

Between-task consistency, temporal stability and the role of posture in simple reach and fishing hand preference in chimpanzees (*Pan troglodytes*)

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ARTICLE INFO

Keywords:

Laterality
Hand preference
Chimpanzee
Posture
Between-task consistency
Temporal stability

ABSTRACT

Studying hand preferences in chimpanzees can provide insights into the evolutionary origins of human hemispheric specialization. Research on chimpanzee hand preference requires careful examination of important factors such as between-task consistency, temporal stability and posture although few studies have investigated all of these factors in combination. We investigated hand preference in simple reach and fishing behaviours in a group of 19 chimpanzees at Chester Zoo in the UK. Simple reach was defined as extending a hand to grasp a small object, then flexing the limb in a continuous motion, and was examined in quadrupedal, sitting and climbing postures. Fish in hole was defined as inserting a stick into a hole in the wall with one hand and then extracting it with the same hand. Between-task consistency of hand preference was assessed by comparing simple reach and fish in hole, while temporal stability was assessed by comparing simple reach from two points in time: 2017 and 2019. The data showed no significant influence of posture on the strength of hand preference, which contrasts with previous research. The findings of this study show temporal stability in simple reach, although only partial between-task consistency. Overall, the results indicate that simple reach elicits laterality at the individual level and is consistent across postures and stable over time, which is consistent with the literature. These results suggest that posture stability may be important in affecting hand preference. Further, whilst there was overall stability in hand preference across time periods, some individuals changed their preferred hand, suggesting there may be individual-level temporal instability of hand preference for certain tasks.

1. Introduction

Hand preference has been widely studied in chimpanzees and other non-human primates (Fitch and Braccini, 2013; Meguerditchian et al., 2013) and it is often focused on when investigating the evolutionary origins of lateralization. Understanding hand preference can create new insights into the origins of lateralization in primates (MacNeillage et al., 1987; Regaiolli et al., 2016), neural correlates of lateralization in the brain (Hopkins et al., 2015; Rogers, 2017) and its link with general aspects of behaviour (Roberts et al., 2019; Rogers, 2009, 2018). As the closest living relatives to humans, studying patterns of hand preference in chimpanzees can provide insights into the evolutionary origins of the left hemisphere specialization seen in humans (Uomini, 2009). In recent years, research has shown that hand preference can be a predictor of certain aspects of personality and cognitive style (Gordon and Rogers, 2010, 2015; Hopkins and Bennett, 1994; Rogers, 2018; Tomassetti et al.,

2019). These aspects of behaviour are known to be temporally stable and, although hand preference is frequently assumed to be temporally stable as well, this stability is not often reported in the literature. Additionally, hand preference is a complex phenomenon that requires researchers to pay close attention to aspects such as postural implications (Braccini et al., 2010; Hopkins, 1993; Llorente et al., 2009) and task-specificity (Hopkins and Pearson, 2000; Hopkins et al., 2013). This study examines chimpanzee hand preference in two tasks: simple reach and fishing behaviour, focusing on three factors: between-task consistency, temporal stability and the influence of posture.

One key question regarding laterality in non-human primates is the extent to which lateral bias is affected by the nature of the manual action (Bailoo et al., 2019; Hopkins et al., 2013; Regaiolli et al., 2016). Simple reaching tasks have been commonly used to study hand preference in chimpanzees, with most studies reporting significant individual-level preferences but failing to find population-level preferences (Bailoo

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<https://doi.org/10.1016/j.applanim.2021.105417>

Received 1 March 2021; Received in revised form 27 July 2021; Accepted 29 July 2021

Available online 31 July 2021

0168-1591/© 2021 The Author(s).

