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Abstract

Arboreal, and in particular suspensory, postures may elicit a preference for the strongest limb to be used in postural support in large bodied primates. However, selection may have favoured ambilaterality rather than a preference for a particular hand in chimpanzees (*Pan troglodytes*) fishing arboreally for ants. To investigate the influence of arboreality on hand preference we recorded handedness in seven captive bonobos (*Pan paniscus*) manipulating a foraging device during terrestrial and arboreal postures in a symmetrical environment, observing 2726 bouts of manipulation. When accessing the foraging device in the arboreal position the bonobos adopted predominantly suspensory postures. There was no population level hand preference for manipulating the foraging device in either the terrestrial or arboreal positions. However, four of seven individuals who interacted with the foraging devices showed a significant preference for one hand (two were left handed, two were right handed) when manipulating the foraging device in the arboreal position whereas only one individual (left handed) showed a preference in the terrestrial position. This suggests that individuals may have a preferred or strongest limb for postural support in a symmetrical arboreal environment, resulting in a bias to use the opposite hand for manipulation. However, the hand that is preferred for postural support differs between individuals. Although our sample is for two captive groups at the same zoo, our findings suggest that the demand of maintaining arboreal postures and environmental complexity influence hand preference.

Key words: *Pan paniscus*; laterality; posture; captivity

Introduction

Laterality of hand use is the preference for using one hand over the other for the majority of the time or for particular tasks (Harris 1974). In humans it is well documented that a preference for one hand (the dominant hand) is associated with enhanced motor

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performance such as strength, speed, and accuracy (Goble and Brown 2008, Janssen et al. 2011, Hughes et al. 2011). Evidence for enhanced performance, such as increased speed or greater accuracy, when the preferred hand is used also exists for other primates (tufted capuchin [*Cebus apella*], Fragaszy and Mitchell 1990; mountain gorilla [*Gorilla gorilla berengei*], Byrne and Byrne 1991; cotton-top tamarin [*Saguinus oedipus*], King 1995; pig-tailed macaque [*Macaca nemestrina*], Rigamonti et al. 1998; chimpanzee [*Pan troglodytes*], Hopkins et al. 2002, McGrew and Marchant 1999, Sanz et al. 2016).

Handedness in non-human primates is multidimensional, and laterality depends on multiple factors, such as the task and the environment in which it is performed (Forester et al. 2012, Forrester et al. 2013, Tabiowo and Forrester 2013, Quaresmini et al. 2014) and the speed of the task (Pouydebat et al. 2014). However, the ability to specialise is important in evolution, not the direction (i.e. which hand is preferred) (Corballis 1989). The ability to specialise with either hand results in neurological benefits for the individual such as increased neural capacity and thus efficiency, for example when one hemisphere is specialised to perform a particular function it frees the opposite hemisphere to perform other or additional processes (Vallortigara and Rogers 2005, Vallortigara et al. 2011, Verendeev et al. 2016). There is also evidence to suggest that ambilaterality (the ability to use either the left or the right hand indiscriminately) may be a predictor of reduced academic performance in humans (Crow et al. 1998) and it has been linked to potentially debilitating conditions such as schizophrenia (Barnett and Corballis 2002, Nicholls et al. 2005, Christman et al. 2008). Furthermore, wild chimpanzees that are strongly lateralised for either the left or the right hand during extractive foraging for termites benefit from increased efficiency compared to ambilateral individuals using either hand indiscriminately (McGrew and Marchant 1999, Sanz et al. 2016). Therefore, it is likely that individual handedness, regardless of direction, plays an important role in increasing evolutionary fitness (Corballis et al. 2008).

Studies of handedness in non-human primates often focus on terrestrial foraging behaviours, including coordinated bimanual food acquisition tasks such as the tube task (e.g. Llorente et al. 2009, Hopkins et al. 2011), tool use (e.g. O'Malley and McGrew

2006, Marchant and McGrew 2007), or gestural communication (e.g. Hobaiter and Byrne 2013, Meguerditchian et al. 2013). However, asymmetries in paired limbs for foraging must also be influenced by the demands of the locomotor and postural behaviours required to access the food source (Hopkins 2006). Few studies have specifically addressed the influence of energetically demanding postures and locomotion (such as suspensory postures where a significant proportion of the body weight is borne by one forelimb) on handedness, but the available evidence indicates a complex interaction between handedness and the type of locomotion or posture (Morcillo et al. 2006, Hopkins 2008, Peters and Rogers 2008).

The Postural Origins Theory suggests that population-level right handedness evident in humans and in some non-human primates for certain tasks may have evolved from a specialisation for postural support in the right limb (MacNeilage et al. 1987). This theory has been developed to suggest that hand use is influenced by a species' ecology, such as the level of arboreality (MacNeilage et al. 2007). For example, arboreal species show a preference for the right hand for postural support in the canopy (and thus a preference for the left hand for manipulations), whereas terrestrial species show a right hand preference for manipulation (Meguerditchian et al. 2013). Some great apes show a left-hand bias for demanding arboreal locomotor and postural behaviours such as descending or hanging (chimpanzees, Morcillo et al. 2006) and gap-crossing (orangutans, Peters and Rogers 2008). Orangutans and white-cheeked gibbons (*Nomascus leucogenys*) also show individual hand preference for foraging behaviours while using a forelimb to support their body weight or for balance (Rogers and Kaplan 1996, Fan et al. 2016). Thus, the demands of maintaining balance or of maintaining body weight are important factors influencing direction and strength of laterality (MacNeilage et al. 1987, Hopkins 1993, Hopkins et al. 1993, Vleeschouwer et al. 1995) and postural and locomotor behaviour, and the degree to which a forelimb provides postural support or contributes to balance (McGrew and Marchant 1997a) should be included in any study that seeks to interpret laterality within an ecological context.

Among the primates, the role of positional behaviour in hand preference is particularly crucial for large-bodied great apes. The arboreal positional behavioural repertoires of great apes (excluding humans) include demanding suspensory postures (Doran 1996, Thorpe et al. 2005). Although chimpanzees and gorillas are habitual terrestrial quadrupeds they still need to move frequently and proficiently in the forest canopy (Remis 1995, Doran 1996). Therefore, arboreal suspensory postures may be of particular importance in the study of laterality of hand use because at least one forelimb is required to support the majority of the body's weight (Hunt 1996). Arboreal postures have been considered in some studies of handedness, with varied results, for example right-handedness for quadrupedal walking, but left-handedness for descending and hanging (Morcillo et al. 2006); individual preference for either the left or the right hand for foraging behaviours when hanging (Rogers and Kaplan 1996, Fan et al. 2016); left hand bias for gap crossing locomotor behaviours (Peters and Rogers 2008); individual hand preference during hanging (Vleeshouwer et al. 1995); and no influence of arborealility on laterality (Harrison and Nystrom 2008, Fletcher and Weghorst 2005, Marchant and McGrew 1996). However, in these studies arboreality was generally defined in terms of height from the ground and did not specify whether demanding suspensory postures were used. The proportion of body weight borne by the limb not being used for manipulation (e.g. providing "major" support) was included in a study of wild chimpanzees fishing for ants arboreally, but no evidence that these postures elicited laterality for foraging behaviours in a complex, natural canopy environment was found (Marchant and McGrew 2007).

