Author(s): Deirdre Birtles, Shirley Anker, Janette Atkinson, Rhiannon Shellens, Alexandra Briscoe, Melissa Mahoney, Oliver Braddick
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Bimanual strategies for object retrieval in infants and young children

Authors: Deirdre Birtles[1], Shirley Anker[1], Janette Atkinson[1], Rhiannon Shellens[2], Alexandra Briscoe[2], Melissa Mahoney[2] & Oliver Braddick[3]

[1]Division of Psychology and Language Sciences, University College London,
26 Bedford Way, London WC1E 6BT, UK

[2]UCL Medical School, University College London,
26 Bedford Way, London WC1E 6BT, UK

[3]Department of Experimental Psychology, Oxford University,
South Parks Road, Oxford OX1 3UD, UK

Address for correspondence:

Professor Oliver Braddick
Dept. of Experimental Psychology
University of Oxford
South Parks Road
Oxford, OX1 3UD
United Kingdom

E-mail: oliver.braddick@psy.ox.ac.uk
Tel: (+44) 01865 281871

Fax: (+44) 01865 271354

Abstract

Age differences in goal-directed bimanual coordination were studied in typically developing infants aged 9 – 29 months, compared to a group of children aged 4-6 years and a group of adults, using an object retrieval task. This task required one hand to open and hold the lid of a transparent box, while the second hand retrieved a small toy from inside the box. Well-coordinated retrieval strategies with differentiated use of the two hands were not established in the majority of infants until 18 months of age. Temporal analysis of the hand actions revealed that, unlike adults who perform the task with close synchronization of the hands at the start, the infants performed the task sequentially and did not activate the second hand until the first hand had started to lift the lid. The children's hand preferences for the two hand actions also contrasted with those of adults. In children aged 27-29 months and 4-6 years there was a preference for using the right hand to lift the lid while in right-handed adults the reverse pattern was observed. The results suggest that although bimanual coordination starts to develop in the second year of life, the adult pattern of performance on this task is not observed before 6 years of age. It is likely that further maturation of the brain networks involved in bimanual coordination, and in particular functional interhemispheric transfer via the corpus callosum, is required before automatization of bimanual hand actions is achieved.

Keywords (4-6 words): Bimanual coordination; Human infants; Goal synchronization, Hand Preference

Introduction

Many everyday skills, such as tying shoelaces or buttoning a shirt, require coordinated use of both hands. Although the actions of the two hands may differ, they are bound together spatially and temporally to achieve a common goal. Studies investigating the development of bimanual coordination in young children generally report that before 12 months of age, infants have trouble performing tasks that require the two hands to carry out different actions simultaneously (e.g. Bruner 1970; Diamond 1991; Fagard 1994; Fagard and Jacquet 1989; Ramsay and Weber 1986). In a task that requires a lid to be held open while a toy is retrieved, young infants tend to adopt inefficient sequential strategies such as lifting the lid of the box with one hand, holding it open with the other, and retrieving the object with the first hand. They also have difficulty dissociating the activity of the two hands so that frequently the hand holding the lid will close it on the hand attempting to retrieve the toy (Bruner 1970; Fagard 1994). Well-coordinated bimanual strategies where one hand lifts and holds the lid and the other hand retrieves the toy are typically not adopted until 15-17 months of age (Bruner 1970; Ramsay and Weber 1986).

Development of coordinated bimanual actions is likely to depend on the maturation of multiple cognitive, sensory, and motor systems combined with relevant activity and motor experience. Diamond (1991) suggests that failure to complete the task in infants below 12 months may be related to immaturity in the frontal lobe. To perform the bimanual box task efficiently the infant must be able to inhibit not only the predominant response to reach directly for the toy, but also the tendency to perform similar actions with the two hands. In addition they must be able to relate the lifting of the lid to retrieval of the toy. Diamond (1991) suggests that while executing a sequence of actions is dependent on the supplementary motor area (SMA) of both hemispheres and their connection via the corpus callosum (CC), a certain level of maturation in the dorsolateral prefrontal cortex (DLPC) is necessary for object retrieval tasks, where infants must not only inhibit a predominant response but integrate information that is separated in time and space.

Brain systems supporting bimanual co-ordination

The results from recent studies of bimanual coordination mechanisms in healthy humans, neurological patients and non-human primates have led to a general agreement that cortical and subcortical areas in a distributed network contribute to bimanual coordination including the SMA, DLPC, CC, cingulate and premotor areas, parietal lobe, and cerebellum (see reviews by Swinnen 2002; Swinnen and Wenderoth 2004; Wiesendanger and Serrien 2004).

Adult patients with specific focal brain damage show coordination disorders. For example patients with mesial frontal lesions involving the SMA sometimes develop bimanual disorders such as intermanual conflict and alien hand syndrome (Wiesendanger et al. 1994; Stephan et al. 1999). With parietal lesions, patients often fail to use their hands in an appropriately coordinated manner for tasks such as buttoning clothes or opening a bottle (e.g., Ghika et al. 1998).

A bimanual pull and grasp drawer task, in which subjects open a loaded drawer with one hand and grasp a small object in the drawer with the other, has been frequently used to study bimanual co-ordination (Wiesendanger et al. 1996; Perrig et al. 1999; Serrien and Wiesendanger 2000). Patients with callosal agenesis can perform familiar everyday bimanual tasks such as tying shoelaces with little impairment, and Serrien and colleagues (2001) demonstrated that these patients showed similar synchronization to control subjects in the drawer task. However, patients with acquired callosal lesions showed more variable performance, with considerable inter-manual delay when vision was excluded. In some respects infants' performance when first learning to coordinate their hand movements resembles these patients in needing greater attention and monitoring of performance and thus greater reliance on exchange of information via the corpus callosum. Diamond (1991) suggested that the presence of coordinated actions may be a useful marker of callosal functioning in infants.

