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RESEARCH ARTICLE

Touch the table before the target: contact with an underlying surface may assist the development of precise visually controlled reach and grasp movements in human infants

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Abstract

Multiple motor channel theory posits that skilled hand movements arise from the coordinated activation of separable neural circuits in parietofrontal cortex, each of which produces a distinct movement and responds to different sensory inputs. Prehension, the act of reaching to grasp an object, consists of at least two movements: a reach movement that transports the hand to a target location and a grasp movement that shapes and closes the hand for target acquisition. During early development, discrete pre-reach and pre-grasp movements are refined based on proprioceptive and tactile feedback, but are gradually coordinated together into a singular hand preshaping movement under feedforward visual control. The neural and behavioural factors that enable this transition are currently unknown. In an attempt to identify such factors, the present descriptive study used frame-by-frame video analysis to examine 9-, 12-, and 15-month-old infants, along with sighted and unsighted adults, as they reached to grasp small ring-shaped pieces of cereal (Cheerios) resting on a table. Compared to sighted adults, infants and unsighted adults were more likely to make initial contact with the underlying table before they contacted the target. The way in which they did so was also similar in that they generally contacted the table with the tip of the thumb and/or pinky finger, a relatively open hand, and poor reach accuracy. Despite this, infants were similar to sighted adults in that they tended to use a pincer digit, defined as the tip of the thumb or index finger, to subsequently contact the target. Only in infants was this ability related to their having made prior contact with the underlying table. The results are discussed in relation to the idea that initial contact with an underlying table or surface may assist infants in learning to use feedforward visual control to direct their digits towards a precise visual target.

Keywords Development of reaching and grasping · Infant reaching and grasping · Prehension · Visually guided reaching and grasping · Dual visuomotor channel theory · Multiple motor channel theory · Peri-hand space · Near-hand space · Development of peripersonal space

Introduction

Prehension, the ability to reach out and grasp an object, is an integral part of the human experience which we use to feed and groom ourselves, build and wield tools, and communicate in gestural and written languages. Multiple Motor Channel theory posits that prehensile movements arise from the coordinated activity of separate neural pathways in parietofrontal cortex, each of which controls a different movement and responds to a unique set of sensory inputs (Karl et al. 2018; Whishaw et al. 2017; Whishaw and Karl 2018). The view that prehension consists of at least two movements, mediated by dissociable neural pathways, is supported by substantial research in both human and non-human primates (Binkofski et al. 1998; Caminiti et al. 2010; Cavina-Pratesi et al. 2010a, b; Culham et al. 2006; Ferrari-Toniolo et al. 2015; Graziano et al. 2002; Greulich et al. 2017; Jeannerod 1981; Jeannorod et al. 1994; Kaas and Stepniewska 2016; Karl and Whishaw 2013; Kastner et al. 2017; Vesia and Crawford 2012; Vesia et al. 2013). A reach movement transports the hand to the target location while a grasp movement opens, shapes, and closes the hand for target acquisition. The neural pathway that mediates the reach involves the human parietal reach region (hPRR) and the dorsal premotor cortex

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(PMd) whereas the neural pathway that mediates the grasp involves the human anterior intraparietal sulcus (hAIP) and the ventral premotor cortex (PMv). In primates, both pathways receive visual input, which allows us to execute the two movements in a simultaneous fashion so that the hand opens, shapes, and closes as we reach towards a visual target (Fig. 1a). Nonetheless, when vision is degraded the action decomposes into its constituent components: an open-handed reach initially locates the target by touching it and then tactile feedback from the target enables accurate shaping and closure of the hand to grasp (Fig. 1b; Hall et al. 2014; Karl et al. 2012, 2013; Karl and Whishaw 2013, 2014). Thus, in healthy human adults, the visual system does not have privileged access to the reach and grasp pathways. The somatosensory system, as well as other sensory systems, can also access and control the reach and grasp movements when needed.

This raises the question: to what extent do vision and somatosensation contribute to the organization and control of prehension at different stages of human development? From soon after birth, young infants produce a large number of spontaneous and exploratory movements. Among these are distinct precursors to functional reach and grasp movements known as pre-reach and pre-grasp movements, respectively. Pre-reach movements include extending the arm and hand to establish self-contact with one's own body (Babik et al. 2017; Lobo and Galloway 2013; Thomas et al. 2015), extending a fisted hand to swat at distal targets without contacting them (von Hofsten 1984), and eventually extending the arm and open hand to touch distal targets (Corbetta et al. 2016; Williams et al. 2015b). Pre-grasp movements include hand babbling, which is characterized by the production of independent digit movements and vacuous pincer or precision grips (Wallace and Whishaw 2003), self-grasping movements (Thomas et al. 2015; Wallace and Whishaw 2003), and the oral and manual exploration of objects held by the mouth or hands (Case-Smith et al. 1998; Rochat 1987, 1989). These pre-reach and pre-grasp movements likely arise from relatively isolated activity in the frontal components of the cortical reach and grasp pathways and their early expression suggests that motoric independence of the reach and grasp is established early in development.

While early studies suggested that infants learn to reach and grasp for distal targets by using vision to align their seen hand with the location of a seen target (Bushnell 1985; McDonnell 1979; Piaget 1952; White et al. 1964), it is now clear that pre-reach and pre-grasp movements are not dependent on visual supervision. For example, young infants rarely look at their own hands when performing self-directed pre-reach and pre-grasp movements (Thomas et al. 2015; Wallace and Whishaw 2003). When they do begin to reach towards distal objects, their reach movements are similar regardless of whether or not they can see their own hand (Clifton et al. 1993, 1994; Lee and Newell 2012) and they do not direct their early reach movements to where they are looking. Rather, they learn to align their visual attention towards their hand after it makes tactile contact with a distal target (Corbetta et al. 2014). When infants eventually do begin to perform successful prehensile actions towards distal targets, their reach and grasp movements are dissociated rather than integrated into a singular hand preshaping movement (Karl and Whishaw 2014). Together, these findings demonstrate that the early reach and grasp movements of young infants are highly reliant on touch and proprioception rather than vision.

