



Review article

Hand preferences in coordinated bimanual tasks in non-human primates: A systematic review and meta-analysis

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ARTICLE INFO

Keywords:

Hand-preference
 Laterality
 Meta-analysis
 Non-human primates
 Tube task
 Bimanual tasks

ABSTRACT

The evolutionary significance of hand preferences among non-human primates and humans has been studied for decades with the aim of determining the origins of the population-level tendency. In this study, a meta-analysis was conducted to statistically integrate data on hand preferences in non-human primates performing the tube task and other bimanual tasks to determine the presence and direction of manual laterality. Significant individual-level lateralization was obtained for these bimanual tasks. In nonhuman primates, 82% of the animals analysed showed right or left-hand preference performing the tube task, this figure being 90% for other bimanual tasks. In contrast with humans, no asymmetry was found at the population level. Additionally, population-level preferences were not found in either of the tasks, although a strong manual preference was found when performing the tube task and other bimanual tasks. Species was studied as a variable moderator throughout the meta-analysis. These results highlight the importance of standardized testing methodologies across species and institutions to obtain comparable data and fill the gaps in the taxonomy.

1. Introduction

Asymmetry and brain lateralization is a widespread phenomenon in humans and other animals (McManus, 2002; Prieur et al., 2019). Laterality research, and particularly that related to cerebral asymmetry, has been largely documented in several phyla of invertebrates (Frasnelli, 2017, 2013) and for all vertebrate classes (Rogers et al., 2013; Ströckens et al., 2013; Vallortigara and Versace, 2017), the results suggesting basic evolutionary advantages. This brain hemispheric specialization provides computational benefits, such as simultaneous processing, avoiding replication of functions and hemispheric competition, behavioral efficiency and the improvement of cognitive abilities (Güntürkün et al., 2020; Rogers et al., 2004; Vallortigara and Rogers, 2005), among others. Functional lateralization has also been linked to differences in cognitive performance (Magat and Brown, 2009), spatial memory (Ecevitoglu et al., 2020), inhibitory control (Lucon-Xiccato et al., 2020), personality (Díaz et al., 2021), social networks (Boeving and Nelson, 2018),

well-being (Berlinghieri et al., 2021) and behavioral strategies (Camerlink et al., 2018) in several non-human animals.

In some primates and marine mammals, a left-hemispheric bias is observed for dynamic actions, while there is a left-hemispheric dominance for vocalization in frogs and mice (Corballis, 2014). It has long been believed that because language is distinctively human (Kivinen and Piironen, 2012), asymmetries must also be (Chance and Crow, 2007). Likewise, other factors must also be taken into account in the phylogeny of language and other cognitive functions (Corballis, 2017, 1989; Ruck, 2014). In fact, it has been argued that it is precisely this relationship with other functions, such as praxis and hand gestures (Arbib, 2005), that constitutes the evolutionary origins of both right-hand dominance and language in humans (Corballis, 2003). Consequently, taking hand preference in humans as an indicator of brain lateralization allows us to investigate cerebral lateralization in non-human primates (NHP) non-invasively (Chapelain et al., 2006).

This research on limb preferences has been the most widely studied

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<https://doi.org/10.1016/j.neubiorev.2022.104822>

Received 1 April 2022; Received in revised form 2 August 2022; Accepted 7 August 2022

Available online 9 August 2022

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behavioral asymmetry for several decades (Forrester, 2017; Ströckens et al., 2013). Historically, hand preferences have been extensively investigated in NHP as a model for understanding the evolutionary processes that have led to human left-hemisphere specialization for language processing and manipulation (Hopkins and Cantalupo, 2004; Meguerditchian et al., 2013). It is widely acknowledged that most humans are right-handed and that this manual dominance or handedness could provide us with information about the roots and evolution of language (Hopkins et al., 2013; Prieur et al., 2018). In the 19th century, anatomical studies revealed a leftward lateralization in the production and decoding of language, involving Broca's and Wernicke's areas (Güntürkün et al., 2020). These areas are located in the left hemisphere in 90–95% of right-handed humans, but also in 70% of the left-handed population (Corballis, 2014, 1983), and Broca's area has been also identified in great apes (Cantalupo and Hopkins, 2001) and Old World monkeys (Becker et al., 2022), using in vivo anatomical magnetic resonance imaging.

In NHP, differences in laterality between species could suggest specific selective pressures, which may in turn have translated into evolutionary mechanisms of handedness and hemispheric specialization (Chapelain and Hogervorst, 2009). These selective pressures consist of both intrinsic (related to demographics and social characteristics) and extrinsic (context-related and behavioral characteristics) factors, which regulate the strength, direction and consistency of manual laterality and may have originated right-handedness in humans (Prieur et al., 2019; Smaers et al., 2012). Specifically, social pressure is considered to be one of the main forces of primate brain evolution (Smaers et al., 2012). Some theories have been posited to study these differences, such as the *Niche Structure Hypothesis* proposed by Mangalam et al. (2015) or the *Postural Origin Theory* (POT) by MacNeilage (2007, 1991). Likewise, Hopkins et al. (2013) hypothesized how genetic factors and postnatal environmental variables may have influenced handedness. However, here we focus on the *Task Complexity Theory* proposed by Fagot and Vauclair (1991), which distinguishes between two levels of manual lateralization tasks: low and high-level tasks. Low-level tasks, like simple food reaching and other unimanual tasks, demand simple and routine actions (Regaioli et al., 2016b). In addition, they yield a symmetrical distribution of hand biases, no population level preferences and thus a lack of specialization in the contralateral hemisphere. These simple tasks could be influenced by situational and random factors, such as posture or object position (Chapelain et al., 2006; MacNeilage, 2007). Conversely, high-level tasks (e.g. object handling or bimanual grooming) require precise motor coordination and complex cognitive processes, which are more likely to elicit stronger hand preference than simple low-level tasks (Lilak and Phillips, 2008; Papademetriou et al., 2005; Zhao et al., 2010). These types of tasks elicit asymmetrical distribution and group-level biases (Hopkins et al., 2003a). Bimanual, precise or sequential manual actions (i.e. high-level tasks) could be considered to be the most sensitive measures for detecting population-level hand preferences and strong individual preferences, reflecting brain hemispheric specialization (Chapelain and Hogervorst, 2009; Meguerditchian et al., 2013; Mosquera et al., 2012). Furthermore, bimanual tasks remove or minimize situational and postural factors (Hopkins, 1995). By way of example, Fletcher (2006) showed the lack of population bias for clapping in wild chimpanzees, while Maille et al. (2013b), studying the box task in guenons and mangabeys, revealed group-level right biases for lifting the lid and a left-hand preference for grasping the item.

One of these sensitive tasks was the *tube task*, proposed by Hopkins (1995), which remained one of the most replicable bimanual tasks for over two decades. This PVC tube elicits a coordinated bimanual movement: the subject has to hold the tube with the subordinate hand while simultaneously removing the food with the opposite, dominant hand (cf. Hopkins, 1995). Hopkins et al. (2011) conducted the most extensive investigation of the tube task with non-human primates ($n = 777$ subjects), specifically with the four species of great apes. Some other species of Strepsirrhines (e.g. Regaioli et al., 2016a), Old World monkeys (e.g.

Vauclair et al., 2005) and Neotropical monkeys (e.g. Nelson and Boeving, 2015) have also been studied using this task. Overall, the above research revealed clear and strong individual preferences (e.g. Caspar et al., 2018; Cubí and Llorente, 2021) and in some cases handedness at the group or population level (e.g. Zhao et al., 2012). Also, Padrell et al. (2019) explored this trait in chimpanzees, finding it to be stable and rising over time. All that being said, the aforementioned research has also displayed several intraspecies and interspecies inconsistencies.