Studies on both humans and non-human primates support the role of the SMA in bimanual goal-oriented tasks. Trained monkeys perform the drawer task with close synchronization of the hands at the start and goal, but unilateral SMA lesions cause a transient delay in movement onset of the contralateral limb (Kazennikov et al. 1998). A similar deficit was observed following reversible inactivation of SMA by muscimol microinfusion, but not with inactivation of other areas including primary motor, dorsal premotor and anterior intraparietal areas (Kermadi et al. 1997). In humans, increased variability in the time interval between the left hand opening the drawer and the right hand starting to move to catch a ball was observed following repetitive TMS to the rostral portion of the SMA (Obhi et al. 2002). Cerebellar patients also exhibit delayed movement onset of the grasping hand in the drawer task (Serrien and Wiesendanger, 2000); however, in the absence of vision, this delay is compensated for by a slowing of the pulling hand which preserves the synchronization of the two hands at the goal. This is hypothesised to be maintained by use of proprioceptive signals.

The present study used a goal-oriented bimanual task, similar to Ramsay and Weber's (1986) box task, to track quantitatively the age related changes of well coordinated bimanual strategies between 9 – 29 months. Earlier studies have characterized the patterns of bimanual action at different developmental stages but have not recorded, in infants who have achieved some coordinated use of the two hands, the relative timing of their actions. We therefore studied the timing of the two hands at the start and the end of the task, in those infants with well coordinated bimanual strategies, and in a group of adults and older children (4-6 year-olds) for comparison.

Role-differentiated hand use

Bimanual tasks frequently involve consistent differentiation of roles for the two hands, taken to reflect a specialization of brain function in motor control (Wiesendanger et al. 1996). In right-handers, the left hand is usually the postural or supporting hand whereas the right hand is used for manipulation. In the drawer task Wiesendanger and colleagues (1996) reported that all 20 right-handed adult subjects spontaneously chose the left hand for pulling the drawer and the right hand for grasping the object. Infants performing bimanual tasks may also show consistently differentiated and complementary roles for the two hands (Fagard and Lockman 2005; Fagard and Marks 2000; Ramsay and Weber 1986). 17-19 month-old infants in the Ramsay and Weber (1986) study showed an overall preference to lift the lid with the right hand and take the toy with the left (R-L). In the younger infants (12-13 months) the reverse pattern was more frequently observed, although differentiated hand strategies were relatively uncommon at this age. To interpret these results, we need to know whether Ramsay and Weber's R-L sequence persists into later childhood for the box task, or whether it changes to the opposite L-R pattern adopted by adults for the drawer task. In this study infants were therefore compared with older children and adults for the occurrence and consistency of various patterns of handedness on this box task.

In summary, this study had three aims.

- Firstly we wanted to track age related changes in bimanual coordination in infants using a goal-oriented task that required differentiated hand use.
- Secondly, we wanted to investigate the temporal sequencing of the task to examine how the synchronization between the hands changes between 12 and 29 months and compare it with older children and adults.
- Thirdly, we wanted to examine the pattern of hand preference in infants' differentiated hand use in this task.

Methods

Participants

Two hundred and thirty two typically developing infant participants (110 boys) were tested aged between 9 and 29 months. Twenty-one of these infants were tested on two separate occasions approximately one year apart (mean interval: 12.0 months; SD 2.3 months). In total, 253 infant testing sessions were included in the analysis. No infant had significant visual problems (e.g. strabismus, refractive error, field deficits) or risk factors for abnormal neurological development (e.g. more than 14 days premature, neonatal abnormalities). A group of 15 adults (undergraduate students, age range 18-23 years) and 19 children aged 4-6 years (mean ± SD, 4.9 ± 0.6 years) were also tested. All the children were recruited from volunteer families within the central London area and attended the Visual Development Unit for testing. Prior to testing, all participants (or their caregivers, as appropriate) gave informed consent. The study was approved by the University Ethics Committee and carried out according to the principles laid down in the 1964 Declaration of Helsinki.

Apparatus

The task required retrieving a small plastic toy (Duplo® people and animals) from a clear Plexiglas box (94 mm high at the rear, 34 mm at the front, 4.5 mm thick) with a hinged sloping lid, similar to that used by Ramsay and Weber (1986). The clear Plexiglas lid (130 x 115 mm x 1.5 mm thick) had a 30 degree slope toward the infant, and was hinged so that it would fall shut if infants did not hold it open. A black plastic handle (19 mm in diameter) was positioned at the front centre of the door. Sessions were recorded with a digital video camera positioned 1.5 m from the infant at a height of approximately 2 m to provide an unobstructed frontal view of the infant's manual activities.

Procedure

The task was performed in a quiet room with the infant seated on the caregiver's lap at a table, directly opposite the experimenter, at the appropriate height for the infant to be able to easily reach the box on the table top. The experimenter placed the box initially out of the infant's reach and then lifted the lid and placed a toy inside while the infant watched. The experimenter then pushed the box across the table to the midline of the infant's reaching space and held it steady while verbally encouraging the infant to retrieve the toy. Once the infant had retrieved the toy and played with it briefly, the box and toy were withdrawn and the procedure was repeated with a new toy. If the infant had not successfully retrieved the toy after several minutes' exploration of the box, the trial was terminated and the box was withdrawn. Three trials were carried out with each infant.

