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Increasing task precision demands reveals that the reach and grasp remain subject to different perception-action constraints in 12-month-old human infants

Jenni M. Karl*, Braydon M. Slack, Alexis M. Wilson, Christopher A. Wilson, Marisa E. Bertoli

Department of Psychology, Thompson Rivers University, Kamloops, BC, Canada

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ABSTRACT

The reach and grasp follow different developmental trajectories, but are often considered to have achieved nearly adult-like precision and integration by 12 months of age. This study used frame-by-frame video analysis to investigate whether increasing precision demands, by placing small reaching targets on a narrow pedestal rather than on a flat table, would influence the reach and grasp movements of 12-month-old infants in a complementary or differential fashion. The results reveal that placing the target atop a pedestal impaired the infants's ability to direct an appropriate digit towards the small target, but did not produce a corresponding decrease in the frequency with which they used an index-thumb pincer grip to grasp the target. This was due to the fact that, although infants were more likely to contact the target with a suboptimal part of the hand in the pedestal condition, a greater proportion of these suboptimal contacts ultimately transitioned to a successful index-thumb pincer grip. Thus, increasing task precision demands impaired reach accuracy, but facilitated index-thumb grip formation, in 12-month-old infants. The differential response of the reach and grasp to the increased precision demands of the pedestal condition suggests that the two movements are not fully integrated and, when precision demands are great, remain sensitive to different perception-action constraints in 12-month-old infants.

1. Introduction

Prehension, the ability to reach out and grasp an object in a single hand, features prominently in the human experience. It can be behaviorally dissociated into at least two movements, a reach and a grasp (Jeannerod, 1981; Karl, Sacrey, Doan, & Whishaw, 2012; Karl & Whishaw, 2013; Schettino, Adamovich, & Tunik, 2017; van de Kamp & Zaal, 2007; Whishaw & Karl, 2019; Zaal & Bongers, 2014). The reach consists of an initial, partially ballistic, phase that transports the hand to the general location of the target followed by a visually-controlled phase that positions an appropriate part of the hand on the target (Arbib, Iberall, & Lyons, 1985; Jeannerod, 1981; Woodworth, 1899). Likewise, the grasp consists of a shaping phase, in which the digits open and shape to match the configuration of the target, followed by a closing phase in which the digits flex and close for target acquisition. In healthy adults, the two movements are often integrated into a single seamless act when reaching for a clearly defined target under foveal visual control. Nonetheless, other sensory modalities such as hapsis, audition, and olfaction, as well as remembered and imagined percepts, can also

* Corresponding author at: Department of Psychology, Thompson Rivers University, 805 TRU Way, Kamloops, BC, V2C 0C8, Canada.
E-mail address: jkarl@tru.ca (J.M. Karl).

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elicit and guide the reach and grasp in an integrated or dissociated fashion depending on task demands (Hall, Karl, Thomas, & Whishaw, 2014; Karl et al., 2012a; Karl, Sacrey, Doan, & Whishaw, 2012; Karl, Schneider, & Whishaw, 2013).

The neural substrates that enable the reach and grasp are also partly dissociable (2018, Cavina-Pratesi, Ietswaart, Humphreys, Lestou, & Milner, 2010, 2010b; Graziano, Taylor, & Moore, 2002; Kaas & Stepniewska, 2016; Kastner, Chen, Jeong, & Mruczek, 2017; Konen, Mruczek, Montoya, & Kastner, 2013; Vesia & Crawford, 2012; Vesia, Bolton, Mochizuki, & Staines, 2013). The reach is enabled largely by a dorsomedial parietofrontal channel involving the human parietal reach region (hPRR) and dorsal premotor cortex (PMd). In contrast, a dorsolateral parietofrontal channel consisting of the human anterior intraparietal sulcus (hAIP) and the ventral premotor cortex (PMv) is largely involved in generating grasp movements. In humans, selective lesions to one channel or the other can produce isolated effects on only one movement (e.g., Binkofski et al., 1998; Cavina-Pratesi, Ietswaart et al., 2010; Cavina-Pratesi, Connolly, & Milner, 2013). Still there is some overlap as the dorsomedial channel plays an important role in integrating the two movements into a seamless act when the hand must open, preshape, and begin to close in anticipation of target contact (Vesia et al., 2017). Finally, corticospinal projections from the parietofrontal reach and grasp areas, in coordination with other descending motor control pathways, contribute to reach and grasp execution (Alstermark & Isa, 2012; Isa, 2019).

That the reach and grasp are dissociable movements is further evidenced by the fact that the two movements are highly dissociated throughout early development (Karl, Sacrey, & Whishaw, 2018). From birth, infants generate a large number of semi-spontaneous movements. These include pre-reach movements, which involve extending the arm and an open or fisted hand to touch the infant's own body or distal objects (DiMercurio, Connell, Clark, & Corbetta, 2018; Thomas, Karl, & Whishaw, 2015; von Hofsten, 1984; Williams, Corbetta, & Guan, 2015), and pre-grasp movements, which consist of independent digit movements, whole-hand grips, precision grips, and pincer grips that may be vacuous, applied to the infant's own body (Babik, Galloway, & Lobo, 2017; Lobo & Galloway, 2013; Wallace & Whishaw, 2003), or applied to an object placed directly into the infant's hand by an experimenter (1989, Case-Smith, Bigsby, & Clutter, 1998; Rochat, 1987). These movements allow young infants to learn about the spatial organization of their own bodies as well as the sensory and functional consequences of moving their limbs in various ways (Corbetta, Williams, & Haynes, 2016; Schlesinger & Parisi, 2001). They also likely facilitate the refinement of distinct muscle synergies and neural representations for separable reach and grasp movements, which may then serve as developmental precursors for functional reach and grasp movements in adulthood (Dominici et al., 2011; Juett & Kuipers, 2019; Thomas et al., 2015).

When infants do begin to reach and grasp for distal objects at about 5 months of age they execute the two movements in a sequential fashion (Karl & Whishaw, 2014). Initially, a relatively fast and jerky reach, characterized by multiple changes in speed and direction (von Hofsten, 1991), is accompanied by exaggerated opening of the digits such that contact with the target is accomplished with an inappropriate part of the hand. Only after target contact does the infant adjust the orientation and configuration of the hand to match the spatial properties of the target and finally close the hand in order to grasp it (Karl & Whishaw, 2014; McCarty & Ashmead, 1999; McCarty, Clifton, Ashmead, Lee, & Goubet, 2001; Schum, Jovanovic, & Schwarzer, 2011; von Hofsten & Rönnqvist, 1988; Witherington, 2005). Thus, the reach and grasp remain largely dissociated and highly dependent on haptic guidance, first to establish initial contact with the object and then to configure the hand in order to grasp it.

Subsequently, the reach and grasp continue to follow different developmental trajectories in relation to the rate at which they achieve adult-like precision and fluidity. Between 9 and 12 months of age infants improve the speed and direction of their reach movement, resulting in much smoother reach trajectories (Berthier & Keen, 2006; von Hofsten, 1991; Sacrey, Karl, & Whishaw, 2012). They also consistently orient their hand prior to target contact (Morrongiello & Rocca, 1989; Schum et al., 2011; von Hofsten & Fazel-Zandy, 1984) and they more reliably contact the target with a part of the hand that is conducive to immediate grasping of the target (Karl & Whishaw, 2014; Karl, Wilson, Bertoli, & Shubear, 2018). At the same time, infants will begin to scale hand opening to target size, but they continue to exaggerate the opening of the hand and greatly delay the onset of grasp closure relative to adults (Karl & Whishaw, 2014; von Hofsten & Rönnqvist, 1988). Thus, by one year of age infants integrate the reach and grasp under visual control, but continue to rely on tactile cues associated with target contact to mediate the grasp (Sacrey, Karl, & Whishaw, 2012).

Early maturationist theories attempted to explain the dissociable nature of the reach and grasp during infancy as the result of a linear developmental progression constrained by neuromaturation (e.g., Gesell, 1952, 1988). According to this view, initially crude reaching movements associated with reflexive whole-hand grasps were mediated by relatively immature descending motor control systems. Then, as increasingly sophisticated descending motor control systems matured, refined reach movements became associated with increasingly dexterous hand movements such as power, and eventually precision and pincer grips (Elliott & Connolly, 1984; Halverson, 1931, 1932; Hohlstein, 1982). This view gained additional traction with subsequent reports that the apparently earlier maturation of the reach could be attributed to earlier maturation of the multisynaptic corticospinal projections that innervate more proximal forelimb muscles for reaching whereas the prolonged development of the grasp was attributed to the delayed maturation of monosynaptic corticospinal projections that innervate the distal muscles of the hand and digits (Lawrence & Hopkins, 1976; Martin, 2005). Jean Piaget (1952) proposed that integration of the reach and the grasp required a significant amount of experience and learning. He argued that, as infants aged, they would learn to use sensory feedback to acquire voluntary control over their initially exploratory movements and to eventually integrate them together into a seamless reach-to-grasp action. While Piaget and others (Bushnell, 1985; McDonnell, 1979; White, Castle, & Held, 1964) acknowledged that other modalities were important, they suggested that vision played the most prominent role in refining early reach and grasp movements and in eventually integrating them into a cohesive reach-to-grasp movement.