The first aim of the present study is to conduct an in-depth review of all non-human primate species that have been evaluated performing the tube task or other bimanual tasks since 1995 and 1991, respectively. In doing so, we will assess descriptive measures of the species studied, number of subjects, taxonomic groups and the bimanual tasks tested. The second aim is to verify their manual preferences at the individual and population level. Finally, we aim to determine the direction and strength of these manual asymmetries. In laterality research, the next decade will be shaped by combining meta-analysis and large-scale database studies to reach unbiased conclusions about true effects and increase the validity and reliability of research findings, thereby improving collaborations and opening a new horizon for novel questions (Ocklenburg et al., 2021). As a first objective in this respect, low statistical power due to the large number of studies with low sample sizes may be improved by introducing replication studies that analyse effects in large samples. And secondly, published datasets can be combined—thereby increasing the overall sample size—to boost statistical power through meta-analytical procedures.

We will therefore focus on the tube task and other bimanual tasks in order to determine differences or similarities between these experimental methods. To this end, three sets of meta-analysis were performed to investigate the following: firstly, whether NHP display manual asymmetries at the individual level, and more specifically whether significantly more animals present a preference for the left or right hand compared to those who are ambilateral. Secondly, whether right-handedness is present in non-human primates in a similar way to humans, which involved evaluating manual asymmetries at the population level, comparing the total number of right-handed individuals with the total number of individuals. And thirdly, two sets of additional meta-analyses were carried out to determine the direction (handedness index) and strength (absolute handedness index) of manual asymmetries. To complement the above, we also evaluated whether species acts as a moderator variable in the expression of laterality for the three sets of meta-analysis.

2. Materials and methods

2.1. Study design and setting

For the purposes of study selection and meta-analysis, we followed the guidelines described in the PRISMA 2020 statement (Page et al., 2021a, 2021b). Data collection began in February and ended in April 2021. The final selection of studies for the meta-analysis followed the procedure outlined below (Fig. 1).

2.2. Search method

The electronic databases Pubmed (<https://pubmed.ncbi.nlm.nih.gov/>), Scopus (<https://www.scopus.com/home.uri>), ScienceDirect (<https://www.sciencedirect.com/>), PsycInfo (<https://www.apa.org/pubs/databases/psycinfo>) and Web of Science (<https://www.webofscience.com/wos/woscc/basic-search>) were used to identify potential studies. Google Scholar (<https://scholar.google.es/>) was excluded due to the very high number of non-precise results. The first search terms used were “non-human primates” AND “tube task” AND “handedness”, with an imprecise result of the topic subject study. This resulted in its modification to “hand preference” AND “bimanual” AND “primates”.

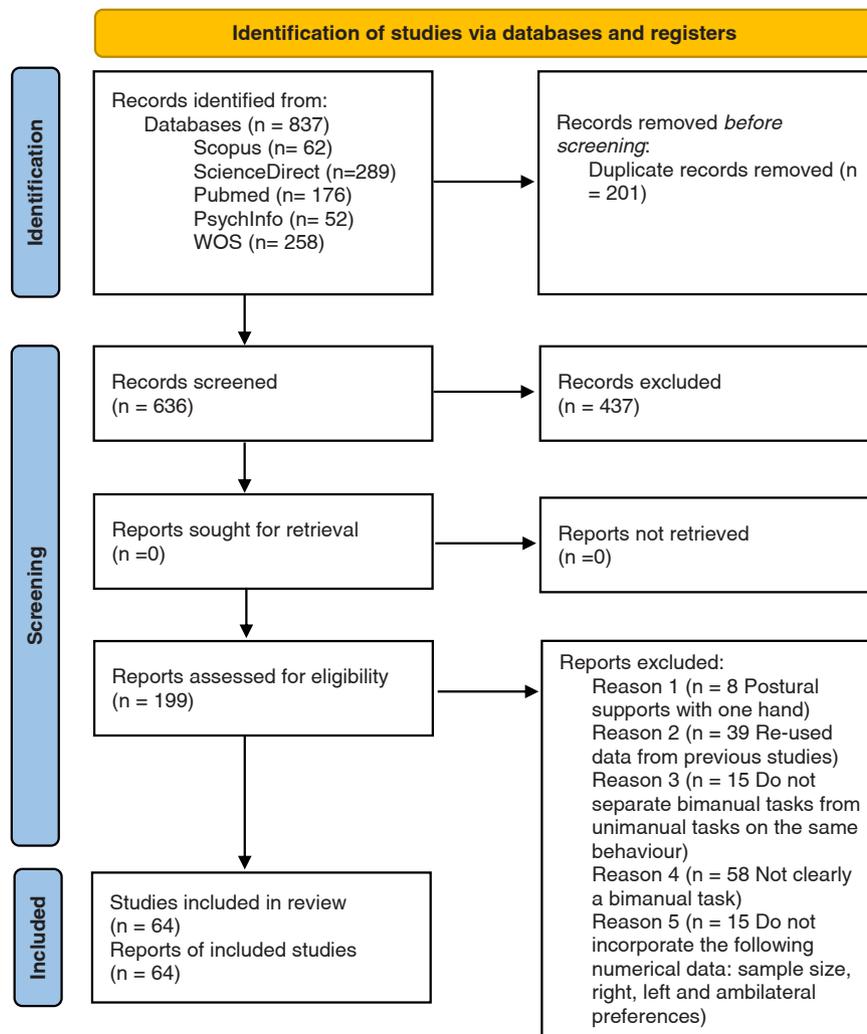


Fig. 1. Flow diagram detailing the different steps and exclusion criteria in our systematic review of publications based on hand preferences in coordinated bimanual tasks in NHP.

Adapted from Page et al. (2021a).

The inclusion and exclusion criteria were decided according to the PICOS elements (Eriksen and Frandsen, 2018; Higgins and Green, 2011). The following criteria were followed to select studies for inclusion:

2.2.1. Population

Data were included from all species of primates except humans.

2.2.2. Intervention

The following studies were considered: those that have used the tube task since 1995 (the original publication by Hopkins) or other bimanual tasks since 1991 (covering three decades of studies). Only “pure” coordinated bimanual tasks (i.e. two hands in different coordinated actions) from empirical articles were included. Only studies in which bimanual tasks were separated from unimanual tasks were included.

2.2.3. Comparison

Manual preferences for the tube task and other bimanual tasks.

2.2.4. Outcomes

In order to be included, the research needed to report the sample size, right, left and ambilateral preferences and frequency or bouts of manual action per individual. All the data had to have been collected from the experiment documented in the article.

2.2.5. Study design

Observational or experimental studies published in English, excluding abstracts, conference proceedings, reviews, thesis dissertations or meta-analyses.

The exclusion criteria comprised any studies that did not meet any of the inclusion criteria described above.

2.3. Selection of the studies

First, we removed duplicate articles and managed the references using the bibliographical software package Mendeley (<https://www.mendeley.com/guides/web>), and then assessed the studies according to the inclusion and exclusion criteria. Two authors (CS, JMMG) worked independently to select which studies to include. Discrepancies in the inclusion and exclusion criteria were resolved by consensus with the help of the third investigator, ML.

