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LACK OF EVIDENCE FOR HAND DOMINANCE IN THE NONHUMAN PRIMATE: DIFFICULTY FOR THE THEORY OF EVOLUTION

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ABSTRACT

Most scientists believe individual nonhuman primates can exhibit hand preference in certain manual tasks, but that there is no population-based hand dominance in prosimians, monkeys or apes like there is in the human. This paper critiques the studies attempting to find hand dominance in nonhuman primates. It also critiques a recent study seeking evidence for brain asymmetry related to hand preference in squirrel monkeys. The investigators felt their data showed that the motor cortex hemisphere contralateral to the preferred hand of squirrel monkeys had a greater number of microstimulation sites that caused forelimb muscle contractions than did the ipsilateral hemisphere. Their conclusion may have been based on faulty reasoning. Any evidence that nonhuman primates have a system homologous to that of human hand dominance (or any correlated brain asymmetry) is very weak indeed. In fact, evidence from these studies of nonhuman primates would support separate ancestries of the different types of nonhuman primates and of humans; although the evidence has not been interpreted in that manner by those who have undertaken the studies.

INTRODUCTION

Hardly any scientist would disagree with the general concept that humans are different from other primates regarding language capability and tool use. The theory that one and/or the other capability were the major factors driving brain asymmetry also has a long history [5, 17, 18]. This general theory even allows nonhuman primates to lack any particular brain asymmetry or hand dominance, and still be consistent with the theory of human origins from nonhuman primates [4], because handedness may not have appeared in the evolutionary chain until after the hominoid line leading to *Homo sapiens* branched off from the nonhuman primate line. Of course, if nonhuman primates show evidence of hand dominance similar to that of humans, this would be consistent with the evolution of man from a nonhuman primate evolutionary ancestor.

There are some investigators who maintain that so-called precursors of language, e.g. vocalizations in nonhuman primate ancestors, were related to some brain asymmetry, and that this lateralized vocalization is homologous to left-sided language centers in humans. Furthermore, these same investigators believe that motor asymmetries (viz., hand preference in particular tasks) exist in present-day prosimians, rhesus monkeys, chimpanzees, and gorillas. They interpret this to mean that they existed in nonhuman primate ancestors of *Homo sapiens* [10, 14]. Even these investigators holding to evidence for hemispheric asymmetry in nonhuman primates would agree that human language and tool use are the result of major evolutionary pressures that have selected for hemispheric asymmetry in humans in the last two million years [18], and especially in the last 30,000 years of evolution of *Homo sapiens*. [10]. These scientists hold that hand dominance in humans may be considerably different than a rudimentary hand preference in nonhuman primates, but that the two are tied in an evolutionary sense.

The controversy this paper will critique is whether hand dominance and related brain asymmetry are evident in present-day nonhuman primates. This critique will not extend into the interesting literature of language and lateralization of speech centers [12], nor into studies of whether anatomical brain asymmetries, e.g. a larger temporal planum in the left cerebral hemisphere, exist in nonhuman primates [1, 11]. The temporal planum is a region in the temporal lobe including much of Wernicke's sensory language area.

GENERAL FINDINGS

After reviewing considerable research, Bock and Marsh reached a controversial conclusion that nonhuman animals, especially primates, exhibit asymmetry or lateralization of some of their functions [4]. Early studies of chimpanzees and rhesus monkeys seemed to indicate that hand preference was a result of experience [7, 22, 23] and probably did not reflect any underlying brain asymmetry [cf. 23]. During the last 20 years a number of studies of the performance of various tasks by chimpanzees, orangutans, gorillas, and certain monkeys showed that some animals preferred using their left hand, some their right, and some did not have a preferred hand [reviewed by 5]. Some even preferred different hands in different tasks. It would seem that nonhuman primates have exhibited some evidence of right or left hand preference for a particular task, with no one preference consistent in either individual animals, a single species, or among all the different nonhuman primates studied [3, 4, 23]. Brain asymmetry and hand preference in nonhuman primates, if it exists at all, would seem to be only a rough analogue of what exists in humans. The general consensus is that handedness in nonhuman primates is not a homologue of human hand dominance in terms of evolutionary continuity [5, 9].

A few investigators, however, have disagreed with this conclusion, as mentioned in the Introduction [6, 10, 14]. MacNeilage, Studdert-Kennedy, and Lindblom, who all have an interest in linguistics [14, cf. also 13], hypothesized that left side prehension was left behind with the advent of bipedality. They hypothesized that left handedness can be seen in present-day prosimians, and it evolved for grasping. They also hypothesized that right handedness evolved for hand manipulation, and furthermore, that right handedness for skilled hand manipulation in more complex tasks requiring bimanual coordination in nonhuman primates is a precursor of right hand dominance in humans.

Peter MacNeilage and his colleagues [14, 13] referred especially to data from stump-tailed macaques, reported by Beck and Barton in 1972 [2], and data from four female gorillas, reported by Fischer and coworkers in 1982 [8], to support their hypotheses. They provided elaborate criticisms of numerous other studies that did not support their ideas. However, commentaries by a number of scientists given at the end of the review by MacNeilage and his colleagues [14] indicate the general skepticism with which their hypotheses are viewed.

