lateral biased (tools, engines,...) than the world of monkeys.
6. Conclusion

This study gives an outline of the hand dominance and hand preference in a population of eight macaques monkeys and twenty human subjects. We have seen that, in no way, it can inform us about the hand dominance and preference at the level of one population. Indeed, the number of subjects is too small, the results (concerning the monkeys), too disparate, to derive a general rules, especially for monkeys. However it was interesting to see the characteristics of each subject. This kind of results will be useful for future studies in our laboratory, for instance in selecting the side of the CNS in which to target a unilateral lesion.

It would be also interesting to conduct further research in this topic to allow still better knowledge of our model, the macaca fascicularis. We could complete our behavioral tests with some observations of the daily life of the animal, as delousing for instance. It could therefore give information about natural behavior in comparison to the “learning” behavior.

We know, thanks to Rogers’study (2009), that the general behavior (dominant/dominated, aggressiveness…) is linked to the handedness and so could help to assess it. We could also perform cortical map to determine if there are differences between both hemispheres and if these differences can be linked to the hand dominance /preference. It would also be interesting to perform again the behavioral tests of this study in six months or one year to establish if the hand preference/dominance is stable throughout the time.

7. Acknowledgments

I want to thank in particular Prof Eric M. Rouiller to have offered me the possibility to work in his research group and for his help and his patience during the supervision of my work.

I also thank all collaborators of the motor system research team for their work in the training of the monkeys for the behavioral tests.

Finally I thank every human subjects for their participation in my study.
8. Appendices

Appendix 1

Human beings subjects, with age and sex.

<table>
<thead>
<tr>
<th>Left-Handers</th>
<th>AB</th>
<th>AH</th>
<th>AP</th>
<th>CC</th>
<th>EK</th>
<th>GC</th>
<th>MB</th>
<th>MF</th>
<th>SB</th>
<th>VC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (years old)</td>
<td>18</td>
<td>27</td>
<td>28</td>
<td>26</td>
<td>28</td>
<td>30</td>
<td>20</td>
<td>27</td>
<td>26</td>
<td>30</td>
</tr>
<tr>
<td>Sex</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Right-Handers</th>
<th>AC</th>
<th>AG</th>
<th>FL</th>
<th>GS</th>
<th>JG</th>
<th>JS</th>
<th>MS</th>
<th>MF</th>
<th>NF</th>
<th>VB</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (years old)</td>
<td>30</td>
<td>25</td>
<td>28</td>
<td>27</td>
<td>23</td>
<td>28</td>
<td>26</td>
<td>25</td>
<td>26</td>
<td>27</td>
</tr>
<tr>
<td>Sex</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
<td>♂</td>
</tr>
</tbody>
</table>

Appendix 2

Chris McManus handedness questionnaire (2009)

**Handedness Questionnaire**

We would like you to answer a few questions about your handedness and that of your family, by ticking the box that best answers, or by ticking in the box. If you are not certain then please leave an item blank, rather than guess.

<table>
<thead>
<tr>
<th>Which hand would you use?</th>
<th>always right</th>
<th>Usually right</th>
<th>Neither</th>
<th>Usually left</th>
<th>Always left</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. To hold a pen while writing a letter?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. To throw a ball at a target?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. To hold a pencil while drawing a picture?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. To hold a dish while drying it?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. To turn the winder on a clock?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. To hold a jar while unscrewing its lid?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. To hold a thread while grading it through the eye of a needle?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8. To hold a knife when eating with a knife and fork?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. To hold a potato while peeling it?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10. As the top of a broom when sweeping the floor?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11. To pick up a glass of water?</td>
<td>❌</td>
<td>✔️</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12. Which foot would you use to kick a ball at a goal?</td>
<td>❌</td>
<td>❌</td>
<td>❌</td>
<td>❌</td>
<td>❌</td>
</tr>
<tr>
<td>13. With which eye would you look through a keyhole?</td>
<td>❌</td>
<td>❌</td>
<td>❌</td>
<td>❌</td>
<td>❌</td>
</tr>
</tbody>
</table>