Video Scoring: Performance and Hand Preference

The infants' object retrieval strategies were classified into the following five behavioural categories (adapted from Fagard and Pezé, 1997; Ramsay and Weber, 1986), scored from 0-3 as indicated in square brackets.

Failure

The infant banged on the lid or outside of the box but was unsuccessful at retrieving the toy even though he or she may have lifted the lid [score=0].

Unimanual

The infants used the same hand to open the lid and retrieve the toy without involvement of the other hand. This was achieved by opening the lid just enough to slide the hand into the box, and allowing the lid to fall on the hand while retrieving the toy [score=1].

Bimanual with hand transfer

One hand opened the lid, the other hand held the lid open, and the leading hand removed the toy. This strategy involves an inefficient division of roles between the two hands since it required three component acts, including a transfer of hand on the lid [score=2].

Bimanual incomplete differentiation

Both hands raised the lid and then one hand removed the toy. This strategy involved incomplete differentiation of roles for the two hands [score=2].

Bimanual complete differentiation

A well-coordinated strategy where one hand opened the lid and held it open, and then the other hand removed the toy. This strategy involved complete differentiation of roles for the two hands [score=3].

A total score was obtained for each child by adding the performance scores of the three trials together, giving a maximum score of 9.

For hand preference, the hand used to open the lid and that used to retrieve the toy were recorded for each trial (trials with hand transfer or incomplete differentiation were not included in this analysis). Analysis was also restricted to second and third trials showing a completely differentiated strategy , since on the first trial infants frequently made initial exploratory actions including lifting of the lid with alternate hands before removing the toy. Trials were coded as either R-L (Right hand lid, Left hand toy) or L-R (Left hand lid, Right hand toy). When the two trials were performed with the same hand preference the infant was categorized as either R-L or L-R. If this differed between the two trials, the handedness was categorized as inconsistent (after Fagard and Lockman, 2005).

Adult participants were asked to complete a handedness questionnaire with 12 items based on the Edinburgh Handedness Inventory (Oldfield 1971), after completion of the experiment. The responses were used to calculate a laterality quotient (LQ) for the individual and classify them as right-handed (N = 13, LQ between +67 and +100) or left-handed (N = 2; LQ between -67 and - 100). For older children (4-6 years, N = 19), the hand used by the child to write their name or draw a picture on a score sheet was recorded as their preferred hand. Seventeen of the children preferred their right hand for writing or drawing and two children preferred to use their left hand.

Video scoring: event latencies

For trials scored as ‘3’ (showing bimanual complete differentiation) discrete temporal events were extracted from frame-by-frame analysis of the video. This allowed examination of the temporal characteristics of bimanual coordination in infants, for comparison with children and adults and comparison with temporal analysis from previous studies.

The time when an infant initiates movement of the first hand can be difficult to register, since infants sometimes reached to grasp the box before it was positioned in front of them, and sometimes spent time haptically exploring the box and handle before attempting to lift the lid. However, inspection of video sequences indicated that the infants did not initiate the second (‘toy’) hand until the first hand had started to lift the lid. Thus the interval between action onset for the lid hand (the frame prior to a visible separation between lid and box) and first frame showing movement of the ‘toy’ hand provided a temporal parameter related to movement onset whose age-related change could be studied. Two identifiable aspects of goal achievement were the lid being fully opened (‘lid peak’) and the grasping hand’s first contact with the toy in the box. The 'lid peak' was defined as the frame in which upward movement of the lid stopped or became minimal. From these onset and goal achievement events we determined the following parameters of interest:

- *total task duration*, i.e. the time between the onset of lid lift and the first touch of the toy.
- *lid-toy hand delay*, i.e. the interval between onset of lid lift and movement onset of the toy hand.
- *lid hand movement*, i.e. from onset of lid lift to lid peak.
- *toy hand movement*, i.e. from first movement of the hand to toy touch.
- *goal synchronization* of the two hands i.e. the interval between lid peak and touch of the toy.

The normalized *movement overlap* time was defined as the interval between initiation of the second (toy) hand and lid peak for the first hand, as a percentage of the total task completion time. If the toy hand was not initiated before lid peak a value of 0% was assigned to that trial.

Analysis of temporal parameters in 24-29 month-old infants, 4-6 year olds and adults

We compared temporal parameters between adults, 4-6 year olds and older infants (24-29 months). Infant trials were only included if (a) they were scored as '3'; (b) the initial start position for the hands was similar to the adults' (i.e. resting on the table either side of the box); (c) the action was completed as a continuous sequence of reaching for the handle, lifting the lid and reaching for the toy with the other hand; (d) it did not involve haptic exploration of box and handle prior to lifting the lid. In comparing these three groups, the first movement of the hand from the table towards the lid was taken as the starting point (Initiate action) and used for determining total duration, total lid-hand and toy-hand times, normalized overlap and initiation delay – the interval between onset of movement of the lid hand and onset of the toy hand. The timing of the lid hand was also recorded as two separate components: the 'reach to grasp handle' and the 'time to open lid' (analogous to lid hand movement in younger infants). Goal synchronization of the two hands, the interval between lid peak and touch of the toy, was identical to the measure used in comparison between infant groups.