2.4. Data extraction and synthesis

Data extraction and synthesis were performed independently by CS, JMMG and ML. Discrepancies with the extracted data were resolved through discussion. The following study data were included: (1) the number of right-handed, left-handed and ambilateral subjects; (2) the number of lateralized and non-lateralized subjects; (3) sample size; (4)

frequency or bouts for left and right hand per individual; (5) the mean handedness index (MHI); and (6) the absolute handedness index (MABSHI). When preference data were not reported, Hopkins (2013) was taken as a reference, assuming HI values higher than 0.20 as right-handed preferences, values lower than -0.20 as left-handed preferences and values between -0.20 and 0.20 ambilateral. The handedness index (HI) value was calculated following Hopkins (1999), by subtracting the number of right responses from left responses and dividing by the sum of the total of right and left responses [$HI = (\#R - \#L)/(\#R + \#L)$]. Using these data, we calculated the “effect size” and evaluated manual asymmetries at the individual and population level. In addition, we also checked the direction and strength of manual asymmetries, which entailed compiling and reporting standard deviation from the MHI and MABSHI. For each study, we also collected data on author, year, source of publication, species, taxon suborder and type of task.

With regard to data synthesis, all of the meta-analyses were performed and weighted estimates obtained using Comprehensive Meta-Analysis (CMA) version 3 (Borenstein et al., 2021). This type of analysis allowed us to calculate heterogeneity between studies and whether there were moderating effects. Publication bias was checked using JASP v.0.16.3 (<https://jasp-stats.org/>). Given use of the CMA, a sample size of below 2 could not be entered in the meta-analysis. Heterogeneity and publication bias were limitations from the meta-analysis (Borenstein et al., 2021).

Three different sets of meta-analyses were conducted, dividing each into two subsections, one according to studies related to NHP performing the “tube task”, and another related to NHP performing “other bimanual tasks”. The first meta-analysis was conducted to assess individual level asymmetries, that is, whether there were significantly more lateralized individuals (i.e. showing right and left-hand preference) than ambilateral animals. This entailed comparing the number of “events” (lateralized animals) with the sample size of each study to obtain the event rate used for the meta-analysis. In the second one, in order to determine population level asymmetries, the number of right-handed individuals was used as “events” to compare with the total number of animals. Finally, in the third meta-analysis, the direction and strength of the manual asymmetries were investigated. To study the former, the mean handedness index (MHI), its standard deviation and the sample size of each study were used to assess a right or left preference. As for the strength of these manual preferences, specifically a strong or weaker preference, data were collected on the mean absolute handedness index (MABSHI), its standard deviation and the sample size included in each study. In the event of significant heterogeneity, “species” was evaluated as a moderator effect for each of the meta-analyses.

For all sets of meta-analysis, a “conditionally random-effects” model and a fixed effects model were used to make an overall estimation (Borenstein et al., 2021, 2010). If statistically significant heterogeneity was detected, a random effects model was run. Z statistics were initially used to test for statistical significance of the overall effect and whether this varied significantly from 0.50. To test heterogeneity, three types of tests were used: the Q statistics, the Tau² statistics and the I² index (Borenstein et al., 2021). Classification of the I² index levels was determined as low (25% or lower), moderate (50%) or high (75% or higher) (Higgins et al., 2003). A moderator variable analysis was performed with the Q statistics, adopting a mixed effects model to test whether species could explain any heterogeneity found between studies. All of these results were visualized in the form of different forest plots. Publication bias analysis was determined using Egger’s t statistical test and the funnel plot graphical test, first by means of forest plot arrays point estimates (effect sizes of all includes studies and the pooled effect size) and confidence intervals (95% CI). Effect size was indicated by a black square and the lines indicated the 95% confidence intervals. Studies with more weight were represented through a larger square size (Borenstein et al., 2021). Secondly, funnel plots were used to display the relationship between effect size and study size. Studies with low

standard error (i.e. large studies) were represented at the top of the y-axis, with high standard error at the bottom. Publication bias was identified by the presence of asymmetry in the plot (Borenstein et al., 2021).

3. Results

3.1. Study selection

A total of 837 studies were screened as a result of the systematic search. First, duplicate studies were removed, then 636 were evaluated for the relevance of their title and abstract. One hundred and ninety-nine full-text articles were found to be eligible. As a next step, those full-text articles not meeting the inclusion criteria were removed. Finally, a total of seventy-six articles published between 1994 and 2021 were included in the meta-analysis (Table 1). The data used in the meta-analysis sets are freely available on OSF (<https://osf.io/8xygn/>).

A total of thirty-eight primate species were evaluated in the selected research: thirty-two for the tube task and thirteen for other bimanual tasks (Table 2). *Lemur catta* aside, the remaining thirty-seven species studied belong to the suborder Haplorrhini. In total, 2891 subjects were included in the meta-analyses. Chimpanzees (*Pan troglodytes*) were the most represented species (34.87% of the sample), followed by baboons (*Papio anubis*; 15.15%), bonobos (*Pan paniscus*; 8.02%) and tufted capuchins (*Sapajus apella*; 7.09%). Fifty percent of the individuals evaluated belonged to the family Hominidae. The mean sample size used across studies was 34.88 subjects (SD=67.07). The minimum sample size was 1 subject and the maximum 536 subjects.

3.2. Meta-analysis 1: lateralized vs. non-lateralized

3.2.1. Presence of laterality in NHP performing the tube task

Thirty-eight studies were included in the first set of analyses, with an overall sample of 2376 primates and thirty different species. The most investigated species were brown capuchins (*Sapajus apella*; ten studies) and chimpanzees (*Pan troglodytes*; seven studies). They all belonged to the haplorrhini taxonomic group and were tested performing the tube task, where hand preference was considered a variable, with three possible outcomes (left, right, ambilateral). Initially, a fixed effects model was used to calculate an overall effect estimation, obtaining an event rate of 0.79 (95% CI [0.77, 0.81]). The model reached significance ($Z = 25.04$, $p < 0.001$). Heterogeneity among data sets was significant ($Q_{(60)} = 95.61$, $p = 0.002$, $Tau^2 = 0.12$), with moderate inconsistency between studies ($I^2 = 27.24\%$).

An effect re-estimation was performed using a random effects model (Suppl. Material, Fig. 1), with an even rate of 0.82 (95% CI [0.79, 0.84]). This model also reached significance ($Z = 16.95$, $p < 0.001$), indicating that NHP performing the tube task displayed individual-level lateralization, with significantly more lateralized (82%) than ambilateral animals (18%). This revealed a range of laterality prevalence in the distribution of populations studied of 79%–84%. Publication bias was identified using Egger’s regression test ($Z = 4.213$, $p < 0.001$). This result displayed statistical significance, suggesting a high effect of publication bias. Visual inspection of the funnel plot graphical test (SM, Fig. 2) revealed that toward the bottom most studies appeared on the right, suggesting the presence of asymmetry. Studies with smaller sample sizes were represented at the bottom and studies with larger sample sizes toward the top of the graph.

3.2.2. Presence of laterality in NHP performing other bimanual tasks

Overall, thirty studies were included, with a total sample of 917 primates; 14 species belonging to two different taxonomic groups, haplorrhini and strepsirrhini, were tested performing other bimanual tasks. The most investigated species were chimpanzees (*Pan troglodytes*; six studies) and gorillas (*Gorilla gorilla*; five studies). A fixed effects model was used to calculate an overall effect estimation, obtaining an

Table 1
Studies included in the meta-analysis of hand preferences in NHP, ordered by author name.