Individuals may have a preferred hand for manipulatory behaviours (such as food processing) or a preferred limb for energetically demanding postural support. In the case of an individual expressing a preferred limb for postural support it could be argued that a hand bias for the opposite hand for manipulatory behaviours may be induced during arboreal suspensory postures, where one limb must be used to maintain a significant proportion of body weight. The stability hypothesis holds that individual laterality increases in arboreal postures where a forelimb is used for postural support due to an increased demand for stability (Vleeschouwer et al. 1995, Peters and Rogers 2008) and limb strength. Handedness is not necessarily in the same direction between individuals

under this hypothesis. For example, an increase in left hand bias in captive bonobos (*Pan paniscus*) was associated with decreasing stability of postures (Vleescouwer et al. 1995). In the same study bonobos also showed individual laterality in an arboreal suspensory posture ("hanging on bars", page 205), which could indicate an individual preference for a particular arm for weight-bearing postural support (Vleescouwer et al. 1995). Similarly, the number of individuals showing hand preference (to either the left or the right) during a reaching task increased in white-cheeked gibbons when reaching from a suspensory posture (Fan et al. 2016). Likewise, the strength of laterality in chimpanzees performing a unimanual tool use task increased in a bipedal posture compared to a quadrupedal posture (Braccini et al. 2010). Furthermore, preference for leading with a particular limb in leaping and landing in marmosets was due to having a greater strength in the preferred limb (Hook and Rogers 2002). When one limb of a pair is preferentially used for demanding postures asymmetric loading (e.g. body weight applied more often to one limb over the other) leads to asymmetry of muscle and bone morphology (Sarringhaus et al. 2005, Carlson et al. 2006, Hopkins 2008, Shaw and Stock 2009).

In contrast to the stability hypothesis, the fatigue hypothesis argues that laterality is reduced (individuals are ambilateral, e.g. use both hands indiscriminately and for equal durations) in arboreal postures where a forelimb is used for postural support because of an increase in change of hands due to fatigue (as found by Marchant and McGrew 2007). Demanding arboreal postures that require the use of a forelimb to maintain body weight or for balance may induce ambilaterality due to fatigue in the limb used for support and an increase in the need to change hands more frequently. In a study of arboreal hand use in wild chimpanzees fishing for ants, eight out of 15 individuals were ambilateral and the frequency of hand changes for the tool using hand and the proportion that the non-dominant hand was used for postural support were positively correlated (Marchant and McGrew 2007).

We investigated the influence of suspensory (arboreal) and compressive (terrestrial) postures on hand preference for manipulating a foraging device to gain a food reward in captive bonobos. Bonobos represent a useful model species as they forage both

terrestrially and arboreally (Susman et al. 1980, de Waal and Lanting 1997) and use suspensory postures (Susman et al. 1980, Susman 1984, Doran 1993). Removing the influence of support availability and the complexity associated with a rainforest canopy by testing arboreal postures in a symmetrical environment reveals the direct influence of demanding postures on laterality. We provided captive bonobos with a foraging device in two testing conditions and recorded hand preference for manipulations and release of the food reward. In the terrestrial condition bonobos could access the foraging device directly from the ground whereas in the arboreal condition they were required to first climb a vertical rope (placed to either side of the foraging device) and maintain a suspensory posture whilst accessing the foraging device.

We predict that if handedness is driven by the need for stability (the Stability Hypothesis), individuals will use one hand significantly more often or for longer durations than the other when feeding in the arboreal condition compared to the terrestrial condition. In contrast, if handedness is driven by fatigue (the Fatigue Hypothesis), we predict that individuals will show reduced preference for a particular hand in the arboreal condition compared to the terrestrial condition, and that the frequency of hand changes will increase with the proportion of use of one hand for postural support.

Methods

NKIH observed bonobos housed at a zoo in the UK. At the beginning of our study the zoo housed 11 bonobos in two groups in adjacent but separate indoor enclosures and a single outdoor enclosure that each group accessed on alternate days. Three adult males and one female infant did not interact with the experimental equipment and so we excluded these individuals from the study. All of the remaining individuals performed in each testing period except one adult female (AdfE) who did not participate in the scattered food condition because she was consistently out-of-sight in the off show areas of the enclosure during data collection (Table 1). We did not include this individual in the correlation analysis as she only manipulated the foraging device six times in the arboreal

experiment, but we show her raw counts, binomial tests and handedness index in the descriptive results. AdfA was the mother of InmA, AdfB was the mother of InfB.

Table 1. Details of the captive bonobos studied between July 2013 and December 2015 in the UK. Individuals are anonymised. Housing group indicates which individuals had access to the experimental foraging devices at the same time.

Individual	Sex	Age group	Age at start of study	Housing group
AdfE	Female	Adult	23 years	1
AdfA	Female	Adult	17 years	1
AdfB	Female	Adult	36 years	2
AdfC	Female	Adult	14 years	1
AdfD	Female	Adolescent	8 years	1
InmA	Male	Infant	3 years	1
InfB	Female	Infant	3 years	2

The indoor enclosures were approximately $167m^2$ in floor area and 5 m in height and were furnished with vertical, angled, and horizontal poles, connected with various ropes and flattened hose pipes. Each enclosure also had 3 separate off-show bed areas that the bonobos had access to throughout the day, except when these areas were being cleaned. There were four viewing windows (where the arboreal foraging device and ropes were positioned), which were 1.5 m x 2 m (width x height).

We observed hand use in three testing conditions: 'scattered food'; 'terrestrial'; and 'arboreal'. We first observed a hand preference for these bonobos in the arboreal testing condition (which ran from July 2013 to September 2013), and therefore included two further conditions, the terrestrial and scattered food testing periods (December 2014 to January 2015). First, we compared hand use for scattered food and foraging devices to determine if this hand preference was elicited by the foraging devices themselves. Second, we compared hand use in the terrestrial and arboreal testing conditions to

determine whether hand preference was driven by the need to maintain an active arboreal posture whilst accessing the foraging devices or by the foraging devices themselves. The length of data collection periods varied because of constraints in access to the enclosure to rearrange ropes and to set the foraging devices. We used foraging devices in the terrestrial and arboreal testing conditions. These were metal mesh cages containing a hollow plastic ball with one small opening. We placed food in the plastic ball so that the bonobos had to pluck or poke the food reward out. One foraging device was spherical (mesh 150 mm^2 – 50 mm^2) and measured 0.4 m diameter, and the other was a cube (mesh size 50 mm^2) measuring 0.16 m across (see Supplementary material Fig. S1). We found no difference in hand preference or use between the different foraging devices. In the terrestrial testing condition (where both foraging devices were available together) 155 manipulations of the spherical foraging device occurred with the left hand and 127 with the right (Binomial test, P = 0.107), and 292 and 252 manipulations of the cube foraging device occurred with the left and right hand respectively (Binomial test, P = 0.094).

In the terrestrial testing condition, we placed two foraging devices in the enclosure 1-1.2 m from the ground suspended from a central horizontal pole so that the bonobos could access them from the ground (when sitting or standing). For the arboreal testing condition, we placed one foraging device 2 m from the ground above a viewing window, with vertical ropes placed on both sides to allow the bonobos to access the foraging device. We placed a second foraging device elsewhere in the enclosure to reduce aggressive competition for the main foraging device, but collected all arboreal data from the central foraging device suspended above the viewing window.

In both the terrestrial and arboreal testing conditions we videoed interactions with the foraging devices (Sanyo Xacti CG10 camera, 30 frames per second) from a central viewing position for 30 minutes from the time the subjects were given access to the enclosure, and analysed videos at a later date. The food reward was usually depleted within the first 15 minutes of each session after which interaction with the foraging device decreased substantially (mean 46 ± 20.5 SD interactions, N = 32 interactions per individual in the first 15 minutes and mean 28 ± 20.7 SD interactions, N = 32 in the last

15 minutes). Although in a related study dominance rank influenced the order in which an individual gained access to the foraging devices (Hanson 2016) all study individuals accessed and retrieved the food reward in most sessions (24 of 32). We replayed videos once at normal speed for each subject that interacted with the foraging devices and collected continuous focal data for each individual for each session (Altmann 1974).