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et al., 2019; Hopkins, 1993, 1995b; Hopkins et al., 2005, 2013, 2015; Llorente et al., 2009; Padrell et al., 2019). However, population-level right-hand preference has been reported for simple reach in bipedal posture (Hopkins and Pearson, 2000) and experimental bimanual tasks (Llorente et al., 2009). Similar results have been found when studying simple reaching as part of spontaneous hand use in the wild (McGrew and Marchant, 2001) and captivity (Fletcher and Weghorst, 2005; Mosquera et al., 2007). Similarly, research has examined lateralised tool use in chimpanzees, particularly “fishing” behaviours, as wild chimpanzees often perform termite-fishing and ant-fishing spontaneously (Marchant and McGrew, 1996). Data indicate that chimpanzees present not only strong individual-level preferences (McGrew and Marchant, 1992) but also a population-level left-hand bias in termite-fishing (Lonsdorf and Hopkins, 2005; Bogart et al., 2012) and a right-hand bias in ant-fishing (Humble and Matsuzawa, 2009), although these results have not always been replicated (Sanz et al., 2016). In particular, differences in fishing technique might explain these contradictory results (Sanz et al., 2016) and, therefore, further research investigating fishing behaviours in different contexts is needed to have a clearer picture of fishing laterality. Fishing behaviours are complex tool-using tasks that chimpanzees perform spontaneously, both in the wild and in captivity, with some research suggesting that fishing performance is heritable (Hopkins et al., 2014, 2019). Fishing behaviours also present an important alternative to experimental tasks, when investigating between-task consistency of hand use, and more research is needed to better understand if hand preference for fishing is consistent with hand preference in other tasks.

An important aspect of hand use that is not often addressed is individual consistency between tasks, since there is evidence in other primate species that population bias can remain the same even though some individuals change their preference from one task to another (Hook and Rogers, 2008). Evidence of between-task consistency is scarce, as studies often report only one behaviour, or a few similar tasks. Hopkins and Pearson (2000) conducted six tasks in a group of 187 captive chimpanzees and found consistency between feeding behaviours and reaching behaviours in three different postures, as well as consistency between two types of bimanual actions, including the tube task and a similar task where the instrument used was shaped as a ball. While there was evidence of right-hand population-level preference in both bimanual tasks as well as feeding and reaching in a bipedal posture, individual preferences for bimanual tasks did not correlate with preferences in feeding and reaching (Hopkins and Pearson, 2000). A more recent study investigated between-task consistency using a more diverse set of behaviours, assessing hand preference for simple reach, tool use, manual gestures and the tube task (Hopkins et al., 2013). Hopkins et al. (2013) found that only the tube task and manual gestures showed a consistent significant right-hand population bias which supports research indicating population biases in these tasks, as both the tube task (Llorente et al., 2009) and manual gestures (Hopkins et al., 2012) show clear population biases in previous research. Interestingly, despite the absence of clear population biases in tool use and simple reach, the four tasks were significantly correlated between each other, showing clear evidence of between-task consistency (Hopkins et al., 2013).

In addition to the nature of the task and between-task consistency, a key factor that is often overlooked in hand preference research is its stability over time. Many studies of hand preference in chimpanzees take a longitudinal approach (Hopkins et al., 2001), collecting data over long periods of time. However, often temporal stability is underreported or only studied through correlational analysis without looking at whether some individuals have important changes in their preferences. Hopkins (1995a) observed that hand preference for simple reach was stable for juvenile chimpanzees over a period of one year. On the other hand, juvenile chimpanzees often show weaker hand preferences (Hopkins, 1995b), which may suggest that hand preference for simple reach consolidates with maturity. Despite this assumption of hand preference consolidating in adulthood, temporal stability in adult life has not been

commonly researched. Hopkins et al. (2001) found moderate correlations between hand preference collected over a five-year period in captive chimpanzees, indicating that hand preference showed some stability over that period of time. In a recent study, Padrell et al. (2019) investigated temporal stability of hand preference in adult chimpanzees in more detail and found that hand preference for simple reach correlated when comparing measures from 2008 and 2011, and from 2008 and 2018. However, there was no correlation in hand preference between 2007 and 2018, although the results were close to being significant, and three out of the 12 chimpanzees studied showed a different hand preference after 10 years. The authors (Padrell et al., 2019) suggest that this lack of correlation might be a consequence of the chimpanzees getting used to interacting with and manipulating the tubes between the periods, although this lack of correlation is also present for simple reach. It is also important to consider that, despite obtaining non-significant results, the small sample size of the study makes their statistical tests have low power, indicating that more research is needed in order to understand the changes over time in hand preference.