Number	Study	Species	Total number of individuals	Task
1	Bailoo et al. (2019)	<i>Macaca mulatta</i> ; <i>Pan troglodytes</i>	N = 22; N = 75	Tube task
2	Bardo et al. (2015)	<i>Pan paniscus</i>	N = 8	Tube task
3	Begg-Reid and Schillaci (2008)	<i>Gorilla gorilla</i>	N = 6	Tube task
4	Blois-Heulin et al. (2006)	<i>Cercocebus torquatus</i>	N = 11	Tube task; other bimanual tasks
5	Blois-Heulin et al. (2007)	<i>Lophocebus albigena</i>	N = 9	Other bimanual tasks
6	Braccini et al. (2010)	<i>Pan troglodytes</i>	N = 46	Tube task
7	Canteloup et al. (2013)	<i>Macaca tonkeana</i>	N = 14	Tube task
8	Caspar et al. (2018)	<i>Hylobates lar</i> ; <i>Hylobates muelleri</i> ; <i>Nomascus gabriellae</i> ; <i>Nomascus leucogenys</i> ; <i>Nomascus siki</i> ; <i>Symphalangus syndactylus</i>	N = 3; N = 1; N = 4; N = 5 N = 4; N = 1	Tube task
9	Chapelain and Hogervorst (2009)	<i>Pan paniscus</i>	N = 29	Tube task
10	Chapelain et al. (2006)	<i>Cercopithecus campbelli</i>	N = 9	Other bimanual tasks
11	Chapelain et al. (2011)	<i>Pan paniscus</i>	N = 77	Tube task
12	Chatagny et al. (2013)	<i>Macaca fascicularis</i>	N = 8	Tube task; other bimanual tasks
13	Corp and Byrne (2002)	<i>Pan troglodytes</i>	N = 38	Other bimanual tasks
14	Cubí and Llorente (2021)	<i>Trachypithecus hatihensis</i> ; <i>Pygathrix cinerea</i>	N = 18; N = 18	Tube task
15	de Andrade and de Sousa (2018)	<i>Sapajus libidinosus</i> ; <i>Sapajus robustus</i> ; <i>Sapajus flavius</i> ; <i>Sapajus xanthosternus</i> ; <i>Sapajus apella</i> ; <i>Cebus albifrons</i> ; <i>Cebus olivaceus</i>	N = 35; N = 7; N = 26; N = 37 N = 33; N = 7; N = 7	Tube task
16	Fan et al. (2017)	<i>Nomascus leucogenys</i>	N = 9	Tube task
17	Fletcher (2006)	<i>Pan troglodytes</i>	N = 18	Other bimanual tasks
18	Forrester et al. (2016)	<i>Pan troglodytes</i>	N = 33	Other bimanual tasks
19	Fu et al. (2019)	<i>Rhinopithecus roxellana</i>	N = 57	Other bimanual tasks
20	Hopkins et al. (2003b)	<i>Gorilla gorilla</i> ; <i>Pongo pygmaeus</i>	N = 31; N = 19	Tube task
21	Hopkins et al. (2007)	<i>Pan troglodytes</i>	N = 125	Other bimanual tasks
22	Hopkins et al. (2011)	<i>Pongo pygmaeus</i> ; <i>Gorilla gorilla</i> ;		Tube task

Table 1 (continued)

Number	Study	Species	Total number of individuals	Task
23	Humble and Matsuzawa (2009)	<i>Pan troglodytes</i> ; <i>Pan paniscus</i>	N = 47; N = 76; N = 536; N = 118	Other bimanual tasks
24	Lambert (2012)	<i>Gorilla gorilla</i>	N = 14	Tube task
25	Leca et al. (2010)	<i>Macaca fuscata</i>	N = 31	Other bimanual tasks
26	Lilak and Phillips (2008)	<i>Sapajus apella</i>	N = 11	Tube task
27	Llorente et al. (2011)	<i>Pan troglodytes</i>	N = 100	Tube task
28	Maille et al. (2013a)	<i>Cercocebus torquatus</i>	N = 12	Tube task
29	Maille et al. (2013b)	<i>Cercocebus torquatus</i>	N = 30	Other bimanual tasks
30	Mangalam et al. (2014)	<i>Macaca radiata</i>	N = 16	Other bimanual tasks
31	Mangalam et al. (2015)	<i>Macaca radiata</i>	N = 16	Other bimanual tasks
32	Margiotoudi et al. (2019)	<i>Papio anubis</i>	N = 74	Tube task
33	Meguerditchian et al. (2010)	<i>Gorilla gorilla</i>	N = 32	Other bimanual tasks
34	Meguerditchian et al. (2012)	<i>Saimiri sciureus</i>	N = 37	Tube task
35	Meunier and Vauclair (2007)	<i>Cebus capucinus</i>	N = 13	Tube task
36	Miller and Paciulli (2002)	<i>Macaca radiata</i>	N = 4	Other bimanual tasks
37	Molesti et al. (2016)	<i>Papio anubis</i>	N = 260	Tube task
38	Motes Rodrigo et al. (2018)	<i>Ateles geoffroyi</i>	N = 14	Tube task
39	Nelson and Boeving (2015)	<i>Ateles fusciceps</i>	N = 9	Tube task
40	Nelson et al. (2011)	<i>Macaca mulatta</i>	N = 16	Tube task
41	Nelson et al. (2015)	<i>Ateles fusciceps</i>	N = 10	Tube task
42	Padrell et al. (2019)	<i>Pan troglodytes</i>	N = 14	Tube task
43	Pan et al. (2011)	<i>Rhinopithecus bieti</i>	N = 6	Other bimanual tasks
44	Phillips and Hopkins (2007)	<i>Sapajus apella</i>	N = 11	Tube task
45	Phillips and Sherwood (2005)	<i>Sapajus apella</i>	N = 7	Tube task
46	Phillips and Sherwood (2007)	<i>Sapajus apella</i>	N = 13	Tube task
47	Phillips et al. (2007)	<i>Sapajus apella</i>	N = 13	Tube task
48	Regaiolli et al. (2016a)	<i>Lemur catta</i>	N = 17	Other bimanual tasks
49	Regaiolli et al. (2018)	<i>Macaca sylvanus</i>	N = 15	Tube task
50	Salmi et al. (2016)	<i>Gorilla gorilla</i>	N = 6	Other bimanual tasks
51	Schweitzer et al. (2007)	<i>Cercopithecus neglectus</i>	N = 12	Tube task; other bimanual tasks
52		<i>Sapajus apella</i>	N = 23	

(continued on next page)

Table 1 (continued)

Number	Study	Species	Total number of individuals	Task
	Spinozzi and Truppa (1999)			Other bimanual tasks
53	Spinozzi and Truppa (2002)	<i>Sapajus apella</i>	N = 23	Other bimanual tasks
54	Spinozzi et al. (1998)	<i>Sapajus apella</i>	N = 26	Tube task
55	Tabiwo and Forrester (2013)	<i>Gorilla gorilla</i>	N = 13	Other bimanual tasks
56	Tamura and Akomo-Okoue (2021)	<i>Gorilla gorilla</i>	N = 21	Other bimanual tasks
57	Trouillard and Blois-Heulin (2005)	<i>Cercopithecus neglectus</i>	N = 6	Other bimanual tasks
58	Vauclair et al. (2005)	<i>Papio anubis</i>	N = 104	Tube task
59	Westergaard and Suomi (1996)	<i>Sapajus apella</i> ; <i>Macaca mulatta</i>	N = 45; N = 55	Tube task
60	Westergaard et al. (1997)	<i>Macaca mulatta</i>	N = 19	Tube task
61	Zhao et al. (2008)	<i>Rhinopithecus roxellana</i>	N = 6	Other bimanual tasks
62	Zhao et al. (2010)	<i>Rhinopithecus roxellana</i>	N = 26	Other bimanual tasks
63	Zhao et al. (2012)	<i>Rhinopithecus roxellana</i>	N = 21	Tube task
64	Zhao et al. (2016)	<i>Macaca leonina</i>	N = 9	Tube task

event rate of 0.75 (95% CI [0.71, 0.79]). The model reached significance ($Z = 10.66$, $p < 0.001$). Heterogeneity among data sets was significant ($Q_{(48)} = 160.289$, $p < 0.001$, $\text{Tau}^2 = 1.357$), with moderate inconsistency between studies ($I^2 = 71.06\%$).

