Dynamic In-Hand Movements in Adult and Young Juvenile Chimpanzees (*Pan troglodytes*)

Jessica Crast,[1]* Dorothy Fragaszy,[1] Misato Hayashi,[2] and Tetsuro Matsuzawa[2]

[1]*Department of Psychology, University of Georgia, Athens, GA 30602*
[2]*Section of Language and Intelligence, Primate Research Institute, Kyoto University, Inuyama, Aichi 484-0056*

KEY WORDS manual dexterity; in-hand movements; object manipulation

ABSTRACT Descriptions of manual function in nonhuman primates have largely focused on static precision and power grasping (as first defined by Napier, 1956), while identification and description of dynamic manual function are rare and incomplete. Here, we describe several forms of in-hand movements used by chimpanzees (*Pan troglodytes*) when manipulating small objects. In-hand movements are defined as the movement of an object within one hand via manipulation of the digits. We presented adult and young juvenile chimpanzees (ages 5–29 years) with a task that required inserting small objects through correspondingly shaped cutouts in a transparent Plexiglas panel. While attempting to insert the objects through the cutouts, the subjects used at least two forms of in-hand movements to change their grip on the object for more precise alignment. We describe in detail the in-hand movements they used and the variability observed in form and execution among the subjects. In general, the adult subjects used in-hand movements more frequently and used a wider variety of forms than did the young juvenile subjects, suggesting that in-hand movements are in the process of fine-tuning around the age of 5 years in chimpanzees. The dexterity exhibited by the adults, however, shows that the neuromuscular and morphological requirements for relatively complex digital manipulation are present in the adult chimpanzee. Am J Phys Anthropol 000:000–000, 2008. ©2008 Wiley-Liss, Inc.

Enhanced manual function and dexterity have proven to be an important adaptation in the order Primates, speculated to have coevolved with bipedalism, tool-making and use, brain enlargement, and language in humans (Wilson, 1998; Mountcastle, 2005). For all primates, the hand is the primary tool for manipulating and interacting with the environment. Primates achieve the daily tasks of foraging, moving around, and socializing using a variety of grips and hand movements (see Fragaszy, 1998). Several authors provide extensive kinematic and descriptive analyses of dynamic hand movements in humans (e.g., Elliott and Connolly, 1984; Exner, 1992; Santello et al., 1998; Braido and Zhang, 2004); however, such documentation is lacking for nonhuman primates. To understand the origins and evolution of fine motor control and dexterity in object manipulation in human and nonhuman primates, a comprehensive investigation of hand anatomy and function—specifically for movement—in nonhuman primates is necessary.

The present study focused on the dynamic aspect of hand movements in chimpanzees (*Pan troglodytes*). We were interested in the movements of the digits to manipulate an object within one hand: a form of precision handling termed "in-hand movements" (*sensu* Exner, 1992; Elliott and Connolly, 1984). Here, precision handling is equated to sophisticated manual dexterity because it involves the manipulation of an object by the distal pulp surfaces of the digits with the thumb opposed (Landsmeer, 1962), requiring a high degree of digital independence. Precision handling, as defined by Landsmeer (1962), is inherently dynamic and derives from Napier's (1956) original descriptions of the power and precision grip. The power grip is used to grasp and stabilize a large object with the whole hand, whereas the precision grip is used for fine control and accuracy in object manipulation, usually involving smaller objects grasped between the pulp surfaces of the thumb and fingertips (Napier, 1956). In the present study, we defined in-hand movements as a form of precision handling in which an object is moved using the surface of the palm and the digits of one hand. Thus, in-hand movements can be thought of as a less sophisticated form of precision handling, as they require some amount of digital independence to move an object within one hand, but do not require an object to be moved by the distal pulp surfaces of the digits.

Our primary objectives were to verify that chimpanzees are capable of in-hand movements and document any variation in the form of execution among chimpanzees of different ages. To do this, we presented an object manipulation task to adult and young juvenile chimpanzees that involved aligning and inserting objects of various shapes through corresponding cutouts in transparent Plexiglas panels [see a similar "fitting" task in a recent study by Örnkloo and von Hofsten (2007) involving human children]. During pilot testing for this study, two of the subjects in this study were tested on this task

Grant sponsors: East Asia and Pacific Summer Institutes of the National Science Foundation; Grant number: 0513078; JSPS-gCOE (A06, Biodiversity); Grant sponsor: MEXT; Grant number: 16002001.

*Correspondence to: Jessica L. Crast, Department of Psychology, University of Georgia, Athens, GA 30602, USA.
E-mail: crastj@uga.edu

Received 8 December 2007; accepted 15 July 2008

DOI 10.1002/ajpa.20925
Published online in Wiley InterScience (www.interscience.wiley.com).

TABLE 1. Synonymous terminology encompassed by the four grip categories defined by Napier (1956), demonstrating functional equivalence in ape and human grasping

	Power grip	Precision grip	Hook grip	Scissor grip
Studies on great ape grip types				
Byrne and Corp, 2001 *Gorilla g. beringei*	Power-grip, squeeze-grip	Pinch-grip, pencil-grip	Hook, loose-grip	Scissor-grip
Marzke and Wullstein, 1996 *Pan troglodytes*	Cup hold	Tip-to-tip hold, pad-to-tip hold, pad-to-side hold	Transverse hook grip, diagonal hook grip, extended transverse hook grip, extended diagonal hook grip	
Tonooka and Matsuzawa, 1995 *Pan troglodytes*		Radial-palmar grasp, imprecise grasp, pincer grip	Ulnar-palmar grasp[a]	Index and middle, finger grip
Studies on human grip types				
Elliott and Connolly, 1984	Squeeze[b]	Pinch,[b] tripod[b]		
Kamakura et al., 1980	Standard type, index finger extension type, extension type, distal type, hook type	Tip prehension, parallel mild flexion grip, surrounding mild flexion grip		Adduction grip
	Intermediate grips (between power and precision grips): Parallel extension grip, lateral grip, tripod grip, tripod variation 1, tripod variation 2			
Wong and Whishaw, 2004		Proper pincer, improper pincer, supported pincer, triangular grasp, improper triangular grasp, four digit flower grasp, five digit flower grasp		

[a] Ulnar digits 4 and 5 hold raisin to pads of metacarpal-phalangeal joints, digits 2 and 3 concurrently flexed, so hand is effectively in a hook-grip position.
[b] Elliott and Connolly (1984) describe these movements as dynamic if the digits flex and extend simultaneously while holding the object in that grip.

and demonstrated their ability to pass (or attempt to pass) the objects through the cutouts without training and also performed what looked like in-hand movements while attempting to do so. We therefore expected the subjects of the current study to attempt to pass the objects through the cutouts and that difficulty in aligning the objects to the cutouts would encourage the use of in-hand movements as a strategy for changing the grip on an object for better alignment to the cutout.

Along with witnessing what looked like in-hand movements during pilot testing, several lines of reasoning support the hypothesis that chimpanzees are capable of in-hand movements. First, chimpanzees routinely manipulate small objects in the wild and in captivity. Chimpanzees are prolific tool-users, often using small objects such as stones and twigs to forage on hard-shelled foods and foods that are hidden and/or must be removed from an embedding substrate (e.g., termites, fruits). Second, the various grip types used by chimpanzees and other great apes while grasping objects are highly comparable to those used by humans (see Boesch and Boesch, 1993; Christel, 1993; Jones-Engle and Bard, 1996; Marzke and Wullstein, 1996; Tonooka and Matsuzawa, 1996; Byrne and Corp, 2001; Corp and Byrne, 2002). Both human and chimpanzee grip types fall into the four grip categories identified by Napier: the precision and power grips (described above), and the hook and scissor grips.[1] Several classification systems used to describe grip types in great apes (a) and humans (b) are summarized in Table 1.