Building on Piaget's work, contemporary proponents of dynamic systems theory (e.g., Newell, Scully, McDonald, & Baillargeon, 1989; Thelen & Smith, 1994; Williams, Corbetta, & Cobb, 2015), posit that the development of mature reach-to-grasp behavior proceeds, not in a linear fashion dictated solely by neuromaturation, but via a series of highly constrained perception-action loops. In simplest terms, the infant generates an initially crude exploratory action and concurrently perceives the functional consequences of generating that action. If the consequences are perceived as valuable, then that action, and the neural processes that enabled it, are selectively refined, reinforced, and repeated in the future; actions that do not generate valuable consequences are not. Most importantly, numerous factors constrain the type of actions an infant can produce, and how the consequences of those actions are perceived, during any particular phase of development. These include the extent of neuromaturation and previous experience, but also current physiological state, environmental context, and task demands. The interplay of these various constraints produces a non-linear developmental progression in which some reach and grasp abilities may emerge, appear to regress, and then re-emerge at a later stage of development. As such, simple precursor movements, such as pre-reach and pre-grasp movements may be subject to differential constraints, refinement, and reinforcement during early infancy. As the infant ages, however, individual constraints on the reach and grasp change and novel perception-action loops that target the reach and grasp concurrently must necessarily emerge in order to facilitate their integration into a cohesive reach-to-grasp movement.

Most developmental scientists currently ascribe to the contemporary view that perception-action loops are the primary driver of prehension development in human infants, but the fact that the reach and grasp follow dissociable developmental profiles is still often attributed to differences in the rate of maturation of the corticospinal tracts for proximal versus distal musculature of the arm and hand. This remains a prominent view, despite substantial evidence that infants between 2 and 6 months of age can perform independent digit movements as well as a variety of precision and pincer grasp movements that are responsive to tactile feedback (Butterworth, Verweij, & Hopkins, 1997; Lee, Liu, & Newell, 2006; Newell et al., 1989; Wallace & Whishaw, 2003); functional monosynaptic corticospinal projections that innervate the hands and digits are present at birth (Eyre, Miller, Clowry, Conway, & Watts, 2000); precision grasping movements can be mediated by cortical commands transmitted via non-monosynaptic corticospinal projections in both healthy non-human primates (Kinoshita et al., 2012) and non-human primates with corticospinal tract lesions (Darling et al., 2014; Isa, 2019; Tohyama et al., 2017), and; precision grasping movements are more likely mediated by neural and muscle synergies rather than the independent digit movements initially thought to be enabled by the monosynaptic corticospinal projections (Hao et al., 2017; Overduin, d'Avella, Roh, Carmena, & Bizzi, 2015). Currently, the extent to which non-neuromaturational constraints contribute to the dissociable developmental profiles of the reach and grasp, as well as their eventual integration, have not been fully explored.

One constraint that may modulate the extent of reach and grasp integration at 12 months of age is the degree of precision required to successfully acquire a small target object. When reaching for small targets, such as Cheerios resting on a flat surface, both adults and 12-month-old infants tend to contact the underlying table upon which the target is resting before they contact the target itself (Karl, Wilson et al., 2018). For adults, initial table contact appears coincidental and inconsequential, but for infants it seems to enhance their ability to subsequently direct an appropriate pincer digit, defined as the distal pad of the thumb or index finger, towards the nearby target. The aim of the present study was to test these prior correlational findings by increasing the precision demands of the task by placing the target atop a narrow pedestal. We hypothesized that if 12-month-old infants do rely on contact with the underlying table to direct their pincer digits toward the target, then placing the target atop the pedestal should impair digit-to-target contact in infants, but not adults. Furthermore, we hypothesized that if the two movements had achieved an adult-like level of integration, then the reach and the grasp should respond in a complementary fashion to the increased precision demands of the pedestal condition. That is, impairments in digit-to-target contact should coincide with a decrease in the subsequent formation of index-thumb pincer grips. Alternatively, if the reach and grasp are not fully integrated, then we would expect that the two movements would respond differently to the increased precision demands. That is, placing the target atop the pedestal might impair digit-to-target contact, but not the subsequent formation of index-thumb pincer grips, in 12-month-old infants.

2. Materials and methods

2.1. Participants

Twenty-one adults (10 male, 11 female, mean age = 19.4 ± 0.73 years) were recruited from introductory psychology classes at Thompson Rivers University and thirty-four 12-month-old infants (16 male, 18 female, mean age = 369 ± 4.54 days) were recruited through online advertisements. All participants had normal vision or wore contact lenses or glasses to correct their vision to normal; had no history of sensory, motor, or neurological disorders; were not allergic to Cheerios, and; if applicable, were right-handed for writing. Adult participants received two percent credit towards an undergraduate psychology class, while infant caregivers received a $25 gift card to The Children's Place clothing store for their participation. All procedures were approved by the Thompson Rivers University Research Ethics for Human Subjects Board.

2.2. Procedures

Adults were randomly assigned to one of two experimental conditions, Table (n = 11) or Pedestal (n = 10). They were then seated in an armless, height-adjustable, chair in front of a glass table, with their feet positioned flat on the floor. The glass table was semi-transparent and did not act as a reflective surface when viewed from the participant's perspective. Participants were instructed to place their right hand in an open and comfortable position with their palm facing down on their upper right thigh at the beginning of each trial. In the Table condition (Fig. 1A), the target, a single ring-shaped piece of cereal (Cheerio, mean diameter = 1.27 cm), was placed directly on the surface of the table and aligned to the participant's midline at a reaching distance normalized to the length of the participant's fully extended right arm. In the Pedestal condition (Fig. 1B) the target was placed atop a 10 cm x 2.5 cm^2 semi-transparent pedestal positioned on top of the table. In both conditions, once the target was in place, participants waited for the

Fig. 1. The experimental setup in the table (A) and pedestal (B) conditions. Visible in the table condition are the target, the semi-transparent tabletop and the position of the three video cameras. Note that the bottom-up view was captured using a mirror placed underneath the table. Visible in the pedestal condition are the target, now placed atop the pedestal, and the infant high chair. Note that the infant is secured only by the waist straps to allow for full movement of the arms.

experimenter to provide a verbal 'one, two, three, go,' command, at which point they used their right hand to reach out, grasp, and withdraw the Cheerio to the mouth for eating. Participants were instructed to perform the task as naturally as possible and to return their hand to the start position on top of their upper right thigh at the end of each trial. Each adult participant completed a total of twenty trials.

Infants were randomly assigned to one of three experimental conditions, Table (n = 17), Pedestal (n = 10), or Adjusted Pedestal (n = 7). The experimental procedures for infants were identical to that of adults, with the following exceptions. First, infants were seated and buckled into a safety-standard, tray-less, height-adjustable highchair in front of the same table. The highchair allowed for free range of movement of the arms, upper waist, and head. In the Table condition, the height of the highchair was adjusted so that infants could comfortably rest their hands on the table's surface with their elbows bent at an approximately 90° angle. The target was aligned to the infant's midline at a reaching distance normalized to the length of the infant's fully extended right arm. In the Pedestal condition, the target was placed atop a 10 cm x 2.5 cm^2 semi-transparent pedestal, which was positioned on top of the table. In the Adjusted Pedestal condition, the target was placed atop the same pedestal and the highchair was raised an additional 10 cm to account for the increased height of the target. Second, the experimenter encouraged the infants to start each trial with their hands positioned in their lap by gently guiding the infant's hand toward the lap prior to placing the target on either the table or pedestal. Third, infants were not able to follow a verbal 'one, two, three, go' signal and thus, reached for the Cheerio at any time that they were willing and with whichever hand that they preferred. Fourth, after grasping the target, most infants withdrew the Cheerio to the mouth and ate it. If an infant did not immediately eat the Cheerio, they were allotted approximately 20 s to handle the Cheerio, after which they were encouraged to return it to the experimenter, who discarded it. Sixth, the infants' guardians remained present for the duration of the study. If infants began to fuss or display any agitation, the testing session was ended immediately and only complete reaching trials in which the infant successfully reached and grasped the Cheerio were included in the analysis. Thus, infants performed a maximum of twenty-five trials to account for the fact that a number of trials were likely to be excluded from analysis due to knocking the Cheerio off of the pedestal.