Evidence from both behavioural and computational studies suggests that tactile feedback arising from contact between the infant's hand and either their own bodies or external objects likely facilitates the initial refinement and reinforcement of separate pre-reach and pre-grasp

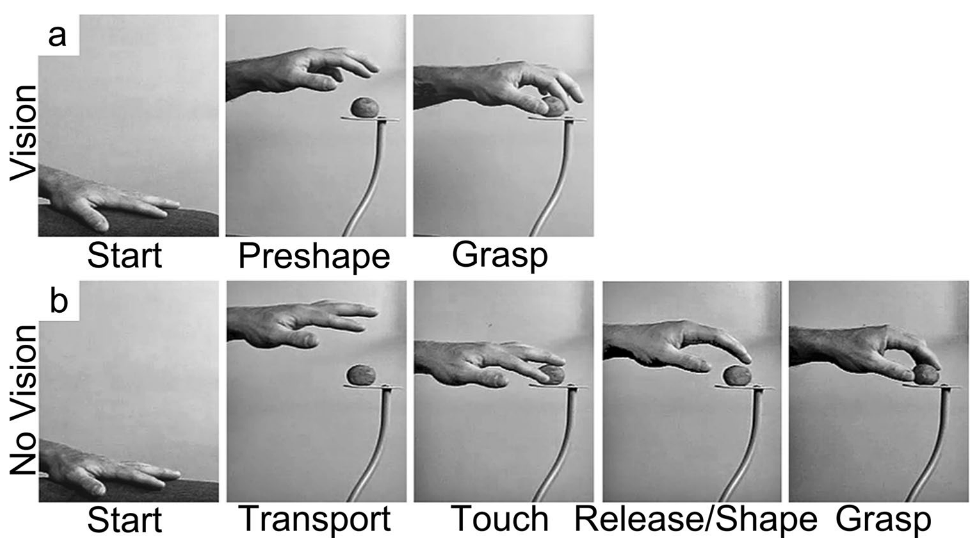

Fig. 1 The adult reach-to-grasp movement performed **a** with and **b** without vision. Sighted adults integrate the reach and grasp by preshaping and closing the hand by the time the they contact the target. Unsighted adults dissociate the reach and the grasp such that the hand does not shape and close to grasp until after target contact. This figure has been adapted from Karl et al. 2012

movements, along with their underlying neural circuits (Schlesinger and Parisi 2001; Sporns and Edelman 1993; Williams et al. 2015a; Williams and Corbetta 2016). Thus, successful contact with a target object refines and reinforces the pre-reach movement that preceded it, whereas successful apprehension of a target object in the hand refines and reinforces the pre-grasp movement that preceded it. Nonetheless, the reach and grasp eventually come under visual control. Feedforward visual control of the reach is present by about 9 months of age and largely mature by 12–15 months of age (Berthier and Carrico 2010; Carrico and Berthier 2008; Corbetta et al. 2012; Karl and Whishaw 2014; Lockman et al. 1984; Morrongiello and Rocca 1989; Schum et al. 2011; von Hofsten and Fazel-Zandy 1984; Wentworth et al. 2000; Witherington 2005). In contrast, feedforward visual control of the grasp continues to mature beyond the 2nd year of life (Barrett and Needham 2008; Karl and Whishaw 2014; von Hofsten and Rönnqvist 1988; Schum et al. 2011). What is currently unclear is how this transition from somatosensory to visual control of the reach and grasp occurs. More specifically, what are the neural and behavioural factors that enable the developing cortical visual system to co-opt these pre-existing reach and grasp movements and coordinate them into a single hand preshaping action?

In an attempt to begin addressing this question, the present study provides a detailed description of infant reach and grasp behaviour during the period that the transition from primarily somatosensory to visual control is proposed to be underway. 9-, 12-, and 15-month-old human infants performed the highly demanding and ethologically relevant task of reaching to grasp small ring-shaped pieces of cereal (Cheerios) located on a transparent tabletop. Their reach and grasp movements were recorded from three different angles using time-synchronized video cameras and analysed using frame-by-frame analyses. Infants were compared to sighted and unsighted adults to determine the extent to which their movements differed from mature visually- and somatosensory-controlled reach and grasp movements, respectively. It was expected that infant reach and grasp movements would feature unique age-specific behaviours related to the developmental transition from somatosensory to visual control.

Materials and methods

All adult participants and infants' guardians provided informed consent prior to participating in the study. All procedures were carried out in the Brain and Behaviour Laboratory at Thompson Rivers University and were approved by the Thompson Rivers University Research Ethics for Human Subjects Board.