Third, chimpanzees possess the neural anatomy that is involved with independent movement of the digits. In all primates, the neurons that synapse with hand musculature are part of the corticospinal tract (CST), which is made up of pyramidal neurons that originate in the primary motor cortex and synapse with motoneurons in the spinal cord (Lemon, 1993; Lemon and Griffiths, 2005). The degree of digital independence and manual dexterity of which a species is capable is influenced by the extent to which corticospinal neurons make direct connections with motoneurons extending to the hand in the ventral gray area of the spinal cord (Pehoski, 1992; Bortoff and Strick, 1993; Lemon, 1993; Lemon and Griffiths, 2005) and the length of the CST down the spine (Heffner and Masterson, 1983; Iwaniuk et al., 1999). Compared to other primates, chimpanzees possess a relatively long CST that extends to the coccygeal vertebrae (Heffner and Masterson, 1983) and have a relatively high number of corticospinal terminations in the ventral gray area of the spinal cord, the site of motoneurons that extend to the hand (Lemon and Griffiths, 2005). This highly developed neuroanatomy supports dexterous finger movements in humans, and likely chimpanzees as well.

In addition to similarities in neuroanatomy, chimpanzees and humans share much in gross skeletal and muscular anatomy (Lewis, 1989; Napier, 1993; Behnke, 2001). However, few important differences may constrain the chimpanzee's ability to perform in-hand movements. First, the chimpanzee thumb is relatively short with respect to the length of their fingers. While the saddle

[1] The hook grip involves flexion of the four fingers, as in holding a suitcase, and the scissor grip involves adduction and abduction of the index and middle fingers (Napier, 1956, 1960, 1993; Napier and Napier, 1985).

joint at the metacarpal joint of the thumb (at the junction of the thumb and wrist) allows the thumb to oppose the other digits (Napier and Napier, 1985), the extent of pad-to-pad surface area contact with the other digits is limited by the short thumb, possibly hindering the maneuverability of objects (Marzke, 1997). In addition, the skeletal morphology of the carpals and metacarpals (wrist and palm bones) severely hinders the chimpanzee's ability to cup the palm (Marzke, 1983; Wilson, 1998). In humans, cupping of the palm likely contributes to precision handling by assisting thumb opposition to the digits, allowing the thumb to achieve pad-to-pad contact with ulnar digits. Second, the amount of force the chimpanzee thumb can apply in a precision grip is less than that of humans due to the lower amount of potential torque the chimpanzee thumb can exert (Marzke, 1997; Marzke et al., 1999). These and other differences in thumb musculature (see Marzke, 1971, 1997; Marzke et al., 1999; Shrewbury et al., 2003) are likely responsible for the chimpanzee's difficulty with manipulating objects within the fingertips (i.e., precision handling; Landsmeer, 1962). Therefore, while overall similarities in neural, skeletal, and muscular anatomy indicate that chimpanzees are capable of in-hand movements, the form of execution is probably very different from that of humans.

One of our principal aims is to make a preliminary investigation into the developmental trajectory of in-hand movements in chimpanzees. Research on the development of manual dexterity in humans has shown that children master some forms of in-hand movements by the age of 3 years (Exner, 1992), and may be capable of simple forms of in-hand movements as early as 1 year (Manoel and Connolly, 1998). Manual skill appears to increase with age, particularly during the second to third (Exner, 1992; Manoel and Connolly, 1998) and fourth years (Pehoski et al., 1997); and children can perform all types of in-hand movements exemplified by adults, though less proficiently, by around 7 (Exner, 1992) to 8 (Manoel and Connolly, 1998) years of age.

This developmental trend appears to be similar in chimpanzees and mountain gorillas, providing a fourth line of reasoning for our expectation of in-hand movements in chimpanzees. Byrne and Corp (2001) and Corp and Byrne (2002) found that wild chimpanzees and mountain gorillas aged 3–4 years and older manipulated certain plant material within the hand when foraging. Actions included rearranging or changing the shape of the items in the hand by movement of the digits alone (termed "manipulation") and combining actions by performing more than one task simultaneously in the same hand for accumulation and increased feeding efficiency (termed "combining" and "unimanual multitasking") (Byrne and Corp, 2001; Corp and Byrne, 2002). Corp and Byrne (2002) showed that the chimpanzees' skill at "unimanual multitasking" was significantly and positively correlated with age, but only until around 6 to 7 years of age.

We therefore expected adult chimpanzees' use of in-hand movements to be more advanced than the young juveniles. The young juveniles were 5 years old by the end of the study, an age during which in-hand movements might have been in the process of fine-tuning. Specifically, we predicted that adult chimpanzees would perform a variety of in-hand movement types to be classified, and that, given the differences between humans and chimpanzees in hand skeletal and muscular anatomy, the adults would execute in-hand movements in a form that differs from the documented human form (see Elliott and Connolly, 1984). Finally, we predicted that the young juveniles would perform fewer types of in-hand movements and/or their forms of execution would be less sophisticated than the adult chimpanzees' in terms of digital control.

TABLE 2. Subject details (Matsuzawa, 1996)

Name	Age at end of study (years)	Sex	Mother	Father
Ai	28	Female	–	–
Pan	21	Female	Puchi	Gon
Popo	23	Female	Puchi	Gon
Akira	29	Male	–	–
Ayumu	5	Male	Ai	Akira
Pal	5	Female	Pan	Akira
Cleo	5	Female	Chloé	Reo

METHODS

Subjects

All the chimpanzees who participated in this study are from the Kyoto University Primate Research Institute. The adult participants included Ai, Pan, Popo, and Akira; the young juvenile participants included Ayumu, Pal, and Cleo (Matsuzawa, 1996). See Table 2 for more details on each subject. All subjects live in an enriched indoor-outdoor compound (about 700 m^2) and were cared for according to the guidelines produced by the Primate Research Institute of Kyoto University. The hands of Pan and Pal were measured during a routine physical to give an estimate of adult and juvenile hand sizes. Palm length and width and the length of each digit were measured. The length of the palm plus the length of the longest digit (D3) gave a measure of hand length, while the width of the palm gave a measure of hand width for both adult and juvenile subject (see Fig. 1a).

Two of the adult subjects (Ai and Pan) and each of the three young juveniles in the present study have experience with this task, as they participated in a previous (unpublished) study involving the same task in September 2001. At that time the young juveniles were 14–17 months old and sat with their mothers or played nearby as their mothers participated in the task. They did not attempt to align and insert the objects through the cutouts during these sessions. Ayumu sat with his mother, Ai; Pal sat with her mother, Pan; Cleo's mother did not participate in the present study. All subjects' hands functioned normally and none were missing any digits.

Materials

The subjects inserted one of five three-dimensional objects, approximately 6 cm × 3 cm × 3 cm (circle, square, triangle, star, and cross) through a corresponding cutout in one of five transparent Plexiglas panels (see Fig. 1b,c). The panels were approximately 37 cm × 27 cm, each with one cutout at approximately 13 cm from the sides and 9 cm from the bottom of the panel. The objects fit through the cutouts with approximately 1 mm of clearance, so the subjects had to align the objects with high precision in order to pass the objects through the panel. Trials were videotaped using Sony DCR-HC88 and DCR-TRV900 digital camcorders.