An effect re-estimation was performed using a random effects model (SM, Fig. 3), obtaining an even rate of 0.90 (95% CI [0.85, 0.93]). This model also reached significance ($Z = 9.53$, $p < 0.001$), indicating that NHP performing other bimanual tasks displayed individual level lateralization with significantly more lateralized (90%) than ambilateral animals (10%). This revealed a range of laterality prevalence in the distribution of populations studied of 85%–93%. A significant publication bias was detected using Egger's test ($Z = 7.355$, $p < 0.001$). Visual inspection of the funnel plot graphical test (SM, Fig. 4) revealed that most studies appeared on the right side toward the bottom and on the left toward the top, suggesting the presence of asymmetry.

3.2.3. Moderator variable analysis

Due to the heterogeneity found in the data sets, a moderator variable analysis was performed to investigate whether the different species included in the meta-analysis could explain differences between studies. A mixed effects model was adopted, in which the effect sizes were used as a random effects variable and study level moderator as fixed effects. Performing the tube task, the moderating effect of classification was found to be near significant ($Q_{(29)} = 42.32$, $p = 0.053$). For other bimanual tasks, the moderating effect of classification was found not to be significant ($Q_{(13)} = 9.448$, $p = 0.738$).

3.3. Meta-analysis 2: right-handedness vs. non-lateralized

3.3.1. Direction of laterality in NHP performing the tube task

Thirty-four studies were included in the second set of analyses, with an overall sample of 2346 primates; 30 different species belonging to the haplorrhini taxonomic group were tested performing the tube task. The

Table 2

Species, sample sizes and evaluated tasks included in the meta-analysis of hand preferences in NHP, ordered by species name.

Species	Other	Tube	Total subjects	% of the sample
<i>Ateles fusciceps</i>		19	19	0.66%
<i>Ateles geoffroyi</i>		14	14	0.48%
<i>Cebus albifrons</i>		7	7	0.24%
<i>Cebus capucinus</i>		13	13	0.45%
<i>Cebus olivaceus</i>		7	7	0.24%
<i>Cercocebus torquatus</i>	41	23	64	2.21%
<i>Cercopithecus campbelli</i>	9		9	0.31%
<i>Cercopithecus neglectus</i>	18	12	30	1.04%
<i>Gorilla gorilla</i>	72	127	199	6.88%
<i>Hylobates lar</i>		3	3	0.10%
<i>Hylobates muelleri</i>		1	1	0.03%
<i>Lemur catta</i>	17		17	0.59%
<i>Lophocebus albigena</i>	9		9	0.31%
<i>Macaca fascicularis</i>	8	8	16	0.55%
<i>Macaca fuscata</i>	31		31	1.07%
<i>Macaca leonina</i>		9	9	0.31%
<i>Macaca mulatta</i>		112	112	3.87%
<i>Macaca radiata</i>	36		36	1.25%
<i>Macaca sylvanus</i>		15	15	0.52%
<i>Macaca tonkeana</i>		14	14	0.48%
<i>Nomascus gabriellae</i>		4	4	0.14%
<i>Nomascus leucogenys</i>		14	14	0.48%
<i>Nomascus sik</i>		4	4	0.14%
<i>Pan paniscus</i>		232	232	8.02%
<i>Pan troglodytes</i>	237	771	1008	34.87%
<i>Papio anubis</i>		438	438	15.15%
<i>Pongo pygmaeus</i>		66	66	2.28%
<i>Pygathrix cinerea</i>		18	18	0.62%
<i>Rhinopithecus bieti</i>	6		6	0.21%
<i>Rhinopithecus roxellana</i>	89	21	110	3.80%
<i>Saimiri sciureus</i>		37	37	1.28%
<i>Sapajus apella</i>	46	159	205	7.09%
<i>Sapajus flavius</i>		26	26	0.90%
<i>Sapajus libidinosus</i>		35	35	1.21%
<i>Sapajus robustus</i>		7	7	0.24%
<i>Sapajus xanthosternus</i>		37	37	1.28%
<i>Symphalangus syndactylus</i>		1	1	0.03%
<i>Trachypithecus hatinhensis</i>		18	18	0.62%
Total	619	2272	2891	

most investigates species were brown capuchins (*Sapajus apella*; nine studies) and chimpanzees (*Pan troglodytes*; five studies). Hand preference was considered as a variable, with three possible outcomes (left, right, ambilateral). We first calculated a fixed effects model to make an overall effect estimation, obtaining an event rate of 0.45 (95% CI [0.43, 0.47]). The model reached significance ($Z = -4.81$, $p < 0.001$). Heterogeneity among data sets was significant ($Q_{(60)} = 99.936$, $p < 0.001$, $\text{Tau}^2 = 0.28$), with moderate inconsistency between studies ($I^2 = 39.96\%$).

We performed an effect re-estimation using a random effects model (SM, Fig. 5), which yielded an even rate of 0.43 (95% CI [0.40, 0.46]). This model reached significance with a negative Z-value ($Z = -4.24$, $p < 0.001$), indicating that NHP performing the tube task did not show a significant right-handed asymmetry at the population level; there were significantly more non right-handed animals than right-handed animals. We detected a significant publication bias was found using Egger's test ($Z = -2.155$, $p = 0.031$). Visual inspection of the funnel plot graphical test (SM, Fig. 6) suggested asymmetry between the right and left side.

3.3.2. Direction of laterality in NHP performing other bimanual tasks

Overall, twenty-eight studies were included, with a sample of 908 primates; thirteen species belonging to two different taxonomic groups, haplorrhini and strepsirrhini, were tested performing other bimanual tasks. The most investigated species were chimpanzees (*Pan troglodytes*; five studies) and gorillas (*Gorilla gorilla*; five studies). A fixed effects model was calculated to make an overall effect estimation, obtaining an event rate of 0.49 (95% CI [0.41, 0.48]). This model reached

significance ($Z = -3.08$, $p = 0.002$). Heterogeneity among data sets was significant ($Q_{(49)} = 122.95$, $p < 0.001$, $\text{Tau}^2 = 0.35$), with moderate inconsistency between studies ($I^2 = 60.15\%$). An effect re-estimation was performed using a random effects model (SM, Fig. 7) with an even rate of 0.47 (95% CI [0.41, 0.53]). This model did not reach significance ($Z = -0.99$, $p = 0.325$), indicating that there was no significant difference between the frequencies of right-handed animals and non-right handed animals. No publication bias was found using Egger's test ($Z = 1.02$, $p = 0.309$). Visual inspection of the funnel plot graphical test (SM, Fig. 8) suggested symmetry between the two halves.