Video-scoring: reliability

Video-scoring of infant performance and hand preference was carried out by four of the authors (DB, AB, RS and MM). One of the authors (DB) then separately coded 62 of the testing sessions (24.5%) spread across the age range (9 – 29 months) and coded by the other authors for reliability of the initial coding. Across the 62 sessions (186 trials) there was 97% agreement for trials performed at Level 3 (bimanual complete differentiation), 90% on Level 2 (bimanual hand transfer or incomplete differentiation), 100% on Level 1 (unimanual) and 96% on Level 0 (failure). There was 100% agreement between coders on hand preference. All the timing parameters were extracted by one of the authors (DB).

Results

Effects of age on bimanual performance

Bimanual performance improved rapidly with age. The changing retrieval strategies are shown in Figure 1 as a proportion of trials averaged across infants. In the youngest age group (9 – 11 months, N = 27) over half the trials were failures where the infant was unable to retrieve the toy. This proportion decreased dramatically in infants aged 12 – 14 months (N = 51) but on a large proportion of trials (40.5%) they used less well-coordinated strategies (Performance Level score = 2), either using both hands to open the lid or swapping hands on the lid in order to retrieve the toy with the first hand. By 15-17 months (N = 73) infants performed over 60% of trials at Level 3 (score=3) with differentiated hand-use in well-coordinated retrieval strategies. Above 18 months, (N = 27, 26, 24, and 25 respectively for the 4 older age groups) all infants used bimanual strategies and over 70% of trials were performed at Level 3, showing differentiated and co-ordinated retrieval strategies.

A total performance score was calculated for each individual by adding the performance scores of the three trials, giving a maximum score of 9 if all three trials were performed at Level 3. The median scores for each group are shown in the top of Figure 1. Analysis of the age trend (Jonckheere-Terpstra Test) indicated a significant improvement in performance with age (J-T statistic = 7.138, $P < 0.001$). Pairwise comparisons of performance (Mann-Whitney Test) between successive age bands showed a significant difference in performance between the youngest group (9-11 months) and 12-14 months (z = -4.704, $P < 0.001$) and between 12-14 months and 15-17 months (z = -2.455, $P = 0.014$). However no differences in performance were observed between the older age groups.

[Figure 1 about here]

Age-related changes in the temporal structure of the object retrieval task

A score of '3' denotes a co-ordinated, differentiated use of the two hands. However, it was evident that infants who achieved this score could still show considerable age-related change in the fluency of the co-ordinated action, which was reflected in our measures of the temporal parameters. As so few of the infants in the youngest age group (9-11 months) achieved scores of '3', only infants over 12 months were included in this temporal analysis. The data obtained from these infants were collapsed into three wider age bands: 12-17 months (N = 54), 18-23 months (N = 38) and 24-29 months (N = 41). To maximize the data for this analysis, timings for the third trial were taken as representative for an individual infant, even if this was the only trial scored as Level 3. Non-parametric tests were used to examine group differences and age trends due to the heterogeneity of variance between the groups and non-normal distribution of the data for several of the parameters.

Overall the majority of the temporal parameters showed a significant trend of improvement with age on the Jonckheere-Terpstra test: Total task duration, movement time for the toy hand, goal synchronization, % hand overlap (all $P \leq 0.001$) and synchronization of the hands at the start (lid-toy hand delay, $P = 0.002$). Lid movement time is the only parameter that did not show a significant age trend ($P = 0.053$). Figures 2a-2f shows this age comparison. Overall, the pattern of results shows that infants under 18 months perform the task slower and more sequentially than older infants, primarily due to the delayed initiation of the toy hand. Infants over 24 months demonstrate closer synchronization of the hands at the goal due in part to faster movement of the toy hand.

[Figure 2 about here]

Suitable records for timing comparisons of adults, children and older infants were obtained from 15 adults, 17 children aged 4-6 years and 21 infants aged 24-29 months. Fig. 3 shows the median timings of key events. For this comparison the start point is the initial movement of the first hand towards the lid. Note that all data in Fig. 3 are illustrated normalized relative to the start and end points. The most marked difference between the three groups is that the children and infants delay the movement initiation of the 'toy' hand until the lid starts to lift, while adults tend to initiate the 'toy' hand before the lid hand reaches the handle. This delay at the start means that the children and infants perform the task in a more sequential manner with less overlap of the two hands compared to the adults. However there is also some variability in performance within the adult group with two out of the 15 subjects initiating their toy hand after their first hand touched the lid.

[Figure 3 about here]

Age-group differences in the temporal parameters were compared using Kruskal-Wallis tests. There was a significant difference between the three groups for all parameters ($P < 0.001$ in most cases). Table 1 gives the actual median values, first and third quartiles and the P values for pair-wise comparisons (Mann-Whitney test) for the temporal parameters. The results show that while many of the temporal parameters are of shorter duration in the adults (Total Duration, Initiation Delay, Goal Synchronization) the movement of the 'toy' hand (toy-hand time) is longer in the adults compared to the children ($z = -3.231$, $P = 0.001$) and infants ($z = -3.214$, $P = 0.001$). In general, the interval between the first hand lifting the lid and the second hand reaching for the toy (lid-toy hand delay) took negative values in the adults indicating the toy hand was initiated prior to the first hand lifting the lid, in contrast these values were positive in the infants and children. In addition, the % overlap for the adult group was significantly greater than that of the other two groups ($P < 0.001$). Age-related improvements in timing between the infant group and the children were observed for a number of parameters including total duration, initiation delay and normalized overlap ($P < 0.05$). The time taken to open the lid to lid-peak (Time to open lid) was similar in children and infants, however, the infants were slower at reaching to grasp the handle (z = -2.497, P = 0.011) and to activate the toy hand (lid-toy hand delay, z = -2.748, P = 0.006).