Exploratory study

Our observations from previous studies indicated that when reaching to grasp Cheerios located on an opaque tabletop, 9- to 15-month-old infants tended to touch the underlying table surface before they contacted the target. Thus, fifteen 12-month-old infants participated in an exploratory study where they reached to grasp Cheerios located on either an opaque tabletop (five male, two female, mean age = 12.26 months) or a transparent safety-tempered glass tabletop (five male, three female, mean age = 12.03 months). Their arm and hand movements were video recorded to determine whether the table's surface influenced how they contacted the table during the reaching task. The results of this exploratory study revealed no differences in the frequency with which infants touched the table before the target when the target was located on an opaque table ($M = 85.62$, SE = 5.71%) compared to a transparent table ($M = 83.34$, SE = 4.66%), $t(13) = 0.288$, $p = 0.778$. There were also no major differences in how infants contacted the table. Infants tended to contact the table with either the pinky finger (opaque = 26.66 ± 8.81%; transparent = 39.35 ± 5.66%) or thumb (opaque = 41.70 ± 5.88%; transparent = 35.02 ± 8.50%) in both conditions. The use of a transparent tabletop affords more detailed video analyses, because the reach and grasp can be video recorded from an additional bottom-up view. Thus, all subsequent data collection and analyses used only a transparent tabletop.

Participants

Adults

Twenty-four young adults (12 male, 12 female, mean age = 20.20 years) were recruited from introductory psychology classes at Thompson Rivers University and were randomly assigned to one of two conditions: Vision (V) or No Vision (NV). All participants self-reported that they were right-handed for writing, had normal or corrected-to-normal vision, were not allergic to Cheerios, and had no history of sensory, motor, or neurological disorders. The data from three female participants (two from the V condition and one from the NV condition) were excluded from analysis due to long artificial fingernails that interfered with their ability to perform the task naturally. All adult participants received 2% credit towards their final grade in their introductory psychology class for participating.

Infants

Thirty-two infants were recruited through online advertisements with local community groups (http://www.kijiji.ca and http://www.facebook.com) and participated in the present study. Nine infants were included in the 9-month-old (9M) age group (one male, eight female, mean age = 9.53 months); ten infants were included in the 12-month-old (12M) age group (seven male, three females, mean age = 12.43 months); and twelve infants were included in the 15-month-old (15M) age group (seven male, six female, mean age = 15.26 months). All guardians reported that infants were born full term (not more than 14 days prior to their due date); had no known sensory, motor, or neurological disorders; did not experience any unexpected birth complications; and were not allergic to Cheerios. Guardians received a $25 gift card to The Children's Place clothing store for allowing their infant to participate.

Procedures

Adults

Prior to testing, the adult participants were seated in a comfortable upright position on an armless chair in front of a transparent safety-tempered glass tabletop. All adult participants were shown the visual location on the table at which the reaching target, a single Cheerio, would be placed. The target's location was centered on the table directly in front of the participant's midline at a distance normalised to the length of the participant's fully extended right arm. Adult 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. Once the Cheerio was in place, participants waited for the experimenter to provide a verbal 'one, two, three, go', signal, 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. Adults in the V condition performed the entire task with full vision. Adults in the NV condition were permitted to view the initial location of the target at the start of the experiment, but then wore a vision occluding blindfold for all twenty reaching trials.

Infants

The experimental task performed by 9-, 12-, and 15-month-old human infants was identical to that of the adult reaching task, with the following exceptions. First, infants were seated and buckled into a safety-standard tray-less highchair in front of the same table. The height of the highchair was adjusted so that infants could comfortably rest their hands on the table's surface. The highchair allowed for free range of movement of the arms, upper waist, and head. 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 Cheerio on the table. 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 as this is a common and natural behaviour for infants of this age (Sacrey et al. 2012a, b). If an infant did not immediately eat the Cheerio, they were allotted approximately 30 s to handle the Cheerio, after which they were encouraged to return it to the experimenter, who discarded it. Fifth, all infants performed the reaching task with full vision and for a maximum of twenty-five trials. 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 (see Table 1).

Data collection

Three digital high-speed video cameras (Sony HD Video Recording HDRPJ440 PJ Handycam Camcorder), operating at a shutter speed of 1/250th of a second and 30 frames per second, were used to record the reach and grasp movements of all participants. As illustrated in Fig. 2, the first camera was positioned in front of the participant and angled down towards a mirror located under the transparent tabletop to capture a bottom-up view of the participant's arm and hand as they reached to grasp the Cheerio. A second camera was positioned sagittal to the participant to capture a medial side view of the participant's right upper thigh, torso, hand, arm, and head as they reached to grasp the Cheerio. A third video camera was positioned in front of the participant to capture a front-on view of the participant's hand, arm, torso, and head. A lamp containing cool LED lights that generate negligible heat was used to illuminate the testing area. Transparent 1 cm^2 graph paper was attached to the underside of the transparent tabletop as well as to a wooden block that

Table 1 Reaches per participant (*n*)

Group	Minimum	Maximum	Mean	Group total
9M	7	22	17.56	158
12M	6	25	16.50	165
15M	4	23	17.42	209
NV	20	20	20.00	220
V	20	20	20.00	200
Total				952

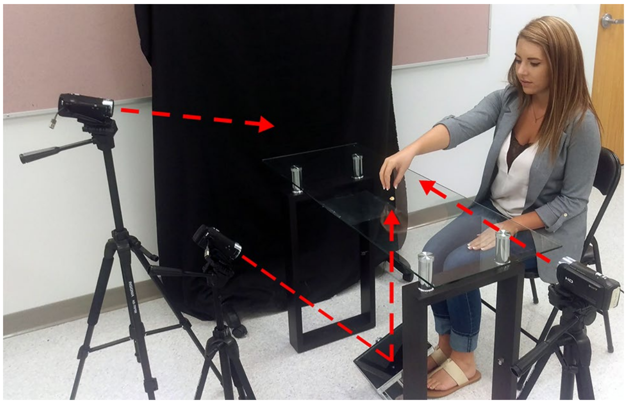

Fig. 2 The experimental setup. Note the positioning of the three video cameras relative to the participant, the reaching target, the mirror underneath the table, and the transparent tabletop

was temporarily presented to the front- and side-view cameras at the start of the experiment. This served as a consistent calibration scale, visible in all three video records, that would later be used to convert distances measured on the video record from pixels to millimetres. After starting the video cameras and presenting the calibration scale to each video camera, the experimenter used the tip of her index finger to quickly tap the surface of the table. This served as a temporal cue that was clearly visible in all three video records and used to manually trim all three video records to a common start frame, thereby time-synchronizing them, in the video editing software Adobe Premiere Pro (http://www.adobe.com/premiere). Offline frame-by-frame analysis of the time-synchronized video records was used to score all behavioural measures.