In the scattered food testing condition we recorded hand preference for ground foraging behaviours (hand-to-mouth feeding and manipulation of food item) on scattered food items. We collected live continuous focal data for each individual for 15 minutes in each session because the distance of the scattered food from the viewing window did not allow for sufficient video quality.

We recorded contextual behaviours, the action of the hands, and associated postures in the arboreal testing condition (Table 2). We recorded the role of each hand as either: dominant (the hand the action was performed with); non-dominant (second hand in bimanual manipulation, the hand not collecting the food item); both hands used equally; rest; postural support; or other. Manipulations of the foraging device (recorded in the arboreal and terrestrial conditions) were touch (touch outer metal cage), power manipulation (hold inner plastic ball in a power grip), and precision manipulation (poke or pluck food out of the opening in the inner plastic ball). Precision manipulations were unimanual (the dominant hand plucked food out of the opening in the inner plastic ball) or bimanual (the inner plastic ball was held by the non-dominant hand while the dominant hand plucked food from the opening). We recorded handedness in bouts with duration in seconds. We recorded a new bout when the role of either hand changed (McGrew and Marchant 2001), when the subject altered their posture, or when the subject had been still for 10 seconds or more (Hopkins 1995). We chose bouts of hand action rather than events to avoid over-inflation of the sample size and to ensure independence of data-points (McGrew and Marchant 1997). We recorded arboreal posture as either: forelimb suspend combination, in which body weight was borne by at least one forelimb in combination with balance or support from hind-limbs in suspension or compression; unimanual

forelimb suspend, in which body weight was borne by one forelimb only; and other, which included rare and brief postures such as hind-limb suspend or leap from the ground.

Table 2. Contextual behaviours, categories of hand action, and arboreal postures observed in captive bonobos in a UK zoo from July 2013 to December 2015. Contextual behaviour is the type of behaviour for which hand use was recorded, hand action describes how the hand was used for each specific behaviour, and arboreal posture describes the type of posture the bonobos adopted when manipulating the foraging device in the arboreal testing condition.

Contextual behaviour	Description
Hand to mouth feeding	Hand transports food to the mouth
Manipulation of food item	Manipulation of food item e.g. tearing or pulling apart
Foraging device manipulation – touch	Touches outer metal cage of the foraging device
Foraging device manipulation – power	Holds inner plastic ball of the foraging device in a power grip
Foraging device manipulation – precision[1]	
- *Unimanual*	Uses one hand to pluck or poke food out of the hole in the inner plastic ball
- *Bimanual*	Plucks or pokes food out of the hole in the inner plastic ball with one hand (dominant) while the other hand (non-dominant) holds the inner plastic ball in a power grip
Hand action[1]	Description
Dominant	Hand is dominant in unimanual or bimanual manipulation tasks, the hand the action is performed with
Non-dominant	Hand is non-dominant during bimanual manipulation task, e.g. supporting the item being manipulated
Both	Both hands are used equally in the same action, e.g. pulling an item

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Rest	Hand is not performing any specific task or is not involved in postural support
Postural support	Hand is weight bearing in postural support
Other	Hand is involved in some other action that does not fall into one of the contextual behaviour categories, e.g. grooming

Arboreal Postures[2]	Description
Forelimb suspend combination	Body weight is borne by at least one forelimb in suspension, a combination of forelimb-hind limb suspend, or a combination of forelimb suspend hind-limb compression
Unimanual forelimb suspend	Body weight is borne by one forelimb in suspension
Other	Other postures included – hind-limb suspend, hind-limb compression (bipedal stand), and leap or jump

[1] adapted from McGrew and Marchant 2001, [2] adapted from Hunt et al. 1996

For the three conditions (scattered food, terrestrial, and arboreal) we used a binomial test (two-tailed, $P = 0.5$) to determine individual handedness using counts of left or right hand use (for a minimum of 6 bouts). We carried out all analyses in R version 3.1.0 (2014-04-10), and set alpha at 0.05. We also calculated a Handedness Index score (HI) according to Hopkins (1999) for each individual for each testing period. We calculated HI using the formula $HI = (R-L)/(R+L)$, where R is the number of responses with the right hand and L is the number of responses with the left hand. This shows the strength and direction of hand use. Negative scores indicate a left hand direction and positive scores indicate a right hand direction.

We analysed sequences of bouts of manipulation of the arboreal foraging device from all individuals ($N = 7$) to test the fatigue hypothesis. Each sequence was made up of a series of behaviours from the point at which the individual first approached the equipment, through any interaction with the foraging device, to the moment they returned to the

ground. We only included sequences that included manipulation of the foraging device (equivalent to Marchant and McGrew's [2007] 'sessions'). This method allowed us to quantify the number of bouts of manipulation of the foraging device and the number of hand changes for each sequence. In addition we obtained the proportion of bouts of manipulation for which one hand was used in postural support. We calculated this by dividing the number of bouts for which one hand was used in postural support by the total number of bouts of manipulation in a sequence. We performed a two-tailed Spearman's rank-correlation to measure the strength and direction of the relationship between number of bouts of manipulation of the foraging device and the number of hand changes per sequence.

Ethical note

We complied with the ethical review requirements of both the University of Birmingham and of the host zoo. Data collection was non-invasive and data were collected from the public viewing areas of the zoo, all practices adhered to the strict health and safety protocols of the University of Birmingham and the host zoo. To avoid any potential disturbance to the bonobos the foraging devices and access ropes were installed and removed during their normal feeding and cleaning routines by the zoo keepers. We used food from the bonobos daily diets as the reward in the foraging devices. For the scattered food testing condition we observed the bonobos during their normal feeding routine.

