Hand Preference during Tool Use in Wild Bearded Capuchins

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Motor skill · Bimanual coordination · Handedness · Brain asymmetry · Cebus

Abstract
The preferential use of one limb (lateralization) has been observed in many species. This lateralization reflects functional asymmetries of the brain. Right-handedness and left-hemisphere dominance seem to be the norm in humans. However, suggestions that vertebrates, particularly non-human primates, show handedness are contentious. Tool use could be a driver of handedness. Here I investigated hand bias during tool use activities in groups of wild capuchins (Sapajus libidinosus). I observed the use of feeding tools in wild capuchin monkeys living in the dry Caatinga forests of the Serra da Capivara National Park, Piauí, Brazil. Capuchins used three major types of feeding tools: (a) tools for probing; (b) tools for pounding/cracking, and (c) digging stones to extract tubers or roots. I recorded hand use in 118 tool use bouts. These different types of tools had different motor demands; digging tools apparently favour right-hand use. The harsh Caatinga habitat poses a strong selective pressure for tool using, which might favour increased laterality and right-hand bias. However, the extent of right-handedness associated with tool use, particularly for digging, can only be fully evaluated following studies with larger sample sizes.

Introduction
Lateralization has been observed in many vertebrate species, from fishes to primates and even in invertebrates [review in Rogers et al., 2013]. This lateralization reflects functional asymmetries of the brain that probably evolved to increase neural processing capacity [Dadda and Bisazza, 2006; Rogers et al., 2013]. There is a consensus that behavioural asymmetries are widespread amongst animals and can reflect specialization of the brain hemispheres [Hopkins et al., 2007; Corballis, 2008; Rogers et al., 2013].
The preferential use of one hand is often used as a proxy for assessing hemisphere specialization, chiefly in primates [Dadda et al., 2006; Hopkins et al., 2007], and Fagot and Vauclair [1991] postulated a possible homology between human and non-human primate laterality. Left-hemisphere dominance and right-handedness seem inextricably linked to fine and skilled motor control, tool use and language [Hammond, 2002; Hopkins et al., 2007; Frey, 2008; Stout et al., 2008; Barber et al., 2012; Forrester et al., 2013]. However, suggestions that vertebrates, particularly non-human primates, show preferential use of one hand at a population level (handedness) are much more contentious mainly because of the variation within species and conflicting results found so far [Corballis, 2008; Uomini, 2009; Marchant and McGrew, 2013].

Fagot and Vauclair [1991] suggested that high-level tasks, such as precise and coordinated bimanual actions, require finer motor control and could lead to preferences in hand use and hemispheric specialization at the group level. Indeed, a considerable body of data shows that high-level motor tasks elicit a more robust, consistent and stronger degree of hand preference than low-level tasks (e.g. reaching) in various species of non-human primates particularly when using the tube task [Hopkins, 2013a; Meguerditchian et al., 2013]. De facto, population-level right-handedness has been reported in captive chimpanzees performing skilled manipulative activities [Hopkins et al., 2011] and neuroimaging data link asymmetries in the motor cortex with right-handed activities such as coordinated bimanual actions [Hopkins et al., 2007; Gilissen and Hopkins, 2013]. The specialized functions of the left hemisphere are essential for skilled movement, language [Serrien et al., 2006; Iturria-Medina et al., 2011] and tool use [Króliczak and Frey, 2009].

Although some authors remain sceptical about right-handedness in non-human primates [McGrew and Marchant, 1997; Fitch and Braccini, 2013; Marchant and McGrew, 2013], there is accumulating evidence of population-level right-handedness in non-human primates, particularly in chimpanzees across captive and wild settings [Lonsdorf and Hopkins, 2005; Humle and Matsuzawa, 2009; Hopkins et al., 2011]. These studies indicate that handedness emerges when tasks being performed are skillful, requiring fine motor control and cognitive abilities that are specific to one hemisphere, such as tool use [Frost, 1980; Fagot and Vauclair, 1990; Hopkins et al., 2007; Iturria-Medina et al., 2011].

