Research

The neural and cognitive correlates of aimed throwing in chimpanzees: a magnetic resonance image and behavioural study on a unique form of social tool use

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It has been hypothesized that neurological adaptations associated with evolutionary selection for throwing may have served as a precursor for the emergence of language and speech in early hominins. Although there are reports of individual differences in aimed throwing in wild and captive apes, to date there has not been a single study that has examined the potential neuroanatomical correlates of this very unique tool-use behaviour in non-human primates. In this study, we examined whether differences in the ratio of white (WM) to grey matter (GM) were evident in the homologue to Broca’s area as well as the motor-hand area of the precentral gyrus (termed the KNOB) in chimpanzees that reliably throw compared with those that do not. We found that the proportion of WM in Broca’s homologue and the KNOB was significantly higher in subjects that reliably throw compared with those that do not. We further found that asymmetries in WM within both brain regions were larger in the hemisphere contralateral to the chimpanzee’s preferred throwing hand. We also found that chimpanzees that reliably throw show significantly better communication abilities than chimpanzees that do not. These results suggest that chimpanzees that have learned to throw have developed greater cortical connectivity between primary motor cortex and the Broca’s area homologue. It is suggested that during hominin evolution, after the split between the lines leading to chimpanzees and humans, there was intense selection on increased motor skills associated with throwing and that this potentially formed the foundation for left hemisphere specialization associated with language and speech found in modern humans.

Keywords: throwing; Broca’s area; chimpanzees

1. INTRODUCTION

Visitors to the zoo are sometimes treated to the sight of chimpanzees throwing objects (often faeces or wet chow) at each other or at them. What most zoo visitors do not appreciate is the rarity with which throwing occurs in non-human animals. Save for a few unsystematic and anecdotal reports of throwing in monkeys and great apes [1–9], there is little evidence that throwing occurs in other animals [10]. Thus, throwing appears to have come under positive selection pressure in hominins. From an evolutionary standpoint, some have suggested that throwing may have offered many advantages to early hominins such as the ability to kill larger prey without putting oneself at risk of being wounded or killed [11]. The ability to kill large game for the purposes of nutrition while simultaneously minimizing one’s personal risk of injury or death (i.e. increased survival) would have been selectively advantageous [12]. Among non-human primates, throwing has most frequently been observed in wild and captive chimpanzees, though there are reports in other great ape species [1,5,6,8] and, to a lesser extent, in monkeys [13–15]. Throwing has been described as a form of tool use in chimpanzees at a number of long-term field sites in Africa, including Gombe, Mahale, Bossou and the Tai forest [16–19]. In the wild and in captivity, throwing has mostly been recorded in the context of both inter- and intraspecies agonistic encounters, although some have described it as a means of initiating play or communication [20–22].

From a psychological and neurological standpoint, aimed throwing is very interesting for several reasons. First, it has been hypothesized that some instances of aimed throwing by chimpanzees reflect foresight or future planning on the part of the apes, an ability often described as uniquely human [23]. For instance, Osvath [7] eloquently describes a zoo-living male

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One contribution of 12 to a Theme Issue ‘From action to language: comparative perspectives on primate tool use, gesture, and the evolution of human language’. 

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Chimpanzee (named Santino) that hides rocks out of sight of the care staff, waiting to reveal and throw them at approaching visitors at the most opportune time. Evidence of planning comes from the observation that Santino searches for the rocks from a moat inside the enclosure prior to the arrival of the care staff and visitors, and caches the rocks out of sight, only to pull them out when the visitors arrive. We have made similar observations of this type of the so-called planning behaviour in the chimpanzees housed at the Yerkes National Primate Research Centre (YNPRC) and the University of Texas M. D. Anderson Cancer Centre [4]. Some of the chimpanzees will pile faeces or wet chow in their cage and wait for visitors to pass by before throwing this at them. We would further argue that aimed throwing in the YNPRC chimpanzees, though often agonistic in function and consequence, is not part of the apes’ display behaviour. Indeed, most instances of aimed throwing that we have observed occur without any accompanying display behaviours such as pilo-erection, hooting or charging, further suggesting an element of planning on the part of the individual ape.

Throwing, as a form of social tool use, is also unique because it likely develops in captive chimpanzees (and possibly wild apes) by way of very different processes and reinforcement contingencies compared with other forms of tool use, notably those described for the purposes of food extraction. For instance, nut-cracking, termite-fishing and ant-dipping are by far the most common forms of tool use observed in wild chimpanzees and each of these is used for the purposes of obtaining otherwise unattainable food. Thus, in purely operant conditioning terms, the subjects learn to use these types of tools and maintain their use because they have been reinforced with food for successful use. Presumably, food is positively reinforcing and therefore increases the probability of subsequent occurrence of tool-use behaviour (though we would acknowledge that some forms of tool use may be maintained without explicit reinforcement).