Data analysis

Reach trials

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 transparent table. They also often contacted the underside of the table with their legs and feet and they frequently visually inspected the edges of the table as well as visible smudges on the surface of the table. Thus, although the table was transparent, the infants had ample opportunity to learn, through both visual and tactile experience, about the structural features of the table and were clearly aware of its presence both prior to and throughout the experiment. These exploratory movements 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 within the immediate vicinity of the target, and ultimately resulted in successful grasping of the target were considered true "reaching" movements and included in the present analysis. Table 1 indicates the minimum, maximum, mean, and total number of reaches per group that were included in the final analysis.

Movement times

The prehensile action of each participant generally consisted of four key behavioural events: Movement start, Table contact, Target contact, and Final grasp. Figure 3 provides an example of these in a(n) sighted adult, unsighted adult, and 12M infant. The temporal organization of these events was determined by stepping frame-by-frame through the time-synchronized video records and noting the individual frame at which each event occurred. Frame numbers were converted to milliseconds for all subsequent analyses.

Movement start

Movement start was defined as the first discernable lifting of the hand away from the upper thigh and towards the target object that resulted in contact with either the target or the surface of the table near the target. If the infant did not begin with the hand placed on the lap, Movement start was defined as the first discernable movement of the hand toward the target that resulted in contact with the target or the surface of the table near the target.

Table contact

Table contact was defined as the first instance of contact between the reaching hand and the surface of the table near the target.

Target contact

Target contact was defined as the first instance of contact between the reaching hand and the target object.

Final grasp

Final grasp was defined as the first instance of complete digit closure, resulting in a secure grasp and hold on the target object.

Total movement time

Total movement time was defined as the temporal difference between Movement start and Final grasp.

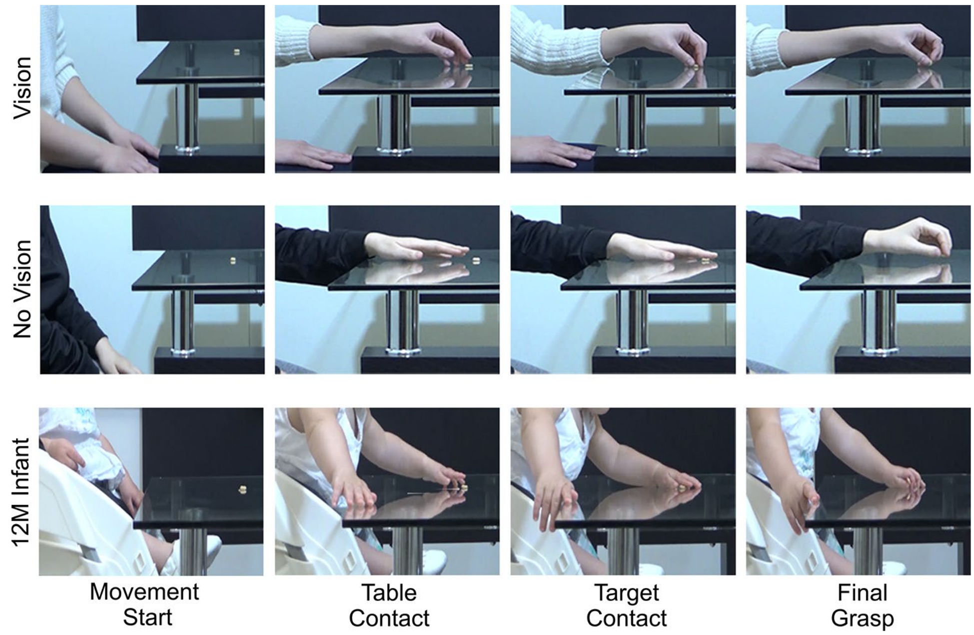

Fig. 3 Representative still frames illustrating the four key behavioural events of Movement start, Table contact, Target contact, and Final grasp in a (top) sighted adult, (middle) unsighted adults, and (bottom) sighted 12-month-old infant

Table contact

The time-synchronized video records were paused on the frame of table contact and the following behavioural measures were scored.

Proportion table contact

For each participant we calculated the proportion of total trials in which they contacted the table before they touched the target.

Part of hand to contact table

The hand was arbitrarily divided into 6 segments and labelled as follows: D1 = thumb, D2 = index finger, D3 = middle finger, D4 = ring finger, D5 = pinky finger, P = palm. For each participant, we calculated the proportion of total trials that each part of the hand made initial table contact. In addition, the raw video data from all participants was combined to generate topographical maps illustrating the part of the hand to initially contact the table, and the location of initial table contact, for each group.