3.3.3. Moderator variable analysis

Due to the heterogeneity detected in the tube task data set, a moderator variable analysis was performed using a mixed effects model. Performing the tube task, the moderating effect of classification was found to be significant ($Q_{(29)} = 57.97$, $p = 0.001$). The species that reached significance in the model were *Macaca tonkeana*, *Pan paniscus*, *Pongo pygmaeus* and *Rhinopithecus roxellana* (SM, Table S1). Performing other bimanual tasks, the moderating effect of classification was also found to be significant ($Q_{(12)} = 22.03$, $p = 0.037$). The species that reached significance in the model were *Rhinopithecus roxellana* (SM, Table S2).

3.4. Meta-analysis 3: to control for the direction (handedness index) and strength (absolute handedness index) of manual asymmetries

3.4.1. Direction of manual asymmetries in NHP performing the tube task

Twenty-five studies were included in the first section of the third set of analyses, with an overall sample of 519 primates and 21 species belonging to the haplorrhini taxonomic group performing the tube task. The most investigated species were brown capuchins (*Sapajus apella*; six studies). A fixed effects model was calculated (SM, Fig. 9) to make an overall effect estimation, obtaining an event rate of 0.007 (95% CI [-0.06, 0.07]). The model did not reach significance ($Z = 0.232$, $p = 0.817$). This indicated that there is no preference in the direction of manual asymmetries when performing the tube task. Heterogeneity among data sets was significant ($Q_{(36)} = 57.80$, $p = 0.012$, $\text{Tau}^2 = 0.02$), with moderate inconsistency between studies ($I^2 = 37.71\%$). No publication bias was found using Egger's test ($Z = -0.870$, $p = 0.384$). Visual inspection of the funnel plot graphical test (SM, Fig. 10) suggested symmetry between the right and left side.

3.4.2. Direction of manual asymmetries in NHP performing other bimanual tasks

Twenty-six studies were included, with an overall sample of 769 primates; twelve species belonging to two different taxonomic groups, haplorrhini and strepsirrhini, were tested performing other bimanual tasks. The most investigated species were western gorillas (*Gorilla gorilla*; five studies) and chimpanzees (*Pan troglodytes*; four studies). A fixed effects model was calculated (SM, Fig. 11) to make an overall effect estimation, obtaining an event rate of -0.03 (95% CI [-0.06, 0.003]). The model did not reach significance ($Z = -1.77$, $p = 0.077$). Heterogeneity among data sets was significant ($Q_{(44)} = 306.81$, $p < 0.001$, $\text{Tau}^2 = 0.09$), with high inconsistency between studies ($I^2 = 85.66\%$). This indicated that there was no preference in the direction of manual asymmetries when performing other bimanual tasks. Publication bias was checked using Egger's test ($Z = -0.614$, $p = 0.539$). Visual inspection of the funnel plot graphical test (SM, Fig. 12) suggested symmetry between the right and left side.

3.4.3. Moderator variable analysis

Heterogeneity was found in the tube task data set, so a moderator variable analysis was performed using a mixed effects model. Performing the tube task, the moderating effect of classification was found to be significant ($Q_{(20)} = 48.29$, $p < 0.001$). The species that reached significance in the model were *Cercopithecus neglectus*, *Macaca sylvanus*, *Pan*

troglodytes, *Pongo pygmaeus* and *Rhinopithecus roxellana* (SM, Table S3). Performing other bimanual tasks, the moderating effect of classification was also found to be significant ($Q_{(11)} = 21.69$, $p = 0.027$). The species that reached significance in the model were *Gorilla gorilla* and *Rhinopithecus roxellana* (SM, Table S4).

3.4.4. Strength of manual asymmetries in NHP performing the tube task

Twenty-four studies were included in the second section of the third set of analyses, with an overall sample of 519 primates and 21 different species belonging to a unique taxonomic group, haplorrhini, performing the tube task. First, a fixed effects model was calculated to make an overall effect estimation, obtaining an event rate of 0.78 (95% CI [0.76, 0.80]). The model reached significance ($Z = 76.31$, $p < 0.001$). Heterogeneity among data sets was significant ($Q_{(36)} = 192.63$, $p < 0.001$, $\text{Tau}^2 = 0.02$), with high inconsistency between studies ($I^2 = 81.31\%$).

An effect re-estimation was performed using a random effects model (SM, Fig. 13), which yielded an event rate of 0.71 (95% CI [0.66, 0.76]). This model reached significance ($Z = 27.22$, $p < 0.001$), indicating that NHP performing the tube task displayed stronger manual preference. Publication bias was checked using Egger's test ($Z = -3.318$, $p < 0.001$). Visual inspection of the funnel plot graphical test (SM, Fig. 14) suggested asymmetry between both sides, in this case the right side was under-represented.

3.4.5. Strength of manual asymmetries in NHP performing other bimanual tasks

Twenty-five studies were included on other bimanual tasks, with an overall sample of 763 primates; 12 species belonging to two different taxonomic groups, haplorrhini and strepsirrhini, were tested performing other bimanual tasks. A fixed effects model was calculated to make an overall effect estimation, obtaining an event rate of 0.72 (95% CI [0.71, 0.73]). The model reached significance ($Z = 136.41$, $p < 0.001$). Heterogeneity among data sets was significant ($Q_{(43)} = 3400.84$, $p < 0.001$, $\text{Tau}^2 = 0.11$), with high inconsistency between studies ($I^2 = 98.74\%$).

An effect re-estimation was performed using a random effects model (SM, Fig. 15), which yielded an event rate of 0.73 (95% CI [0.63, 0.83]). This model reached significance ($Z = 14.37$, $p < 0.001$), indicating that NHP performing other bimanual tasks displayed stronger manual preference. No publication bias was found using Egger's test ($Z = -1.23$, $p = 0.218$). Visual inspection of the funnel plot graphical test (SM, Fig. 16) suggested symmetry between the left and right sides.

3.4.6. Moderator variable analysis

Due to the heterogeneity found in the tube task data set, a moderator variable analysis was performed using a mixed effects model. Performing the tube task, the moderating effect of classification was found to be significant ($Q_{(20)} = 134.44$, $p < 0.001$). All of the species reached significance in the model, with the exception of *Cercocebus torquatus* (SM, Table S5). Performing other bimanual tasks, the moderating effect of classification was found to be significant ($Q_{(11)} = 44.31$, $p < 0.001$). All of the species reached significance in the model, with the exception of *Rhinopithecus bieti* (SM, Table S6).

The results of all the meta-analyses performed in this study are summarized in Table 3.

4. Discussion

The aim of the present study was to statistically integrate reports on hand preferences in NHP performing the tube task and other bimanual tasks in order to determine the presence and direction of manual laterality. Furthermore, the direction and strength of these motor asymmetries were also determined using weighted estimates in the form of several meta-analyses.

In the first set of meta-analyses, individual-level asymmetries were explored in NHP performing bimanual tasks. This was done by screening studies that had investigated hand preference as a variable with three

Table 3

Summary of the data obtained in the results section.