In contrast, the rewards associated with throwing are quite different because they are not nutritive in form. Throwing in wild chimpanzees is seldom, if ever, observed for the purposes of obtaining food, but rather is almost always directed towards other chimpanzees or humans. In captivity, it is difficult to imagine that human caretakers would overtly reward a chimpanzee with food immediately after they had just been soiled with faeces by the same ape. In short, what appears to be the main reward for throwing is the simple ability to control or manipulate the behaviour of the targeted individual (ape or human). For example, in our laboratory, chimpanzees will patiently wait for strangers or visitors to approach and then will throw at them. They do not conceal their intentions and they will often stand bipedal and threaten to throw by cocking their arm with the projectile in their hand in preparation for throwing (figure 1). The passers-by can see this and will often try and negotiate with the chimpanzees to put down the projectile, or they will try to trick the ape by stopping, then dashing rapidly past the ape enclosure. This seems to be the reaction the apes hope to get from the humans and, in operant conditioning terms, is the only ‘reward’ the chimpanzees receive for throwing.

Neurologically, throwing is complex because it demands coordinated precision in timing the velocity and release window of a projectile in relation to the speed of movement and distance of the target (i.e. prey). Some have suggested that the increased selection for neural synchrony of rapid muscular sequencing routines associated with actions such as throwing are similar to the motor programming demands of language and speech, and therefore engage similar neural systems, notably Broca’s area [24]. Moreover, because the left hemisphere is dominant for language, some have argued that the foundations for left hemisphere lateralization in language may have evolved from an initial preadaptation for right-handedness in throwing [11]. In Western cultures, a significant majority of individuals self-report preferring the right-hand for throwing [25], and studies in non-traditional societies have reported right-hand biases in throwing actions, such as in the use of spears [26]. Two previous studies have reported that captive chimpanzees show population-level right-handedness for throwing, which suggests left hemisphere dominance [4]. Hopkins et al. [4] have also found that posture influences handedness for throwing. Within the subsample of 89 chimpanzees that were observed to reliably throw by Hopkins et al. [4], 90 per cent of right-handed individuals preferred to throw overhead compared with underhand. A majority of the overhead throws were made when the chimpanzees were standing bipedally. In contrast, a significant majority of the left-handed individuals threw underhand.

Figure 1. Four sequential frames demonstrating a chimpanzee throwing a polyvinylchloride (PVC) pipe towards a human in a tower above the subject. The chimpanzee stands bipedally, brings the PVC pipe back and then throws the object. Note that the force of the chimpanzees’ throw causes him to leave the ground. This reflects the whole body function of throwing in some of the chimpanzees.
when they were in a quadrupedal posture. Thus, handedness was strongly linked to the posture and style of throwing adopted by the apes. Despite the long-standing theoretical interest in throwing in relation to brain evolution, few studies to date have examined the potential neural correlates of throwing in non-human primates, notably chimpanzees [27]. In a previous study, Cantalupo & Hopkins [27] found that chimpanzees that had learned to throw reliably had significantly larger cerebella than those that had not. Throwing offers a unique opportunity to consider cortical plasticity in chimpanzees because, as noted already, there are considerable individual differences in terms of its occurrence and lateralization.

One aim of this study was to examine whether variation in either grey matter (GM) or white matter (WM) within premotor and primary motor cortex was associated with the occurrence and lateralization of throwing in captive chimpanzees. Specifically, magnetic resonance image (MRI) scans were obtained in 76 chimpanzees and the proportions of WM to GM in the left and right hemispheres were computed for two cortical motor regions, including the motor-hand area of the precentral gyrus (termed the KNOB) and the inferior frontal gyrus (IFG). The KNOB was selected as a region of interest because it is the anatomical region of the precentral gyrus where the hand is represented, and studies in humans and chimpanzees have shown that asymmetries in this brain area are associated with hand preference [28–30]. Additionally, we measured the IFG because it is the homologue to Broca’s area in the human brain [31,32] and previous studies in humans and chimpanzees have shown that variation in asymmetries in this region are associated with hand use for tool use [33–35]. If handedness for throwing is associated with asymmetries in these two motor regions, then we hypothesized that right-handed throwers would show leftward asymmetries while left-handed throwers would show rightward asymmetries. We further hypothesized that if learning to throw promotes the development of connections between cortical regions, then chimpanzees that reliably throw would show increased WM within the IFG and KNOB regions compared with individuals that have not learned to throw. We were particularly interested in WM because recent diffusion tensor imaging (DTI) studies have shown that training experiences can have a significant effect on cortical connectivity. For instance, Scholz et al. [36] measured WM connectivity in a sample of naive human participants and subsequently had them learn how to juggle. Post-training DTI imaging revealed increased cortical WM in several brain regions, but notably in regions underlying the intraparietal sulcus. More germane to this study, Quallo et al. [37] imaged three monkeys before and after training them on a tool-use task. Using voxel-based morphometry, significant increases in GM were found in several regions, including the intraparietal and superior temporal sulci. Furthermore, increased levels of WM were found bilaterally in the cerebellum—a brain structure that is critically involved in motor learning and coordination—after learning the tool-use task.