Lastly, the influence of posture on hand preference is an important aspect that cannot be overlooked. The Postural Origins Theory (MacNeilage et al., 1987) argues that a left-hand specialization in supporting the body would have freed the right hand, which would have consequently specialised in manipulating objects. Examining how posture influences hand use in chimpanzees can provide insights into the role of posture in the evolution of left-hemisphere motor specialisation in humans, as evidence shows that more demanding postures result in stronger preferences (Braccini et al., 2010; Hopkins, 1993; Llorente et al., 2009). Chimpanzees show stronger hand preferences when using tools in a bipedal posture rather than sitting (Braccini et al., 2010; Hopkins, 1993) or quadrupedal posture (Bailoo et al., 2019). Interestingly, chimpanzees show stronger hand preferences when doing simple reaching tasks from a sitting posture, compared to a quadrupedal posture (Llorente et al., 2009). This may not be due to task difficulty, but to situational convenience. For example, when approaching the object or piece of food, one hand might be closer to it due to the asymmetric nature of quadrupedal locomotion. It is also important to note that while posture has an effect on the strength of hand preference, it does not seem to influence the direction of hand preference (Bailoo et al., 2019). While previous studies have investigated the effects of bipedal posture (Bailoo et al., 2019; Braccini et al., 2010; Hopkins, 1993) and sitting (Llorente et al., 2009), other less common postures such as climbing still require further investigation.

The objective of the present study is to assess hand use in chimpanzees in captivity in two tasks: simple reach and fishing behaviours. This research explores individual- and group-level laterality, while examining the influence of between-task consistency, temporal stability and posture on laterality. We propose three hypotheses: 1) hand indices will show positive relationships between tasks (Hopkins et al., 2013), 2) hand indices in 2017 will show positive relationships with indices in 2019 (Padrell et al., 2019), and 3) more demanding postures result in stronger preferences (Braccini et al., 2010; Hopkins, 1993; Llorente et al., 2009), therefore climbing should result in stronger preferences than sitting and quadrupedal postures, and sitting postures should result in stronger preferences than quadrupedal postures.

2. Method

2.1. Sample and housing

The subjects were 19 chimpanzees (*Pan troglodytes*) (Table 1) housed in a single group at the chimpanzee colony of Chester Zoo in the United Kingdom. The exhibit consists of two enclosures: the indoor breeding centre and the outdoor island. The breeding centre is an indoor enclosure (approximately 13 m high and 4.3 m in diameter) containing climbing structures with resting sites, ropes and nets. The island is an outdoor area of approximately 0.2 ha connected with the breeding

Table 1
Chimpanzees at Chester Zoo, UK, indicating sex and age (2017).

Name	Sex	Age (years)
Carlos	M	12
Eric	M	14
Dylan	M	30
Friday	M	41
Nicky	M	48
Wilson	M	49
Boris	M	51
Tina	F	8
Pattie	F	20
Chrissie	F	21
Vila	F	22
Zee Zee	F	23
Layla	F	25
Alice	F	26
Sally	F	29
Sarah	F	31
Mandy	F	40
Farthing	F	42
Rosie	F	44

centre, with wide vegetation patches and climbing posts connected with ropes and nets. Water was continually available and feeding involves scattering food on the indoor and outdoor areas, hiding food in the vegetation on the outdoor area in the morning, and food distribution in the indoor area between 1 pm and 3 pm each day. Additional enrichment food was occasionally offered in the form of yogurt or honey inside small holes on a wall in the inside enclosure that was easily visible for observers, which the chimpanzees could access by using thin branches to “fish” for the food.

2.2. Ethical note

The study was approved by the Ethics Committee of the School of Psychology at the University of Chester and the Research Committee of Chester Zoo. The study required only observational data; no manipulation of the animals or their environment was needed, and animals were observed only during their normal display hours at the zoo.