Digit flexion

The extent of digit flexion at the time of table contact (or target contact if the participant did not contact the table prior to the target) was coded on a scale from 0 to 4. As illustrated in Fig. 4, 0 = fully extended, 1 = up to ¼ flexed, 2 = up to ½ flexed 3 = up to ¾ flexed, 4 = fully flexed. Each individual digit received a single flexion score and then a total flexion score was calculated by summing the five individual digit flexion scores for each trial. An average total flexion score was then calculated for each participant.

Reach accuracy

Healthy sighted adults consistently direct the tip of the index finger towards the target by the time they contact the table and/or target. Thus, the distance between the tip of the index finger and the center of the target at the time of table contact (or target contact if the participant did not initially contact the table) was measured from the bottom-up camera view using the ruler tool in Adobe Photoshop (Fig. 5a) and served as an indicator of reach accuracy at the time of table contact. The 1 cm^2 grid paper attached to the bottom of the tabletop

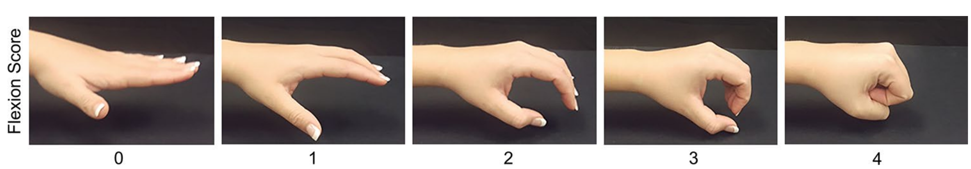

Fig. 4 Representative still frames illustrating the coding system used to quantify digit flexion at the time of table/target contact. Each digit was coded separately and then a single total flexion score for the trial was calculated by summing the scores of all five digits

was used to convert reach accuracy measures from pixels to millimetres and the raw video data from all participants was combined to generate topographical maps illustrating reach accuracy at the time of table/target contact for each group.

Lean

The side-view video records were imported into kinematic software (http://www.kinovea.com) and the displacement of a stable body marker (the center of the shoulder joint) was traced from the time of movement start to the time of table contact (or target contact if there was no initial table contact) for each reaching trial. We then calculated the linear horizontal displacement of this marker, which served as a measure of how far forward infants leaned during each reaching trial.

Target contact

The time-synchronized video records were paused on the frame of target contact and the following behavioural measures were scored.

Part of hand to contact target

Healthy sighted adults almost always use the most distal phalange of either the thumb or index finger to contact the target and to subsequently grasp it. Thus, we computed the proportion of total trials that each participant used the most distal phalange of either the thumb or index finger (termed "pincer digits") to contact the target. In addition, the combined raw video data from all participants was used to generate topographical maps illustrating the part of the hand to make first contact with the target for all participants in each group.

Aperture

The distance (aperture) between the central tip of the index finger and the central tip of the thumb at the time of target contact was measured from the bottom-up camera view, using the ruler tool in Adobe Photoshop (Fig. 5b). To control for differences in hand size, we also calculated aperture at target contact as a proportion of maximum hand aperture, defined as the distance between the central tip of the thumb and the central tip of the index finger when the thumb and index finger formed a 90° angle.

Final grasp

The time-synchronized video records were paused on the frame of final grasp and the following behavioural measure was scored.

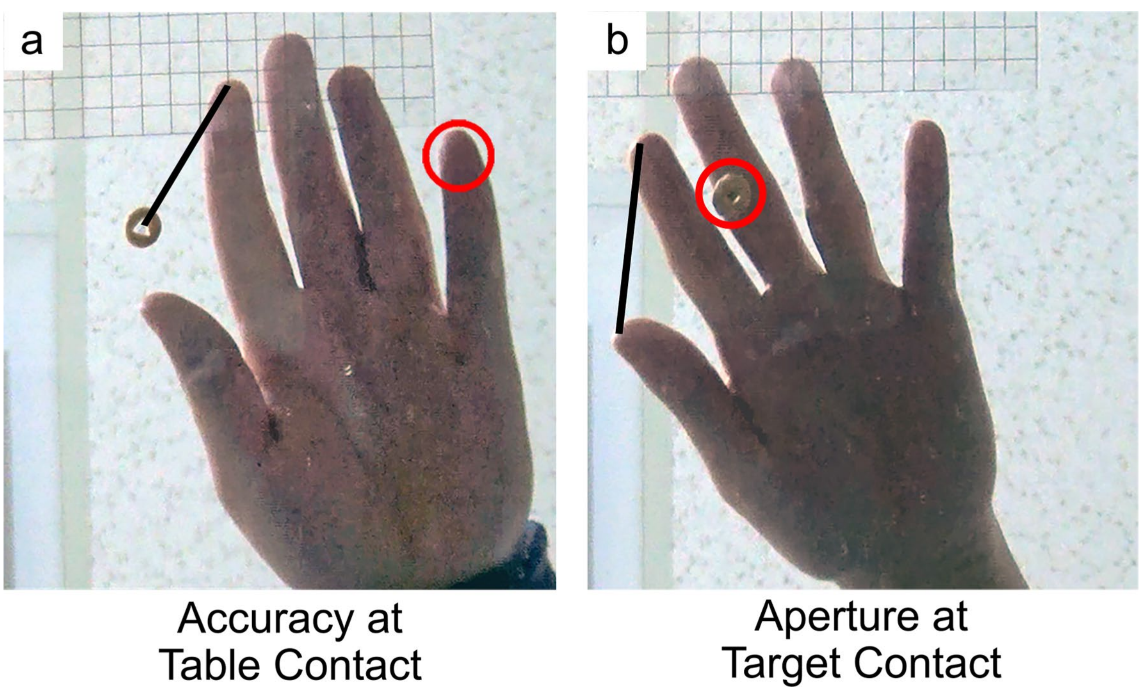

Fig. 5 Still frames illustrating the measures of Reach accuracy and Aperture from the bottom-up view. **a** Reach accuracy is the distance between the central tip of the index finger and the center of the reaching target (black line) at the time of table contact (circle). **b** Aperture is the distance between the central tips of the thumb and index fingers (black line) at the time of target contact (circle)

Grip type

The grip used to grasp and hold the target was coded as either a D1D2 pincer grip (the target was gripped between the distal pads of the thumb and index finger); a D1D3 pincer grip (the distal pads of the thumb and middle finger); a tripod grip (the distal pads of the thumb, index finger, and middle finger); or an alternative grip (any other grip configuration). For each participant, we calculated the proportion of total trials that they used each grip type to grasp the target.