A second aim of this study was to test whether chimpanzees that have learned to throw are socially more sophisticated or intelligent than those that have not. As noted above, we and others have noted that chimpanzees that throw exhibit a considerable degree of planning in their actions and seem to know that they can use their throwing actions to manipulate or change the behaviours of other social beings, notably naive human observers. This suggests that these apes are more sensitive to how their actions influence the behaviours of others. Leavens et al. [38] argued that most ape gestural communication observed in captive individuals’ functions in a similar manner. That is, when apes point to otherwise unattainable foods in the presence of humans, they are instrumentally controlling or manipulating the human to get the food for them, or in essence the human becomes the tool. For this reason, we hypothesized that apes that throw might be more socially or communicatively sophisticated than those that have not learned to throw. We tested this hypothesis by comparing the chimpanzees that reliably throw to non-throwers on a series of cognitive tasks that quantify physical and social cognition in apes. Specifically, Herrmann et al. [39] have described a series of tasks, referred to as the primate cognition test battery (PCTB), which allegedly measures the abilities of human children and non-human primates to use social and physical cues to solve different types of learning problems. Broadly, the tasks assess communication abilities, comprehension of causality, spatial cognition and memory, quantity discrimination and theory of mind. We have recently tested more than 90 chimpanzees on these tasks [40] and, in this study, we compared the performance of throwing and non-throwing apes to examine whether performance differences were evident in these groups.

2. METHODS
(a) Subjects
Magnetic resonance images were obtained from a sample of 78 chimpanzees, including 24 males and 54 females. The subjects ranged in age from 6 to 51 years (mean = 23.05, s.d. = 11.80). All the chimpanzees were members of a captive colony housed at YNPRC in Atlanta, GA, USA. Within the sample, there were 38 chimpanzees that reliably threw, and these individuals were matched on the basis of sex, age and scanning protocol with 38 chimpanzees that did not reliably throw. This was done to control for these potential confounding variables within the sample.

(b) Image collection and procedure
For the in vivo scanning, subjects were first immobilized by ketamine injection (10 mg kg$^{-1}$) and subsequently anaesthetized with propofol (40–60 mg (kg h$^{-1}$)$^{-1}$) following standard procedures at the YNPRC. Subjects were then transported to the MRI facility. The subjects remained anaesthetized for the duration of the scans as well as the time needed to transport them between their home cage and the imaging facility (total time approximately 2 h). Subjects were placed in the scanner chamber in a supine position with their head fitted inside the human-head coil. Scan duration ranged between 40 and 60 min as a function of brain size.
A portion of the subjects were scanned using a 1.5 T scanner (Phillips, Model 51), while the remaining chimpanzees were scanned using a 3 T scanner (Siemens Trio, Siemens Medical Solutions USA, Inc., Malvern, Pennsylvania, USA) at the YNPRC.

For all chimpanzees scanned in vivo using the 1.5 T machine, T1-weighted images were collected in the transverse plane using a gradient echo protocol (pulse repetition = 19 ms, echo time = 8.5 ms, number of signals averaged = 8, and a $256 \times 256$ matrix). For the chimpanzees scanned using the 3 T scanner, T1-weighted images were collected using a three-dimensional gradient echo sequence (pulse repetition = 2300 ms, echo time = 4.4 ms, number of signals averaged = 3, matrix size = $320 \times 320$).

After completing MRI procedures, the subjects scanned in vivo were returned to the YNPRC and temporarily housed in a single cage for 6–12 h to allow the effects of the anaesthesia to wear off, after which they were returned to their social group. The archived MRI data were transferred to a PC running Analyze 7 (Mayo Clinic, Mayo Foundation, Rochester, MN, USA) software for post-image processing. Prior to data collection, two raters blind to the hemisphere and handedness of the chimpanzees independently measured the IFG and KNOB in 10 specimens. Inter-rater correlations between the two tracings were positive and significant for both regions [30,41]. Prior to measurement, the raw T1-weighted MRI scans were aligned in the axial, coronal and sagittal planes along the AC-PC line.