There is accumulating evidence supporting the link between tool use and the preponderance of right-hand use seen in humans [Uomini, 2009; Cochet and Byrne, 2013; Forrester et al., 2013]. The importance of tool use and bimanual coordination for the emergence of right-handedness in humans has been highlighted in a number of studies [review in Cochet and Byrne, 2013], and studies with non-human primates are vital for detecting which factors favour the expression and variation in the preference of hand use. Ecological factors, for example, are an important aspect that can affect tool use and the selective pressures that might promote handedness. The ability to use tools is particularly important for obtaining essential food resources during lean times or in impoverished habitats [Yamakoshi, 1998; Moura and Lee, 2004], and capuchin monkeys inhabiting the dry forest areas of central and north-eastern Brazil use tools customarily [Ottoni and Izar, 2008; Canale et al., 2009]. Individuals living under these conditions are probably under strong pressure for improved neural circuits associated with skilled actions and finer motor control. Given the association between tool use, finer motor control and the leading role of the left hemisphere for
highly demanding processes [Fagot and Vauclair, 1991; Hammond, 2002; Iturria-Medina et al., 2011], right-handedness could be expected. Although there are some studies that show a left-hand bias during tool use in non-human primates [Westergaard, 1991; McGrew and Marchant, 1992; Anderson, 1996; Bogart et al., 2012; Phillips and Thompson, 2013], they focused on tool use involving probing, which probably requires more tactile input. The left-hand preference could reflect asymmetry favouring the right cerebral hemisphere for its haptic sensory inputting [Cochet and Byrne, 2013; Phillips and Thompson, 2013]. Lonsdorf and Hopkins [2005] found that termite fishing in wild chimpanzees is left-handed at population level, while nut cracking elicits right-handedness, and they suggest that differential cognitive, sensory and motor demands of these tool activities might be responsible for the directional biases in hand use.

Capuchin monkeys, macaques and chimpanzees seem to converge in tool technology [McGrew and Marchant, 1997; Gumert et al., 2009] providing a unique opportunity to evaluate whether ecological factors and tool use prompt increased right-handedness. Unfortunately, there is a dearth of studies evaluating the link between habitual tool use and right-handedness in wild non-human primates, and most existing studies are done with non-human apes [Humle and Matsuzawa, 2009]. In macaques only Leca et al. [2010] have studied stone handling and laterality, finding strong lateralization in hand preferences at an individual level. Garber et al. [2008] compared two species of capuchin monkeys during three visually guided tool foraging tasks and found a significant population-level right-hand bias when combining the data for the two species. For capuchin monkeys this is the first study reporting hand preference during tool use. Here I suggest that tool use might be an important selective force driving right-handed phenotypes in the population.

Methods

Study Site
Capuchins were studied in the Serra da Capivara National Park (about 130 km²; 8°26′–8°54′ S and 42°19′–42°45′ W), Piauí state, north-eastern Brazil. The mean annual rainfall over 7 years was 781 ± 177 mm (1 SD), and a marked dry season occurred from May to October, but there was great variability in the amount of rainfall from year to year [Moura, 2004].

Study Groups and Subjects
Observations of tool use and hand preference were made during the period February 2001 to March 2002. Most of the data originated from the main study group (Oitenta), with whom I accumulated over 317 contact hours. This group was composed of 2 adult males, 5 adult females and 3 juveniles [further details in Moura and Lee, 2010]. I also collected data sporadically from a neighbouring group (Baixa Grande), consisting of about 18 individuals, and from another group (Baixao da Vaca); the total contact time with both groups was less than 4 h. Data were collected using slow scan sampling at each half-hour, both focal animal continuous records and 60-second interval focal animal sampling during 10-min sessions, and all occurrences [Altmann, 1974; for detailed methods, see Moura and Lee, 2010].