Results

Over the three different testing conditions we observed 2726 bouts of manipulations of the foraging devices or feeding behaviours, with a mean of 105 bouts (± 34 SD, N = 6 individuals) per individual in the scattered food testing period, a mean of 118 bouts (± 70 SD, N = 7 individuals) per individual in the terrestrial testing condition and a mean of 214 bouts (± 164 SD, N = 7 individuals) per individual in the arboreal testing condition. The majority of arboreal postures included the use of a forelimb as the main weight bearing limb, of these 89.5% were forelimb suspend combination (Fig. 1).
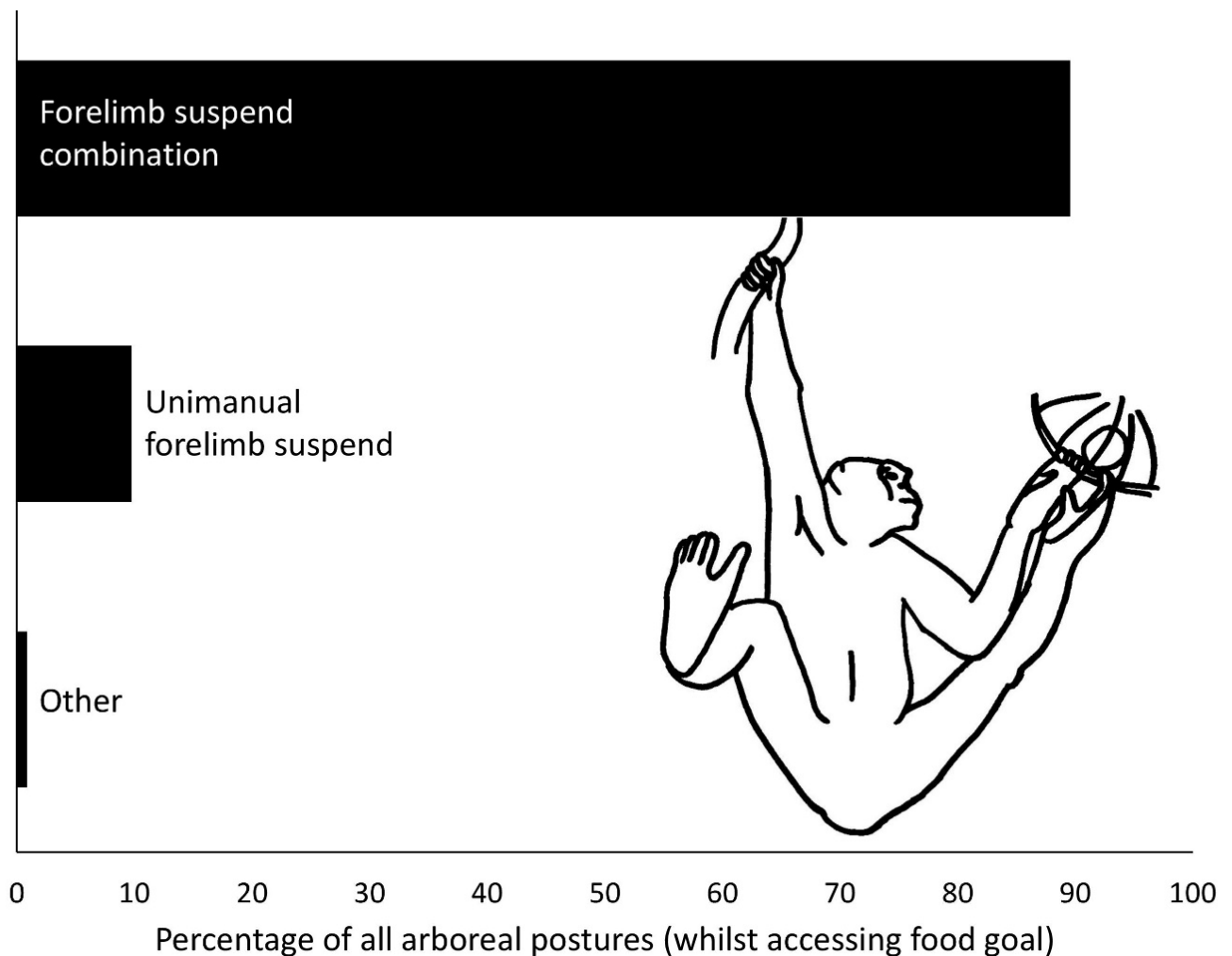
Fig. 1 Percentages of different postures used by captive bonobos in a UK zoo to access an arboreal foraging device during an arboreal testing condition (July - September 2013). Diagram is an example of the most common posture (forelimb suspend combination) drawn by NKIH

Two individuals were lateralised in the scattered food condition and one individual was lateralised in the terrestrial testing condition (Table 3). In contrast four individuals were lateralised in the arboreal testing condition: two were right handed and two were left handed. Handedness Index scores revealed that direction of hand use was consistent

across the different testing periods for two out of seven individuals (AdfC and AdfD). Direction of hand use was different depending on testing period for all other individuals.

Table 3. Individual laterality of captive bonobos in a UK zoo when manipulation foraging devices or food under three testing conditions (July 2013 - December 2015). In the scattered food condition bonobos manipulated food foraged from the ground during normal feeding routines. In the terrestrial condition bonobos manipulated two foraging devices accessible from the ground. In the arboreal condition the bonobos had to maintain an active arboreal posture to access the same foraging devices. HI is handedness index score, calculated according to Hopkins (1999). For binominal tests (B test), P values <0.05 are shown in bold, with the dominant hand.

Ind.	Scattered food		Terrestrial		Arboreal	
	Count (L/R)	B test	Count (L/R)	B test	Count (L/R)	B test
	HI	Direction	*HI*	Direction	*HI*	Direction
AdfE	-	-	48/32	P = 0.093	5/1	P = 0.219
			-0.200	Left	*-0.667*	Left
AdfA	99/96	P = 0.886	85/85	P = 1	73/124	**P < 0.001**
	-0.015	Left	*0.000*	Not lat.	*0.259*	**Right**
AdfB	33/14	**P = 0.008**	16/18	P = 0.864	58/65	P = 0.589
	-0.404	**Left**	*0.059*	Right	*0.057*	Right
AdfC	28/57	**P = 0.002**	17/27	P = 0.174	3/41	**P < 0.001**
	0.341	**Right**	*0.227*	Right	*0.864*	**Right**
AdfD	41/34	P = 0.489	90/43	**P < 0.001**	115/39	**P < 0.001**
	-0.093	Left	*-0.353*	**Left**	*-0.494*	**Left**
InfB	48/45	P = 0.836	129/99	P = 0.055	237/264	P = 0.245
	-0.032	Left	*-0.132*	Left	*0.054*	Right
InmA	63/70	P = 0.603	62/75	P = 0.305	167/80	**P < 0.001**
	0.053	Right	*0.095*	Right	*-0.352*	**Left**

Furthermore, individuals with a preference for using a particular hand at the foraging device had a longer mean duration of arm use for postural support for the opposite arm