(i) Inferior frontal gyrus
The IFG was quantified separately for the left and right hemispheres in the axial (transverse) plane following procedures that have been described elsewhere [41] (figure 2a). The most dorsal point of the IFG slice was defined as the slice on which both the precentral inferior (PCI) and fronto-orbital (FO) sulci could be seen. Using a freehand tool, PCI was traced to the lateral portion of the brain and was followed until meeting FO. FO was then traced to its most medial point and the most medial points of FO and PCI were then connected with a straight line to create an estimate of the area of the gyrus between these two sulci for each slice. Both sulci had to be present to be considered a traceable slice. Successive 1 mm slices were traced using these landmarks until either FO or PCI were no longer visible. The areas within the traced regions were subsequently summed to derive volumes of the IFG for each hemisphere. These IFG object maps for the right and left hemispheres were saved for each individual subject and subsequent application to the segmented volumes.

(ii) Motor-hand area or KNOB
As with the IFG, the KNOB was quantified separately for the left and right hemispheres in the axial (transverse) plane (figure 2b) following procedures previously used in human and chimpanzee brain specimens [29,42]. The dorsal and ventral edges of the KNOB along the central sulcus (CS) served as markers for defining the boundaries of the area. The area of the entire KNOB was traced on each slice and hemisphere using a mouse-driven pointer (figure 2b). The areas within the traced regions were subsequently summed to derive volumes of the KNOB for each hemisphere. These KNOB tracings for the right and left hemispheres were saved for each individual subject.

(c) Image segmentation and region of interest measurements
The aligned T1-weighted MRI scans were skull-stripped and subsequently segmented into GM, WM and cerebral spinal fluid (CSF) tissue using FSL (Analysis Group, FMRIB, Oxford, UK) [43] (figure 2a,b). Because the segmented volumes were in the same stereotaxic space as the T1-weighted scans on which the object maps for the IFG and KNOB were drawn, the object maps were then applied to the segmented GM and WM, and the number of voxels that fell inside the object maps were calculated for each region, subject and hemisphere. We then divided the number of voxels by the total size of the object maps and multiplied by 100 to compute the percentage of GM or WM within each region and hemisphere. To simplify the analyses, we calculated WM-to-GM ratios for each hemisphere and region by dividing the WM percentage by the GM percentage (WM-GM ratio). Thus, the left and right hemisphere WM percentages for the KNOB and IFG were divided by the left and right GM percentages. We then computed average WM-to-GM ratios for the KNOB (WMGM_KNOB) and IFG (WMGM_IFG) by adding the values for the left and right hemispheres and dividing by two. We also computed asymmetry quotients (AQ) for the KNOB_AQ and IFG_AQ by using the formula $AQ = (R - L)/(R + L) \times 0.5$, where $R$ and $L$ reflect the WM-to-GM ratios for the right and left hemispheres. Positive AQ values reflected right hemisphere excess volume.
asymmetries, while negative values indicated left hemisphere biases.

**d) Primate cognition test battery**

(i) **Procedures**

Subjects were tested on a modified version of the PCTB originally described by Herrmann et al. [39]. The PCTB attempts to assess subjects’ abilities in various areas of physical and social cognition. For our study, some aspects of the original PCTB were eliminated owing to time and housing constraints. The previously published procedures were followed as closely as possible but some tasks were modified to better address the questions at hand, given the past experience and environmental constraints of our subjects. Each task is described briefly below with notes made when procedures were altered from those described by Herrmann et al. [39]. Subjects were generally tested in the order that the tasks are presented below and testing was completed over three to five testing sessions, depending on the motivation and attention of the subject. Most subjects were tested alone; however, some individuals are uncomfortable being separated from their group. These individuals were tested with one other conspecific with whom they were comfortable. All testing was done in the subject’s home enclosure.

(e) **Physical cognition tasks**

Eight tasks were used in the ‘Physical Cognition’ portion of our test, including tasks exploring the apes’ spatial memory and understanding of spatial relationships, ability to differentiate between quantities, understanding of causality in the visual and auditory domains and their understanding of tools. Our test differed from the original PCTB in several ways. We excluded the Addition task as well as certain components of the Tool Properties tasks.

(i) **Spatial memory (three trials)**

This test assessed subjects’ ability to remember the locations of food rewards. In this subject, the subject watched as food was hidden in two of three possible locations (opaque cups turned upside down) on a test table in front of them. The subject was then allowed to search the locations one by one. If the subject located one of two hidden food rewards, they were given the reward and allowed to search for the second hidden reward. Subjects that located both hidden food items without searching the un baited location were scored as successful. Each subject received all three possible combinations of baited locations.