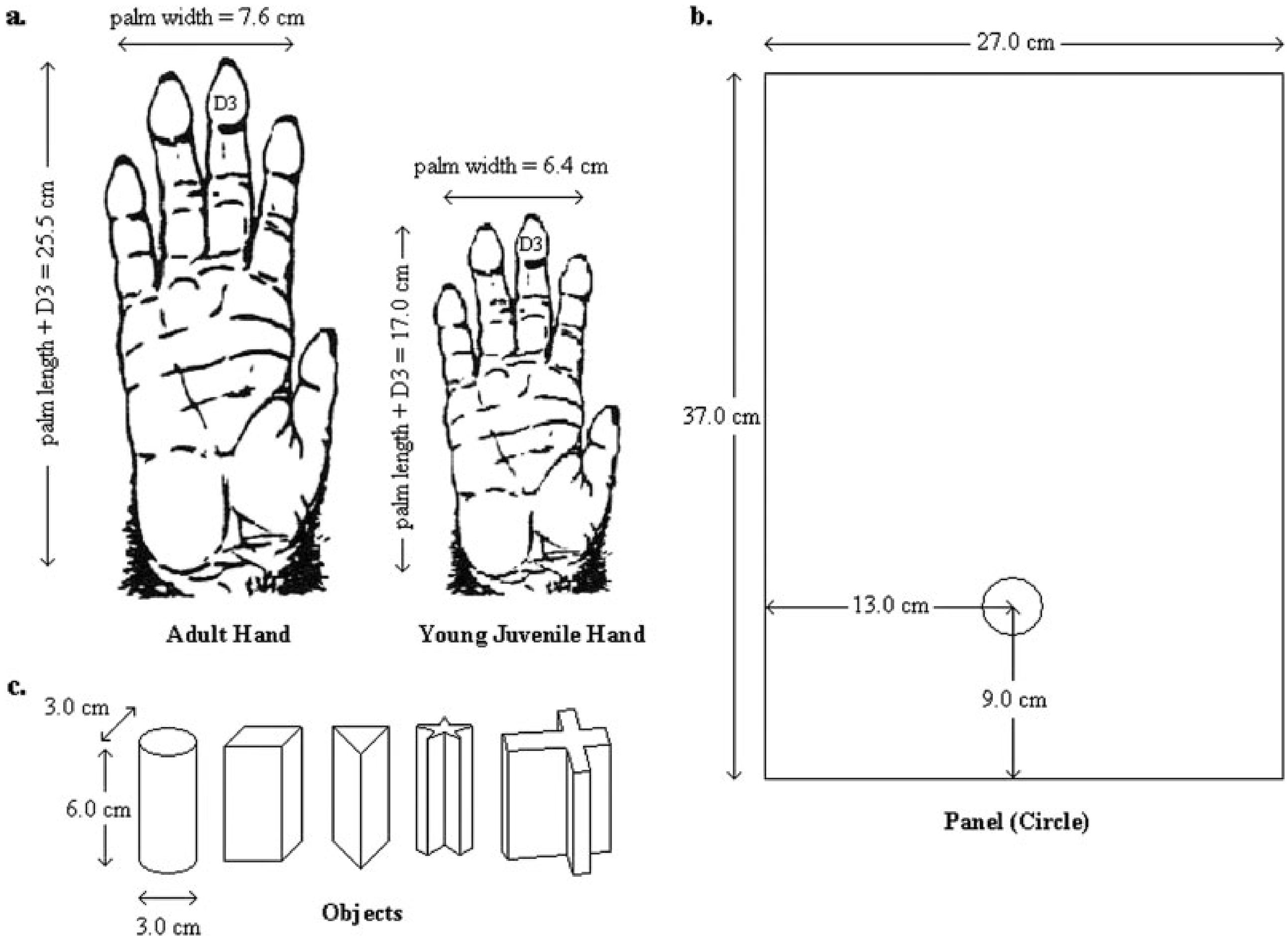


Fig. 1. (**a**) Drawings of the chimpanzee hand with the adult and juvenile hand lengths scaled to the panel size and object sizes (adapted from Schultz, 1969). (**b**) Drawing of the Plexiglas panel used in testing, drawn to scale with (a) and (c) (the circle cutout is shown). (**c**) Drawings of the objects used in testing, drawn to scale with (a) and (b).

Testing situation and procedure

Each subject participated in three testing sessions, each testing session consisting of five blocks trials. A block consisted of three trials with one object type and blocks were administered in the order of circle, square, triangle, star, and asymmetrical cross. During each testing session, the subject sat on the floor across from the human tester inside an enclosed playroom with transparent windows (see Fig. 2). A trial began with the human tester and subject sitting across from one another and the tester placing the panel vertically (cutout nearest the floor) between him or herself and the subject, and the corresponding object placed between the tester and the panel. The tester then began a trial by moving the panel to the other side of the object, indicating to the subject to pick it up. Each subject had a 1-min time limit to align the object to the cutout and pass it through to the tester (beginning when the object was first touched and ending when the object was passed through the cutout or 1 min was reached).

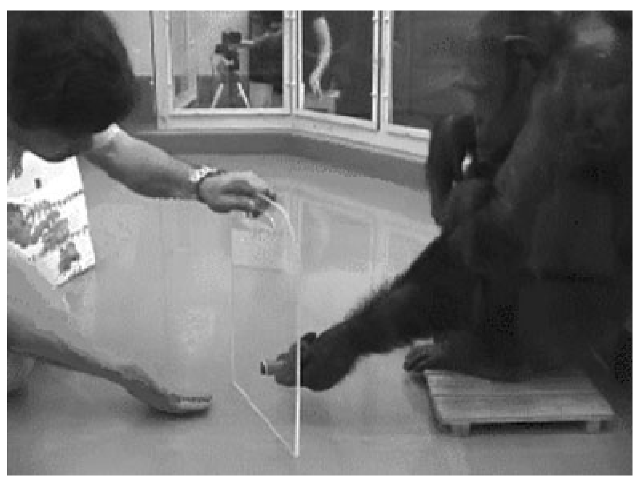


Fig. 2. Testing situation: adult chimpanzee with human tester.

If the subject failed to insert the object within the time limit, the tester requested that the chimpanzee return the object and then began the next trial. For adults, after a failed trial, the panel was turned to a horizontal position on the subsequent trial within the same block, and stayed horizontal if the subject failed a second time within a block. If the next trial was the first trial of the next block, the panel was kept vertical. Turning the panel horizontal allowed the adult subjects to see the cutout more clearly (see Fig. 2) and this procedure was used for a few reasons: first, to make the task a little

TABLE 3. In-hand movement definitions: coded behaviors and synonymous terminology

Category	Type	Subtype	Synonymous terminology (humans)	Synonymous terminology (apes)
Simple movements: a single movement that involves digits moving in opposite directions simultaneously (short duration).	Thumb abduction/ adduction (TAB/TAD): thumb movement alone moves object: Thumb abduction: thumb moves away from midline of hand		Simple movements–reciprocal synergies[a] and shift[b] and simple rotation[b]	
	Thumb adduction: thumb moves toward midline of hand.		Roll–twiddle,[a] rock,[a] radial roll,[a] index roll,[a] and full roll[a]	
	Roll (ROL): object is held between two digits; digits move opposite to one another to twist or roll the object along one axis. *Example*: turning a small screw with the thumb and index.	Thumb push (THP): a type of Roll in which the object is first stabilized or resting in the palm (vs. the distal ends of the digits); digits squeeze inward and thumb extends and abducts, pushing the object out of the palm. *Example*: holding a pen and pushing the cap off with the thumb while squeezing the digits inward toward the palm.	Thumb push–palmar combination[a]	
Complex movements: the digits grasp and regrasp the object using a sequence of grasps and simple movements (longer duration).	Rotation (ROT): the object is turned about one or more axes by a series of grasps and simple movements; object may be grasped and regrasped several times. Rotation ceases when object does not move in the hand for 2 s.	Turnover (TUR): a specific rotation pattern in which the object is picked up with a scissor grip and rolled around the index finger to be grasped between the thumb and index (see Fig. 8). Follows the order: scissor grip, pencil-grip, roll, pinch (with or without support by digits 4 and 5).	Complex movements–sequential patterns[a] and complex rotation[b] Rotation–rotary step,[a] digital step,[a] linear step[a]	Rotation–manipulate[c]

[a] Elliott and Connolly, 1984.
[b] Exner, 1992.
[c] Byrne and Corp, 2001.

easier following a failed trial, and second, to create a slight change in the task to maintain the subjects' motivation to keep working. The turning of the panel was not expected to significantly affect their use of in-hand movements. When a young juvenile subject failed to insert the object within the time limit, the tester did not turn the panel to a horizontal position, but simply moved to the next block of trials. This measure was taken to decrease the young juveniles' discouragement upon failure and maintain interest in the task (the young juvenile subjects tended to be more impatient than adult subjects). If a subject abandoned the task within the first 30 s of a trial, the trial was ended and started over. However, if a subject worked at the task for at least 30 s, the tester continued to encourage participation and the trial was counted. If a subject became too discouraged or refused to participate, the session was cancelled. Subjects were rewarded for their participation regardless of success.