Meta-Analysis	Question	Result	N studies	N sample	N species	Model significance	Heterogeneity	Publication bias	Moderator effect
MA1: Lateralized vs. non-lateralized	Presence of laterality tube task?	82% lateralization	38	2376	30	Yes	Yes (moderate)	Yes	No
	Presence of laterality in bimanual tasks?	90% lateralization	30	917	14	Yes	Yes (moderate)	Yes	No
MA2: Right-handedness vs. non-lateralized	Direction of laterality in tube task?	No population level asymmetry	34	2346	30	Yes	Yes (moderate)	Yes	Yes
	Direction of laterality in bimanual tasks?	No population level asymmetry	30	908	13	No	Yes (moderate)	No	Yes
MA3: Direction and strength of manual asymmetries	Direction in the tube task	No preference in the direction	25	519	21	No	Yes (moderate)	No	Yes
	Direction in bimanual tasks	No preference in the direction	26	769	12	No	Yes (high)	No	Yes
	Strength in the tube task	Strong manual preference	25	519	21	Yes	Yes (high)	Yes	Yes
	Strength in bimanual tasks	Strong manual preference	25	763	12	Yes	Yes (high)	No	Yes

possible outcomes (left-handed, right-handed and ambilateral) in accordance with the procedure used in similar previous studies (Manns et al., 2021; Ocklenburg et al., 2019). The results manifested a clear presence of laterality for both tube tasks and other bimanual tasks performed by NHP. For the former, the model yielded an average event rate of 82% lateralized NHP, with a range of laterality prevalence in distribution of the populations studied of between 79% and 84%. For other bimanual tasks, the model yielded an event rate of 90% lateralized animals and a range of 85%–93%. The percentages of lateralized NHP performing the tube task and other bimanual tasks is comparable with those of paw preference in other mammals such as mice, rats, cats and dogs, estimated in two meta-analysis studies with the following event rates: 81% lateralized mice, 84% rats, 78% cats and 68% dogs (Manns et al., 2021; Ocklenburg et al., 2019). Nevertheless, handedness in humans has been reported for > 98% of the population, with nearly 90% classified as right-handed and 10% as left-handed (Cuéllar-Partida et al., 2021; Papadatou-Pastou et al., 2020).

The aim of the second set of meta-analyses was to determine whether there was a right-handed asymmetry at the population level in executing the tube task or other bimanual tasks. This meant comparing the number of right-handed animals with the total number of individuals. The random effects model reached significance with a negative Z-value in NHP executing the tube task, indicating that these subjects did not display a significant right-handed asymmetry at the population level when performing the tube task, so there were more non-right-handed (57%) than right-handed animals (43%). For other bimanual tasks, the random effects model did not reach significance, indicating that there was no significant difference between the frequencies of right-lateralized animals (47%) and non right-lateralized animals (53%). Both models were initially run using an informative fixed-effects model. Heterogeneity was found to be moderate in both tube tasks and other bimanual tasks, but no publication bias was found in either of the two. As a result of the heterogeneity found, a moderator effect was run, the results being significant in both cases.

Our results with NHP are in line with previous findings for other mammal species (e.g. mice, rats, cats and dogs) (Manns et al., 2021; Ocklenburg et al., 2019) that did not verify the population-level lateralization identified for humans. The lack of this population-level lateralization may be explained by the heterogeneity and diversity of NHP species at the behavioral, ecological, anatomical or cognitive levels (Fleagle, 2013; Gebo, 2014; Llorente, 2019), among others. In the case of the tube task, the model reached significance with a negative Z-value, showing that non right-handedness was more frequent than right-handedness. For NHP executing other bimanual tasks, on the other

hand, the model did not reach significance, equal frequencies being observed between right-handedness and non right-handedness.

The aim of the first section of the third set of meta-analyses was to study direction —i.e. a left or right manual preference— in NHP performing the tube task or other bimanual tasks. Both models indicated that there is no preference in the direction of manual asymmetries in NHP performing any of said tasks. Heterogeneity was found to be moderate in the tube task, but high in other bimanual tasks. No publication bias was found for either task. As a result of the heterogeneity reached, a moderator effect was run and the results were significant in both cases. The second section of the third set of meta-analyses investigated the strength of manual asymmetries in NHP performing the tube task and other bimanual tasks (ranging between weak and strong preferences). For the tube task, a random effects model was performed, with an event rate of 71% of NHP with strong manual preference versus 29% of NHP with a weaker manual preference performing the tube task in NHP. For other bimanual tasks, a strong manual preference (73%) was identified for other bimanual tasks versus 27% for the weaker manual preference. Heterogeneity was found to be high in the tube task and in other bimanual tasks, but publication bias was only found in NHP performing the tube task. As a result of the heterogeneity found, a moderator effect was run and the results were significant in both cases. Globally, we can state that although neither bimanual task presented a significant preference at population-level (right-handedness; left-handedness), they did elicit strong manual preferences. Thus, based on the third meta-analysis, we might assume that overall NHP would not present a handedness direction as biological order. Again, differences in anatomy, ecological niches, sociality, diet or cognitive capacities among primate species (Antinucci, 2010; Fleagle, 2013; Gebo, 2014; Llorente, 2019; Strier, 2021) may drive the evolution of different selective pressures related to manual skills and cerebral hemispheric specialization. By way of example: anatomies, manual abilities and locomotor systems are diverse among different primate taxonomic groups (Ankel-Simons, 2010) and may influence brain evolution (Sawaguchi, 1990); some ecological variables (e.g. home range size, diet or activity period) are associated with brain size (DeCasien et al., 2017; Fish and Lockwood, 2003; Powell et al., 2017); we find solitary but also highly social species (Dunbar, 1988), where social learning and modeling may be important aspects in the development of manual preference (Boulinguez-Ambroise et al., 2022); and, finally, although cognitive complexity is a general characteristic of all primates, there are differences in both neuroanatomical (e.g., brain size) and cognitive capacities among primates (Barton, 2006) that may influence their manual performance and lateralization.

As we have seen, four of the eight meta-analyses performed (50%) had publication biases. We can affirm that publication bias would be a problematic confound in the present meta-analysis, as it is in most meta-analyses (Begg and Berlin, 1988; Thornton and Lee, 2000). However, even in the presence of these significant publication biases, we consider this meta-analysis to be meaningful for several reasons. Firstly, this study reviews the state of the art of manual laterality studies in non-human primates with those tasks (coordinated bimanual actions) that are potentially more sensitive and precise for measuring manual preferences. To date, we have not found any published review or meta-analysis comparable to this one, except for a recent pre-print that includes some of our database and incorporates new data not included in the present meta-analysis (Caspar et al., 2021). Secondly, it highlights the great heterogeneity of procedures, assessments and sample sizes used in laterality research in nonhuman primates. Thus, as we will detail later, it is necessary to standardize procedures and tasks (such as the tube task), in the same way collaborative initiatives such as Many-Primates have done for cognitive research (ManyPrimates et al., 2019b). Finally, we detected a significant bias in the number of species evaluated. According to our review (see Table 2), only 32 species have been used in tube task and 13 in bimanual tasks. Nevertheless, this would seem to have been strongly affected by publication bias. Although studies of hand preferences in additional species may have been conducted, a lack of significant findings may have prevented these studies from being published. Therefore, it would be necessary to evaluate other primate species that have not yet been studied in order to be able to carry out a more in-depth phylogenetic and evolutionary analysis.