Three digital video cameras (Sony HD Video Recording HDRPJ440 PJ Handycam Camcorder), operating at a shutter speed of 1/250^{th} of a second and 30 frames per second, recorded the participant's reaching movement from a front, lateral, and bottom-up view. Transparent 1 cm^2 graph paper attached to the underside of the table and a wooden block that was presented to each camera at the start of each testing session were used to convert distances measured on the video record from pixels to millimeters. At the start of

Table 1
Number of Reaches Included in Final Analysis.

Age	Condition	Minimum	Maximum	Mean	Total
Infants	Table	6	25	15.2	258
	Pedestal	9	22	16.2	270
Adults	Table	19	20	19.9	219
	Pedestal	16	22	18.9	189
Total					936

Note. Infants in the Pedestal and Adjusted Pedestal conditions are combined in this table.

each testing session the experimenter used the tip of his/her index finger to quickly tap the top of the table/pedestal, providing a temporal cue to all video cameras, that was then used to manually trim all three videos to a common start frame, thereby time-synchronizing them, in the video editing software Adobe Premiere Pro (www.adobe.com/premiere).

Once seated in the highchair, infants engaged in a number of movements that appeared exploratory in nature. These included using the arms and hands to swat, bang, slap, wipe, push, and/or scratch the top and edges of the table and pedestal. They also often contacted the underside of the table with their legs and feet and they frequently visually inspected the edges of the table and pedestal as well as visible smudges on the surface of the table and pedestal. Thus, although the table and pedestal were semi-transparent, the infants had ample opportunity to learn, through both visual and tactile experience, about the structural features of both and were clearly aware of their presence both prior to and throughout the experiment. In addition, the infants did occasionally knock the Cheerio off of the pedestal without successfully grasping it. These exploratory movements and movements that knocked the Cheerio off the pedestal were intentionally excluded from analysis. Only arm and hand movements that were clearly directed towards the target, resulted in contact with the target or the table/pedestal within the immediate vicinity of the target, and that ultimately resulted in successful grasping of the target were considered true “reaching” movements and included in the present analysis. In addition, previous work has revealed that the reach and grasp movements of 12-month-old infants are not significantly different when reaching to a Cheerio on a semi-transparent table compared to an opaque table (Karl, Wilson et al., 2018). Table 1 indicates the minimum, maximum, mean, and total number of reaches that were included in the final analysis.

2.3. Frame-by-frame video analysis

Frame-by-frame analysis of the time-synchronized video records (Karl, Kuntz et al., 2018) was used to score a number of behavioral measures. Measures of movement timing included: *1) Movement Start*, defined as the frame at which the hand made its first discernable movement towards the target object resulting in contact with either the target or the nearby table/pedestal surface; *2) Target Contact,* defined as the frame of first contact between the hand and the target object, and; *3) Final Grasp,* defined as the frame that digit closure was complete, resulting in a secure grasp and hold on the target object. From these, *Reach Duration*, defined as the time from movement start to target contact, and *Grasp Duration,* defined as the time from target contact to final grasp, were calculated.

Additional measures taken at the time of target contact included: *1) Terminal Reach Velocity,* defined as the mean velocity (m/s) of the most proximal knuckle of the index finger during the three video frames preceding target/table/pedestal contact as measured using the kinematic software Kinovea (www.kinovea.org). On a small number of trials infants initially missed the target and had to reverse their reach movement to return to the target location. In these instances the three video frames prior to the first pass of the target were used to calculate terminal reach velocity; *2) Aperture*, defined as the distance between the central tip of the index finger and the central tip of the thumb at the time of target contact as measured from the bottom-up camera view, and; *3) Part of Hand to Contact Target*, healthy sighted adults almost always use the pads of either the thumb or index finger to contact the target and to subsequently grasp it. Thus, we calculated the proportion of trials that each participant used the distal pads of either the thumb or index finger to contact the target.

Measures taken at the time of final grasp consisted of *Grip Type,* defined as the grip configuration used to grasp and lift the target from the table/pedestal, which was coded as: *1) D1D2 pincer grip*, defined by gripping the target between the distal pads of the thumb and index fingers; *2) D1D3 pincer grip*, defined by gripping the target between the distal pads of the thumb and middle fingers; *3) Tripod grip*, defined by gripping the target between the distal pads of the thumb, index, and middle fingers; or *4) Alternative grip*, defined by gripping the target with any other hand configuration.

2.4. Inter-rater reliability

A subset of 5 trials per age and condition (n = 20 trials) were scored by two independent but trained experimenters (Hallgren, 2012). The inter-rater reliabilities for the following variables were assessed using two-way, mixed, average-measures intraclass correlation co-efficients (ICC) with absolute agreeability: *Frame of Movement Start* ICC = 1.00, *Frame of Target Contact* ICC = 1.00, *Frame of Final Grasp* ICC = 1.00, and *Aperture* ICC = 0.984. The inter-rater reliabilities for the following variables were assessed using Cohen’s (1960) kappa: *Part of Hand to Contact Target,* $\kappa = 0.82$, $p < 0.0005$ and *Grip Type,* $\kappa = 1.00$, $p < 0.0005$. These analyses indicated that the coding method used in the present study produced very high inter-rater reliability and that all measures were scored similarly by different raters.

Table 2
Infant Reaches in the Pedestal vs. Adjusted Pedestal Conditions.

Dependent Variable	Pedestal Mean (*SD*)	Adjusted Pedestal Mean (*SD*)	*t* value	*p* value
Reach Duration	35.43 (*8.27*)	36.34 (*5.78*)	0.251	0.806
Grasp Duration	40.54 (*26.72*)	26.26 (*8.47*)	1.356	0.195
Terminal Velocity	0.21 (*0.09*)	0.14 (*0.09*)	1.482	0.159
Aperture	3.43 (*1.17*)	3.16 (*0.67*)	0.558	0.585
D1 or D2 Contact	0.35 (*0.29*)	0.37 (*0.17*)	0.160	0.875
D1D2 Pincer Grip	0.32 (*0.31*)	0.25 (*0.13*)	0.537	0.599
D1D3 Pincer Grip	0.06 (*0.07*)	0.08 (*0.07*)	0.629	0.539
Tripod Grip	0.09 (*0.09*)	0.11 (*0.12*)	0.334	0.743
Alternative Grip	0.52 (*0.10*)	0.55 (*0.19*)	0.214	0.834

Note. Infants in the two conditions did not differ significantly from each other on any of the dependent variables.

3. Results

A detailed description of the results of adult and infant participants in the table condition have been reported previously (Karl, Wilson et al., 2018) so the current analysis focused on the comparison of participants in the table condition versus the pedestal condition. Statistical analyses were conducted using SPSS (v. 22). All raw data were transformed into either a mean score (reach duration, grasp duration, terminal reach velocity, aperture) or a proportion score (part of hand to contact target, grip type) for each participant. First, independent t-tests were used to compare infant performance on all measures in the Pedestal vs. Adjusted Pedestal conditions. As there were no significant differences between infants in these two conditions (Table 2), their data were combined for all subsequent analyses. Second, the data from adult and infant participants were analyzed separately using analyses of variance (ANOVAs) to determine whether any gender differences existed for any of the dependent variables. This analysis revealed that male and female infants employed D1D2 pincer grips with equal frequency; nonetheless, when they did not use a D1D2 pincer grip, male and female infants differed slightly in the extent to which they employed D1D3, tripod, and alternative grips ($p = 0.013$) with male infants slightly more likely to employ alternative grips than female infants. Data from male and female participants were combined for all subsequent analyses. All transformed scores were treated as dependent variables in separate two-way ANOVAs with Age (infants vs. adults) and Condition (table vs. pedestal) as independent between-subjects variables. A p value of < 0.05 was considered significant and post hoc analyses were subject to bonferroni correction. The results of this analysis are displayed in Table 3.

Fig. 2A illustrates results for the measure of reach duration, that is, the amount of time required to reach out and establish tactile contact with the target. The statistical analysis revealed a significant effect of Age [$F(1,51) = 10.985, p = 0.002$, partial $\eta^2 = 0.177$], but not Condition [$F(1,51) = 1.269, p = 0.265$, partial $\eta^2 = 0.024$] or Age X Condition [$F(1,51) = 0.740, p = 0.394$, partial $\eta^2 = 0.014$], for reach duration. Thus, infants took longer to reach out and contact the Cheerio than adults did, regardless of whether the Cheerio was located on the table or pedestal. Placing the Cheerio atop the pedestal did not significantly increase or decrease the reach duration of either infant or adult participants.

Fig. 2B illustrates results for the measure of grasp duration, that is, the amount of time required to transition from initial contact

Table 3
ANOVA Results.