Coding and analysis

Behaviors were coded from video playback using The Observer 5.0, Noldus Corporation. Five types of in-hand movements were coded, including movement of the thumb alone, rolling the object between the thumb and digits, ejecting the object out of the hand (as in pushing off a pen-cap), and rotating the object within the hand (two types). Each in-hand movement consisted of finger manipulations that resulted in a new grasp on the object. The in-hand movement categories were created by observing the subjects' movements and modifying Elliott and Connolly's (1984) system for characterizing in-hand movements in adult humans. We simplified their "reciprocal" and "sequential" movements to "simple movements" and "complex movements," respectively. Table 3 provides definitions of each behavior within each category and shows equivalent terminology used by Elliott and Connolly (1984) and in other studies looking at hand movement in humans and apes.

As each in-hand movement was coded, the digits that were in contact with the object during the movement were coded, as well as any use of the surface of the panel (if any) while performing an in-hand movement. Use of the surface of the panel was termed "surface-assistance," and was defined as bracing an object against a surface such as the cutout, panel, mouth, or floor as a method of assisting an in-hand movement by relieving some of the effects of gravity and allowing the digits to move more freely. The digit combinations that were coded for each in-hand movement included (digits labeled 1-5 beginning with 1 = thumb): 1-2 (e.g., precision grip), 2-3 (e.g., scissor grip), 1-2-3, 1-3, 1-2-3-4, 1-2-3-4-5, 2-3-4, and 2-3-4-5 (the latter two allowing for rotations against the palm).

To identify and define the behavioral categories and coded behaviors, the coder made two passes through the data. In the first pass, trial durations, trial success (passing the object through the cutout within 1 min), in-hand movements, and other strategies for manipulating the object (i.e., bimanual actions—using both hands to manipulate or regrasp the object, and use of the mouth to regrasp or attempt insertion) were recorded.[2] During the first pass, the movement definitions and coding process were refined; the second pass then focused solely on in-hand movements. For the second pass, a subset of the data was chosen in order to standardize the duration of time coded for each subject so that rates (frequency per minute) of each type of in-hand movement could be determined based on a common timeframe. During the first pass, it was noted that the circle object did not elicit many in-hand movements and trial durations were relatively short. Therefore, the trials chosen for the second pass through the data were square, triangle, star, and cross trials. Trials were chosen until the standardized time was reached: approximately 457 s, or 7.6 min (this time based on the subject with the lowest total trial time, which was Ai with 457 s).

From the second pass, we obtained the following measures for each subject: overall rate of in-hand movements, the percent of in-hand movements that were surface-assisted, the percent of each digit combination (listed above), and mean rate of in-hand movements per object type. In addition, for each movement type we found the rates and percent of total in-hand movements for each subject, and the percent surface-assisted and the percent of each digit combination that was used within each movement type for each subject. As the development of in-hand movements was one of our interests *a priori*, we compared each of these measures in adults and young juveniles. We analyzed differences in trial durations and percent success across object types using a one-way analysis of variance (ANOVA). Intrarater reliability was determined by recoding in-hand movements in 15% of the second pass trials (trials were chosen semirandomly so that 15% of the total trial time was recoded) and calculating the mean percent agreement and mean Cohen's Kappa across subjects. The mean percent agreement of in-hand movements across subjects was 97.35% and mean Kappa was 0.95.

[2] In the Results section, we present overall rates (frequency per minute) of bimanual actions and mouth use in this article for subjects who used one of these movement types as their primary strategy for changing their grip on the object (see Other Strategies).

TABLE 4. Occurrence of each movement type and overall rates (frequency per minute) of in-hand movements for each subject

	In-hand movements					
Subjects	TAB/D	ROL	THP	ROT	TUR	Overall rate
Ai	✓	✓		✓	✓	7.65
Pan	✓	✓	✓	✓	✓	6.75
Popo	✓	✓		✓	✓	5.99
Akira	✓	✓			✓	1.84
Ayumu	✓	✓				0.26
Pal	✓	✓				0.52
Cleo	✓	✓		✓		0.65

RESULTS

General patterns

All subjects attempted to insert each object type through the cutouts and used at least one type of in-hand movement (see Table 4). Objects were presented in the order: circle, square, triangle, star, and cross, on the prediction that this order would present a step-wise increase in difficulty as the number of sides and angles increased, and ended with an asymmetric object. While we cannot demonstrate how the subjects experienced "difficulty" during trials, Figures 3 and 4 show that our choice of presentation order was appropriate in that we began with a small challenge (circle), moved to moderate challenges (square, triangle, and star), and ended with a larger challenge (cross). First, Figure 3 shows that mean trial durations increased in this order, with cross trials being significantly higher than all other object types ($F(4,30) = 22.794$, $P < 0.001$) and circle being significantly lower than both star and cross ($F(4,30) = 22.794$, $P = 0.018$). Second, Figure 4 shows that the mean percent of successful trials for both adults and young juveniles was above 85% on each object except cross, which was significantly lower for both adults and juveniles ($F(4,30) = 19.566$, $P < 0.001$). Circle was the only object with which both adults and young juveniles achieved 100% successful trials. In addition, Figure 5 shows that the rates of in-hand movements were highest on square, triangle, star, and cross trials.

Our results confirm that chimpanzees are capable of in-hand movements. Table 4 shows the occurrence of each movement type and overall rates of performing in-hand movements for each subject. There were individual differences in the subjects' tendency to use a surface while performing in-hand movements (shown in Fig. 6). The adults braced the object against a surface between 8 and 19% of total in-hand movements. The most frequent form of surface assistance was bracing the object against the panel or cutout (13 of 16 instances of surface assistance). Only Popo performed three rotations against her mouth. None of the young juveniles used the surface of the panel to assist rolls or thumb movements (TAB/D), except the one rotation performed by Cleo. When performing an in-hand movement, both the adults and young juveniles preferred using digits 1 and 2 or digits 1, 2, and 3. The adults used digit combinations 1-2 and 1-2-3 for a mean of 92.5% of the total in-hand movements performed; the young juveniles used these digit

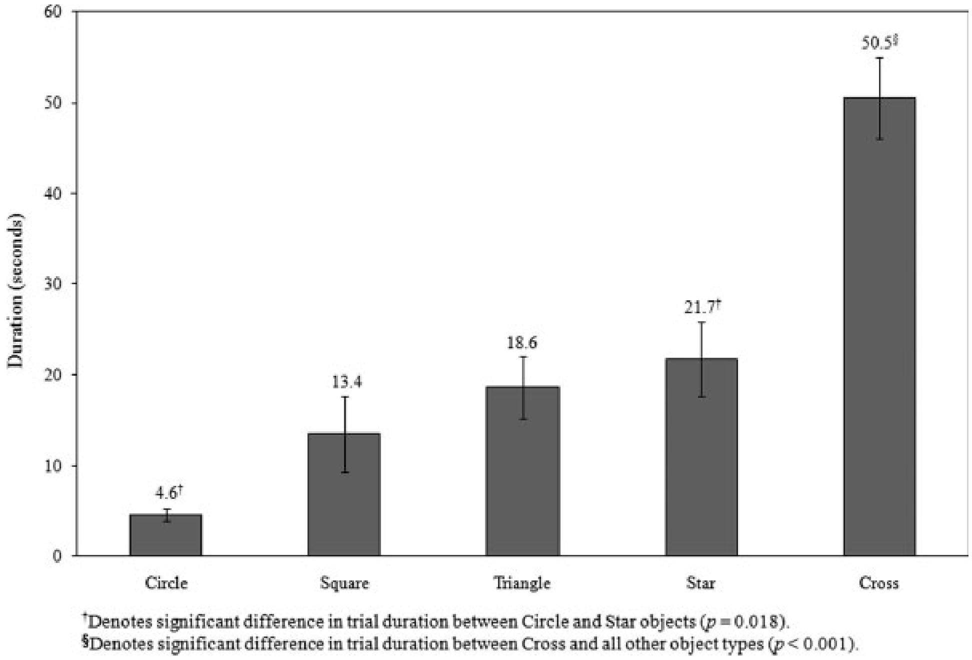


Fig. 3. Mean trial durations per object type across subjects.