(see Supplementary material Fig. S2). The frequency of hand changes was significantly negatively correlated with the proportion of use of one hand for postural support (Spearman's rank-correlation coefficient two-tailed, -0.074, N = 288, S = 4681, P < 0.005, Fig. 2). However, a low R^2 value ($R^2 = 0.006$), suggests that only 0.6% of the variance in the proportion of bouts with postural support can be explained by variance in frequency of hand changes.
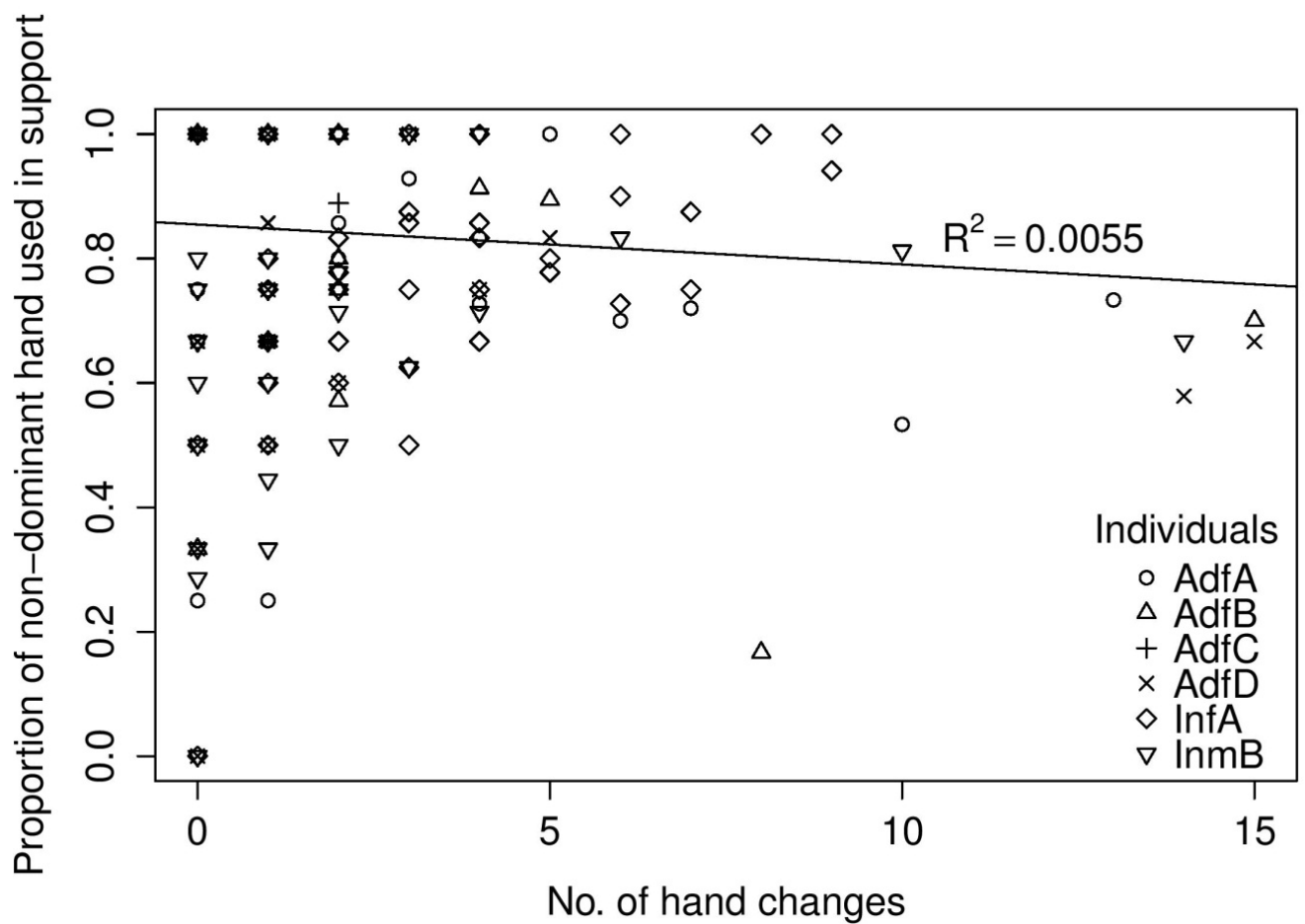

Fig. 2 Proportion of bouts in which captive bonobos used their non-dominant hand (the hand not manipulating an arboreal foraging device) for support in relation to the number of changes in hand used to manipulate the foraging device. Data are for bonobos in a UK zoo, July-September 2013.

Data availability

The data sets analysed and presented in this study are available from the corresponding author on reasonable request.

Discussion

Our findings suggest that bonobos have a preferred hand for maintaining demanding arboreal postures. We found no evidence for ambilaterality in these postures due to fatigue in forelimbs used to support body weight in suspensory postures in a symmetrical environment. Four of seven individuals had a preferred hand when accessing the foraging device in the arboreal testing condition, whereas only one individual exhibited a hand preference for manipulating the same foraging device in the terrestrial testing condition. There was no consistent direction of handedness across the population. HI scores indicate that directionality across the different testing conditions was consistent for two individuals.

More individuals were lateralised in the arboreal testing condition than in the terrestrial testing condition. This may suggest individual preference for maintaining active and predominantly suspensory postures. However, four of seven individuals is a small majority and one lateralised individual (InmA) was an infant and may not have yet developed limb preference (McManus et al. 1988). The two infants in this group did not follow the direction or laterality of their mothers, supporting previous studies showing no hereditary influence on laterality (Hopkins et al. 1994).

To test the fatigue hypothesis we predicted that the rate of change of the manipulating hand would be positively correlated with the proportion of bouts in which the non-dominant hand provides postural support due to fatigue (as in Marchant and McGrew 2007). However, we found no evidence of support for the fatigue hypothesis. We found a weak but significant negative correlation between the proportion of non-dominant hand use for postural support and number of hand changes in the arboreal testing condition.

Meaning, the more individuals used a forelimb in postural support the less they changed hands, contrary to the findings of Marchant and McGrew (2007). Furthermore, mean duration of limb use for postural support in the arboreal testing condition was longer for the opposite arm than that used for manipulation, suggesting individuals' maintained longer weight bearing postures for a preferred limb (see Supplementary Material). For example, if an individual was lateralised for the left hand for manipulating the foraging device in the arboreal testing condition they maintained significantly longer durations of arboreal postures when using their right arm for postural support.

The most frequent arboreal postures we recorded were suspension adjacent to or underneath the foraging device. In the majority of cases (89.5%) body weight was borne by a forelimb suspend combination posture (in which at least one forelimb was weight bearing), and a further 9.7% of cases were unimanual suspend (body weight borne by a single forelimb). In a previous study arboreal handedness was recorded for postures that included a forelimb as the "major support", however, the authors did not categorise positional behaviour in terms of forelimb suspension or compression (Marchant and McGrew 2007). It is likely that the differences in arboreal laterality we observed are due to the more demanding suspensory postures required, suggesting an individual preference for a particular limb for demanding postural support.

Wild chimpanzees fishing for ants arboreally are ambilateral, and it is suggested that this is because the locations of available supports in relation to ant holes is random and unpredictable in a natural canopy so chimpanzees have to use each hand indiscriminately for support and for fishing for ants (Marchant and McGrew 2007). However, the authors did not quantify the location of the ant holes or the available supports relative to selected supports in their analysis, and so this cannot be tested directly. In our study we kept the location of the foraging device constant in relation to available supports, and the foraging device itself could provide postural support. This would have enabled the bonobos to express their preferred hand for suspensory postures. Therefore, the results of our study suggest that laterality is more pronounced in postures where one hand is required for postural support due to individuals having a preferred hand for postural support. This is

in line with the stability hypothesis, (that individuals would be lateralised for a preferred limb to maintain body weight in demanding suspensory postures) and is consistent with previous findings (Vleeschouwer et al. 1995, Peters and Rogers 2008).

Evidence for population-level laterality of hand use in bonobos is mixed. For example there is evidence for: group level right handedness (Shafer 1997, Ingmanson 2005); group level left handedness (Vleescouwer et al 1995); and a right and left bias for different behaviours (Hopkins et al. 1993, Hopkins and de Waal 1995). Furthermore, several studies have found no evidence of group level handedness (McGrew and Marchant 1997b, Ingmanson 1998, Harrison and Nystrom 2008, Chapelain and Hogervorst 2009, Chapelain et al. 2011). However, most studies have found individual preference for either the right or the left hand (our study, Hopkins et al. 1993, Hopkins and de Waal 1995, Ingmanson 1998, Ingmanson 2005, Chapelain and Hogervorst 2009, Chapelain et al. 2011). It has been argued that hand preference for either the left or the right hand is dependent on: the complexity of the task for which handedness is recorded (Fagot and Vauclair 1991); the environment in which it is performed (Forester et al. 2012, Forrester and Quaresmini 2013, Tabiowo and Forrester 2013, Quaresmini et al. 2014); and the speed with which the task is performed (Pouydebat et al. 2014). Our findings suggest that the physical demand of a task (such as maintaining arboreal suspensory postures) could also elicit individual handedness. This could benefit the individual through enabling a longer duration of manipulation of an arboreal food resource, as seen in our study in the mean duration of arm use in the arboreal testing condition. Similarly, wild chimpanzees have been shown to benefit from individual lateralisation (to either the left of the right) for an ant-fishing task (McGrew and Marchant 1999).