(ii) **Object permanence (nine trials)**

Here, we tested an individual’s ability to follow a food reward after invisible displacement, given three different possible displacements. During single displacement trials, only one of three possible locations was manipulated and thus potentially baited. In the double displacement trials, two of three possible locations were manipulated, meaning that either location could potentially be baited. Double displacement trials were further divided by whether or not the baited locations were adjacent to one another. In order to be considered successful, the subject must locate the hidden food item without searching in the location that was not manipulated.

(iii) **Rotation (nine trials)**

In the third task, subjects’ ability to track a food reward as it is spatially rotated either 180° or 360° was examined. In this task, subjects watched as a food reward was hidden in one of the three locations (opaque cups turned upside down) lined up on a platform. The platform was then rotated on a horizontal plane, with the three locations being rotated as a unit. Three different manipulations were employed. In 180° middle trials, the middle location was baited and the platform was turned 180°. In 360° side and 180° side trials, either the left or right location was baited, and the platform was then rotated 360° or 180°, respectively. Subjects successfully completed a Rotation trial by tracking and identifying the correct location of the hidden reward.

(iv) **Transposition (nine trials)**

In this task, subjects watch as a food reward is hidden in one of three possible locations and then as the baited location is changed in one of the three ways. In one condition, the baited location is switched with one of the un baited locations. In the second condition, the baited location is switched with one of the unbaited locations and then the two unbaited locations are switched. In the last condition, the baited location is switched with one of the unbaited locations and then with the other unbaited location. Subjects received three trials of each condition. To be considered successful on this task, the subject must track the reward and choose the baited location.

(v) **Relative numbers (13 trials)**

In the fifth task, subjects were tested for their ability to discriminate between different quantities by being presented with two plates containing different amounts of equally sized food pieces. Each subject received the same set of 13 different quantity pairings as those used in the original PCTB (1 : 0, 5 : 1, 6 : 3, 6 : 2, 6 : 4, 4 : 3, 3 : 2, 2 : 1, 4 : 1, 4 : 2, 5 : 2, 3 : 1 and 5 : 3). During each trial, the subject was allowed to choose only one plate and received whatever reward was on the chosen plate. A correct response was recorded when the subject chose the plate containing the larger quantity of food. We did not include the task by Herrmann et al. [39] referred to as Addition Numbers.

(vi) **Causality noise (six trials)**

In the sixth task, subjects’ understanding of causal relationships based on sound was assessed. In this task, the experimenter placed a hard food reward (i.e. peanut) in one of the two metal containers such that the container with the food reward made a sound when shaken, while the un baited container did not. In ‘Full’ trials, the metal container containing the food reward was lifted and shaken and then the un baited container was lifted. In the ‘Empty’ trials, the empty container was lifted and shaken and then
the baited container was lifted. Subjects were then allowed to choose one of the two containers. A correct choice was recorded when the subject chose the baited container.

(vii) Causality visual (six trials)
In the seventh task, subjects were tested for their causal understanding of the physical world in the visual domain. Specifically, in one trial type, a food reward was placed underneath one of two boards lying flat on the testing table. The food caused the baited board to be tilted, while the unbaited board remained flat. In the second trial type, a food reward was placed underneath one of two pieces of cloth laying flat on the testing table. The reward created a visible bump in the baited cloth, while the unbaited cloth lay flat. Subjects received three trials with both the board and cloth. In both trial types, the subject had to choose the baited item to be considered successful.

(viii) Tool properties (six trials)
The last Physical Cognition task explored the apes’ understanding of the physical properties of tools and how those relate to achieving a goal. In each task, the subject is presented with a choice between two similar tools. However, one tool can be used to obtain a food reward, while the other tool is ineffective. For the first task, subjects are presented with two identical pieces of paper. One piece of paper has a food reward sitting on top of the far end, while the second piece of paper has a food reward sitting beside it. The subject could pull either piece of paper into their cage, but only by pulling the paper with the food sitting on top of it would they be able to retrieve the food reward. In the second task, one tool was identical to the effective tool in the first task. The second tool consisted of two smaller pieces of paper with a small gap between them, visually emphasizing that they are disconnected. The food reward is placed on the out-of-reach piece of the two disconnected pieces of paper. The subject could pull in the reward using the effective tool, but pulling the piece of the disconnected paper is ineffective in obtaining the reward. Each subject received three trials for each tool property task. Note that we did not include three tool properties tasks from the original PCTB, ‘Bridge’, ‘Broken Wool’ and ‘Tray Circle’ [39].

(f) Social cognition tasks
The tasks designated as ‘Social Cognition’ in the PCTB that we used are fourfold. The first two are designed to test the apes’ ability to understand and to produce communicative signals. The third set of tasks assesses their sensitivity to the attentional state of an experimenter and their ability to use appropriate communicative modalities based on this information. The last social cognition task is designed to assess rudimentary aspects of Theory of Mind by testing their ability to follow gaze. Owing to housing and time constraints, we excluded the Social Learning tasks done in the original PCTB and made some modifications to several of the other Social Cognition tasks noted as follows.