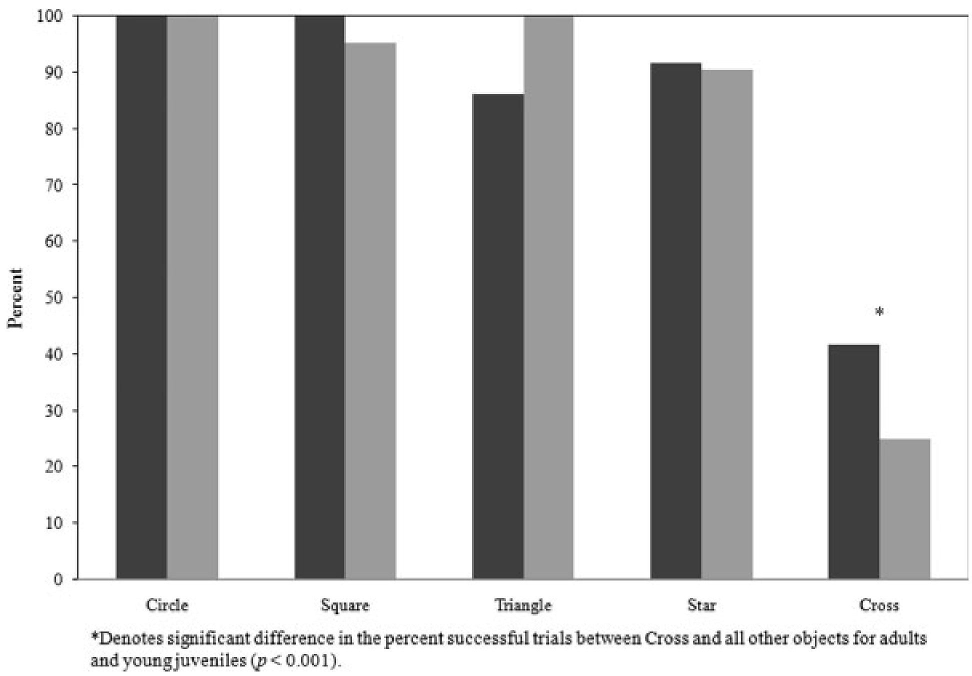


Fig. 4. Mean percent of successful trials per object type in adults and young juveniles.

combinations for a mean of 91.7% of the total in-hand movements performed.

In-hand movements

The adults proved quite capable of using in-hand movements as a method of changing their grasp on an object to align it to the cutout. Figure 7 shows the variability in rates of each type of in-hand movement across subjects. Overall, frequencies per minute and mean percents of total in-hand movements for roll, rotation, and turnover were approximately equal in the adults (see Fig. 7 for rates; means of 27.4% of in-hand movements were rolls, 26.6% rotations, and 26.3% turnovers). The frequencies per minute and mean percent of total in-hand movements for roll and thumb movements were approximately equal for the young juveniles (see Fig. 7 for rates; means of 45% of total in-hand movements were rolls and 48.3% were thumb movements). Cleo was the only young juvenile to perform a surface-assisted

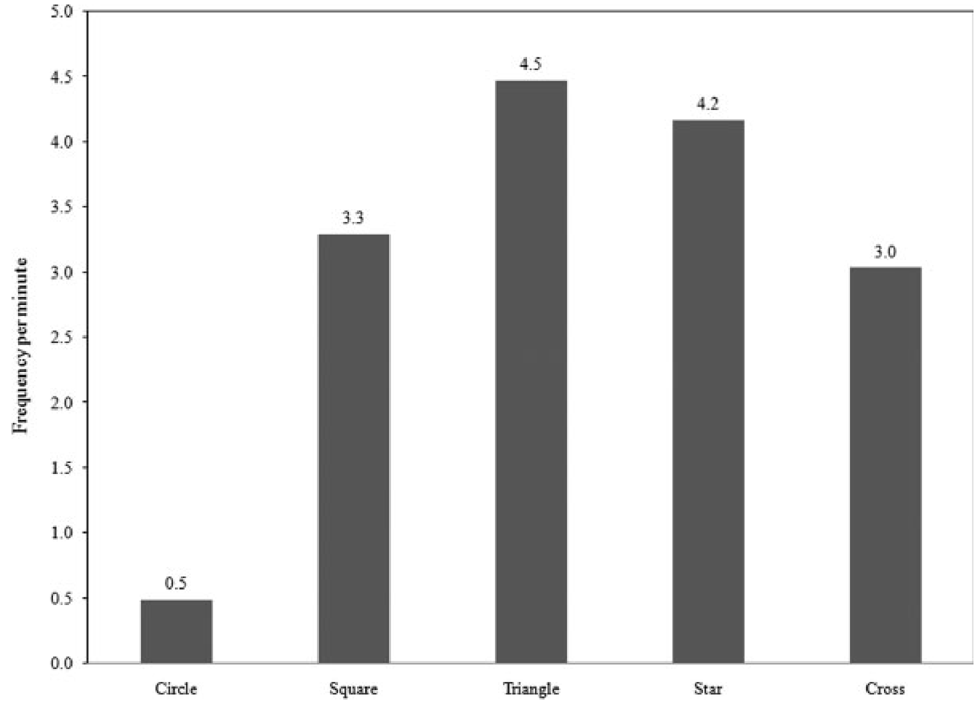


Fig. 5. Mean rates of in-hand movements per object type across subjects.

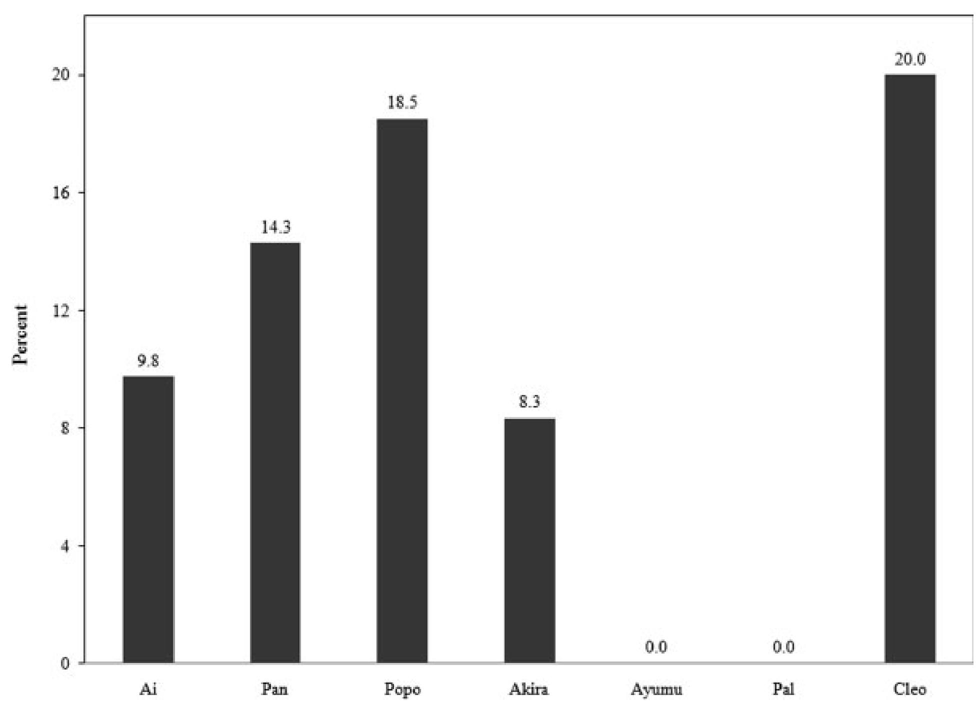
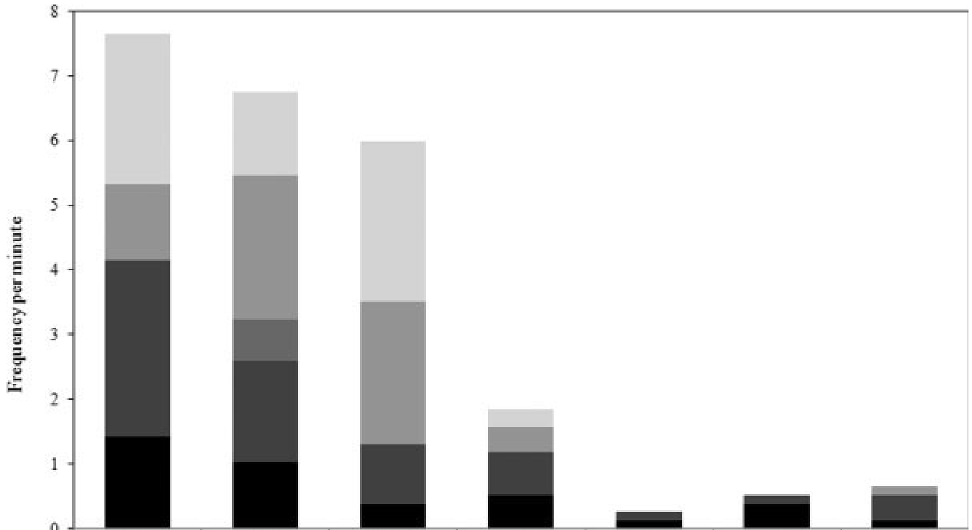