Inter-rater reliability

A subset of five trials per group ($n = 25$ trials) was scored by two independent experimenters (Hallgren 2012). The inter-rater reliability of all interval and ratio variables was assessed using two-way, mixed, average-measures intraclass correlation co-efficients (ICC) with absolute agreeability. For *Frame of Movement Start* ICC = 1.000, *Frame of Table Contact* ICC = 1.000, *Frame of Target Contact* ICC = 1.000, *Frame of Final Grasp* ICC = 1.000, *Total Flexion Score* ICC = 0.978, *Reach Accuracy* ICC = 0.945, and *Aperture* ICC = 0.934. The inter-rater reliability of the nominal variables was assessed using Cohen's (1960) kappa: *Part of Hand to Contact Table,* $\kappa = 0.773$; *Part of Hand to Contact Target,* $\kappa = 1.000$; and *Grip Type,* $\kappa = 1.000$. These analyses indicated that the frame-by-frame video analysis produced very high inter-rater reliability and that all measures were scored similarly by different raters.

Statistical analysis

All raw data were transformed into either a mean score for each participant (Movement Times, Reach Accuracy, Digit Flexion, Aperture) or a proportion score for each participant (Proportion of Table Contact, Part of Hand to Contact Table, Part of Hand to Contact Target, and Grip Type), which then served as dependent variables with Group (9M, 12M, 15M, V, and NV) as the independent between-subjects variable. The data did not always meet the assumptions of normality and homogeneity of variances that are required for analyses of variance (ANOVA) so all group differences were analyzed using the non-parametric Kruskal–Wallis *H* test and follow-up pairwise comparisons using Dunn's (1964) procedure with a Bonferroni correction for multiple comparisons. Adjusted *p* values are presented. Point biserial correlations were used to determine whether infants that leaned farther forward were more likely to contact the underlying table before they contacted the target. Chi square (χ^2) tests were used to determine if there was a relationship between whether or not the participant made initial contact with the underlying table and whether or not they used a pincer digit, defined as the tip of either the index finger or thumb, to make initial contact with the target. All statistical analyses were conducted using SPSS (v. 22) statistical software and *p* values of 0.05 or less were considered significant.

Results

Summary

Infants and unsighted adults frequently contacted the table before they contacted the target and they contacted the table in a similar way, usually with the tip of the thumb and/or pinky finger, a relatively open hand, and poor reach accuracy. This differed from sighted adults who contacted the table less frequently, and when they did, they tended to use the tips of the lateral digits, a flexed and closed hand, and had much higher reach accuracy. Still, there was one notable way in which infants were similar to sighted adults. Despite relatively poor reach accuracy, lack of hand preshaping, and tendency to touch the table before the target, infants were similar to sighted adults in that they tended to use a pincer digit, defined as the tip of either the index finger or thumb, to subsequently contact the target object. Only infants were significantly more likely to use a pincer digit to contact the target if they had made prior contact with the underlying table. Sighted adults tended to use a pincer digit to contact the target, whereas unsighted adults tended to use an alternate part of the hand to contact the target, regardless of whether or not they had made prior contact with the underlying table. These results suggest that initial contact with an underlying surface may assist 9- to 15-month-old infants in learning to use vision to direct a pincer digit to a precise target location.

Movement times

A general description of the temporal organization of the reach-to-grasp action is provided in Fig. 6. All participants took a similar amount of time to contact the table, but 9M infants took significantly longer to subsequently contact the target compared to all other groups. In addition, sighted adults were much faster at transitioning from first contact to final grasp of the target compared to all other groups. These results were confirmed by the statistical analyses (Table 2), which found that the time of table contact did not differ between groups, but the amount of time required to contact the target and complete final grasp did.

Table contact

Figure 7a illustrates the frequency with which participants contacted the table before they contacted the target. 9M

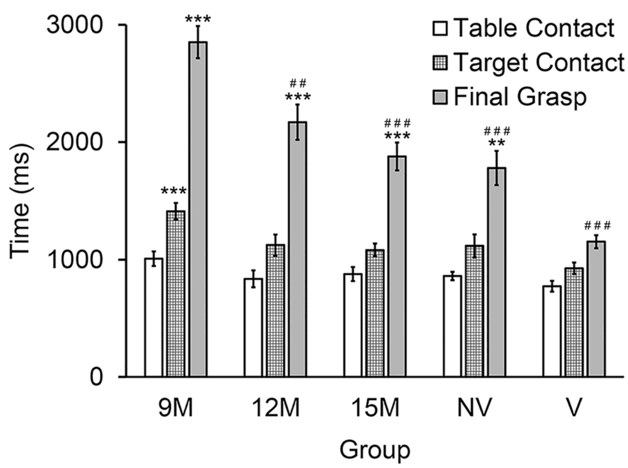

Fig. 6 The amount of time (mean ± SE) required to establish Table Contact, Target Contact, and Final Grasp for each group of participants. All groups took the same amount of time to establish Table Contact, but infants and unsighted adults took significantly longer than sighted adults to establish Final Grasp. *Significant difference compared to sighted adults. #Significant difference compared to 9M infants (*** or ###$p < 0.001$; ** or ##$p < 0.01$; * or #$p < 0.05$)

infants, 12M infants, and unsighted adults frequently contacted the table before the target, sighted adults contacted the table prior to the target about 60% of the time, and 15M infants appeared to be in a state of transition regarding this behaviour. These results were confirmed by the statistical analyses (Table 3) which found that 9M infants, 12M infants, and unsighted adults contacted the table prior to the target significantly more often than sighted adults.