[Table 1 about here]

Bimanual hand preferences

A total of 132 infants aged 12 – 29 months performed both the second and the third trial with a differentiated hand strategy and could be included in the analysis. In the youngest age group (9-11 months), only three infants performed two trials at Level 3, so this age group was not included in the analysis of hand preference. Table 2 summarizes the frequency of hand preference patterns (R-L, L-R or inconsistent) as a function of age group. The *Consistent* R-L pattern (right-hand opens lid and left hand extracts toy) was the most frequently used strategy in each age group although there were a substantial proportion of infants who were inconsistent between the two trials. The preference for the R-L pattern over the L-R pattern only reached significance in the 27-29 month age group (Binomial test, P<0.001). Age-related differences in the preference for the R-L pattern as opposed to L-R or the inconsistent pattern were observed between the 27-29 month old group and three of the other age groups; 15-17 month old infants (χ^2 (1) = 4.22, P = 0.04); 21-23 month old infants (χ^2 (1) = 6.51, P = 0.01) and 24-26 month old infants (χ^2 (1) = 5.31, P = 0.02). There was increased R-L versus L-R pattern use in the 27-29 month old infants compared to the 12-14 month old infants (P = 0.047, Fishers Exact Test) but differences in hand preference between 27-29 month olds and 18-20 month olds did not reach significance. No other age-related differences were observed.

[Table 2 about here]

To determine whether there was any further age-related change in hand-preference for the task we compared the hand preference patterns for the oldest group of infants (27-29 months, N = 19) with those for the 4-6 year old children (N = 19) and adults (N = 15). Seventeen of the 4-6 year olds could be classified as right-handed on their choice of hand for writing. The hand-preference patterns for the right-handed 4-6 year olds were similar to those observed in the older infants, with 70.6% of the children using an R-L pattern (P = 0.43, Fisher's Exact Test). The two left-handed child participants used the opposite pattern i.e. L-R. In the right-handed adults (N = 13) the R-L pattern was rarely used (N = 3) and the most commonly observed hand preference pattern was L-R (76.9%). The hand preference pattern observed in the adults was significantly different from that of the older infants (P = 0.001, Fisher's Exact Test) and the 4-6 year-olds (P = 0.025).

Discussion

Age related changes in strategy in infancy

Our results indicated that in line with previous cross-sectional studies (Bruner 1970; Fagard 1994; Ramsay and Weber 1986), less than half of the youngest infants (9-11 months) were able to co-ordinate the two hands to retrieve the toy from the box. Performance improved rapidly with age, and the majority of infants over 18 months performed the task with a well-coordinated strategy demonstrating differentiated hand use. Quantitatively, our results agree well with Ramsay and Weber (1986) who found 50% of 12-13 month olds used a completely differentiated strategy (48% of 12-14 month-olds in this study) compared to 78% of 17-19 month olds (73% of 18-20 month-olds in this study).

This age-related change is likely to depend on a combination of neurological development and motor experience. Several brain areas implicated in the ability to perform bimanual tasks such as the corpus callosum, DLPFC and cerebellum, do not reach full maturity until adolescence (Diamond 2000). The corpus callosum increases in size as a result of myelogenesis up to the age of 18 years (Giedd et al. 1999; Thompson et al 2000) and interhemispheric transfer time has been shown to be relatively slow in young children (Brizzolara et al. 1994; Hagelthorn et al. 2000). In addition, the changes occurring in the corticospinal motor system around 12-15 months (Martin 2005) are likely to play a major role in the development of efficient bimanual coordination. The improvement in bimanual performance observed around 15 months coincides with the withdrawal of ipsilateral corticospinal projections and faster growth of axonal diameters in the contralateral projections in typically developing children (Eyre et al. 2001). In children with unilateral damage to the motor cortex, displacement of contralateral projections from the damaged hemisphere with ipsilateral projections may explain why clear signs of hemiplegia only emerge at around 18 months (Eyre et al. 2007).

Temporal Analysis of bimanual completely-differentiated retrieval strategies

Even after differentiated, coordinated hand use is achieved, our results show that the pattern of timing changes with age. The youngest infants (12-17 months) had the most difficulty coordinating their hands at the onset of movement, delaying the movement of the hand that will grasp the toy. Once initiated, the individual movement times of the two hands were no different between the youngest and middle age groups (18-23 months). The oldest infants (24-29 months) showed similar synchronization to the middle group at the start of movement, but improved synchronization at the goal (lid peak to toy touch), associated with faster movement of the 'toy' hand once activated.

Timing for the older infants (24 – 29 months), children (4-6 years) and adults could be compared in trials starting with a standard hand position. The timing for the first (lid) hand could be analyzed as two components, reaching for the handle followed by lifting the lid. Age-related improvements between infants and 4-6 year old children were observed in the timing of the lid hand and the synchronization between the hands at the start of the action: the older children were quicker to reach for the handle and activate the toy hand compared to the infants. However synchronization at the goal and the duration of the reach for the toy were similar in the two groups. The adults were significantly quicker overall and showed more overlap of the two hands' movements compared to both infants and children: adults synchronized the hands at the start much more closely, moving the toy hand before the first hand had reached the handle of the box. In contrast the infants and children performed the task sequentially, only activating the toy hand after the lid started to lift.