Dependent Variable	*df*	*F* value	*p value*	Partial η^2
Main Effect of Age				
Reach Duration	1,51	10.985	0.002**	0.177
Grasp Duration	1,51	47.018	0.000***	0.480
Terminal Velocity	1,51	7.096	0.010**	0.122
Aperture	1,51	41.719	0.000***	0.450
D1 or D2 Contact	1,51	57.785	0.000***	0.531
D1D2 Pincer Grip	1,51	27.995	0.000***	0.354
Main Effect of Condition				
Reach Duration	1,51	1.269	0.265	0.024
Grasp Duration	1,51	0.258	0.614	0.005
Terminal Velocity	1,51	36.857	0.000***	0.420
Aperture	1,51	0.225	0.637	0.004
D1 or D2 Contact	1,51	2.474	0.122	0.046
D1D2 Pincer Grip	1,51	0.035	0.853	0.001
Interaction Effect of Age x Condition				
Reach Duration	1,51	0.740	0.394	0.014
Grasp Duration	1,51	0.174	0.678	0.003
Terminal Velocity	1,51	0.339	0.563	0.007
Aperture	1,51	0.063	0.803	0.001
D1 or D2 Contact	1,51	11.998	0.001***	0.190
D1D2 Pincer Grip	1,51	1.002	0.322	0.019

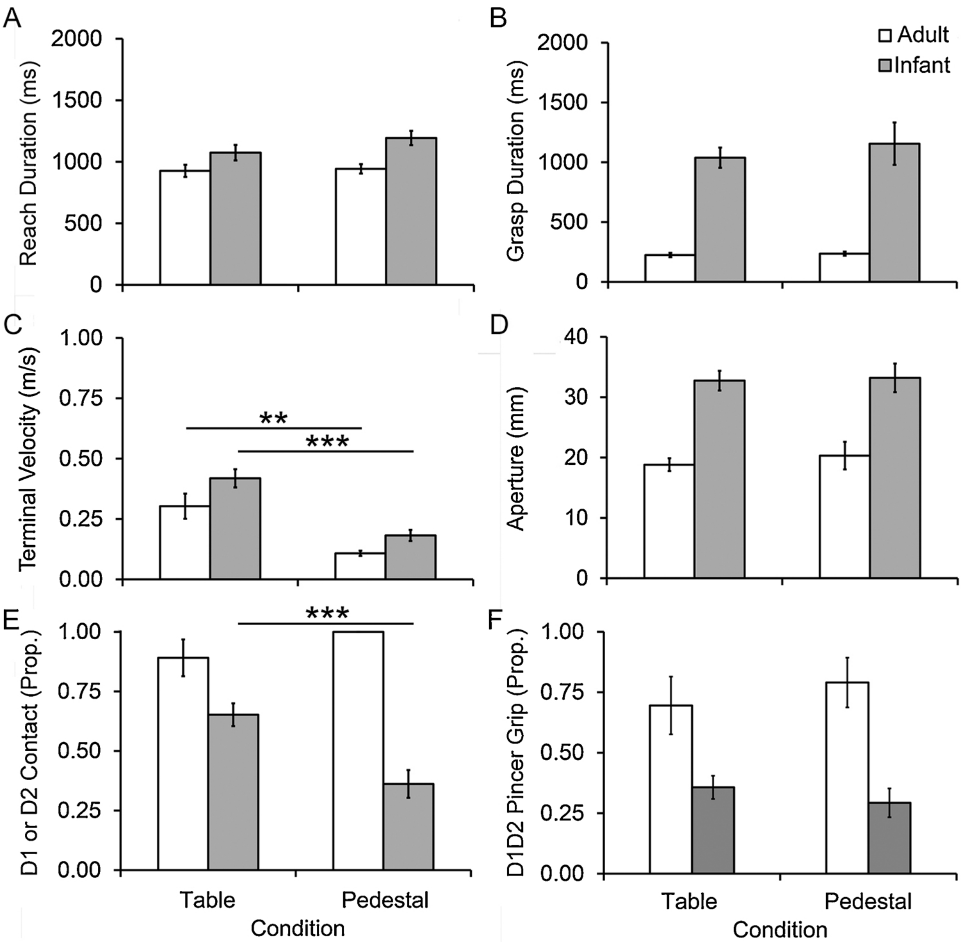

Fig. 2. Results of the frame-by-frame video analysis (mean ± SE). Reach durations (A); grasp durations (B); Terminal reach velocity (C); Aperture at target contact (D); Proportion of trials on which a pincer digit (pads of D1 or D2) was used to make first contact with the target (E); Proportion of trials in which a D1D2 pincer grip was used grip the target (F). $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

to final grasp of the target. The statistical analysis revealed a significant effect of Age [F(1,51) = 47.018, $p < 0.0005$, partial $\eta^2 = 0.480$], but not Condition [F(1,51) = 0.258, $p = 0.614$, partial $\eta^2 = 0.005$] or Age x Condition [F(1,51) = 0.174, $p = 0.678$, partial $\eta^2 = 0.003$] for grasp duration. Thus, infants took longer to grasp the Cheerio after touching it than adults did, regardless of whether the Cheerio was located on the table or the pedestal. Placing the Cheerio atop the pedestal did not significantly increase or decrease grasp duration for either infants or adults.

Fig. 2C illustrates results for the measure of terminal reach velocity, that is, the speed of the hand just prior to target contact (or initial pass of the target). The statistical analysis revealed significant effects of Age [F(1,51) = 7.096, $p = 0.010$, partial $\eta^2 = 0.122$] and Condition [F(1,51) = 36.857, $p < 0.0005$, partial $\eta^2 = 0.4420$], but not Age x Condition [F(1,51) = 0.339, $p = 0.420$], for terminal reach velocity. Thus, infants displayed a greater terminal reach velocity than adults, regardless of whether the target was located on the table or pedestal. Nonetheless, placement of the Cheerio atop the pedestal led to an almost equivalent reduction in terminal reach velocity in both infants ($p = 0.003$) and adults ($p = 0.001$), indicating that, like adults, infants were able to reduce the speed of their hand on approach to the target when it was located atop the pedestal.

Fig. 2D illustrates results for the measure of index-thumb aperture at the time of target contact. The statistical analysis revealed a significant effect of Age [F(1,51) = 41.719, $p < 0.0005$, partial $\eta^2 = 0.450$], but not Condition [F(1,51) = 0.225, $p = 0.637$] or Age x Condition [F(1,51) = 0.063, $p = 0.803$, partial $\eta^2 = 0.001$], for aperture. Thus, infants maintained a larger index-thumb aperture at the time of contact with the Cheerio than adults did, regardless of whether the Cheerio was located on the table or the pedestal. Placing the Cheerio atop the pedestal did not affect the hand aperture at the time of target contact for either infants or adults.

Fig. 2E illustrates the proportion of trials that participants used a pincer digit, defined as the distal pad of either the thumb (D1) or index finger (D2), to make first contact with the target. The statistical analysis revealed significant effects of Age [F(1,51) = 57.785, $p < 0.0005$, partial $\eta^2 = 0.531$] and Age x Condition [F(1,51) = 11.998, $p = 0.001$, partial $\eta^2 = 0.190$], but not Condition [F(1,51) = 2.474, $p = 0.122$], for part of hand to contact target. Thus, when the target was located on the table, infants were slightly less likely than adults to contact it with a pincer digit. Placement of the target atop the pedestal did not affect how adults contacted

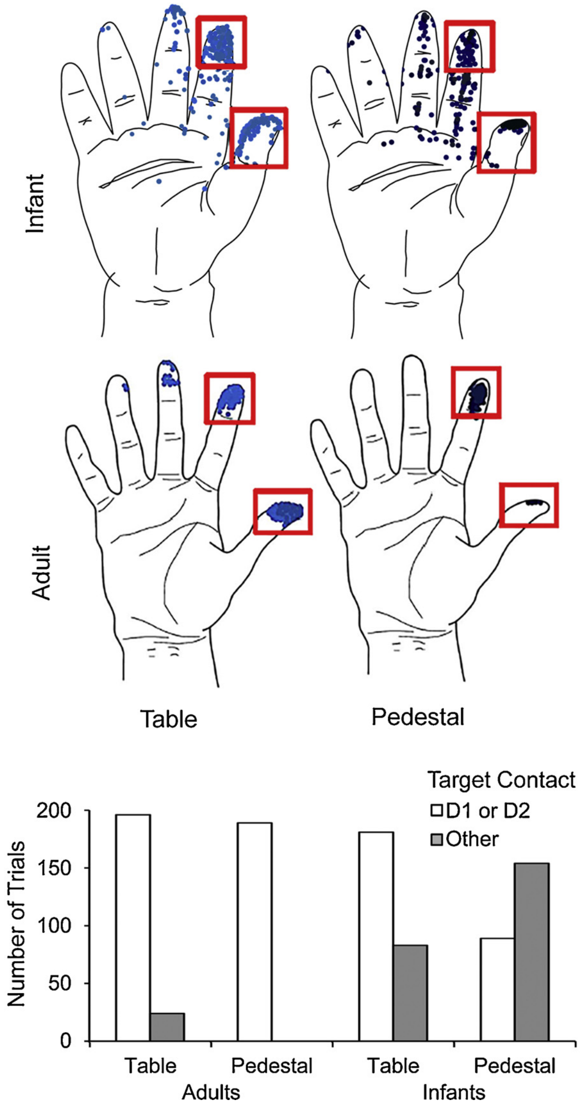

Fig. 3. Topographical maps (top) showing the part of the hand to make first contact with the target. Each dot represents the part of the hand to make first contact the Cheerio. The number of trials (bottom) in which either the pads of D1 or D2 or another part of the hand was used to make first contact with the Cheerio.

the target, but significantly reduced the frequency with which infants used the thumb or index finger to contact the target (p = 0.009).