4.1. Evolutionary significance of individual and population-level lateralization

Our results suggest that there is a robust individual-level lateralization in NHP, but not at the population-level. In contrast, with humans, around 90% of the population are right-handed (Annett, 2006; Papadatou-Pastou et al., 2020). The presence of population-level right-side bias has also been identified in the fossil record for some hominin species such as *Homo neanderthalensis* (Lozano et al., 2017; Uomini, 2011) or *Homo habilis* (Frayer et al., 2016). In addition, great apes have displayed population-level handedness for some tasks (e.g. grooming, manual gestures, throwing; Hopkins, 2006), and particularly strong right-handedness for the bimanual tube task (Hopkins et al., 2011). Although handedness has historically been connected to language in humans, there is currently considerable debate on this association (Boulinguez-Ambroise et al., 2022; Corballis, 2003; Llorente et al., 2008). That being said, the relationship between hand preference and communicative gestures (Hopkins et al., 2012; Meunier et al., 2013) and its connection to asymmetry in some “language-like” brain areas (Becker et al., 2022; Tagliatela et al., 2008, 2006) has been documented for several primate species. For baboons, some studies reported that direction and degree of hand preference for tube tasks correlate with contralateral hemispheric depth asymmetry of the central sulcus, corresponding to the motor hand area (Margiotoudi et al., 2019). This pattern in central sulcus depth and in the primary motor cortex has also been reported for capuchin monkeys (Phillips and Sherwood, 2005), squirrel monkeys (Nudo et al., 1992) and chimpanzees (Dadda et al., 2006; Hopkins and Cantalupo, 2004). In humans, the association between handedness and motor cortex is related to other complex lateralization patterns in the temporal, parietal, prefrontal and frontal cortex (Fischer et al., 1991; Morita et al., 2020). Recent studies suggest that reaching and fine manipulation of objects are more likely to recruit larger group of muscles correlating with the anatomical asymmetries of large fronto-parietal tracts rather than projection pathways (Howells et al., 2018). Nevertheless, further studies are needed regarding the neuroanatomical correlates of hand preferences in both NHP and humans.

Our meta-analysis has addressed the results of all non-human

primate species investigated in bimanual actions, while various studies have documented population-level handedness for several species of non-human primates (Hopkins and Rabinowitz, 1997; Meguerditchian et al., 2010). It would be especially relevant in future studies to test whether hand preference is linked to phylogeny and species-level predictors (e.g. vocal repertoire, dietary breadth, group size, terrestriality, home range or feeding budget) through phylogenetic analysis (Caspar et al., 2021). That is, to identify the possible factors that drive or influence this trait along the phylogenetic tree.

4.2. Potential moderator variables

There are several possible moderator variables that could influence hand preference in NHP. In this meta-analysis, we tested whether species—but not taxonomic group or level—played a role in the heterogeneity of the results. As mentioned previously, it would be necessary to assess whether differences in anatomy, behavioral ecology, sociality or cognitive capacities may produce different selective pressures on the evolution of manual laterality in primates. Also, another potential factor necessary for inclusion in future studies and meta-analyses is rearing history and developmental context (Nelson, 2022). Contradictory results have been reported on this issue. Some authors have reported that differential rearing has no influence on the development of hand preference in chimpanzees (Hopkins et al., 2006; Lambert, 2012; Llorente et al., 2011) and bonobos (Chapelain et al., 2011), whereas other studies in the literature have reported a significant effect of rearing history. For example, Hopkins (1994) assessed hand preference for bimanual feeding in 140 captive chimpanzees, determining that mother-reared chimpanzees were more lateralized than nursery-reared chimpanzees. In rhesus macaques (*Macaca mulatta*), nursery-reared monkeys exhibited greater left-hand bias than mother-reared ones in the tube task (Bennett et al., 2008). Finally, more recently Heldstab et al. (2020) documented whether manipulation skills developed and changed over a 7-year period in 36 species of primates. Unfortunately, such information on rearing background is absent from most studies or not analysed, and we have therefore been unable to include it in our analysis.

In addition to the above, sex and age may act as a potential moderator with regard to hand preference. By way of example, the direction and strength of wild *Rhinopithecus roxellana* in bimanual feeding or bimanual grooming differed between adults and juveniles, while no significant differences were found between the sexes (Fu et al., 2019). In *Macaca leonina*, no significant sex or age differences were identified in direction and strength when performing the tube task. Finally, the last proposal of moderator variables is related to how data have been recorded: i.e. bouts vs. events (Hopkins, 1999). Historically, these different methodological issues in the assessment of hand preference have represented a problem when comparing results across different studies (Hopkins, 1999; McGrew and Marchant, 1997). Due to this, and a lack of consensus among researchers, we recommend that both methods be used and both results reported, even if similar results may be found (e.g. Cubi and Llorente, 2021).

Future studies should include these variables (e.g. rearing, sex, locomotion or bouts/events) in order to statistically test the moderator effect of these factors. We also recommend a more in-depth analysis of species as a moderating variable (i.e. an in-depth discussion of the groups and subgroups of species and how they work in each meta-analysis and influence the results).

4.3. Heterogeneity in the use of different bimanual tasks

In accordance with research on complexity in bimanual and unimanual tasks, Fagot and Vauclair (1991) proposed the Task Complexity Theory, where they discussed whether high and low-level tasks differ cognitively. Bimanual coordinated tasks seem critical for detecting consistent hand preferences in NHP (Hopkins et al., 2003b; Schweitzer et al., 2007; Zhao et al., 2010) due to the cognitive and

neural demands of these tasks. In contrast to unimanual actions, bimanual tasks require interhemispheric information transfer (Mooshagian et al., 2021) and a more complex coordination of both hands that relies on extensive cortical and subcortical neural networks (Donchin et al., 1998; Puttemans et al., 2005; Swinnen, 2002), including the cerebellum (van Dun et al., 2021). Specifically, some studies with NHP have revealed that manual preferences are correlated to neuroanatomical asymmetries within the primary motor cortex during the bimanual tube task (Hopkins and Cantalupo, 2004; Phillips and Sherwood, 2005), but also in complex unimanual task requiring skilled finger manipulation (Nudo et al., 1992). This is why some authors assume that rather than "bimanuality", it is the complexity of the task that facilitates cerebral hemispheric specialization (Koenke et al., 2004).

In conclusion, our results reveal the presence of laterality in NHP when performing the tube task and other bimanual tasks. However, when studying the population level, we obtained a non-significant model in NHP performing other bimanual tasks, supporting a greater efficiency of the tube task versus other bimanual tasks. In the case of direction, significance was not observed in either of the two types of task, whereas a significant model was obtained in both cases with regard to strength. Given this, we hypothesize that the direction and strength of manual asymmetries may work independently of the requirements of the task.

Following on from the previous point, we opted to unify all of the bimanual tasks here, and given the results obtained, it would appear to be a good idea to use the tube task as the only one for evaluating manual preferences in NHP, due to its greater efficacy and the possibility of comparing studies and making replicas.

Finally, we would like to emphasize the importance of standardizing testing methodologies across species and institutions to obtain comparable data. Also, despite the effort to obtain large and diverse samples of primates, certain taxa are over-represented while others are absent. Phylogenetic targeting (Arnold and Nunn, 2010; MacLean et al., 2012) of species before data collection is crucial in manual laterality studies. That is why we encourage further initiatives like that of the Many-Primates Project (cf. ManyPrimates et al., 2019a,b), and the building of a global consortium of researchers and study sites to collaboratively construct open datasets of manual laterality to include a wide range of species and individuals. In addition, it would be important to be able to publish those studies that do not find statistically significant differences in hand use, that is, studies with negative results. This practice would help to reduce publication bias, a concern not only for this area of research, but for many others in neuroscience and psychology.

Funding

This work was supported by the Regional Government of Catalonia—Generalitat de Catalunya (2017 SGR-1040); Universitat Rovira i Virgili (2019PFR-URV91); the Spanish Ministerio de Ciencia e Innovación (PID2020-118419GB-I00); and the Universitat de Girona (Programa d' Ajuts de Suport a la Recerca del Departament de Psicologia 2021). Open Access funding was provided thanks to the CRUE-CSIC agreement with Elsevier.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data used in the meta-analysis sets are freely available on OSF (<https://osf.io/8xygn/>).

Acknowledgments

We are grateful to the University of Girona for funding the acquisition of the CMA software.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.neubiorev.2022.104822](https://doi.org/10.1016/j.neubiorev.2022.104822).

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