In conclusion our findings do not support the previous hypothesis that ambilaterality during arboreal postures results from fatigue in the limb being used in postural support, as reported for wild chimpanzees for an arboreal ant fishing activity (Marchant and McGrew 2007). Our data suggest that the role of the forelimbs in demanding suspensory postures, such as arm hanging, may result in a preferred limb for these postures and this is likely due to individual limb strength. Data for hand preference for postural support,

recorded in relation to available supports relative to a food resource, in a natural canopy are needed to further explore the influence of the arboreal environment on laterality. We suggest that arboreal suspensory postures should be included in studies of laterality and that along with increasing complexity (such as more dextrous or tool use tasks), tasks with increasing physical demand (such as energetically demanding postures) can elicit individual hand preference. The majority of primates use the arboreal environment and therefore the study of non-human primate behavioural ecology, such as the study of laterality, should consider the influence of this physically demanding environment.

References

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227-266

Barnett, K. J. & Corballis, M. C. (2002) Ambidexterity and magical ideation. *Laterality: Asymmetries of Body, Brain and Cognition*. 7(1), 75-84

Braccini, S., Lambeth, S., Schapiro, S., & Fitch, W. T. (2010) Bipedal tool use strengthens chimpanzee preferences. *Journal of Human Evolution*, 58, 234-241

Byrne, R. W. & Byrne, J. M. (1991). Hand preferences in the skilled gathering tasks of Mountain Gorilla (*Gorilla g. berengei*). *Cortex*, 27(4), 521-546

Carlson, K. J., Doran-Sheehy, D. M., Hunt, K. D., Nishida, T., Yamanaka, A., & Boesch, C. (2006) Locomotor behaviour and long bone morphology in individual free-ranging chimpanzees. *Journal of Human Evolution*, 50, 394-404

Chapelain, A. S. & Hogervorst, E. (2009). Hand preference for bimanual coordination in 29 bonobos (*Pan paniscus*). *Behavioural Brain Research*, 196, 15-29

Chapelain, A. S., Hogervorst, E., Mbonzo, P., & Hopkins, W. D. (2011). Hand preferences for binomial coordination in 77 bonobos (*Pan paniscus*): Replication and extension. *International Journal of Primatology*, 32, 491-510

Christman, S. D., Henning, B. R., Geers, A. L., Propper, R. E., & Niebauer, C. L. (2008) Mixed-handed persons are more easily persuaded and are more gullible: interhemispheric interaction and belief updating. *Laterality: Asymmetries of Body, Brain and Cognition.* 13(5), 403-426

Corballis, M. C. (1989). Laterality and Human evolution. *Psychological Review*, 96(3), 492-505

Corballis, M. C., Hattie, J., & Fletcher, R. (2008) Handedness and intellectual achievement: an even-handed look. *Neuropsychologia*, 46(1), 374-378

Crow, T. J., Crow, L. R., Done, D. J., & Leask, S. (1998). Relative hand skill predicts academic ability: global deficits at the point of hemispheric indecision. *Neuropsychologia*. 36(12), 1275-1282

de Waal, F. & Lanting, F. (1997). Bonobo: The forgotten ape. University of California Press, Ltd

Doran D. M. (1993). Comparative locomotor behavior of chimpanzees and bonobos: the influence of morphology on locomotion. *American Journal of Physical Anthropology.* 91(1) 83-98

Doran, D. M. (1996). Comparative positional behaviour of the African apes. *In Great ape societies, Eds. McGrew, Marchant, and Nishida.* (pp. 213-224). Cambridge University Press.

Fagot, J. & Vauclair, J. (1991). Manual laterality in nonhuman primates: A distinction between handedness and manual specialization. *Psychological Bulletin*. 109(1), 76-89

Fan, P., Liu, C., Chen, H., Liu, X., Zhao, D., Zhang, J., & Liu, D. (2016). Preliminary study on hand preference in captive norther white-cheeked gibbons (*Nomascus leucogenys*). Primates. 58(1), 75-82

Fitch, W. T. & Braccini, S. N. (2013) Primate laterality and the biology and evolution of human handedness: a review and synthesis. *Annals of the New York Academy of Sciences.* 1288(1), 70-85

Fletcher, A. & Weghorst, J. (2005). Laterality of hand function in naturalistically housed chimpanzees (*Pan troglodytes*). *Laterality: Asymmetries of Body, Brain and Cognition*. 10(3), 219-242

Forester, G. S., Quaresmini, C., Leavens, D. A., Spiezio, C., & Vallortigara, G. (2012) Target animacy influences chimpanzee handedness. *Animal Cognition*, 15, 1121-1127

Forrester, G. S., & Quaresmini, C. (2013) The right hand man: manual laterality and language. In *Behavioural Lateralization in Vertebrates* (pp125-141), Springer Berlin Heidelberg

Forester, G. S., Quaresmini, C., Leavens, D. A., Mareschal, D., & Thomas, M. S. C. (2013) Human handedness: an inherited evolutionary trait. *Behavioural Brain Research*, 237, 200-216

Fragaszy, D. M. & Mitchell, S. R. (1990). Hand preference and performance on unimanual and bimanual tasks in Capuchin Monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 104(3), 275-282

Goble, D. J. & Brown, S. H. (2008) The biological and behavioural basis of upper limb asymmetries in sensorimotor performance. *Neuroscience and Biobehavioural Reviews*. 32, 598-610

Hanson, N.K.I. (2016) Cognitive and locomotor strategies of arboreal locomotion in non-human apes and humans. PhD Thesis, University of Birmingham, UK

Harris, A. J. (1974). Harris test of lateral dominance (3rd ed.). The Psychological Corp, New York

Harrison, R. M. & Nystrom, P. (2008). Handedness in captive bonobos (*Pan paniscus*). *Folia Primatol*, 79, 253-268

Hobaiter, C. & Byrne, R. W. (2013) Laterality in the gestural communication of wild chimpanzees. *Annals of the New York Academy of Sciences*, 1288(1), 9-16

Hook, M. A. & Rogers, L. J. (2002). Leading-limb preferences in marmosets (*Callithrix jacchus*): walking, leaping, and landing. *Laterality*. 7, 145-162

Hopkins, W. D. (1993). Posture and reaching in chimpanzees *(Pan troglodytes*) and orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 107(2), 162-168

Hopkins, W. D. (1995). Hand preferences for simple reaching in juvenile chimpanzees (*Pan troglodytes*): Continuity in development. *Developmental Psychology*, 31(4), 619-625

Hopkins, W. D. (1999). On the other hand: Statistical issues in the assessment and interpretation of hand preference data in nonhuman primates. *International Journal of Primatology*, 20(6), 851-866

Hopkins, W. D. (2004) Laterality in maternal cradling and infant positional biases: implications for the development and evolution of hand preferences in non-human primates. *International Journal of Primatology*, 25(6), 1243-1265

Hopkins, W. D. (2008). Brief communication: Locomotor limb preferences in captive chimpanzees (*Pan troglodytes*): Implications for morphological asymmetries in limb bones. *American Journal of Physical Anthropology*. 137, 113-118

Hopkins, W. D., Bennet, S. L., Bales, J. L., & Ward, J. P. (1993). Behavioural laterality in captive bonobos (*Pan paniscus*). *Journal of Comparative Psychology*. 107(4), 403-410

Hopkins, W. D., Bales, S. A., & Bennet, A. J. (1994) Heritability of hand preference in chimpanzees (*Pan*). *International Journal of Neuroscience*. 74(4), 17-26