Behavioural Observations
I analysed the use of tools in obtaining food or to facilitate an activity related to obtaining food. The capuchins used three types of tools for obtaining food: probing – branches or twigs used to probe tree holes and rock crevices; cracking/pounding – use of stones to crack open diverse materials (seeds, dry branches, etc.); digging – the use of a stone for digging up tubers/roots.
Probing tools were used more often by males; females rarely used probing tools probably due to the higher proportion of failure to obtain a reward [Moura and Lee, 2010].

Data on hand use are presented as bouts. When using a stone to dig, an individual held it with one hand and hit the ground quickly, while simultaneously scooping the soil away with the other hand. Another pattern was to hit the ground quickly with a stone held in one or both hands, then to release the stone and dig using both hands. A bout of tool digging ended only when the individual found a tuber/root or discarded the tool and moved away. I considered a new bout of digging to have occurred if the individual stopped digging, chose another stone or changed the hand being used to hold the stone. For probing and cracking, the tool use bout was defined as the total duration of tool manipulation in each clearly defined activity, e.g. a bout of seed cracking ended only when the individual obtained the food resource or moved away [Moura and Lee, 2010]. The use of bouts potentially underestimates or favours the null hypothesis (no hand preference) [Hopkins, 2013b], hence the results presented here are conservative.

Analysis

To evaluate individual laterality in hand use, I followed Hopkins [1999] and used the handedness index (HI) following the formula: (#R – #L)/(#R + #L). The HI produces scores ranging from −1 to +1. A right-hand bias is reflected by a positive HI, while negative scores indicate a preference for the left hand. I used the one-sample Wilcoxon signed-rank test on the combined HI values to check for population-level handedness, and I used absolute values of HI to characterize strength of lateralization independent of direction.

Previous research has linked hand preference in tool use to the motor actions employed [Lonsdorf and Hopkins, 2005; Humle and Matsuzawa, 2009] and, ideally, I would analyse each type of tool separately, but due to the small number of bouts of tool use actually observed I combined them to test for population level handedness. Combining these bouts seemed unproblematic as capuchin monkeys demonstrate consistency of hand use across different tasks [Lilak and Phillips, 2007], and more recently Hopkins [2013b] has argued in favour of characterizing hand preferences based on consistency between tasks.

Nevertheless, in order to estimate if the different types of tool use could prompt the preferential use of one hand or both hands I summed the bouts of tool use for each type of tool where one or both hands were used. I then tested the values via a $\chi^2$ goodness of fit test. All statistical tests are two-tailed.

Results

In a sample of 118 bouts of tool use (data from 17 individuals), the individuals used a single hand 75.4% of the time, and in the tool use bouts where only a single hand was used (n = 89; table 1) the capuchin held the tool in the right hand in 64.8% of the bouts. Although capuchins showed a trend towards right-handedness (mean HI = 0.25 ± 0.31 SE, n = 6), a one-sample Wilcoxon signed-rank test on the HI scores (only individuals with a minimum of 4 bouts) found no group level bias ($Z = 1.21, n = 6, p = 0.22$). The monkeys showed lateralization of hand use (mean absolute HI = 0.67, n = 6).

When tools were used for digging, there was a strong bias for right-hand use (mean HI = 0.63, n = 4; only individuals with a minimum of 4 bouts). When the monkeys used a stone for cracking/pounding, there was a bias for holding the stone with the right hand (mean HI = 0.19, n = 3).

There appeared to be consistency of hand preference for the different types of tool use in the 4 individuals with the highest frequency of tool use (>6 bouts; Boludo, Cara-Branca, Adtmale and JuvII), and the direction of laterality did not vary in relation to different types of tools used (table 1). Although I did not record hand prefer-
I observed the alpha male Boludo on 2 occasions carrying stones with his left hand, which was also his preferred hand for tool use (table 1). Individuals that used a specific hand for a particular type of tool kept using the same hand across the different types of tool use.