(i) Comprehension (six trials)
For the first task, we chose a slightly different strategy from that of Herrmann et al. [39] to assess the apes’ abilities to comprehend communicative signals. The original task implemented the same table-and-cup set-up as used in many of the other physical cognition tasks. However, in our task, a target was placed on the left and right sides of the enclosure, while the subject was centred. The experimenter then used either gaze (three trials) or gaze combined with a manual point (three trials) to direct the subject to one of the two targets. The subject had to move to and touch the designated target to be considered successful on this task. Note that we did not include the ‘Mark’ condition conducted by Herrmann et al. [39].

(ii) Production (four trials)
For the second task, following the established PCTB methods, the apes’ ability to produce communicative signals to indicate a hidden food item was tested in four trials [39]. In this task, the ape watched as an experimenter baited a location on either the left or right side of the enclosure. A second experimenter then approached the cage, centred the subject and waited for the subject to indicate which location contained the hidden food. The subject was given 60 s to indicate the correct location using an overt communicative signal, such as a manual gesture towards the hidden food.

(iii) Attentional state (eight trials)
In the third task, we followed the methods outlined by Herrmann et al. [39] but added an additional test. First, an experimenter placed a piece of food on the ground outside of the subject’s enclosure. Then a second experimenter approached the cage and altered their attentional state in one of four ways. In the first trial, the experimenter’s face and body were directed towards the food item and the subject. In the second trial, the experimenter’s body faced the subject, but her face was turned away. In the third trial, the experimenter stood with her body facing away from the enclosure, but then turned her head to look at the subject. In the last trial, the experimenter’s body and face were oriented away from the subject. In order to be successful, the subject had to use a communicative signal in the modality appropriate to the experimenter’s attentional state. For example, if the experimenter was looking at the subject, he/she could use a visual signal, such as a manual gesture to indicate the food. However, if the experimenter was facing away from the subject, the subject had to first use an auditory or tactile signal, such as a cage bang or a spit to get the attention of the experimenter and then once the experimenter was looking at him/her, use a visual signal to indicate the food. To further explore this topic, we added an additional set of four trials using the same basic conditions. However, the trials were conducted in a more familiar setting with the experimenter sitting at the testing table, placing a piece of food on the table and then carrying out the four variations of attentional state. The same requirements regarding modality-specific communication.

Phil. Trans. R. Soc. B (2012)
were required for the subject to be considered successful on any given trial.

(iv) Gaze following (three trials)
For the last social cognition test, we examined each ape’s ability to follow gaze in three trials. In this task, an experimenter sat on a stool approximately 1 m from the subject’s enclosure. The experimenter captured the subject’s attention and centred him/her by offering a piece of food. The experimenter then shifted her head and eyes to gaze at a point directly above her head for a period of 10 s. In order to be successful, the subject had to follow the gaze of the experimenter by looking upward. Note that we did not test our subjects on two of the gaze following tasks, ‘Back’ and ‘Eyes’, used in the original PCTB [39].

(v) Data analysis
The mean proportion of correct trials was calculated for each of the 12 tasks. From these data, we computed average performance scores for the five basic cognitive dimensions originally described by Hermann et al., which include COMMUNICATION (Comprehension, Production and Attentional State), CAUSALITY (Visual Causality, Tool Properties and Noise), SPACE (Spatial Memory, Object Permanence, Rotation and Transposition), QUANTITY (Relative Numbers) and THEORY OF MIND (Gaze Alternation).

3. RESULTS
(a) Neuroanatomical correlates
In our initial analyses, we compared the proportion of WM to GM within the IFG and KNOB between males and females. These analyses were compared on both the WMGM_KNOB and WMGM_IFG and KNOB_AQ and IFG_AQ values. For both analyses, no significant main effects or interactions were found. Thus, male and female chimpanzees did not differ in the proportion of WM to GM nor in lateralization for the IFG and KNOB.

We next considered the influence of throwing on the proportion of WM to GM within the KNOB and IFG. For this analysis, we performed a mixed model analysis of variance (ANOVA) with region (WMGM_IFG, WMGM_KNOB) serving as the within-subject factor, while throwing classification (THROW+, THROW−) was the between-group factor. Significant main effects for region ($F_{1,74} = 41.02, p < 0.001$) and throwing classification were found ($F_{1,74} = 5.6820, p < 0.03$). The proportions of WM found within the region object maps were significantly higher for the KNOB compared with those for IFG. Moreover, for both regions, the proportion of WM was significantly higher in the THROW+ than in the THROW− chimpanzees. The mean WMGM_KNOB and WMGM_IFG in THROW+ and THROW− chimpanzees are shown in figure 3.