Fig. 6. Mean percent of in-hand movements during which subjects used surface-assistance.

rotation, which comprised a mean of 6.7% of their in-hand movements.

Movement of the thumb alone (coded TAB/D to denote thumb abduction or adduction) to move the object within one hand was considered the least complex of the in-hand movements because it involved movement of a single digit in a single direction. The mean percent of total in-hand movements was 17.3% for adults and 48% for young juveniles. The adults averaged 0.9 TAB/D per minute (ranging from 0.4 to 1.4, see Fig. 7); the young juveniles averaged 0.2 TAB/D per minute (ranging from 0.1 to 0.4, see Fig. 7). Neither adults nor young juveniles used the surface of the panel to assist a TAB/D. These movements were typically made between the thumb and



	Ai	Pan	Popo	Akira	Ayumu	Pal	Cleo
TUR	2.33	1.30	2.47	0.26	0	0	0
ROT	1.17	2.21	2.21	0.39	0	0	0.13
THP	0	0.65	0	0	0	0	0
ROL	2.72	1.56	0.91	0.66	0.13	0.13	0.39
TAB	1.43	1.04	0.39	0.53	0.13	0.39	0.13

Fig. 7. Rates of each type and subtype of in-hand movement performed by each subject.

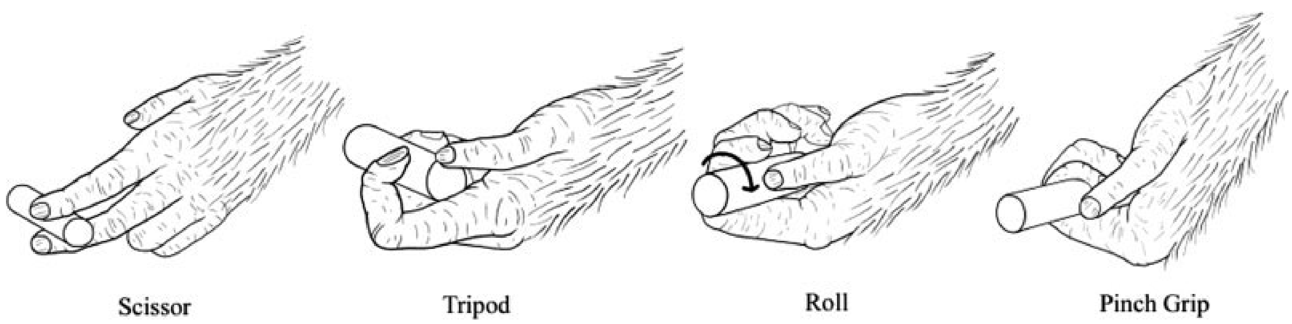


Fig. 8. Turnover sequence. Drawn by Cheryl Reese.

digits 2 and 3, with the arm in a supine position, the object supported by digits 2 and 3, and the thumb then moving either away from the palm (abduction) or toward the palm (adduction) to turn the object about its longitudinal axis.

The roll (ROL) was considered a slightly more complex movement than TAB/D, as two digits were required to move simultaneously in opposing directions (see "roll" in Fig. 8), but was still considered a simple movement. Rolls comprised 27.4% of adult in-hand movements and 45% of young juvenile in-hand movements. The adults averaged 1.46 ROL per minute (ranging from 0.7 to 2.7, see Fig. 7); the young juveniles averaged 0.2 ROL per minute (ranging from 0.1 to 0.4, see Fig. 7). Surface-assistance was uncommon for both adults and young juveniles for ROL: a mean of 4.8% of total rolls were surface-assisted for adults; the young juveniles did not use any surface-assistance for rolls. The chimpanzee roll was very similar to the human form. As described by Elliott and Connolly (1984), humans often roll objects between the thumb and index finger. The adult chimpanzees did this frequently, but also often used their middle digit to support the object as well. For the adults, digit combinations 1-2 or 1-2-3 were used in 77.4% of total rolls. The remaining percent of rolls used digit combination 2-3 (predominately by Popo). Two typical methods of executing a roll were observed in both adult and young juvenile subjects: by holding the object between the tip of the thumb and radial side of the index (and sometimes also the radial side of the third digit as well), or between the tip of the thumb and the pulp (volar) surface of the entire length of the index (and sometimes also those surfaces of the third and fourth digits as well). When rolls were performed using the latter method, it appeared that the object was cradled in the digit(s) as the thumb-tip opposed. The arm and palm were often, but not always, in a supine position during rolls.

The thumb push (THP), a type of roll, was a simple movement in which the digits and thumb moving in opposite directions simultaneously (refer to "roll" in Fig. 8, but imagine the thumb flexes and contacts the object from behind and extends to push it out of the hand while the other digits flex toward the palm). The only subject to use THP was Pan (adult female). She never used the surface of the panel to assist the movement, always used digits 1-2 or 1-2-3 (80% of her thumb pushes were using 1-2-3), and held her arm in a supine position with the digits cradling the object.

Rotations were considered a more "complex" in-hand movement because the digits were required to move in a sequence involving more than one simple movement. Rotations comprised a mean of 26.6% of in-hand movements for adults and performed a mean of 1.5 times per minute (ranging from 0.4 to 2.2, see Fig. 7). Cleo was the only young juvenile to perform a rotation. The adults' rotations appeared clumsy compared to adult humans, yet always were a sequence of actions (grasps and simple movements) and the objects were always held between the finger tips or cradled in the digits (2, 2-3, or 2-3-4) while the thumb opposed. The movement patterns that were coded as rotations appeared highly variable; there was not a particular sequence of actions to characterize a rotation. Because of the relatively high degree of independent digital control required to perform a rotation, we suspected that surface-assistance would be employed during a high percentage of rotations. This idea was not supported in our data set as only a mean of 31.4% of adult rotations were surface-assisted, although Cleo's rotation was surface-assisted. For the adults, 91.2% of rotations were performed with digit combinations 1-2 or 1-2-3. The remaining rotations comprised one instance of Popo using digit combination 1-2-3-4, and one instance of Popo using digit combination 1-3. The subjects' arms were in a supine position during most rotations, most likely to support the object with the palm during the movement.