2.3. Procedure

Data collection for the study was conducted from January to April 2017, with additional data collected from June to August 2019 to assess temporal stability. Data were collected both indoors and outdoors using focal subject sampling of 10 min, switching focal subject when an animal moved out of sight in the outdoor enclosure to maximize data collection. Focal observations that were stopped this way were resumed later when the individual was visible again. All observations were collected from approximately 10am until 3 pm, during standard zoo opening hours.

2.4. Simple reach

Simple reaching behaviours were defined as behaviours in which the focal chimpanzee extends a limb and grasps a small object, then flexes the limb in one continuous motion (Fletcher and Weghorst, 2005; Marchant and McGrew, 1996). Simple reach bouts were registered when the chimpanzee had both hands free from previous object possession. No unsuccessful attempts were observed. Chimpanzees were fed by scattering pieces of food throughout the indoor and outdoor enclosure. Postural information was collected for simple reach and fish in hole, recording if the animal was in a quadrupedal position, sitting, standing bipedally or climbing with two legs and one arm for support. Providing food in the indoor enclosure also occasionally resulted in pieces of food remaining in the nets of the ceiling and walls of the enclosure, which elicited climbing postures.

2.5. Fish in hole

When performing this behaviour, chimpanzees hold a stick with one hand and insert it into a hole in the wall. The inside of the hole is covered in yogurt or honey, which covers the stick. The chimpanzee then extracts the stick to lick the food from it. The holes on the walls of the enclosure are meant to replicate ant- and termite-fishing behaviours observed in the wild. Postural information for fish in hole was collected, although most bouts were performed from a climbing posture due to the location of the holes (see Fig. 1). While the hand performing the action was clearly visible for the observer, sometimes grass/straw obscured the details of finger placement and, therefore, information regarding grip morphology (Llorente et al., 2009; Meguerditchian et al., 2015) was not collected.

Both behaviours were recorded using bouts (Hopkins, 1999; McGrew and Marchant, 1997) separated by: i) another behaviour (for example, if a chimpanzee is using the right hand to pick up objects, then scratches with the right hand, then resumes picking up, that would be considered as two bouts of picking up with the right hand), by ii) the use of the opposite hand (if a chimpanzee is picking up objects with the right, then starts picking up with the left, that would be considered as one bout with either hand) or by iii) a period of inactivity of five or more seconds.

2.6. Data analysis

Individual hand preferences were assessed by calculating binomial tests on the data for each individual, obtaining z-scores to evaluate if they were significantly lateralized; chimpanzees were classified as significantly lateralized if they had a z-score over 1.96 or under -1.96, they were classified as ambipreferent if their z-score was between 1.96 and -1.96 (Fletcher and Weghorst, 2005; Hopkins, 1999; Padrell et al., 2019). Additionally, handedness indices (HI) were computed for each behavioural category using the formula $HI = (R - L) / (R + L)$ (Hopkins, 1995a), where R was the frequency of right-hand use and L was the frequency of left-hand use. HI ranges from -1, indicating a left-hand preference through to 1, indicating a right-hand preference, with values close to 0 indicating no particular preference. Absolute measures for HI (Wiper, 2017) were used to study strength of hand preference, independent of the direction of the preference. Only animals with a