Figure 7b, c depict the extent to which participants preemptively flexed and closed the hand by the time they contacted the table (or the target if there was no prior table contact). A low total flexion score is indicative of an open hand with extended digits and vice versa. 9M infants were similar to unsighted adults in that they maintained a relatively open hand up until the moment of table/target contact. In contrast, sighted adults displayed significant digit flexion and closure at the time of table/target contact. 12M and 15M infants fell in between. These results were confirmed by the statistical analyses, which found that sighted adults flexed the hand significantly more than 9M infants, 12M infants, and unsighted adults (Table 3).

Figure 8a, b illustrate which part of the hand was used to contact the table and the location of table contact relative to the target. Infants and unsighted adults were more variable than sighted adults on both of these measures. They tended to use the thumb (D1) and/or pinky finger (D5) to contact the table, whereas sighted adults tended to use the tips of the middle (D3), ring (D4), and/or pinky (D5) fingers, but rarely the thumb (D1), to contact the table. These results were confirmed by the statistical analyses, which found that there

Table 2 Movement times

Group	Descriptives				Kruskal–Wallis *H* test		
	Median	Mean	SD	SEM	*H*	*df*	*p*
Time to table contact (ms)					8.692	4	0.069
9M	998.33	1008.33	186.67	62.33			
12M	735.67	836.33	229.00	72.33			
15M	806.00	877.33	207.00	59.67			
NV	866.67	861.00	117.67	35.67			
V	758.33	861.00	145.33	46.00			
All	812.33	868.67	189.33	26.33			
Time to target contact (ms)					16.365	4	0.003**
9M	1408.00	1410.00	212.00	70.67			
12M	1057.33	1122.33	281.67	89.00			
15M	1070.67	1082.00	183.67	53.00			
NV	1083.33	1115.67	321.33	97.00			
V	960.00	926.67	163.00	49.00			
All	1061.00	1120.00	275.00	37.67			
Time to final grasp (ms)					35.425	4	0.001***
9M	2720.00	2852.00	410.67	137.00			
12M	2132.00	2170.00	476.33	150.67			
15M	1806.67	1877.67	412.67	119.00			
NV	1641.67	1779.00	484.67	146.00			
V	1166.67	1151.33	180.33	54.33			
All	1768.67	1927.00	666.67	91.67			

**$p < 0.01$, ***$p < 0.001$

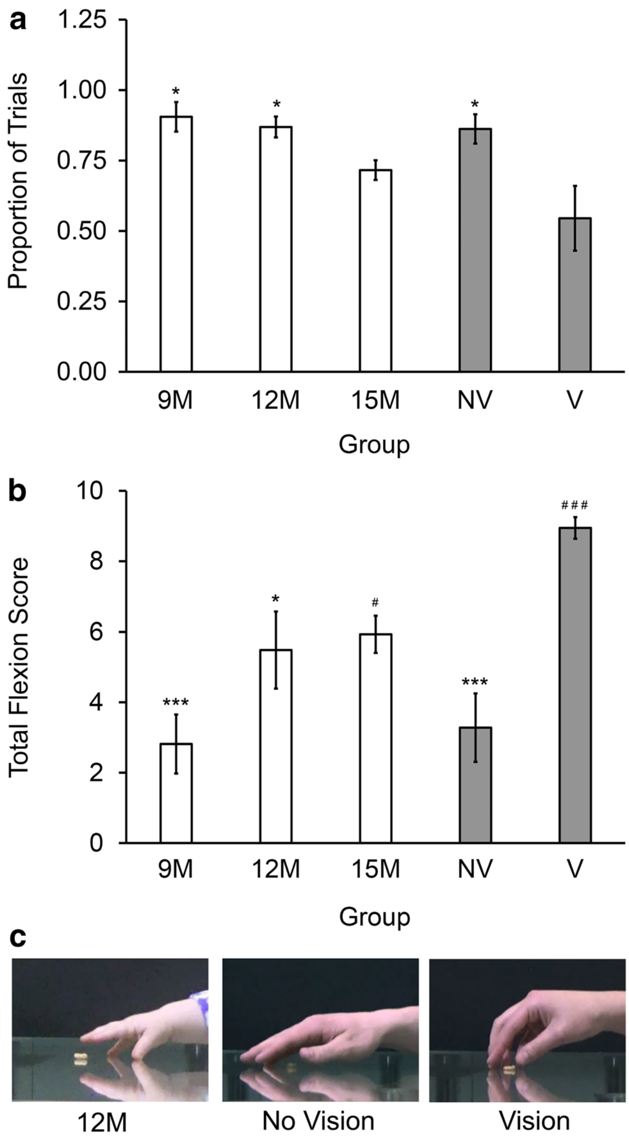

Fig. 7 **a** The proportion of total trials (mean ± SE) that the hand contacted the table before the target for each group; **b** the total flexion score (mean ± SE) at the time of table (or target) for each group, and; **c** representative still frames illustrating the extent of digit flexion at the time of table contact for a 12M infant, unsighted adult, and sighted adult. *Significant difference compared to sighted adults. #Significant difference compared to unsighted adults (*** or ###$p<0.001$; * or #$p<0.05$)

were significant group differences as to which part of the hand was used to contact the table: the thumb $\chi^2(4)=24.893$, $p<0.001$, the index finger $\chi^2(4)=13.719$, $p=0.008$, and the palm $\chi^2(4)=15.188$, $p<0.004$.