At 4-6 years children are very familiar with opening containers and removing objects, suggesting that the continuing immaturity in achieving an adult-like coordination pattern is unlikely to result from lack of experience but may reflect a lack of functional interhemispheric transfer via the corpus callosum which only develops around 6 years of age (Franz and Fahey 2007). By this age the major growth of the anterior region of the corpus callosum is completed enabling more efficient transfer of information between motor areas of the frontal lobes (Thompson et al. 2000). These results can be related to the findings of Hung et al. (2004) who compared typically developing 8-16 year olds with children with hemiplegic cerebral palsy. In a version of the pull and grasp drawer task the control children generally initiated the movement of the grasping hand before the first hand reached the handle of the drawer and the movement times overlapped by 50-70% (compare the 55% overlap in adults in the present study). Comparison of these older children with our 4-6 year olds and adults suggests that the ability to synchronize the hands at the start of an asymmetric goal-directed task does not develop until middle childhood.

Maturation of cerebellar function may also be an important element for the normal development of merging of separate actions into a coherent movement program. In developmental disorders such as Attention Deficit Hyperactivity Disorder (ADHD), autism, dyslexia and developmental coordination disorder, motor impairments associated with cerebellar dysfunction have been reported including effects on timing precision on bimanual tasks (Wolff, Michel, Ovrut & Drake, 1990) and decreased connectivity and cerebellar activity during motor task performance (Mostofsky et al. 2009).

Although the infants and children performed the task sequentially there appeared to be some attempt to compensate for the initiation delay and achieve synchronization of the hands at the goal: individual movement time of the toy hand was significantly shorter than in the adults. A similar compensatory strategy was observed in the work by Hung et al. (2004) on children with cerebral palsy. When their impaired hand led in opening the drawer the non-impaired hand waited for the drawer to be opened, but then reached with an increased velocity towards the goal, compared to controls.

In the current study this apparent compensation by speeding the 'toy' hand to achieve goal synchronization was observed at 24-29 months but not in younger infants. The neural basis of this compensation is not yet known. Young infants start to reach and grasp objects successfully from 4 months of age. However, initially their arm movements are erratic and the goal is approached using a series of submovements (von Hofsten, 1991; Berthier, 1996). Stereotypic kinematic motor patterns in reaching (straight hand paths with a smooth velocity profile) are not produced until 12-15 months of age and only become adult-like and established around 2 years of age (Konczak and Dichgans 1997). Hence the faster reaching for the toy and improved goal synchronization observed in the 24-29 month olds may be due to maturation of the posterior parietal cortex and its connections with motor and premotor cortices which are involved in spatio-temporal control of unilateral arm movements (Rizzolatti et al. 1998; Wise et al. 1997).

Bimanual Hand Preferences

When two hand actions (lift lid, grasp toy) become differentiated and coordinated, does the infant assign them to particular hands? The bias toward the R-L strategy was not statistically significant until a strong shift at 27-29 months, when it was shown by over 80% of the infants. Fluctuations in hand preference for manual activities have been linked to the emergence of new motor skills such as independent walking (Corbetta and Bojczyk 2002) and language development (Bates et al. 1986), where a burst typically occurs in the acquisition of grammatical morphology around 28 months.

The R-L pattern also dominated in our 4-6 year-old group, with the L-R pattern observed in two children that were left-handed for writing. This is the reverse pattern to that adopted by adults who use their dominant hand to retrieve the toy. In the discussion of the temporal structure of the task, we suggested that the sequential performance observed for the infants and children may be partly due to a lack of functional interhemispheric transfer between frontal areas. More generally, the L-R strategy requires anticipatory planning that the hand preferred for grasping should be deployed second, which presumably requires inhibition of a preponderant tendency to use the preferred hand for initially grasping the lid handle. Such inhibition is commonly associated with frontal lobe function. In a (unimanual) task where initial grasp determines the end-state comfort of the final hand position, children's selection of this grasp does not anticipate the end state until about age 7 (Smyth and Mason 1997). Motor planning appears to require both frontal and parietal areas (Marois 2002); the maturation required for the L-R sequence may therefore be a function either of commissural connections of these areas, or of the areas themselves.

Summary and conclusions

Age related changes in bimanual co-ordination shows a sequence of landmarks from age 12 months onwards, which may reflect the maturation of components of the underlying neural systems:

1. The differentiated use of the two hands to achieve a goal appears soon after 12 months in some infants and is generally achieved by around 18 months; developments in frontal areas, commissural connections, and the corticospinal system may be required.
2. Initially these bimanual actions are executed sequentially; from 24 months children can control the timing of the second hand which retrieves the toy to synchronize actions at the goal, but their actions are not well synchronized at the onset.
3. Infants by 27 months have a reliable assignment of roles of the two hands, but unlike adults use the preferred hand for the first phase of the action (lid lift).
4. Four- to six-year-old children do not yet show synchronized initiation of the two hands in bimanual actions, and still tend to use the preferred hand for lid rather than toy manipulation, similar to the older infants. This may reflect immaturity of a network of frontal (SMA) and parietal areas, and their callosal interconnections, which allows adult-like temporal patterning only after 6 years of age.