We distinguished the turnover as a particular form of rotation because it always occurred in the characteristic sequence and always to pick up an object from the floor. It is not a movement that has been described in humans and only adult chimpanzees performed the turnover (comprising 26.3% of in-hand movements). In a turnover, subjects used a scissor grip with digits 2-3 to pick the object up off the floor, with the arm in a supine position, and rolled the object around the index digit to a pinching grasp, with the arm either supine or prone (or something in between), with the object between the thumb and side of index (1-2), occasionally with the middle digit remaining in contact (see Fig. 8). Thus, all recorded turnovers were performed with digits 1-2-3.

Other strategies

A few subjects preferred strategies other than in-hand movements for changing their grip on the object. Bimanual actions included turning the object over repeatedly using both hands and placing the object in the other hand to be regrasped in a different way. Ayumu (the young juvenile male) appeared to use bimanual actions more frequently than the other subjects (6.6 per minute); Ai (adult female) did not use bimanual actions at all. The other subjects used between 0.3 and 1.6 bimanual actions per minute. Mouth use included placing the object in the mouth to be regrasped, manipulating the object with the mouth, and attempting to insert the object through the cutout with the mouth. The rates of mouth use for the adult females were lowest (ranging from 0.3 to 0.7 per minute); young juveniles had higher rates (ranging from 4.6 to 6.2 per minute) and Akira (adult male) used his mouth much more often than all of the other subjects (12.4 per minute). The predominant form of mouth use that Akira employed was to place the object in the mouth to be regrasped (99% of mouth uses). The young juveniles were the only subjects to attempt insertion with the object placed in the mouth, however placing the object in the mouth to be regrasped was also predominant (75% of mouth uses).

DISCUSSION

This study unequivocally showed that chimpanzees are capable of using dynamic in-hand movements while manipulating objects. These behaviors were not trained, but were spontaneous reactions to the problem we presented. Most of our predictions were supported: the adults performed a greater number of in-hand movement types than the young juveniles; adults performed the more complex movement types while juveniles on the whole did not; and the adult form of execution appeared different than the adult human form. In general, the chimpanzees' digit movements during in-hand movements seemed to be performed more haphazardly than precisely, as seen in human precision handling. For example, the chimpanzees often cradled the objects in the palm and/or proximal pulp surfaces of the digits during a movement. However, of the types of in-hand movements that the both adults and young juveniles performed, the young juveniles' form did not appear less sophisticated than the adult form. The chimpanzees' lesser refinement in digit movement compared to humans may reflect neurological differences or other anatomical limitations. The following discussion considers the implications of our findings with regard to our specific task, the individual differences observed, the development of in-hand movements, and the evolution of complex manual skill.

The fitting task

The fitting task proved sufficient in eliciting in-hand movements in chimpanzees. We chose to use a variety of objects and presented them in an order that we perceived as increasing in difficulty. Figures 3 and 4 support our choice in the order of object presentation and Figure 5 shows that moderate challenges elicited in-hand movements as a strategy for changing one's grasp of the object, though not the primary strategy used by all subjects. Other strategies for manipulating the objects may be representative of how chimpanzees avoid using in-hand movements if such movements are difficult for an individual to achieve for some reason (e.g., age, handicap, and individual preference). The majority of the subjects' in-hand movements did not use surface assistance, indicating that the subjects could support the object adequately in the hand throughout the entire movement.

Individual differences

Beyond showing that chimpanzees are capable of using in-hand movements, we were interested in the variation in in-hand movements among the subjects. Their rates of each type of in-hand movement and the use of bimanual actions and the mouth reveal how each subject dealt with the problem of changing its grip on the object for more effective placement while aligning it to the cutout. There appears to be some differences between the adults and young juveniles, but also between the adult females and the adult male subject. The latter difference may be due to some unaccounted variable, such as hand/body size differences between males and females. Of course, a larger sample of individuals is needed to determine the consistency of age and sex differences in chimpanzees. The adult females performed in-hand movements at a higher rate than the adult male and young juveniles. As predicted, the young juveniles did not perform as many types of in-hand movements as the adults did, but performed simple movements nearly exclusively (the sole exception was the one rotation performed by the young juvenile female, Cleo). Simple and complex movements seemed to be equally achievable by adults. We did not attribute the lack of complex movements in young juveniles to the size of the objects, as the objects were large enough to be easily grasped by both adults and young juveniles (see Fig. 1). More likely, the necessary digital control required to perform the more "complex" movements like rotation and turnover had not yet fully developed in the young juvenile subjects. However, use of the fitting task in future work would benefit from scaling the object sizes to the various hand sizes of the subjects.

Mouth use, particularly for regrasping, was a major strategy for the adult male (especially) and the young juveniles; adult females rarely used their mouth to change their grip on the object. The young juveniles were the only subjects to attempt aligning the object to the cutout directly with the mouth ("mouth attempt"). Perhaps their smaller body size accounted for their inclination to lean very close to the floor in order to make the mouth attempt. The young juvenile male Ayumu used bimanual actions more frequently than mouth use, while bimanual actions were not used frequently by the other subjects. The manipulation of objects with both hands and the mouth seemed to be a natural way to explore and handle the objects, as has been seen in other studies of object manipulation by young chimpanzees (see Takeshita, 2001; Hayashi, 2007).

The variation among the subjects in in-hand movements, bimanual actions, and mouth use shows the diversity of methods available to chimpanzees when manipulating objects and suggest that personal preference may affect how the task is approached, not necessarily their propensity for using a particular form of manipulation in other contexts. For example, the adult male was proficient at using in-hand movements, but preferred using his mouth to regrasp the object over all other methods; this may not be indicative of his ability to use in-hand movements in other situations.

Development of in-hand movements

The patterns discussed above imply that the adult females performed in-hand movements with greater ease than the young juveniles. However, it is possible that the young juveniles were actually capable of performing the more complex forms of in-hand movements, and we may have observed them if we gave the young juveniles a smaller object to handle or more time with the task. Nevertheless, our results suggest that these more complex movements seem to be in the process of development, as demonstrated by Cleo, the young juvenile female who used a surface-assisted rotation. It seems that the young juveniles follow a similar developmental timeline of this motor skill to that of human children. At 5 years of age, human children use many of the forms of in-hand movements used by human adults, though with less proficiency (Exner, 1992; Manoel and Connolly, 1998). Similarly, 5-year-old chimpanzees possess at least two of the five forms of in-hand movements we identified that were observed in the adults (TAB/D and ROL). It will be useful in future studies to determine the age at which these simple movements first appear in young chimpanzees.

The task proved a perceptual and cognitive challenge to the subjects, requiring them to line up the many sides and angles of the objects to a cutout on a transparent panel. As with 22-month-old human children (Örnkloo and von Hofsten, 2007), each of the chimpanzee subjects consistently lined the longitudinal axis of the objects up to the apertures, showing that they perceive some of the relevant features of the objects as they relate to the cutout and anticipate how the objects must be passed through the cutouts. However, unlike older human children and adults, the chimpanzees did not always automatically orient the sides of the objects' cross-sections to that of the cutout and pass the objects through on the first try. Although this was easiest to achieve with the circular object (as any orientation will allow it to pass through as long as the longitudinal axis is lined up), it seemed as though the chimpanzees did not perceive all relevant features of the objects as they related to the cutouts. While this difficulty undoubtedly elicited the use of in-hand movements, which was pertinent to our research aims, it is interesting to note the motor and perceptual differences between adult humans and adult chimpanzees in this seemingly easy task. Further work with this same task may probe questions regarding the chimpanzees' perception of the spatial relationships between objects and the planning of appropriate motor action.