Fig. 3 illustrates the part of the hand participants used to contact the Cheerio in the table and pedestal conditions. Adults almost always contacted the Cheerio with the distal pads of the thumb or index finger, regardless of whether the target was located on the table or pedestal. While infants appeared to approximate this adult-like behaviour when the Cheerio was located on a table, the true extent to which they differ from adults was revealed when the precision demands of the task were increased by placing the Cheerio atop the pedestal. In this condition, infants were much more likely to use some other part of the hand to contact the target.

Fig. 2F illustrates the mean proportion of trials that participants used an index-thumb (D1D2) pincer grip to grasp the target. The statistical analysis revealed a significant effect of Age [$F(1,51) = 27.995$, $p < 0.0005$, partial $\eta^2 = 0.354$], but not Condition [$F(1,51) = 0.035$, $p = 0.853$] or Age x Condition [$F(1,51) = 1.002$, $p = 0.322$, partial $\eta^2 = 0.019$], for proportion of D1D2 pincer grips. Thus, infants employed a D1D2 pincer grip significantly less than adults in both the table and pedestal conditions. Placement of the Cheerio atop the pedestal had no significant effect on the frequency with which either infants or adults used the D1D2 pincer grip to grasp the target.

Fig. 4 provides a more detailed description of the grip types used by infant and adult participants to acquire the Cheerio in the table and pedestal conditions. As mentioned above, adults almost always used a D1D2 pincer grip to grasp the target. On occasions when a D1D2 was not used, adults tended to adopt a tripod grip. They almost never employed a D1D3 pincer grip or an alternative grip, regardless of whether the Cheerio was located on the table or the pedestal. In contrast, infants were most likely to employ an

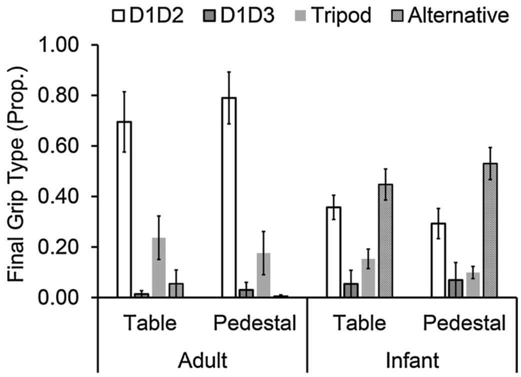

Fig. 4. Detailed grip configuration profiles of adults and infants when reaching to grasp Cheerios off of a table versus a pedestal.

alternative grip. Their second preference was to use a D1D2 pincer grip. Infants employed D1D3 and tripod grips very infrequently, regardless of whether the Cheerio was located on the table or the pedestal. Thus, the composition of the grip profile differed significantly between infant and adult participants with infants splitting their use between alternative and D1D2 grips, whereas adults clearly preferred the use of a D1D2 pincer grip. Placing the Cheerio atop the pedestal did not significantly alter the grip profile of either infant or adult participants.

Surprisingly, placing the Cheerio atop the pedestal reduced the frequency with which infants used the distal pad of the thumb and/or index finger to contact the target, but did not produce a corresponding decrease in D1D2 pincer grips. Thus, we examined the frequency with which a D1D2 pincer grip was preceded by contact with either the thumb or index finger versus some other part of the hand. Interestingly, when adults formed a D1D2 pincer grip, this was always preceded by either a D1 or D2 contact (100 ± 0%), regardless of whether the target was located on the table or the pedestal. When infants reached for the target on the table their D1D2 grips were preceded by a D1D2 contact 87.44 ± 0.05% of the time. In contrast, when they reached for the target on the pedestal their D1D2 grips were preceded by a D1D2 contact only 74.25 ± 0.07% of the time. Thus, although infants in the pedestal condition were more likely to contact the target with an alternative part of the hand, they were also more likely to subsequently transition to a D1D2 pincer grip after that alternative contact.

In sum, infant reach and grasp movements differed significantly from adults on all measures, regardless of whether the target was located on the table or the pedestal. Increasing task precision demands by placing the target atop the pedestal produced only two significant effects. First, both adults and infants slowed the terminal velocity of their reach to a greater extent when reaching for the target atop the pedestal compared to the table. Second, the frequency with which infants used the distal pad of the thumb or index finger to contact the target decreased significantly when reaching for the target atop the pedestal. Despite this, infants employed an index-thumb (D1D2) pincer grip with equal frequency regardless of whether the target was located on the table or the pedestal because, in the pedestal condition, a greater proportion of trials in which the target was initially contacted with an alternative part of the hand were ultimately followed by a successful D1D2 pincer grip.

4. Discussion

Twelve-month-old infants and healthy adults reached to grasp Cheerios located on a flat table or a narrow pedestal with the expectation that the increased precision demands in the pedestal condition would reduce the digit-to-target contact accuracy of infants but not adults. The experimental design also allowed us to investigate whether the reach and grasp movements of 12-month-old infants would respond to the increased precision demands of the pedestal condition in a complementary or differential fashion. Our initial expectation was confirmed in that infants were less likely to contact the Cheerio with the distal pads of the thumb and/or index finger when it was located on the pedestal. Nonetheless, they continued to employ an index-thumb pincer grip with the same frequency as in the table condition. This was due to the fact that, although infants were more likely to contact the Cheerio with a suboptimal part of the hand in the pedestal condition, a greater proportion of these suboptimal contacts ultimately transitioned to a successful index-thumb pincer grip. Thus, placing the Cheerio atop the pedestal impaired reach accuracy, but facilitated pincer grasp formation, in 12-month-old infants. The differential response of the reach and grasp to the increased precision demands of the pedestal condition indicate that the two movements are not fully integrated and respond differently to high precision task constraints in 12-month-old infants.

The results of the present study indicate that the first phase of the reach, which is visually-elicited, largely ballistic, and serves to transport the hand to the general location of the target (Arbib et al., 1985; Jeannerod, 1981; Woodworth, 1899), may be approaching adult-like maturity by 12 months of age. This is evidenced by the fact that, while infants displayed slightly longer reach durations than adults, both infant and adult reach durations were unaffected by placing the target atop the pedestal. In addition, infants displayed slightly greater terminal reach velocities than adults, but both groups slowed their hand on approach to the target to a greater extent in the pedestal condition. These results are in agreement with previous research revealing that many gross aspects of the reach movement show significant developmental improvements by 12 months of age, including a reduction in the number of movement units that constitute the reach (Konczak, Borutta, Topka, & Dichgans, 1995; von Hofsten, 1991; Rönnqvist & Domellöf, 2006), better alignment of the arm and hand with the orientation of the target (Karl & Whishaw, 2014; von Hofsten & Fazel-Zandy, 1984), smoother acceleration and deceleration of the arm (Berthier & Keen, 2006), and altered kinematics in response to removing vision of the hand and the surround (Berthier & Carrico, 2010; Carrico & Berthier, 2007).

In contrast, the second phase of the reach, which is visually-guided and serves to position an appropriate part of the hand on the target (Arbib et al., 1985; Jeannerod, 1981; Woodworth, 1899), remained more sensitive to subtle changes in task precision demands in 12-month-old infants compared to adults. In both the table and pedestal condition, adults almost always consummated their reach movement by using the distal pads of either the thumb or index finger to contact the target as this type of contact is presumably most conducive to the subsequent formation of an index-thumb pincer grip. Infants, on the other hand, contacted the target with the thumb or index finger significantly more reliably when the target was located on the table as compared to the pedestal. This suggests that the second phase of the reach is not yet fully mature as infants, but not adults, likely rely on contact with underlying supportive surfaces to achieve precise digit-to-target contact with small target objects. Thus, placing the target in a location that lacks an underlying supportive surface impedes the infant's, but not adult's, ability to direct the appropriate grasping digits toward the target.