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Figure Captions

Fig. 1 Movement retrieval strategies used by infants from 9 months to 29 months expressed as a percentage for each group. Retrieval strategies were categorized as Failure [0], Unimanual [1], Bimanual incomplete differentiation [2], Bimanual complete differentiation [3]. See text for further description. The median Total Performance Score (sum of three trials) for each age group are shown at the top of the Figure.

Fig. 2 Boxplots of event timing parameters for bimanual object retrieval (Level 3) for the 3 infant groups, 12 – 17 months (N = 54), 18 – 23 months (N = 38), 24 – 29 months (N = 41). a) lid-toy hand delay b) goal synchronization c) lid hand movement d) total task duration e) toy hand movement f) normalized movement overlap. See text for parameter definitions. Box illustrates median (line) and 25th – 75th percentile, whiskers represent 10th and 90th percentile.

Fig 3 Boxplots illustrating median values for key temporal events during bimanual object retrieval (Level 3). a) 24-29 month-old infants (N = 21), b) 4-6 year old children (N = 17) and c) adults (N = 15). For this comparison the start point is the initial movement of the first hand towards the lid (Initiate action) and the end point is first touch of the toy (Toy touch). Time scale is normalized relative to the start and end points. Box illustrates median (line) and 25th – 75th percentile, whiskers represent 10th and 90th percentile.

Table 1 Summary of temporal event comparisons for older infants (24 – 29 months, N = 21), children (4 - 6, years, N = 17) and adults (N = 15). Median values and 25th and 75th percentiles are shown along with the *P* values of U from pair-wise Mann-Whitney tests.

Table 2 Frequency of hand preferences (%) for completely differentiated bimanual performance (Level 3) as a function of age. Infants categorized as *Consistent R-L* use the right hand to lift the lid and the left hand to remove the toy for both trials with the reverse preference for infants categorized as *Consistent L-R*. Infants categorized as *Inconsistent* exhibit different hand preferences for the two trials. The very youngest infants (9-11 months, N = 27) have been excluded as so few were able to perform two trials of the task at Level 3.

* Significant at 0.05 level

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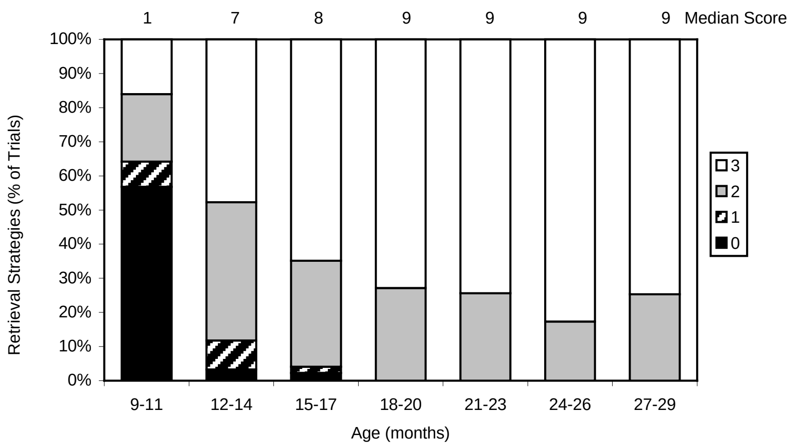

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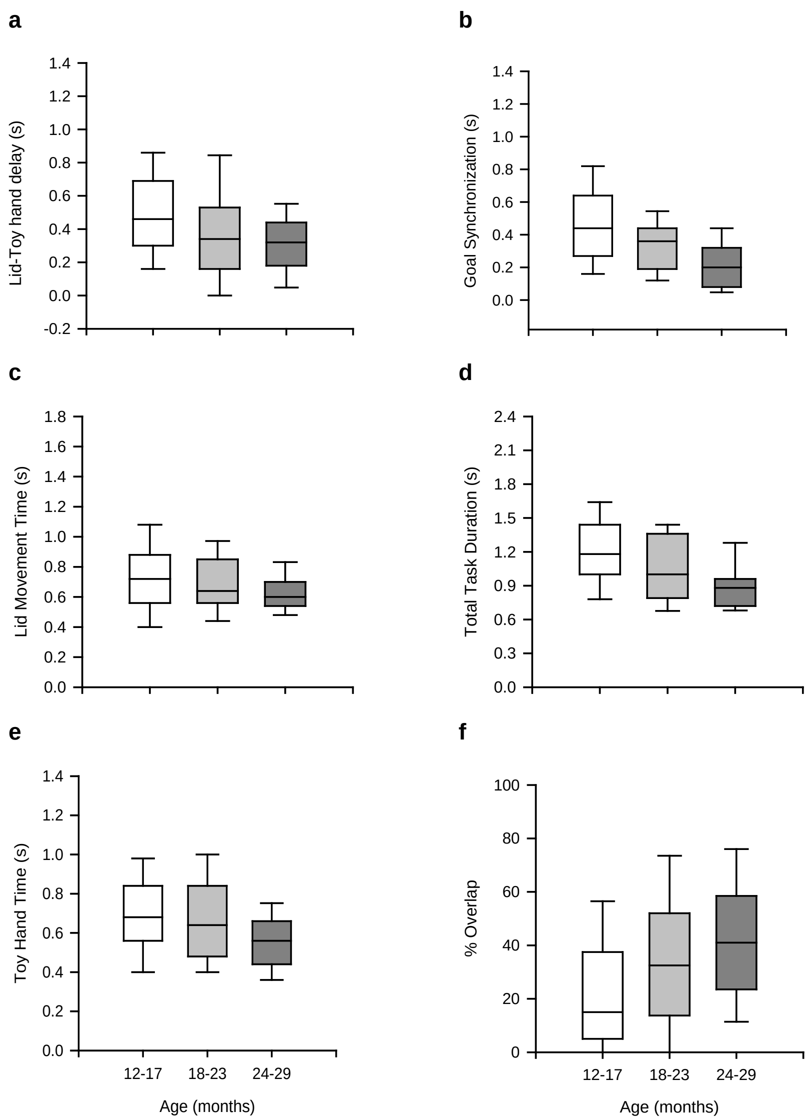