Hopkins, W. D. & de Waal, F. B. M. (1995). Behavioural laterality in captive bonobos (*Pan paniscus*): Replication and extension. *International Journal of Primatology*, 16(2), 261

Hopkins, W. D., Cantalupo, C., Wesley, M. J., Hostetter, A. B., & Pilcher, D. L. (2002). Grip morphology and hand use in chimpanzees (*Pan troglodytes*): Evidence of a left hemisphere specialization in motor skill. *Journal of Experimental Psychology: General*. 131(3), 412-

Hopkins, W. D., Phillips, K. A., Bania, A., Calcutt, S. E., Gardner, M., Russell, J., Schaeffer, J., Lonsdorf, E. V., Ross, S. R. & Schapiro, S. J. (2011). Hand preferences for

coordinated bimanual actions in 777 great apes: Implications for the evolution of handedness in Hominins. *Journal of Human Evolution*. 60, 605-611

Hughes, C. M. L., Reibig, P. & Seegelke, C. (2011). Motor planning and execution in left- and right-handed individuals during a bimanual grasping and placing task. *Acta Psychologica*. 138(1), 111-118

Hunt, K. D., Cant, J. G. H., Gebo, D. L., Rose, M. D., Walker, S. E., & Youlatos, D. (1996). Standardised descriptions of primate locomotor and postural modes. *Primates*. 37(4), 363-387

Ingmanson, E. J. (1998). Right and left hand use preferences in a power grip task among *Pan paniscus* at Wamba, Zaire. *American Journal of Physical Anthropology*. suppl. 26, 125

Ingmanson, E. J. (2005). Hand-use preferences among *Pan paniscus* (bonobos) at Wamba, Democratic Republic of Congo. *American Journal of Primatology*. 66(suppl 1), 69-70

Janssen, L., Meulenbroeck, R. G. J., & Steenbergen, B. (2011). Behavioural evidence for left-hemisphere specialisation of motor planning. *Experimental Brain Research*. 209, 65-72

King, J. E. (1995). Laterality in hand preferences and reaching accuracy of cotton-top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, 109(1), 34-41

Llorente, M., Mosquera, M. & Fabre, M. (2009). Manual laterality for simple reaching and bimanual coordinated task in naturally housed *Pan troglodytes. International Journal of Primatology*. 30, 183-197

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987) Primate handedness reconsidered. *Behavioural and Brain Sciences*, 10, 247-303

MacNeilage, P. F. (1993). Implications of primate functional asymmetries for the evolution of cerebral hemispheric specializations. *In Primate Laterality*. (pp. 319-341). Springer New York

MacNeilage, P. F. (2007) Present status of the postural origins theory. In *W. D. Hopkins (Ed.) The Evolution of Hemispheric Specialization in Primates* (pp. 59-91) Amsterdam: Elsevier

Marchant, L. F. & McGrew, W. C. (2007). Ant fishing by wild chimpanzees is not lateralised. *Primates*. 48, 22-26

McGrew, W. C. & Marchant, L. F. (1997a). On the other hand: Current issues in and meta-analysis of the behavioural laterality of hand function in non-human primates. *Yearbook of Physical Anthropology*. 40, 210-232

McGrew, W. C. & Marchant, L. F. (1997b). Using the tools at hand: Manual laterality and elementary technology in *Cebus spp.* and *Pan spp. International Journal of Primatology*. 18(5), 787-810

McGrew, W. C. & Marchant, L. F. (1999). Laterality of hand use pays off in foraging success for wild chimpanzees. *Primates*. 40(3), 509-513

McGrew, W. C. & Marchant, L. F. (2001). Ethological study of manual laterality in the chimpanzees of the Mahale Mountains, Tanzania. *Behaviour*. 138(3), 329-358

McManus, I. C., Sik, G., Cole, D. R., Mellon, A. F., Wong, J., & Kloss, J. (1988) The development of handedness in children. *British Journal of Developmental Psychology*. 6, 257-273

Meguerditchian, A. Vauclair, J., & Hopkins, W. D. (2013) On the origins of human handedness and language: a comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. *Developmental Psychobiology*, 55(6), 637-650

Morcillo, A., Fernandez-Carriba, D., & Loeches, A. (2006). Motor asymmetries in locomotion and postural control in chimpanzees. *American Journal of Primatology*. 68, 802-811

Nicholls, M., Orr, C., & Lindell, A. (2005) Magical ideation and its relation to lateral preference. *Laterality: Asymmetries of Body, Brain and Cognition.* 10(6), 503-515

O'Malley, R. C. & McGrew, W. C. (2006). Hand preferences in captive orangutans (*Pongo pygmaeus*). *Primates*. 47, 279-283

Peters, H. H. & Rogers, L. J. (2008). Limb use and preferences in wild orangutans during feeding and locomotor behaviour. *American Journal of Primatology*. 70, 261-270

Pouydebat, E., Borel, A., Chotard, H., & Fragaszy, D. (2014) Hand preference in fast-moving versus slow-moving actions in capuchin, *Sapajus* spp., and squirrel monkeys, *Saimiri sciureus*. *Animal Behaviour*, 97, 113-123

Quaresmini, C., Forrester, G. S., Spiezio, C., & Vallortigara, G. (2014) Social environment elicits lateralised behaviours in gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 128(3), 276

Remis, M. (1995). Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. *American Journal of Physical Anthropology*. 97(4), 413-433

Rigamonti, M. M., Previde, E. P., Poli, M. D., Marchant, L. F., & McGrew, W. C. (1998). Methodology of motor skill and laterality: New test of hand preference in *Macaca nemestrina*. *Cortex*. 34(5), 693-705

Rogers, L. J. & Kaplan, G. (1996) Hand preferences and other lateral biases in rehabilitated orangutans, *Pongo pygmaeus pygmaeus*. *Animal Behaviour*. 51(1), 13-25

Sanz, C. M., Morgan, D. B., & Hopkins, W. D. (2016) Lateralisation and performance asymmetries in the termite fishing of wild chimpanzees in the goualougo triangle republic of Congo. *American Journal of Primatology*. 78(11), 1190-1200

Shafer, D. D. (1997). Hand preference behaviours shared by two groups of captive bonobos. *Primates*. 38(3), 303-313

Shaw, C. N. and Stock, T. (2009). Habitual throwing and swimming correspond with upper limb diaphyseal strength and shape in modern human athletes. *American Journal of Physical Anthropology*. 140, 160-172

Susman R., Badrian N., & Badrian A. (1980). Locomotor behavior of *Pan paniscus* in Zaire. *American Journal of Physical Anthropology.* 53, 69-80

Susman, R. L. (1984). The locomotor behavior of *Pan paniscus* in the Lomako forest. *In The pygmy chimpanzee: Evolutionary biology and behaviour*. (pp. 369-393). Springer US

Tabiowo, E., & Forrester, G. S. (2013) Structured bimanual actions and hand transfers reveal population-level right-handedness in captive gorillas. *Animal Behaviour*, 86, 1049-1057

Thorpe, S. K. S. & Crompton, R. H. (2005). Locomotor ecology of wild orangutans (*Pongo pygmaeus abelii*) in the Gunung Leuser Ecosystem, Sumatra, Indonesia: a multivariate analysis using log-linear modelling. *American Journal of Physical Anthropology*. 127(1), 58-78

Vallortigara, G. & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioural and Brain Sciences*. 28, 575-633

Vallortigara, G., & Chiandetti, C. (2011) Brain asymmetry (animal). *Wiley interdisciplinary reviews: Cognitive Science*, 2(2), 146-157