### Number of Hands Used and Type of Tool

Capuchin monkeys showed differences in number of hands used between the three types of tools (fig. 1). When using a stick to probe for food in rock crevices or holes in tree trunks, capuchins invariably used a single hand ($\chi^2 = 11.267$, d.f. = 1; $p < 0.01$), in the 15 bouts recorded for probing there was just a single case of using both hands when Peta (a captive female released in the area) used a twig as a probe. The action of digging was strongly lateralized with the tool being held preferentially with one hand ($\chi^2 = 21.622$; d.f. = 1; $p < 0.01$). However, when using tools for cracking/pounding, there was no significant difference between bouts where a single hand or both hands were used to hold the tool ($\chi^2 = 1.690$; d.f. = 1; $p > 0.1$).

### Discussion

This is the first study examining the possible link between tool use and hand preference in wild groups of capuchin monkeys. The use of stones as pounding and cutting tools elicits right-hand bias at population level in captive capuchins [Westergaard and Suomi, 1996b], but my results do not indicate population level bias in hand use. Although derived from a small sample size, my results highlight interesting...
trends in hand use associated with tools. There is a strong lateralization in hand use, the type of tool activity affects hand use and apparently there is consistency of hand preference between different types of tool use.

The preferential use of the same hand across different tool activities seemed to occur. The three adult capuchins (Boludo, Adtmale and Cara-Branca) and a juvenile with the highest number of tool use bouts recorded showed consistency in hand use across different tool activities (table 1). This agrees with findings by Lilak and Phillips [2007] showing that captive capuchins display consistency of hand preferences across tasks that require similar motor actions.

The capuchins showed strong individual lateralization in hand use. The high degree of lateralization in capuchins has been highlighted in a series of studies in captive groups tested with bimanual tasks and in tool use [Westergaard and Suomi, 1996a, b; Spinozzi et al., 1998; Lilak and Phillips, 2007; Meunier and Vauclair, 2007], which could indicate asymmetries in the motor cortex [Fagot and Vauclair, 1991; Phillips and Thompson, 2013]. Tool use, particularly nut cracking, has been associated with strong individual laterality and also population-level right-handedness in communities of wild chimpanzees [Boesch, 1991; Lonsdorf and Hopkins, 2005; Humle and Matsuzawa, 2009; but see Marchant and McGrew, 2013] and in captive groups of capuchin monkeys the use of tools to pound/crack is right-handed [Westergaard and Suomi, 1996b].

However, my data indicate that the monkeys tended to hold the tool with a single hand when probing and digging, but when pounding/cracking they typically used both hands. The use of both hands to hold the tool might be mediated by ecological factors, type of activity and level of force required by the task when using the tool. For example, using both hands to hold a larger stone could increase the energy of impact for breaking hard nuts or dry branches. The exclusive use of one hand was most prevalent for probing and digging. The use of tools for digging seems to be the most cognitively complex task, requiring a complementary coordinated action of both hands, and might require finer motor control. Although this study provides an indication of
individual hand preferences, it did not find evidence for population-level laterality. Nonetheless, it is possible that the capuchins from Serra da Capivara are under selective pressure in specific brain areas associated with handedness and finer motor control.

Digging with stones is the most common form of tool use in Serra da Capivara [Moura and Lee, 2004; Mannu and Ottoni, 2009], while in a nearby site (Boa Vista, Gilbues) it is rare. In over 4,000 observation hours, only a single event of digging with a tool was observed in capuchin monkeys from Gilbues [Spagnoletti et al., 2012]. That digging with tools might be a catalyst for right-handedness deserves further investigation.

It is premature to draw conclusions without a larger sample size. Nevertheless, if tool use favours the emergence of right-hand bias in the capuchins from Serra da Capivara, the following predictions can be made: (a) a larger sample size will reveal right-handedness at the population level in Serra da Capivara, particularly in digging with tools, and (b) capuchin monkeys from Boa Vista (Gilbues) will, comparatively, present a lower level of right-handedness since they have a strong pressure for using both hands, which is necessary to lift heavy stones and provide a more effective strike [Liu et al., 2009].

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References