The grasp also consists of two phases. In the initial hand shaping phase the digits open and shape to match the size and shape of the target and in the second digit closing phase the digits close onto appropriate contact points on the target in order to apprehend it. Interestingly, increasing precision demands by placing the target on the pedestal had no effect on either phase of the grasp for infant and adult participants. Infants consistently displayed a larger index-thumb aperture at the time of contact and took longer to form a final grasp configuration regardless of whether the target was located on the table or the pedestal. As such, infants, unlike adults, tended to complete the majority of their hand shaping, as well as hand closure, *after* initial target contact. These results are in agreement with previous research showing that 12-month-old infants do not preshape the hand to the same extent as adults when reaching for a variety of objects (Karl & Whishaw, 2014; von Hofsten & Rönnqvist, 1988). Nonetheless, both infants and adults were capable of forming an index-thumb pincer grip on the target. Adults clearly favored this grip configuration in both the table and pedestal conditions, whereas infants showed a slight preference for alternative grip configurations with a secondary preference for index-thumb pincer grips. These characteristic infant and adult grip profiles remained consistent across both the table and pedestal conditions. The observation that 12-month-old infants can perform functional pincer grips, together with previous work on younger infants (Butterworth et al., 1997; Newell et al., 1989; Wallace & Whishaw, 2003), suggests that maturation of monosynaptic corticospinal projections likely plays a much more nuanced role in explaining the dissociable developmental profiles of the reach and grasp than previously thought.

Initially, we were surprised to observe that, for infants, increasing precision demands by placing the Cheerio on the pedestal reduced the frequency of thumb and/or index finger contacts with the target, but did not produce a corresponding decrease in index-thumb pincer grips. This suggests that the way in which the hand contacts the target does not directly relate to the subsequent use of index-thumb pincer grips in 12-month-old infants as appears to be the case in adults. Rather, even though infants were more likely to make suboptimal contact with the target in the pedestal condition, a greater proportion of these suboptimal contacts ultimately transitioned to a successful index-thumb pincer grip. This may have been because the infants experienced increased incentive and drive to form a secure index-thumb pincer grip, despite an initial suboptimal contact with the target, in order to avoid knocking or dropping the Cheerio off of the pedestal. Thus, it appears that at 12 months of age the reach and grasp respond differently to variations in task precision requirements. Contact with the underlying table seems to facilitate the refinement of the reach, specifically the second phase of the reach that directs an appropriate part of the hand towards the target; but at the same time, the table's presence seems to actually hinder developmental refinement of the grasp by deincentivizing the subsequent formation of an index-thumb pincer grip by providing sufficient physical support to enable the infant to apprehend the target, without knocking it away, using a wide variety of alternative grips.

To quote Williams et al. (2015a, p.7), "Infants who are initially learning to reach need to first discover a solution to bring the hand (s) into contact with a target object. Following that discovery, infants will then explore and discover an adaptive reach-to-grasp solution." This previous observation combined with the current results suggests that, at 12 months, the infant is likely still learning how to make precise digital contact with the target. Achieving this motor outcome likely takes precedence over preshaping the hand, which is less useful if one can't actually contact the target appropriately, and thus, the infant reaches with an open hand and contacts the underlying table which in turn facilitates index and/or thumb contact with the target despite the fact that it might also reduce the drive to subsequently form an index-thumb pincer grip. Nonetheless, increasing precision demands by placing the Cheerio atop the pedestal reveals that the infant can indeed generate successful index-thumb pincer grips to acquire the target, even after an initially suboptimal digit-to-target contact. Thus, we hypothesize that infants may not preshape the hand until they are able to direct an appropriate digit to the target *without the assistance of an underlying surface*, and only then will the frequency of index-thumb grips more closely mirror the rate of index and/or thumb target contacts, all key features of an integrated reach-to-grasp strategy, regardless of whether the target is located on a table or pedestal.

Within a broader context, the results of the present study seem to suggest that development of the reach-to-grasp movement may be characterized by at least four key perception-action loops, which appear to map onto the four phases of the adult reach-to-grasp movement: 1) transport the hand to the general location of the target, 2) make precise contact with the target, 3) preshape the hand prior to target contact, and 4) close the hand to grasp the target using an appropriate grip configuration. Importantly, because the specific actions that the infant generates during early development are highly constrained, they may differ substantially from the actions that will eventually constitute the fully mature reach-to-grasp movement. In this case, the infant may contact the target with the thumb or index finger one way when first learning it – by touching the table with an open hand and then directing an appropriate digit towards the target – but in a very different way once that particular motor goal must be incorporated into the larger overall reach-to-grasp action, in which case contact with the table may be avoided, or at least not used to assist digit-to-target contact, in order to enable hand preshaping and subsequent index-thumb pincer grip formation.

The results of the present study, together with previous work (Karl, Wilson et al., 2018), suggest that the reach and grasp remain sensitive to different perception-action constraints at 12 months of age. The presence of an underlying surface likely facilitates reach development in 12-month-old infants by helping them to direct an appropriate digit towards the visually-identified target. After target contact, however, the table's presence might actually hamper development of precision grips by reducing the incentive to practice forming functional index-thumb pincer grips. We conclude that apparent differences in the maturity of the reach and grasp during different stages of infancy may be strongly related to the fact that the two movements tend to respond differently to subtle contextual factors, such as precision demands, which may bias the refinement and reinforcement of one component of prehension over the other.

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References

Alstermark, B., & Isa, T. (2012). Circuits for skilled reaching and grasping. *Annual Review of Neuroscience, 35*, 559–578. https://doi.org/10.1146/annurev-neuro-062111-150527.

Arbib, M., Iberall, A., & Lyons, T. D. (1985). Coordinated control program for movements of the hand. In A. W. Goodman, & I. Darian-Smith (Eds.). *Hand function and the neocortex* (pp. 135–170). Berlin, Germany: Springer.

Babik, I., Galloway, J. C., & Lobo, M. A. (2017). Infants born preterm demonstrate impaired exploration of their bodies and surfaces throughout the first two years of life. *Physical Therapy, 97*(9), 915–925. https://doi.org/10.1093/ptj/pzx064.

Berthier, N. E., & Carrico, R. L. (2010). Visual information and object size in infant reaching. *Infant Behavior & Development, 33*(4), 555–566. https://doi.org/10.1016/j.infbeh.2010.07.007.

Berthier, N. E., & Keen, R. (2006). Development of reaching in infancy. *Experimental Brain Research, 169*(4), 507–518. https://doi.org/10.1007/s00221-005-0169-9.

Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., et al. (1998). Human anterior intraparietal area subserves prehension: A combined lesion and functional MRI activation study. *Neurology, 50*(5), 1253–1259.

Bushnell, E. W. (1985). The decline of visually guided reaching during infancy. *Infant Behavior & Development, 8*(2), 139–155. https://doi.org/10.1016/S0163-6383(85)80002-3.

Butterworth, G., Verweij, E., & Hopkins, B. (1997). The development of prehension in infants: Halverson revisited. *The British Journal of Developmental Psychology, 15*(2), 223–236. https://doi.org/10.1111/j.2044-835X.1997.tb00736.x.

Carrico, R. L., & Berthier, R. L. (2007). Vision and precision reaching in 15-month-old infants. *Infant Behavior and Development, 31*(1), 62–70. https://doi.org/10.1016/j.infbeh.2007.07.005.

Case-Smith, J., Bigsby, R., & Clutter, J. (1998). Perceptual-motor coupling in the development of grasp. *American Journal of Occupational Therapy, 52*(2), 102–110. https://doi.org/10.5014/ajot.52.2.102.

Cavina-Pratesi, C., Connolly, J. D., & Milner, A. D. (2013). Optic ataxia as a model to investigate the role of the posterior parietal cortex in visually guided action: Evidence from studies of patient M.H. *Frontiers in Human Neuroscience, 7*, 336. https://doi.org/10.3389/fnhum.2013.00336.

Cavina-Pratesi, C., Connolly, J. D., Monaco, S., Figley, T. D., Milner, A. D., Schenk, T., et al. (2018). Human neuroimaging reveals the subcomponents of grasping, reaching, and pointing actions. *Cortex, 98*, 128–148. https://doi.org/10.1016/j.cortex.2017.05.018.

Cavina-Pratesi, C., Ietswaart, M., Humphreys, G. W., Lestou, V., & Milner, A. D. (2010). Impaired grasping in a patient with optic ataxia: Primary visuomotor deficit or secondary consequence of misreaching? *Neuropsychologia, 48*(1), 226–234. https://doi.org/10.1016/j.neuropsychologia.2009.09.008.