13. Has injury, damage or disease ever meant you were unable to use your normally dominant hand? No / Yes
   If Yes: How old were you? __ years Which hand/arm was injured or damaged? Right / Left
   Was the effect temporary or permanent? Temporary / Permanent if temporary, how long?
   Please describe the problem briefly:

16. Has any person ever tried to change your handedness? No / Yes
   If Yes: Was it? From using the right hand to using the left hand / From using the left hand to using the right hand.
   How old were you when the attempt was made? __ years
   Who was the person who tried to change your handedness?
   How successful was the attempt? Very successful / Moderately / Storvay / Not at all successful
Appendix 3

Mk-AN: Scores for the left and the right hand when the use of the hand was imposed in the Brinkman board task.
Appendix 4

Mk-AT: Scores for the left and the right hand when the use of the hand was imposed in the Brinkman board task.
Appendix 5

Mk-CA: Scores for the left and the right hand when the use of the hand was imposed in the Brinkman board task.
Appendix 6

Mk-DI: Scores for the left and the right hand when the use of the hand was imposed in the Brinkman board task.
Appendix 7

Mk-LO: Scores for the left and the right hand when the use of the hand was imposed in the Brinkman board task.
Appendix 8

Mk-MA: Scores for the left and the right hand when the use of the hand was imposed in the Brinkman board task.
Appendix 9

Mk-MI: Scores for the left and the right hand when the use of the hand was imposed in the Brinkman board task.
Appendix 10

Mk-TH: Scores for the left and the right hand when the use of the hand was imposed in the Brinkman board task.
Appendix 11

Mk-AN: CT for the left and the right hand when the use of one hand was imposed.
Appendix 12

Mk-AT: CT for the left and the right hand when the use of one hand was imposed.
Appendix 13

Mk-CA: CT for the left and the right hand when the use of one hand was imposed.
Appendix 14

Mk-DI: CT for the left and the right hand when the use of one hand was imposed.
Appendix 15

Mk-LO: CT for the left and the right hand when the use of one hand was imposed.

[Graphs showing contact time vs. sessions for left and right hands with different slot orientations]
Appendix 16

Mk-MA: CT for the left and the right hand when the use of one hand was imposed.
Appendix 17

Mk-MI: CT for the left and the right hand when the use of one hand was imposed.
Appendix 18

Mk-TH: CT for the left and the right hand when the use of one hand was imposed.
Appendix 19

Mk-AN: Scores for vertical and horizontal slots when the use of hands was free in the Brinkman board task.

Appendix 20

Mk-AT: Scores for vertical and horizontal slots when the use of hands was free in the Brinkman board task.
Appendix 21

Mk-CA: Scores for vertical and horizontal slots when the use of hands was free in the Brinkman board task.

Appendix 22

Mk-DI: Scores for vertical and horizontal slots when the use of hands was free in the Brinkman board task.
Appendix 23

Mk-LO: Scores for vertical and horizontal slots when the use of hands was free in the Brinkman board task.

Appendix 24

Mk-MA: Scores for vertical and horizontal slots when the use of hands was free in the Brinkman board task.
Appendix 25

Mk-MI: Scores for vertical and horizontal slots when the use of hands was free in the Brinkman board task.

Appendix 26

Mk-TH: Scores for vertical and horizontal slots when the use of hands was free in the Brinkman board task.
Appendix 27

Total scores for left-handed human subjects.

Score of AB

Score AH

Score AP

Score CC

Score EK

Score GC

Score MB

Score MF
Appendix 28

Total scores for right-handed human subjects.
9. References

9.1 Papers


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9.2 Books


9.3 Web sites

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http://www.ucl.ac.uk/medical-education/other-studies/laterality/laterality-questionnaires/NotesOnBriefHandednessQuestionnaire2009.pdf (March 2011)