(b) Neuroanatomical correlates of laterality in throwing
We next considered whether interhemispheric differences in the ratio of WM to GM were found for left- and right-handed chimpanzees on the basis of their preferred hand for throwing. For this analysis, we performed a mixed model ANOVA with the KNOB_AQ and IFG_AQ values serving as the within-subject factor, while throwing preference (LEFT, RIGHT) was the between-group factor. A significant main effect for throwing hand was found ($F_{1,36} = 5.462, p < 0.03$; figure 4). Right-handed throwers rather than left-handed throwers showed significantly greater leftward asymmetries in the WM-to-GM ratio for the IFG and KNOB.

(c) Cognitive correlates of throwing
As noted earlier, our laboratory has administered the PCTB test to 91 chimpanzees, and within this sample, there were 39 apes that threw consistently (THROW+) and 52 that did not (THROW−). In this next analysis, we compared THROW+ and THROW− individuals in their performance on the PCTB task. To test whether differences in cognitive abilities were evident between the two groups, we conducted a multiple analysis of variance (MANOVA) with the mean PCTB scores serving as dependent measures, while sex and throwing group served as the between-group factors. The MANOVA revealed a significant
main effect for throwing group ($F_{5,86} = 3.642, \ p < 0.001$). Subsequent univariate $F$-tests indicated that the only significant difference between the throwing groups was for COMMUNICATION ($F_{1,87} = 11.388, \ p < 0.001$) with THROW$^+$ apes performing significantly better than the THROW$^-$ individuals (figure 5). No other significant differences were found.

4. DISCUSSION

In terms of the neuroanatomical correlates of throwing, the results reported here indicate that the presence of throwing skills in chimpanzees is correlated with increased cortical connectivity in Broca’s area as well as in the motor-hand area of the precentral gyrus. The principal result in support of this conclusion is the observation that THROW$^+$ apes had significantly higher proportions of WM to GM within the IFG and KNOB regions than THROW$^-$ individuals. Because increased WM indicates more myelinated interneurons that connect different cortical regions, this result would suggest that learning to throw may alter the connectivity between premotor and primary motor cortex in the chimpanzee. The results from comparing right- and left-handed throwers also support this conclusion, because differences in WM are hemisphere-specific and contralateral to the preferred hand that the chimpanzees use for throwing. The association between hand preferences for throwing and asymmetries within the IFG and KNOB are also consistent with previous studies showing that handedness for other forms of tool use, such as simulated termite-fishing and nut-cracking, is linked to lateralization in the cortical language area homologues of chimpanzees [33,44]. It should also be noted that asymmetries in hand use for manual gestures are associated with asymmetries within the IFG [45]. Thus, the results reported here are consistent with the evolutionary hypothesis that throwing may have served as a preadaptation for the neural adaptation of motor programmes necessary for complex motor actions, including language and speech [11].

It should also be noted that hand preferences for throwing are linked to variation in handedness for other measures of tool use and communication, but not non-tool-use measures of manual action. For instance, we have a large sample of hand preference data in chimpanzees for actions such as simple reaching, coordinated bimanual actions, simulated termite-fishing tool use and manual gestures [46–49]. Interestingly, right- ($n = 44$) and left-handed ($n = 37$) throwers differ significantly in their handedness for simulated termite fishing $t_{79} = -2.50, \ p < 0.02$ and manual gestures $t_{79} = -2.59, \ p < 0.02$, but not for simple reaching $t_{79} = -1.20$, n.s. or for coordinated bimanual actions $t_{79} = -0.62$, n.s. (figure 6). Thus, as with the neuroanatomical data, there is an explicit link between throwing, simulated termite fishing and gestural communication in terms of lateralization of function.

We also found that chimpanzees that have learned to throw are better at communication tasks than chimpanzees that have not. Interestingly, these two cohorts of chimpanzees do not differ on cognitive tasks that assess dimensions of physical cognition. These results suggest an explicit association between the cognitive foundations for throwing and the ability to engage in successful interspecies communication, at least as assessed by the PCTB. Leavens et al. [38] have argued that, in captivity, chimpanzees learn to gesture to humans for foods that are otherwise unavailable to them by solving the referential problem space. That is, the chimpanzees want the food, but the food cannot be reached owing to physical barriers preventing the apes from attaining the foods. What the chimpanzees have learned to do with their gestures and other signals, such as attention-getting sounds,
is to manipulate humans to obtain the food for them. Thus, in essence, the human becomes a tool for them. Indeed, we would argue that if a physical tool was available in these contexts, such as a long stick, the chimpanzees would use them to get the food rather than wait for a human caretaker to come by and retrieve the food for them.