Cavina-Pratesi, C., Monaco, S., Fattori, P., Galletti, C., McAdam, T. D., Quinlan, D. J., et al. (2010). Functional magnetic resonance imaging reveals the neural substrates of arm transport and grip formation in reach-to-grasp actions in humans. *Journal of Neuroscience, 30*(31), 10306–10323. https://doi.org/10.1523/JNEUROSCI.2023-10.2010.

Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and Psychological Measurement, 20*, 37–46. https://doi.org/10.1177/001316446002000104.

Corbetta, D., Williams, J. L., & Haynes, J. M. (2016). Bare fingers, but no obvious influence of "prickly" Velcro! In the absence of parents' encouragement, it is not clear that "sticky mittens" provide an advantage to the process of learning to reach. *Infant Behavior & Development, 42*, 168–178. https://doi.org/10.1016/j.infbeh.2015.05.001.

Darling, W. G., Morecraft, R. J., Rotella, D. L., Pizzimenti, M. A., Ge, J., Stilwell-Morecraft, K. S., et al. (2014). Recovery of precision grasping after motor cortex lesion does not require forced use of the impaired hand in Macaca mulatta. *Experimental Brain Research, 232*(12), 3929–39398. https://doi.org/10.1007/s00221-014-4068-9.

DiMercurio, A., Connell, J. P., Clark, M., & Corbetta, D. (2018). A naturalistic observation of spontaneous touches to the body and environment in the first 2 months of life. *Frontiers in Psychology, 18*(9), 2613. https://doi.org/10.3389/fpsyg.2018.02613.

Dominici, N., Ivanenko, Y. P., Cappellini, G., d'Avella, A., Mondi, V., Cicchese, M., et al. (2011). Locomotor primitives in newborn babies and their development. *Science, 334*(6058), 997–999. https://doi.org/10.1126/science.1210617.

Elliott, J. M., & Connolly, K. J. (1984). A classification of manipulative hand movements. *Developmental Medicine and Child Neurology, 26*(3), 283–296. https://doi.org/10.1111/j.1469-8749.1984.tb04445.x.

Eyre, J. A., Miller, S., Clowry, G. J., Conway, E. A., & Watts, C. (2000). Functional corticospinal projections are established prenatally in the human foetus permitting involvement in the development of spinal motor centres. *Brain, 123*(1), 51–64. https://doi.org/10.1093/brain/123.1.51.

Gesell, A. (1952). *Infant development: The embryology of early human behavior.* New York: Harper & Brothers.

Gesell, A. (1988). *The embryology of behaviour: The beginnings of the human mind.* Oxford: Blackwell Scientific Publications.

Graziano, M. S., Taylor, C. S., & Moore, T. (2002). Complex movements evoked by microstimulation of precentral cortex. *Neuron. 34*(5), 841–851.

Hall, L. A., Karl, J. M., Thomas, B. L., & Whishaw, I. Q. (2014). Reach and grasp reconfigurations reveal that proprioception assists reaching and hapsis assists grasping in peripheral vision. *Experimental Brain Research, 232*(9), 2807–2819. https://doi.org/10.1007/s00221-014-3945-6.

Hallgren, K. A. (2012). Computing inter-rater reliability for observational data: An overview and tutorial. *Tutorials in Quantitative Methods for Psychology, 8*(1), 23–34. https://doi.org/10.20982/tqmp.08.1.p023.

Halverson, H. M. (1931). An experimental study of prehension in infants by means of systematic cinema records. *Genetic Psychology Monographs, 10*, 107–286.

Halverson, H. M. (1932). A further study of grasping. *The Journal of General Psychology, 7*(1), 34–64.

Hohlstein, R. R. (1982). The development of prehension in normal infants. *The American Journal of Occupational Therapy, 36*(3), 170–176. https://doi.org/10.5014/

ajot.36.3.170.

Hao, Y., Zhang, S., Zhang, Q., Li, G., Chen, W., & Zheng, X. (2017). Neural synergies for controlling reach and grasp movement in macaques. *Neuroscience, 357*, 372–383. https://doi.org/10.1016/jneuroscience.2017.06.022.

Isa, T. (2019). Dexterous hand movements and their recovery after central nervous system injury. *Annual Review of Neuroscience, 8*(42), 315–335. https://doi.org/10.1146/annurev-neuro-070918-050436.

Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In J. Long, & A. Badeley (Eds.). *Attention and performance IX* (pp. 152–169). Hillsdale, NJ: Lawrence Erlbaum Associates.

Juett and Kuipers (2019). Learning and acting in peripersonal space: Moving, reaching, and grasping. *Frontiers in Neurorobotics, 13*, 4. https://doi.org/10.3389/fnbot.2019.00004.

Kaas, J. H., & Stepniewska, I. (2016). Evolution of posterior parietal cortex and parietal-frontal networks for specific actions in primates. *The Journal of Comparative Neurology, 524*(3), 595–608. https://doi.org/10.1002/cne.23838.

Karl, J. M., Kuntz, J. R., Lenhart, L. A., & Whishaw, I. Q. (2018). Frame-by-frame video analysis of idiosyncratic reach-to-grasp movements in humans. *Journal of Visualized Experiments, 131*. https://doi.org/10.3791/56733 e56733.

Karl, J. M., Sacrey, L. A., Doan, J. B., & Whishaw, I. Q. (2012a). Hand shaping using hapsis resembles visually guided hand shaping. *Experimental Brain Research, 219*(1), 59–74. https://doi.org/10.1007/s00221-012-3067-y.

Karl, J. M., Sacrey, L. A., Doan, J. B., & Whishaw, I. Q. (2012b). Oral hapsis guides accurate hand preshaping for grasping food targets in the mouth. *Experimental Brain Research, 221*(2), 223–240. https://doi.org/10.1007/s00221-012-3246-x.

Karl, J. M., Sacrey, L. A., & Whishaw, I. Q. (2018). Multiple motor channel theory and the development of skilled hand movements in human infants. In D. Corbetta, & M. Santello (Eds.). *Reach-to-grasp behavior: Brain, behavior and modelling across the life span* (pp. 542–548). Abingdon, UK: Routledge Taylor & Francis.

Karl, J. M., Schneider, L. R., & Whishaw, I. Q. (2013). Nonvisual learning of intrinsic object properties in a reaching task dissociates grasp from reach. *Experimental Brain Research, 225*(4), 465–477. https://doi.org/10.1007/s00221-012-3386-z.

Karl, J. M., & Whishaw, I. Q. (2013). Different evolutionary origins for the reach and the grasp: An explanation for dual visuomotor channels in primate parietofrontal cortex. *Frontiers in Neurology, 4*, 208. https://doi.org/10.3389/fneyr.2013.00208.

Karl, J. M., & Whishaw, I. Q. (2014). Haptic grasping configurations in early infancy reveal different developmental profiles for visual guidance of the Reach versus the Grasp. *Experimental Brain Research, 232*(10), 3301–3316. https://doi.org/10.1007/s00221-014-4013-y.

Karl, J. M., Wilson, A. M., Bertoli, M. E., & Shubear, N. S. (2018). *Experimental Brain Research*. https://doi.org/10.1007/s00221-018-5293-4 Epub ahead of print.

Kastner, S., Chen, Q., Jeong, S. K., & Mruczek, R. E. B. (2017). A brief comparative review of primate posterior parietal cortex: A novel hypothesis on the human toolmaker. *Neuropsychologia, 105*, 123–134. https://doi.org/10.1016/j.neuropsychologia.2017.01.034.

Kinoshita, M., Matsui, R., Kato, S., Hasegawa, T., Kasahara, H., Isa, K., et al. (2012). Genetic dissection of the circuit for hand dexterity in primates. *Nature, 487*(7406), 235–238. https://doi.org/10.1038/nature11206.

Konczak, J., Borutta, M., Topka, H., & Dichgans, J. (1995). The development of goal-directed reaching in infants: Hand trajectory formation and joint torque control. *Experimental Brain Research, 106*(1), 156–168. https://doi.org/10.1007/BF00241365.

Konen, C. S., Mruczek, R. E., Montoya, J. L., & Kastner, S. (2013). Functional organization of human posterior parietal cortex: Grasping- and reaching-related activations relative to topographically organized cortex. *Journal of Neurophysiology, 109*(12), 2897–2908. https://doi.org/10.1152/jn.00657.2012.

Lawrence, D. G., & Hopkins, D. A. (1976). The development of motor control in the rhesus monkey: Evidence concerning the role of corticomotoneuronal connections. *Brain, 99*(2), 235–254. https://doi.org/10.1093/brain/99.2.235.

Lee, M. H., Liu, Y. T., & Newell, K. M. (2006). Longitudinal expressions of infants' prehension as a function of object properties. *Infant Behavior and Development, 29*(4), 481–493.