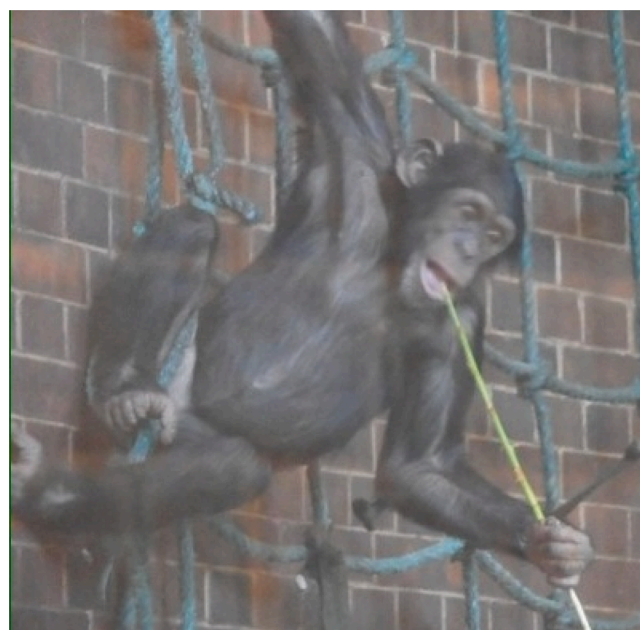


Fig. 1. Juvenile chimpanzee licking a stick after performing “fish in hole” from a climbing posture.

minimum number of observations of eight bouts were included in the analysis. Since a sample size of five is usually considered extremely small (Bishara and Hittner, 2012; de Winter et al., 2016), only tasks with six or more individuals with enough data were considered for the subsequent analysis. These were: simple reach in quadrupedal, sitting and climbing positions and fish in hole in climbing position. Due to the lack of sufficient data on different postures for “fish in hole” behaviours, this study does not evaluate posture across tasks.

Non-parametric statistics were used where available based on the small sample sizes and exploration of histograms and Q-Q plots. One sample t-tests were used to investigate group-level preferences by testing significant differences from 0 (Llorente et al., 2011; Mosquera et al., 2007), using Bonferroni's correction to avoid increasing the type-1 error. Spearman's ρ was used to investigate between-task consistency by correlating HI between simple reach and fish in hole as well as to assess temporal stability by correlating HI in simple reach measures obtained in 2017 and 2019. Simple reach measures were used to assess temporal stability as most individuals had sufficient observations in both periods. The effects of posture on simple reach were evaluated by correlating different postures using Spearman's ρ . Friedman's test was used to investigate differences between strength of HI between postures for simple reach.

3. Results

3.1. Data used

The categories used in the analysis and total number of bouts recorded for quadrupedal, sitting and climbing simple reach as well as fish in hole while climbing can be seen in Table 2. The number of bouts per individual for quadrupedal simple reach ranged from 59 to 364 (mean = 123, SD = 80).

3.2. Individual- and population-level laterality

Based on the z-scores, the majority of the chimpanzees were significantly lateralised in simple reaching behaviours, in quadrupedal and sitting position, while only half of the chimpanzees showed a significant lateralization for simple reach when climbing and a third were lateralised for fishing (Table 3). T-tests adjusted using Bonferroni correction ($p < .012$) did not find significant population-level laterality for any of the behaviours.

3.3. Between-task consistency

Table 4 shows the individual classification of hand preference for overall observation, including data collected in 2019 and 2017. Of the 19 individuals, six showed perfect consistency, significantly using the same preferred hand, although five were only measured in quadrupedal and sitting simple reach, with one, Sally, being consistent in

Table 3

Hand use measures, showing the number of lateralised individuals, the mean handedness index (HI) for the group and the result for the t -test.

	Simple Reach			Fish in Hole
	Quadrupedal (n = 19)	Sitting (n = 19)	Climbing (n = 8)	Climbing (n = 9)
Lateralised individuals	14	12	4	3
Mean HI (SD)	0.028 (0.533)	−0.095 (0.607)	0.41 (0.361)	0.109 (0.309)
T	0.229	−0.679	3.218	1.065
P	.821	.506	.015	.318

Table 4

Posture and between-task consistency of hand preference for simple reach and fish in hole, based on z-scores.