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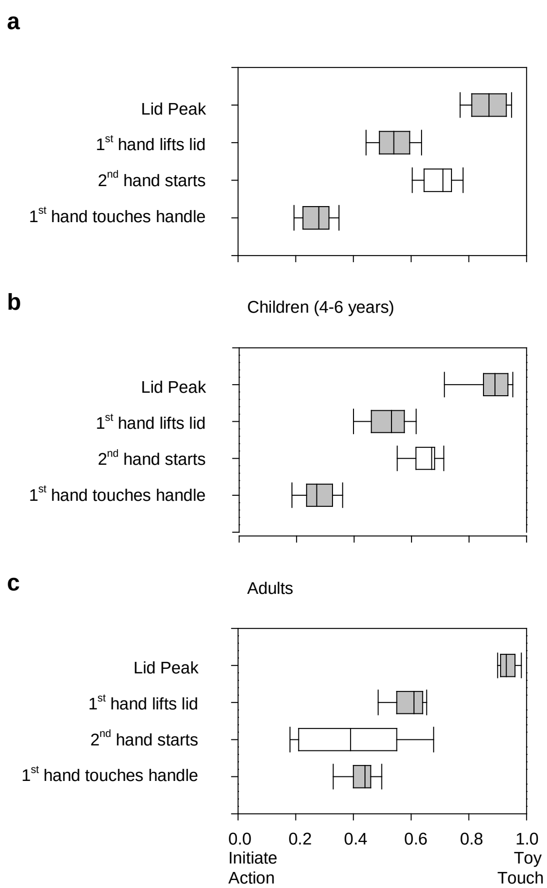

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Table 1. Summary of temporal event comparisons for older infants (24 – 29 months, N = 21), children (4 - 6, years, N = 17) and adults (N = 15).

	Median values (25th, 75th percentiles)			*P* values		
Temporal Parameter	Infants 24-29 months (N = 21)	Children 4-6 years (N = 17)	Adults (N = 15)	Infants – Children	Infants – Adults	Children – Adults
Total Duration (s)	2.10 (1.86, 2.28)	1.68 (1.51, 1.88)	1.37 (1.33, 1.65)	0.002*	0.000*	0.009*
Reach to grasp handle (s)	1.07 (0.96, 1.27)	0.88 (0.73, 1.09)	0.86 (0.73, 1.04)	0.011*	0.007*	0.682
Time to open lid (s)	0.62 (0.59, 0.73)	0.63 (0.52, 0.69)	0.49 (0.41, 0.55)	0.296	0.007*	0.004*
Total Lid-hand Time (s)	1.74 (1.54, 2.0)	1.50 (1.32, 1.65)	1.27 (1.21,1.57)	0.005*	0.000*	0.082
Initiation Delay (s)	1.41 (1.29, 1.69)	1.16 (0.94, 1.28)	0.61 (0.26,0.84)	0.000*	0.000*	0.000*
Lid-toy hand delay (s)	0.35 (0.24, 0.46)	0.21 (0.15, 0.28)	-0.25 (-0.52, -0.04)	0.006*	0.000*	0.000*
Toy-hand Time (s)	0.61 (0.52, 0.71)	0.57 (0.50, 0.67)	0.76 (0.65, 0.99)	0.746	0.001*	0.001*
Goal Synchronization (s)	0.25 (0.13, 0.38)	0.16 (0.12, 0.28)	0.09 (0.05, 0.12)	0.176	0.000*	0.001*
Normalized Overlap (%)	19.0 (10.0, 24.0)	25.0 (20.0, 31.0)	59.0 (40.0, 70.0)	0.026*	0.000*	0.000*

Median values and 25th and 75th percentiles are shown along with the *P* values of U from pair-wise Mann-Whitney tests.

* Significant at 0.05 level

Table 2. Frequency of hand preferences (%) for completely differentiated bimanual performance (Level 3) as a function of age.

Age Group (months)	Total infants *N* *N*	Performing at Level 3 *N* *N*	Hand Preference (% Group) (% Group)			Binomial Test difference from (R-L) = (L-R) *P*=
			Consistent R-L	Consistent L-R	Inconsistent	
12-14	51	10	60.0	40.0	0.0	0.754
15-17	73	37	56.8	27.0	16.2	0.071
18-20	27	21	57.1	19.1	23.8	0.077
21-23	26	20	45.0	30.0	25.0	0.607
24-26	24	22	50.0	31.8	18.2	0.332
27-29	25	19	84.2	5.3	10.5	<0.001*

Infants categorized as *Consistent R-L* use the right hand to lift the lid and the left hand to remove the toy for both trials with the reverse preference for infants categorized as *Consistent L-R*. Infants categorized as *Inconsistent* exhibit different hand preferences for the two trials. The very youngest infants (9-11 months, N = 27) have been excluded as so few were able to perform two trials of the task at Level 3.

* Significant at 0.05 level

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