Lobo, M. A., & Galloway, J. C. (2013). The onset of reaching significantly impacts how infants explore both objects and their bodies. *Infant Behavior & Development, 35*(1), 14–24. https://doi.org/10.1016/j.infbeh.2012.09.003.

Martin, J. H. (2005). The corticospinal system: From development to motor control. *The Neuroscientist, 11*(2), 161–173. https://doi.org/10.1177/1073858404270843.

McCarty, M. E., & Ashmead, D. H. (1999). Visual control of reaching and grasping in infants. *Developmental Psychobiology, 35*(3), 620–631. https://doi.org/10.1037/0012-1649.35.3.620.

McCarty, M. E., Clifton, R. K., Ashmead, D. H., Lee, P., & Goubet, N. (2001). How infants use vision for grasping objects. *Child Development, 72*(4), 973–987. https://doi.org/10.1111/1467-8624.00329.

McDonnell, P. M. (1979). The development of visually guided reaching. *Perception & Psychophysics, 18*(3), 181–185. https://doi.org/10.3758/BF03205963.

Morrongiello, B. A., & Rocca, P. T. (1989). Visual feedback and anticipatory hand orientation during infants' reaching. *Perceptual and Motor Skills, 69*(3), 787–802. https://doi.org/10.1177/00315125890693-115.

Newell, K. M., Scully, D. M., McDonald, P. V., & Baillargeon, R. (1989). Task constraints and infant grip configurations. *Developmental Psychobiology, 22*(8), 817–831. https://doi.org/10.1002/dev.420220806.

Overduin, S. A., d'Avella, A., Roh, J., Carmena, J. M., & Bizzi, E. (2015). Representation of muscle synergies in the primate brain. *Journal of Neuroscience, 35*(37), 12615–12624. https://doi.org/10.1523/JNEUROSCI.4302-14.2015.

Piaget, J. (1952). *The origins of intelligence in children.* New York: Basic Books.

Rochat, P. (1987). Mouthing and grasping in neonates: Evidence for the early detection of what hard or soft substances afford for action. *Infant Behavior & Development, 10*(4), 435–449. https://doi.org/10.1016/0163-6383(87)90041-5.

Rochat, P. (1989). Object manipulation and exploration in 2- to 5- month old infants. *Developmental Psychology, 25*(6), 871–884. https://doi.org/10.1037/0012-1649.25.6.871.

Rönnqvist, L., & Domellöf, E. (2006). Quantitative assessment of right and left reaching movements in infants: A longitudinal study from 6 to 36 months. *Developmental Psychobiology, 48*(6), 444–459. https://doi.org/10.1002/dev.20160.

Sacrey, L. A., Karl, J. M., & Whishaw, I. Q. (2012a). Development of rotational movements, hand shaping, and accuracy in advance and withdrawal for the reach-to-eat movement in human infants aged 6-12 months. *Infant Behavior & Development, 35*(3), 543–560. https://doi.org/10.1016/j.infbeh.2012.05.006.

Sacrey, L. A., Karl, J. M., & Whishaw, I. Q. (2012b). Development of visual and somatosensory attention of the reach-to-eat movement in human infants aged 6 to 12 months. *Experimental Brain Research, 223*(1), 121–136. https://doi.org/10.1007/s00221-012-3246-x.

Schettino, L. F., Adamovich, S. V., & Tunik, E. (2017). Coordination of pincer grasp and transport after mechanical perturbation of the index finger. *Journal of Neurophysiology, 117*(6), 2292–2297. https://doi.org/10.1152/jn.00642.2016.

Schlesinger, M., & Parisi, D. (2001). Multimodal control of reaching – Simulating the role of tactile feedback. *IEEE Transactions on Evolutionary Computation, 5*(2), 122–128. https://doi.org/10.1109/4235.918433.

Schum, N., Jovanovic, B., & Schwarzer, G. (2011). Ten- and twelve-month-olds' visual anticipation of orientation and size during grasping. *Journal of Experimental Child Psychology, 109*(2), 218–231. https://doi.org/10.1016/j.jecp.2011.01.007.

Thelen, E., & Smith, L. B. (1994). *A dynamic systems approach to the development of cognition and action.* Massachusetts: The MIT Press.

Thomas, B. L., Karl, J. M., & Whishaw, I. Q. (2015). Independent development of the Reach and the Grasp in spontaneous self-touching by human infants in the first 6 months. *Frontiers in Psychology, 5*, 1526. https://doi.org/10.3389/fpsyg.2014.01526.

Tohyama, T., Kinoshita, M., Kobayashi, K., Isa, K., Watanabe, D., Kobayashi, K., et al. (2017). *Proceedings of the National Academy of Sciences, USA, 114*(3), 604–609. https://doi.org/10.1073/pnas.1610787114.

van de Kamp, C., & Zaal, F. T. (2007). Prehension is really reaching and grasping. *Experimental Brain Research, 182*(1), 27–34. https://doi.org/10.1007/s00221-007-0968-2.

Vesia, M., Barnett-Cowan, M., Elahi, B., Jegatheeswaran, G., Isayama, R., Neva, J. L., et al. (2017). Human dorsomedial parieto-motor circuit specifies grasp during the planning of goal-directed hand actions. *Cortex, 92*, 175–186. https://doi.org/10.1016/j.cortex.2017.04.007.

Vesia, M., Bolton, D. A., Mochizuki, G., & Staines, W. R. (2013). Human parietal and primary motor cortical interactions are selectively modulated during the transport and grip formation of goal-directed hand actions. *Neuropsychologia, 51*(3), https://doi.org/10.1016/j.neuropsychologia.2012.11.022 410/417.

Vesia, M., & Crawford, J. D. (2012). Specialization of reach function in human posterior parietal cortex. *Experimental Brain Research, 221*(1), 1–18. https://doi.org/10.1007/s00221-012-3158-9.

von Hofsten, C. (1984). Developmental changes in the organization of prereaching movements. *Developmental Psychology, 20*(3), 378–388. https://doi.org/10.1037/0012-1649.20.3.378.

von Hofsten, C. (1991). Structuring of early reaching movements: A longitudinal study. *Journal of Motor Behavior, 23*(4), 280–292. https://doi.org/10.1080/00222895.1991.9942039.

von Hofsten, C., & Fazel-Zandy, S. (1984). Development of visually guided hand orientation in reaching. *Journal of Experimental Child Psychology, 38*(2), 208–219. https://doi.org/10.1016/0022-0965(84)90122-X.

von Hofsten, C., & Rönnqvist, L. (1988). Preparation for grasping an object: A developmental study. *Journal of Experimental Psychology: Human Perception and Performance, 14*(4), 610–621. https://doi.org/10.1037/0096-1523.14.4.610.

Wallace, P. S., & Whishaw, I. Q. (2003). Independent digit movements and precision grip patterns in 1-5-month-old human infants: Hand-babbling, including vacuous then self-directed hand and digits movements, precedes targeted reaching. *Neuropsychologia, 41*(14), 1912–1918. https://doi.org/10.1016/S0028-3932(03)00128-3.

Whishaw, I. Q., & Karl, J. M. (2019). The evolution of the hand as a tool in feeding behavior: The multiple motor channel theory of hand use. In V. Bels, & I. Q. Whishaw (Eds.). *Feeding in vertebrates: Evolution, morphology, behavior, biomechanics* (pp. 159–186). Switzerland: Springer.

White, B. L., Castle, P., & Held, R. (1964). Observations on the development of visually directed reaching. *Child Development, 35*(2), 349–364. https://doi.org/10.2307/1126701.

Williams, J. L., Corbetta, D., & Cobb, L. (2015). How perception, action, functional value, and context can shape the development of infant reaching. *Movement & Sport Sciences, 89*, 5–15. https://doi.org/10.1051/sm/2015005.

Williams, J. L., Corbetta, D., & Guan, Y. (2015). Learning to reach with “sticky” or “non-sticky” mittens: A tale of developmental trajectories. *Infant Behavior & Development, 38*, 82–96. https://doi.org/10.1016/j.infbeh.2015.01.001.

Witherington, D. C. (2005). The development of prospective grasping control between 5 and 7 months: A longitudinal study. *Infancy, 7*(2), 143–161. https://doi.org/10.1207/s15327078in0702_2.

Woodworth, R. S. (1899). Accuracy of voluntary movement. *The Psychological Review: Monograph Supplements, 3*(3), https://doi.org/10.1037/h0092992 i-114.

Zaal, F. T., & Bongers, R. M. (2014). Movements of individual digits in bimanual prehension are coupled into a grasping component. *PloS One, 9*(5), https://doi.org/10.1371/journal.pone.0097790 e97790.