		Simple Reach			Fish in hole	Consistency
		Quadrupedal	Sitting	Climbing	Climbing	
Carlos	A	R	A			2/3
Eric	L	L		R		2/3
Dylan	L	L				2/2
Friday	L	L				2/2
Nicky	A	A				2/2
Wilson	R	R				2/2
Boris	L	L				2/2
Tina	R	R	R	A		3/4
Patti	R	A	A	A		3/4
Chrissie	R	R	A			2/3
Vila	R	A	R	R		3/4
ZeeZee	R	A	R	L		2/4
Layla	R	A	R			2/3
Alice	A	R		A		2/3
Sally	A	A		A		3/3
Sarah	R	A		A		2/3
Mandy	A	L				0/2
Farthing	R	R		A		2/3
Rosie	L	L	A			2/3

Note: R: right hand preference, L: left hand preference, A: ambipreferent. Consistency is the extent to which chimpanzees demonstrating the same hand preference across different tasks and postures.

quadrupedal and sitting simple reach as well as climbing fish in hole. Of the remaining individuals, twelve were measured in at least three tasks and were consistent in at least two of them. One individual, Mandy, was measured in quadrupedal and sitting simple reach but was not consistent in her preferred hand.

Table 5 shows the results for the Spearman correlations investigating between-task consistency. Simple reach in quadrupedal position showed a moderate positive correlation with simple reach while sitting ($r_s(17) = .661$, $p = .001$) and a strong positive correlation with simple reach in climbing posture ($r_s(6) = .881$, $p = .002$).

Table 2

Total number of chimpanzees and observations per behaviour.

	N. of chimpanzees with 8 or more observations	Mean (SD) of bouts per individual	Minimum and maximum bouts per individual	Total number of bouts
Quadrupedal simple reach				
Total	19	123 (80)	59–364	2335
2019	17	55 (40)	15–168	928
2017	19	74 (60)	20–277	1407
Sitting simple reach				
Total	19	127(76)	16–267	2424
2019	15	49 (29)	8–129	760
2017	19	88 (65)	9–238	1664
Climbing simple reach*	8	23(22)	9–80	190
Fish in hole Climbing*	9	44(20)	17–79	406

Note: Climbing simple reach represents the total amount of observation between 2017 and 2019. Fish in hole was only observed in 2019.

Table 5

Spearman's correlation coefficients for simple reach in quadrupedal, sitting and climbing position and fish in hole.

	Simple reach sitting	Simple reach climbing	Fish in hole
Simple reach quadrupedal	.661*	.881*	-.250
Simple reach sitting		.119	-.483
Simple reach climbing			0

Note: the correlation coefficient between simple reach climbing and fish in hole was lower than .001.

* Indicates significant correlations at $p < .01$, adjusting using a Bonferroni correction.

3.4. Temporal stability

Table 6 shows the individual classification of hand preference for quadrupedal and sitting simple reach in 2017 and 2019. Examining the significance of z-scores shows that six individuals showed temporal stability in both postures and eight showed stability in only one posture. Four chimpanzees only had enough data to be assessed in one posture: two of them showed stability while the other two did not. Of the 12 chimpanzees that did not show full stability, all changed from showing a significant preference, either left or right, to ambipreferent; or from ambipreferent to showing a significant preference. No individual switched from right preference to left preference or vice versa. The Spearman's tests revealed significant, strong positive relationships between the HI of quadrupedal simple reach in 2017 and 2019 ($r_s(15) = .735$, $p = .001$) as well as between the HI of sitting simple reach in 2017 and 2019 ($r_s(13) = .849$, $p < .001$).

3.5. Posture

A Friedman's test was conducted in order to test if the strength of hand preference (absolute value of the handedness indices) varied in simple reach depending on the posture. The test did not find significant differences between the strength of hand preference in simple reach using quadrupedal, sitting or climbing postures ($\chi^2(2) = 4.75$, $p = .093$).

Table 6

Temporal stability between 2017 and 2019 of simple reach in quadrupedal and sitting postures based on z-scores.