Cognitively, we believe that the development and acquisition of throwing skills by chimpanzees operates in a manner similar to the emergence of manual gestural communication. As noted previously, the motivation for throwing in chimpanzees is largely to alter the behaviour of other individuals (be it human visitors or conspecifics). For this reason, the apes that have learned to throw have acquired an ability to understand how their behaviour affects the behaviours of others. If the same individuals apply these basic skills within the context of (i) understanding gestures, (ii) producing gestures, and (iii) using attention-getting behaviours when a human experimenter is inattentive to them, then it would follow that the THROW+ individuals should outperform the THROW− apes on the PCTB test. Moreover, these same skills may not offer any advantage in tasks that are not communicative in function.

We have focused on aimed throwing by chimpanzees in this paper, but some discussion of the prevalence of throwing in other species seems warranted within the context of the underlying cognitive processes that appear to accompany this ability in apes. In particular, capuchin monkeys have been reported to engage in aimed throwing [14] and they have well-documented tool-using abilities both in the wild and in captivity [50–56]. On the basis of our results in chimpanzees, this leads to the suggestion that capuchin monkeys might also engage in some forms of gestural communication during intraspecies interactions; however, this has not been frequently reported in the literature [57]. Thus, the interconnection in social cognitive abilities between throwing and gestural communication may not be well developed in the capuchin monkey. We would also point out that, though the capuchin monkeys in the studies by Westergaard & Suomi [15] did learn to throw, their behaviour was explicitly shaped by the investigators by initially having the subjects throw an object into a bucket containing peanut butter (a preferred food). The peanut-butter-covered object was then handed to the subject and thereby the monkeys were reinforced with food for throwing. Thus, the acquisition of throwing by capuchin monkeys (at least in this study) appears to be mediated by a different type of reward when compared with the chimpanzees we have described in this paper.

There are limitations to the present study that warrant some discussion. First, it could be argued that the associations we found between throwing and WM reflect inherent differences in cortical organization rather than developing as a consequence of learning to throw. In other words, it may be the case that chimpanzees that learn to throw have inherently higher levels of WM within the KNOB and IFG regions and that this enabled them to learn to throw (rather than the increased WM emerging as a consequence of their experience). Similarly, though we found an association between throwing ability and communication skills on the PCTB tasks, it is not clear whether increased communication abilities are a consequence of learning to throw or vice versa. Neither of these alternative explanations can be ruled out based on the findings reported here.

One approach to address this issue would be to identify THROW− apes that differ with respect to WM volumes or asymmetries and then train them to throw. If inherent differences in WM explain the results reported here, then the prediction would be that individuals with larger WM volumes would acquire throwing abilities much faster than individuals with smaller volumes. In terms of communication, a similar approach could be used by performing a pre–post-test of communication abilities in two groups of apes, where one group is taught to throw and the other group is not. If learning to throw enhances communication abilities, then apes taught to throw should perform significantly better on the communication tasks in the post-test compared with apes that are not taught to throw.

Second, we examined the proportion of GM and WM within gyri comprising the regions of interest in this study (IFG and KNOB). This is a relatively crude measure of WM organization. Ideally, studies comparing THROW+ and THROW− apes using more sensitive measures of WM connectivity, such as DTI, would be more informative of the possible changes in cortical connectivity between the IFG and KNOB in these cohorts of apes [58,59].

In summary, we believe that this is the first evidence linking throwing with aspects of cortical organization and asymmetries in non-human primates as well as with differences in communicative abilities. The brain areas distinguishing right- and left-handed throwing chimpanzees show considerable overlap with cortical regions involved in language processing by humans.
Our findings that (i) chimpanzees are predominantly right-handed for throwing [4], and (ii) relative WM volumes within two frontal lobe regions distinguish right- from left-handed throwers suggest that the left hemisphere was specialized for the planning of complex motor actions prior to the split between the lines leading to humans and chimpanzees. Increasing selection for aimed throwing in a context of hunting or predator defence in hominins may have refined the neural architecture of the left hemisphere so as to eventually support other complex motor sequencing actions, including language and speech.

All procedures used with the chimpanzees were approved by the Institutional Animal Care and Use Committee of Emory University. This research was supported in part by NIH grants NS-42867, HD-60563 and HD-56232. The Yerkes Centre is fully accredited by the American Association for Accreditation of Laboratory Animal Care. American Psychological Association guidelines for the ethical treatment of animals were adhered to during all aspects of this study. We are grateful for the helpful assistance of the entire veterinary staff at the Yerkes Centre in collection of the MRI scans.

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Phil. Trans. R. Soc. B (2012)