Beck and Barton [2] examined 17 different hand tasks by 10 stump-tail macaques. The tasks were grouped into six subgroups: 1) simple reach, 2) complex reach, 3) expose and reach, 4) stabilize and reach, 5) manipulate and reach, and 6) stabilize and manipulate and reach. Beck and Barton arranged their data so that higher median percentages of left preferences for reaching occurred when reaching was done in combination with a bimanual complex task. For example, the median of left hand preference for simple reaching for 10 monkeys was 35%; whereas the median of left hand preference for reaching in combination with finger manipulation of a hasp container ranged from 50-100%. However, the average of median percentages of left hand preferences for all reaching tasks in 10 monkeys was only 64.7%. In contrast, Beck and Barton maintained that tasks using manipulation showed an average of the medians of right hand preference of 72.8%. (The medians ranged from 53-97% for eight tasks involving manipulation.) In other words, the data were arranged such that trends supporting their hypotheses of left-hand preference for reaching and right-hand preference for manipulation were emphasized.

The other study MacNeilage and his colleagues [14] said was consistent with their hypotheses was Fischer, Meunier, and Hunt's [8] study of four female gorillas. All four animals used their right hand to grasp food or other objects more than 80% of the time. Left hand support of a baby gorilla by the four female mothers was observed 64% of the time. This data, they said, supported the theory that right hand preference for manipulation was similar to right hand dominance in humans. In contrast to the data reported by Fischer and colleagues, another study of 10 male and female gorillas by Preilowski and Leder (referenced by MacNeilage et al. [14]) showed no interindividual hand preferences.

Several recent studies of prosimians [21], capuchins and macaques [24], and gorillas, macaques, and baboons [6] were interpreted by Fagot and Vauclair to support a so-called "nonhuman primate precursor of human hand dominance hypothesis" [6]. Like MacNeilage and coworkers [14], Fagot and Vauclair reviewed previous studies that they felt supported this hypothesis in light of their more recent data [6]. However, other scientists, viz. Hamilton and Vermeire [9], interpreted the more recent evidence [6, 21] to show that hand preference by nonhuman primates in various tasks is related to cognitive specializations that may only be coincidentally similar to those of humans. Once again, support for hand preference in nonhuman primates being continuous with human hand dominance is a very debatable interpretation.

A SPECIFIC STUDY OF MOTOR CORTEX IN MONKEYS TO LOOK AT BRAIN ASYMMETRY

A team of five investigators [15] at the University of California Medical Center in San Francisco looked for hand dominance in squirrel monkeys. They sought evidence that the motor cortex hemisphere contralateral to the dominant hand had a greater number of sites that when stimulated caused forelimb muscle contractions than did the ipsilateral hemisphere. Even if this kind of research *could* be thorough, which it cannot be, it still is not very

surprising that one hemisphere had a greater density of neurons projecting to forelimb muscles, and that this hemisphere was opposite to the hand used the most. (Finding stimulation sites is a somewhat hit-and-miss technique as I have experienced personally in a technically similar research project [16], even with a grid pattern like they used.) Numerous environmental enrichment studies have shown that neuronal density is related to environmental stimulation and usage [20]. Therefore, it would seem that hand preference in nonhuman primates would develop randomly, and that the motor cortex responsible for the "preferred" hand would be used more, and therefore would have a greater density of neurons projecting to hand muscles.

This study by Nudo and his coworkers [15] at the UC Medical Center at San Francisco was conducted using a modified "Kluver board" from which the monkey removed food from wells; other studies have shown that hand preference varied from task to task [reviewed by 5]. Of the six monkeys studied, four were found to have a strong left-hand preference for this task (84.35% - 99.3% preference score). One was less strongly left-handed (55.3% preference score), and one had a strong right-hand preference (86% preference score). After the investigators determined the hand-preference of the monkeys, they anesthetized the monkeys, and applied microstimuli to the right and left motor cortex hemispheres of the monkeys. The hemisphere contralateral to the preferred hand had a greater number of stimulation sites that caused hand movements. This was interpreted to mean that the hemisphere contralateral to the preferred hand had a greater density of neurons projecting to forelimb muscles.

One criticism of this study is the fact that the investigators were not blinded to the preference results as they undertook the stimulation study. Another criticism has to do with their statistics. An enormous number of different tests using the parametric analysis of variance and the Student *t* tests were performed using results from only five monkeys with a documented preferred hand. Parametric tests are usually not valid for a sample of only five because assumptions of normal distributions and equal variances are difficult to meet with small samples [25]. Beyond that, the major criticism of this study should be that this kind of hand preference could be thought to be similar to hand dominance in humans. This data simply showed that 4/6 squirrel monkeys had a left-hand preference for removing food from a "Kluver board". Four out of six is not even statistically significant with a nonparametric test [19]. These data also showed that contralateral brain sites with neurons projecting to hand muscles of the preferred hand used in this task were easier to find by investigators with a hit-and-miss strategy that were not blinded as to results needed to support their hypothesis. These data cannot be extrapolated to support the concept that hand preference in monkeys is an intermediate condition in an evolutionary lineage leading to hand dominance in humans.

CONCLUSIONS

Evidence of consistent hand preference exhibited by any type of prosimian, monkey or ape has not been well demonstrated, and cannot be considered homologous to the hand dominance seen in humans. Brain asymmetries correlated with hand preference have not been investigated to any great extent. There has been only one study examining motor cortex and hand preference in the squirrel monkey [15], and it provided no concrete evidence of handedness with a correlated contralateral brain asymmetry like that seen in the human. Studies of hand preference in nonhuman primates would seem to support separate ancestries of individual types of nonhuman primates, and of the human.

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