	Quadrupedal		Sitting		Stability
	2017	2019	2017	2019	
Carlos	A		R		–
Eric	L	L	L	A	1/2
Dylan	L	A	L	L	1/2
Friday	L		L	A	0/1
Nicky	L	A	A	A	1/2
Wilson	R	R	R	R	2/2
Boris	L	A	L	L	1/2
Tina	R	R	R	R	2/2
Patti	A	R	A	A	1/2
Chrissie	R	A	R	R	1/2
Vila	R	R	L		1/1
ZeeZee	R	A	A	A	1/2
Layla	R	R	A		1/1
Alice	A	A	R	R	2/2
Sally	A	A	A	A	2/2
Sarah	R	A	A		0/1
Mandy	A	A	L	L	2/2
Farthing	R	R	R		2/2
Rosie	L	A	L	L	1/2

Note: R: right hand preference, L: left hand preference, A: ambipreferent. Stability is the extent to which chimpanzees demonstrating the same hand preference from 2017 to 2019 for quadrupedal and sitting simple reach.

4. Discussion

This study presents a detailed examination of hand preference in captive chimpanzees, adding important considerations such as between-task consistency, temporal stability and posture. The results show no significant influence of posture on the strength of hand preference in simple reach, contrary to what was predicted. Additionally, while there is consistency between simple reaching tasks in different postures, there is no between-task consistency between simple reach and fish in hole. The data indicate significant temporal stability in simple reach over a period of two years.

The first hypothesis related to between-task consistency and proposed that there would be a positive relationship between hand preference in different postures, and between the simple reach tasks and the fish in hole task. The results show, for simple reach, there was a positive correlation when quadrupedal and sitting and when quadrupedal and climbing, but not when climbing and sitting. More interestingly, fish in hole did not significantly correlate with any of the other tasks and most individuals did not display a significant hand preference in this task. In the wild, termite fishing behaviours often elicit strong hand preferences (McGrew and Marchant, 1992) and population level left-hand preference (Lonsdorf and Hopkins, 2005). However, the artificial context in which this behaviour is emulated at Chester Zoo might constrain important aspects of the behaviour. For example, although studies of termite-fishing in the wild often do not give details of posture during the behaviour (Lonsdorf and Hopkins, 2005; McGrew and Marchant, 1992), the position and distribution of termite holes on the ground make them easily accessible from a sitting or quadrupedal posture. In contrast with this, the positioning of the holes at Chester Zoo often made it difficult for all individuals to access them at once unless they climbed on a nearby net, and it is possible that a climbing posture requires the use of the right hemisphere for keeping a more balanced posture (Rogers and Vallortigara, 2015), constraining the use of the left hand that would otherwise be used for fishing. Previous studies have reported significant, albeit small, associations between hand use measures when investigating simple reach and experimental tasks, including fishing tasks (Hopkins et al., 2013). Again, posture might be at the root of these diverging results. Although Hopkins et al. (2013) do not report posture during the fishing task, it is likely that chimpanzees performed this behaviour from the ground. Overall, correlations indicate consistency in hand preference between quadrupedal and sitting simple reach, as well as quadrupedal and climbing simple reach, but not between simple reach and fish in hole.

Regarding the second hypothesis and temporal stability, results are similar to previous research (Hopkins et al., 2001; Padrell et al., 2019), showing strong correlations between handedness indices for simple reach measures in 2017 and 2019. Much is still unknown regarding temporal stability in the medium-term. Padrell et al. (2019) found that, while hand preference in simple reach correlated between 2008 and 2018, it did not correlate between 2007 and 2008. Also, it is important to consider that, even when there is a significant correlation in the overall handedness indices (HI) between two time periods, there might be an important number of individuals that experience changes in their preferred hand. In the current study, 12 out of 19 chimpanzees changed their hand preference from significantly lateralized to ambipreferent or from ambipreferent from significantly lateralized, while no chimpanzee changed from left to right or vice-versa. The results from Padrell et al. (2019) were similar, as 4 out of 12 showed a similar change while only one displayed a change from left to right preference. This is indicative that, while the overall indices might remain similar, it is likely that there are individual factors that contribute to changes in hand preference.