CONCLUSIONS

We have established that chimpanzees are capable of in-hand movements that are similar to human forms and that these abilities develop significantly through the chimpanzee's young juvenile years. In-hand movements appear to enhance foraging efficiency with plant material (Corp and Byrne, 2002) and likely aid tool manufacture and use as well; for instance, when stripping twigs for ant-dipping, or when handling stone, anvil, and nuts for nut cracking. The chimpanzees' relatively advanced manual dexterity, combined with that which has been documented in gorillas (Byrne and Corp, 2002), implies that the neural and muscular anatomy required for in-hand movements evolved in a common ancestor to humans, Pan, and Gorilla. Modern human hand morphology and neural control may have evolved as the use of in-hand movements expanded to more complex tool-making and became important in other areas of daily life.

In addition, our findings may inform investigations of the timeline of the appearance of tool-making and use in human ancestors, as the chimpanzees demonstrated an ability to manipulate objects within one hand despite lacking a relatively long thumb and the enhanced thumb musculature that humans possess (see Susman, 1994; McGrew et al., 1995; Marzke, 1997). Meanwhile, continued documentation of the forms and development of sophisticated manual function in primates will further our understanding of the evolution of these important adaptations in both humans and the great apes, and the importance of dynamic in-hand movements in the daily lives of extinct and extant primates.

ACKNOWLEDGMENTS

We would like to acknowledge the help of several people on this project. We thank Sana Inoue and Etsuko Nogami for assistance during data collection, Hika Kuroshima for advice and help coding, and Cheryl Reece for drawing Figure 8.

LITERATURE CITED

Behnke RS. 2001. Kinetic anatomy. Champaign, IL: Human Kinetics.

Boesch C, Boesch H. 1993. Different hand postures for pounding nuts with natural hammers by wild chimpanzees. In: Preuschoft H, Chivers DJ, editors. Hands of primates. New York: Springer-Verlag. p 91–108.

Bortoff GA, Strick PL. 1993. Corticospinal terminations in two New-World primates: further evidence that corticomotoneuronal connections provide part of the neural substrate for manual dexterity. J Neurosci 13:5105–5118.

Braido P, Zhang X. 2004. Quantitative analysis of finger motion coordination in hand manipulative and gestic acts. Hum Mov Sci 22:661–678.

Byrne RW, Corp N. 2001. Manual dexterity in the gorilla: bimanual and digit role differentiation in a natural task. Anim Cog 4:347–361.

Christel M. 1993. Grasping techniques and hand preferences in Hominoidea. In: Preuschoft H, Chivers DJ, editors. Hands of primates. New York: Springer-Verlag. p 91–108.

Corp N, Byrne RW. 2002. The ontogeny of manual skill in wild chimpanzees: evidence from feeding on the fruit of *Saba florida*. Behaviour 139:137–168.

Elliott JM, Connolly KJ. 1984. A classification of manipulative hand movements. Dev Med Child Neurol 26:283–296.

Exner CE. 1992. In-hand manipulation skills. In: Case-Smith J, Pehoski C, editors. Development of hand skills in the child. Bethesda, MD: American Occupational Therapy Association. p 1–11.

Fragaszy D. 1998. How non-human primates use their hands. In: Connolly KJ, editor. The psychobiology of the hand. London: Mac Keith Press. p 77–96.

Hayashi M. 2007. Stacking of blocks by chimpanzees: developmental processes and physical understanding. Anim Cog 10: 89–103.

Heffner RS, Masterson RB. 1983. The role of the corticospinal tract in the evolution of human digital dexterity. Brain Behav Evol 23:165–183.

Iwaniuk AN, Pellis SM, Whishaw IQ. 1999. Is digital dexterity really related to corticospinal projections?: a re-analysis of the Heffner and Masterson data set using modern comparative statistics. Behav Brain Res 101:173–187.

Jones-Engle LE, Bard KA. 1996. Precision grips in young chimpanzees. Am J Primatol 39:1–15.

Kamakura N, Matsuo M, Ishii H, Mitsuboshi F, Miura Y. 1980. Patterns of static prehension in normal hands. Am J Occup Ther 34:437–446.

Landsmeer JMF. 1962. Power grip and precision handling. Ann Rheum Dis 21:164–170.

Lemon RN. 1993. Cortical control of the hand. Exp Physiol 78:263–301.

Lemon RN, Griffiths J. 2005. Comparing the function of the corticospinal system in different species: organizational differences for motor specialization? Muscle Nerve 32:261–271.

Lewis OJ. 1989. Functional morphology of the evolving hand and foot. Oxford: Clarendon Press.

Manoel EJ, Connolly KJ. 1998. The development of manual dexterity in young children. In: Connolly KJ, editor. The psychobiology of the hand. London: Mac Keith Press. p 177–198.

Marzke MW. 1971. Origin of the human hand. Am J Phys Anthropol 34:61–84.

Marzke MW. 1983. Joint functions and grips of the *Australopithecus afarensis* hand, with special reference to the region of the capitate. J Hum Evol 12:187–211.

Marzke MW. 1997. Precision grips, hand morphology, and tools. Am J Phys Anthropol 102:91–110.

Marzke MW, Marzke RF, Linscheid RL, Smutz P, Steinberg B, Reece S, An KN. 1999. Chimpanzee thumb muscle cross sections, moment arms and potential torques, and comparisons with humans. Am J Phys Anthropol 110:163–178.

Marzke MW, Wullstein KL. 1996. Chimpanzee and human grips: a new classification with a focus on evolutionary morphology. Int J Primatol 17:117–139.

Matsuzawa T. 1996. Sociocognitive development in chimpanzees: a synthesis of laboratory and fieldwork. In: Matsuzawa T, Tomonaga M, Tanaka M, editors. Cognitive development in chimpanzees. Tokyo: Springer-Verlag. p 3–33.

McGrew WC, Hamrick MW, Inouye SE, Ohman JC, Slanina M, Baker G, Mensforth RP. 1995. Thumbs, tools, and early humans. Science 268:586–589.

Mountcastle VB. 2005. The sensory hand: neural mechanisms of somatic sensation. Cambridge, MA: Harvard University Press.

Napier JR. 1956. The prehensile movements of the human hand. J Bone Joint Surg Br 1956;38:902–913.

Napier JR. 1960. Studies of the hand of living primates. Proc Zoo Soc London 134:647–657.

Napier J. 1993. Hands (revised edition). Princeton, NJ: Princeton University Press.

Napier JR, Napier PH. 1985. The natural history of the primates. Cambridge, MA: The MIT Press.

Örnkloo H, von Hofsten C. 2007. Fitting objects into holes: on the development of spatial cognition skills. Dev Psychol 43:404–416.

Pehoski C. 1992. Central nervous system control of precision movements of the hand. In: Case-Smith J, Pehoski C, editors. Development of hand skills in the child. Bethesda, MD: American Occupational Therapy Association, p 1–11.

Pehoski C, Henderson A, Tickle-Degnen L. 1997. In-hand manipulation in young children: rotation of an object in the fingers. Am J Occup Ther 51:544–552.

Santello M, Flanders M, Soechting JF. 1998. Postural hand synergies for tool use. J Neurosci 18:10105–10115.

Schultz AH. 1969. The life of primates. London: Weidenfeld and Nicolson.

Shrewsbury MM, Marzke MW, Linscheid RL, Reece SP. 2003. Comparative morphology of the pollical distal phalanx. Am J Phys Anthropol 121:30–47.

Susman RL. 1994. Fossil evidence for early Hominid tool use. Science 265:1570–1573.

Takeshita H. 2001. Development of combinatory manipulation in chimpanzee infants (*Pan troglodytes*). Anim Cog 4:335–345.

Tonooka R, Matsuzawa T. 1995. Hand preferences of captive chimpanzees (*Pan troglodytes*) in simple reaching for food. Int J Primatol 16:17–35.

Wilson FR. 1998. The hand: how its use shapes the brain, language, and human culture. New York: Pantheon Books.

Wong IJ, Whishaw IQ. 2004. Precision grasps of children and young and old adults: individual differences in digit contact strategy, purchase pattern, and digit posture. Behav Brain Res 154:113–123.