Vleeschouwer, K. D., Elsacker, L. V., & Verheyen, R. F. (1995). Effect of posture on hand preferences during experimental food reaching in bonobos (*Pan Paniscus*). *Journal of Comparative Psychology*, 109(2), 203-207

Verendeev, A., Chet, S. C., & Hopkins, W. D. (2016). Organisation and evolution of the neural control of the hand in primates: Motor systems, sensory feedback, and laterality. *In The Evolution of the Primate Hand*. (pp. 131-153). *Springer New York.*
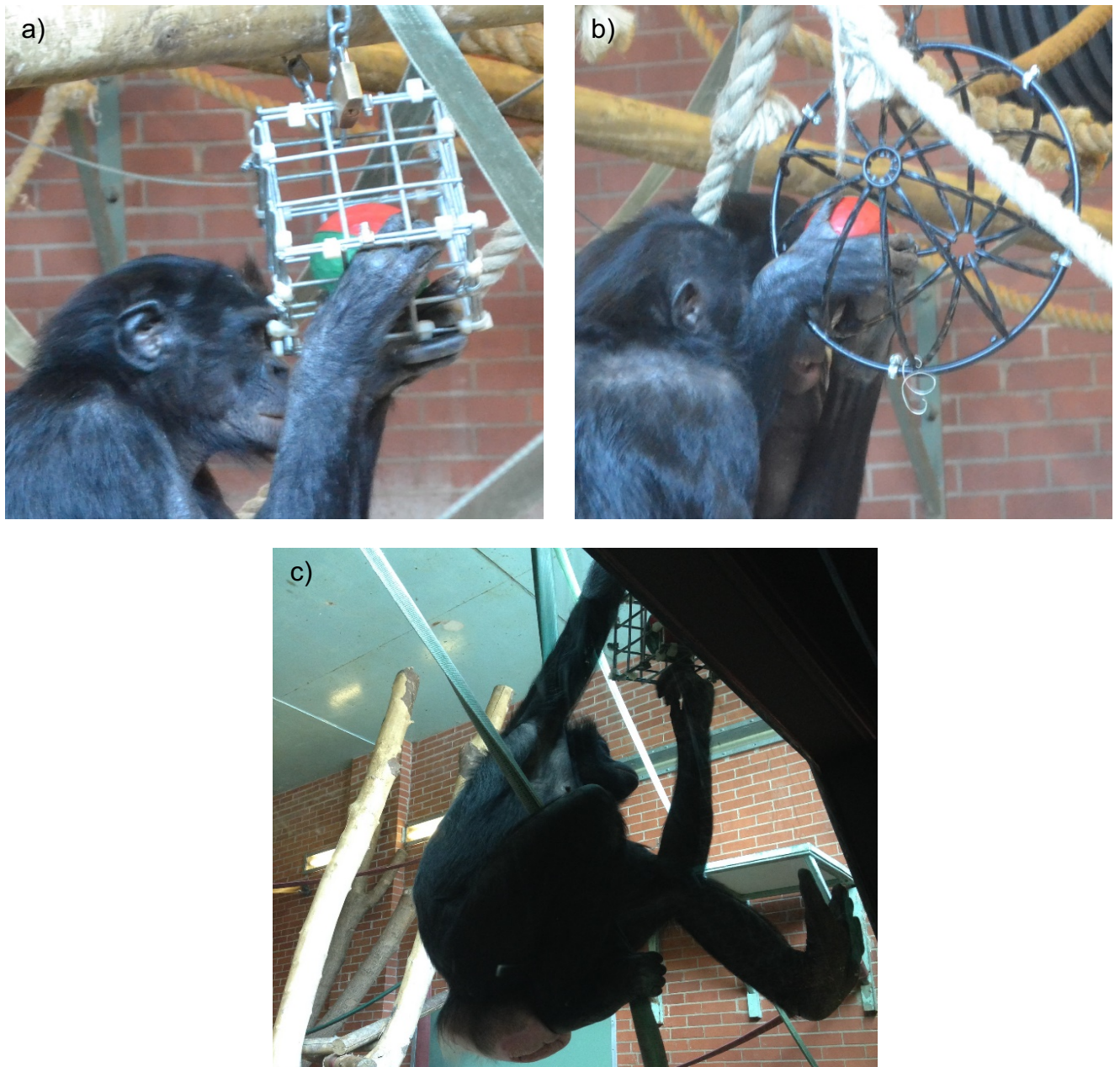
Fig. S1 Photographs of captive bonobos (UK, July 2013-December 2015) accessing food reward in the terrestrial testing condition with the a) cube and b) spherical foraging devices, in this position the bonobos were able to access the foraging devices from the ground. In the arboreal testing condition bonobos were required to maintain an active arboreal posture whilst accessing the foraging device (c).
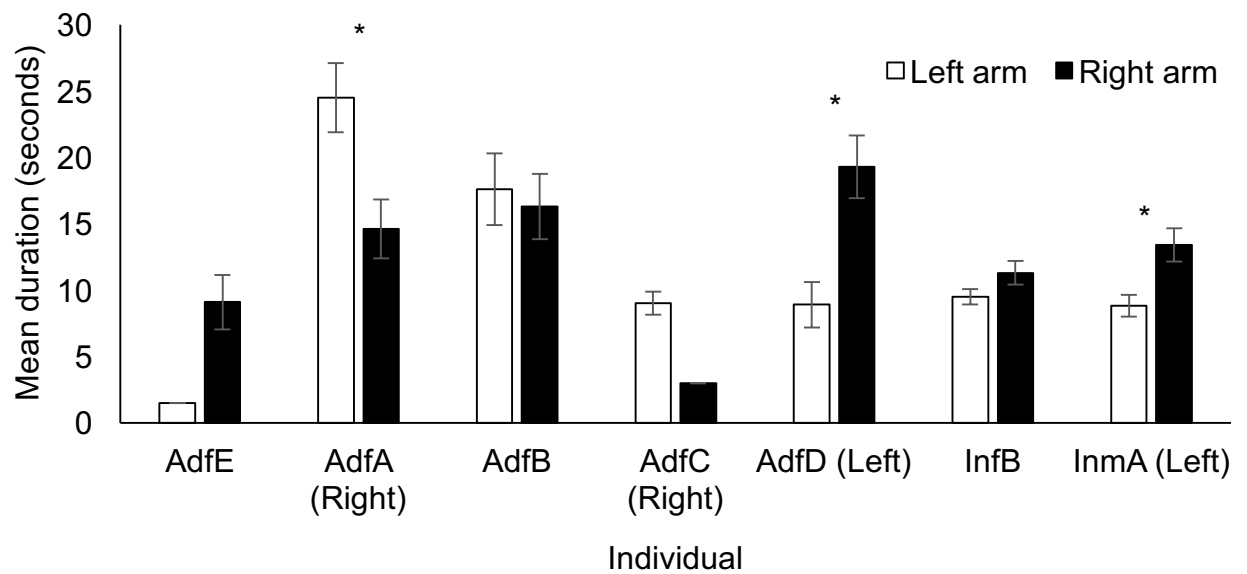
Fig. S2 Mean duration of arm use in seconds (and standard error bars) for postural support whilst accessing a foraging device for captive bonobos studied between July and September 2013. Individuals that showed a significant difference in mean duration are indicated with an * (Kruskal-Wallis Test, P < 0.05). Direction is shown in (brackets) for lateralised individuals on the X axis. Two individuals AdfE and AdfC used their left and their right arm (respectively) only once to maintain posture and so standard error could not be calculated.