The third hypothesis of this study proposed that more demanding postures such as climbing would result in stronger hand preferences. This was based on past research that indicates that posture is an important factor in the evolution of hand preference in primates (MacNeilage et al., 1987) and that it has an important effect on the strength,

but not the direction, of hand preference. Llorente et al. (2009) found stronger hand preferences in sitting simple reach than in quadrupedal simple reach, while Hopkins (1993) found stronger hand preferences in bipedal postures than in quadrupedal simple reach. Similarly, Braccini et al. (2010) reported stronger hand preferences in a bipedal posture compared to sitting when using tools with one hand and Bailoo et al. (2019) showed stronger hand preferences in bipedal posture compared to quadrupedal postures. Fletcher and Weghorst (2005) measured climbing postures but do not include an analysis of their effect on the strength or direction of hand preference. The current study attempted to account for these four postures (quadrupedal, sitting, bipedal and climbing), although bipedal posture was not considered in the analysis due to its infrequent observation. Importantly, the results of the present study fail to replicate these past findings, as there was no significant difference in the strength of hand preference between quadrupedal, sitting and climbing simple reach. These findings could challenge the notion that more complex postures elicit stronger hand preferences, although they must be interpreted with caution due to the small number of observations of climbing simple reach, in comparison to quadrupedal and sitting simple reach. A likely interpretation of the results might be that climbing does not present the same challenging postural demands as bipedalism has been suggested to do in previous studies (Braccini et al., 2010; Hopkins, 1993). This is in line with Bailoo et al.'s (2019) suggestion that postural instability is at the root of changes in the strength of hand preference in simple reach and, while climbing postures appear to have more postural demands than sitting or quadrupedal, it offers good stability and balance for chimpanzees. Given the low frequency in which climbing simple reach was observed in this study, further studies investigating the effect of climbing posture are needed to gain a clearer picture. Future research comparing climbing with bipedal postures might shed more light on the demands of both postures and how they impact hand preference.

These findings also highlight the need to carefully consider not only the task, but also the time-frame that studies use to collect hand preference, in particular when studying the association between hand preference and other aspects of behaviour. In recent years, new areas of research have begun investigating links between hand preference and general patterns of behaviour that are known to be stable over time (Gordon and Rogers, 2010, 2015; Rogers, 2009). The findings of the current study, along with previous findings by Padrell et al. (2019), suggest that it is important to carefully consider the stability over time of hand preference in these cases and/or to undertake data collection for hand preference and other behaviours during the same period of observation.

However interesting the current findings are, there are some limitations in the present study that require careful consideration. This study did not account for grip morphology, which is known to play an important role in hand use and hand preference, as right-handed chimpanzees tend to use precise grips more often, using their index finger and thumb (Hopkins et al., 2002; Meguerditchian et al., 2015). However, Llorente et al. (2009) failed to find a difference in hand preference between grip types and, following those findings, subsequent studies investigating simple reach with their chimpanzees do not consider grip types (Padrell et al., 2019). Nonetheless, it would be valuable to investigate grip morphology in future research conducted with the chimpanzee group at Chester Zoo since, to our knowledge, no data has been published on it to date.

5. Conclusion

This study assessed hand use in chimpanzees in simple reach and fishing behaviours, contributing to previous research by expanding the investigation of between-task consistency and temporal stability, as well as examining the effects of posture. The lack of an effect of posture on the strength of hand preference indicates that postural stability, rather than posture complexity, might mediate the manifestation of hand

preference, as climbing postures, while requiring more complex coordination, are likely more stable than bipedal postures investigated in previous research (Bailoo et al., 2019; Braccini et al., 2010; Hopkins, 1993). Another important finding of the study shows that, while results support previous findings showing that hand preference correlates between time periods (Hopkins et al., 2001; Padrell et al., 2019), some individuals show changes in their preferred hand, pointing towards the need to carefully consider individual scores when studying hand preference from a longitudinal approach.

Author contributions

SD, LM and SR conceived the study. SD collected and analysed the data and wrote the manuscript. LM and SR contributed to the design of the methodology. LM, SR and PR provided editorial advice. This research received no funding.

Declaration of Competing Interest

Authors declare no conflict of interest.

Acknowledgments

We would like to thank the research team and the primate keepers at Chester Zoo for all their assistance with this research. We would also like to thank the editor and two anonymous reviewers for their feedback and insight on the manuscript.

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