Differences in reach accuracy, or the extent to which a participant was able to direct the tip of the index finger towards the target by the time they contacted the table and/or target are illustrated in Fig. 9a, b. In general, all infants demonstrated relatively poor reach accuracy, similar to unsighted adults, in that the tip of their index finger remained an average 23–30 mm from the target at the time of table/target contact. In contrast, sighted adults displayed greater reach accuracy of about 12 mm. These results were confirmed by the statistical analysis (Table 3), which found that sighted adults had significantly better reach accuracy than all other groups.

The relationship between lean and table contact in all infant participants is depicted in Fig. 10. These results reveal that infants tended to contact the table before the target regardless of how far forward they leaned during the reaching trial. Overall, there was no relationship between how far forward infants leaned and whether or not they contacted the table before the target. These results were confirmed by the statistical analysis, which found no significant relationship between lean and table contact in 9M infants, $r_{pb}=0.120$, $p=0.141$; 12M infants, $r_{pb}=0.017$, $p=0.835$; or 15M infants, $r_{pb}=0.029$, $p=0.681$.

Target contact

The extent to which participants used a pincer digit, defined as the tip the index finger or thumb, to contact the target is illustrated in Fig. 11. Despite the fact that infants had relatively poor reach accuracy, they were similar to sighted adults in that they tended to use the tip of either the index finger or thumb to subsequently contact the target. In contrast, unsighted adults, whose reach accuracy was similar to that of infants, were significantly less likely to use a pincer digit to contact the target. On trials where infants did not initially contact the target with a pincer digit, they tended to contact the target with a more proximal part of the hand. Such contacts were common in unsighted adults, but never occurred in sighted adults. Thus, on the relatively few occasions that infants did not use a pincer digit to contact the target, the way in which they contacted the target was more similar to that of unsighted adults. These results were confirmed by the statistical analysis (Table 4), which found that unsighted adults were significantly less likely to use a pincer digit to contact the target compared to all other groups, but 9M, 12M, and 15M infants did not differ from sighted adults.

Figure 12 illustrates hand aperture (the distance between the central tip of the thumb and the central tip of the index finger) at the time of target contact in both millimetres (Fig. 12a) and as a proportion of maximum hand aperture (Fig. 12b). These measures indicate the extent to which the participant preemptively closed the hand in preparation to grasp the target before touching it. When correcting for differences in maximum hand aperture, 9M, 12M, and 15M infants all maintained a larger hand aperture at the time of target contact compared to both sighted and unsighted adults. These results were confirmed by the statistical analysis as shown in Table 4.

Table 3 Measures of table contact

Group	Descriptives				Kruskal–Wallis *H* test		
	Median	Mean	SD	SEM	*H*	*df*	*p*
Table contacts[a]					13.569	4	0.009**
9M	0.95	0.90	0.16	0.05			
12M	0.87	0.87	0.12	0.04			
15M	0.72	0.72	0.12	0.04			
NV	0.90	0.86	0.17	0.05			
V	0.60	0.55	0.38	0.12			
Total	0.88	0.77	0.25	0.03			
Digit flexion (Total Score)					23.689	4	0.001***
9M	1.62	2.81	2.51	0.84			
12M	4.56	5.49	3.46	1.10			
15M	5.84	5.93	1.83	0.53			
NV	2.80	3.28	3.22	0.97			
V	9.00	8.95	1.02	0.31			
Total	5.17	5.39	3.29	0.45			
Reach accuracy (mm)					23.692	4	0.001***
9M	23.52	23.71	8.70	2.89			
12M	26.10	26.42	6.00	1.92			
15M	25.17	28.22	9.61	2.83			
NV	25.08	29.87	10.33	3.07			
V	11.82	12.34	3.68	1.12			
Total	23.51	24.02	10.32	1.44			

*$p<0.05$, **$p<0.01$, ***$p<0.001$

[a]Proportion of trials

Final grasp

Figure 13 shows the type of grip used to grasp the target by each group of participants. Sighted adults were the most likely to use a D1D2 pincer grip, followed by 9M, 12M, and 15M infants, and finally unsighted adults used a D1D2 pincer grip the least. Infants and sighted adults rarely used a D1D3 pincer grip, but this was the favoured grip of unsighted adults. Infants also frequently employed a variety of alternative grips. These results were confirmed by the statistical analysis as shown in Table 5.

Relationship between table contact and target contact

Figure 14 illustrates the relationship between 'whether or not the participant contacted the table before the target' and 'whether or not the participant used the tip of either the index finger or thumb to contact the target'. When examined separately, there were no significant differences between 9M, 12M, and 15M infants on this analysis. Thus, we collapsed their data into a single, infant, group. For infants, there was a significant relationship between having made prior contact with the table and the tendency to subsequently use a pincer digit to contact the target χ^2 (1, $N=531$) = 14.172, $p<0.001$, Cramer's $V=0.163$. On trials where infants did not make initial contact with the underlying table, they were equally likely to use either a pincer digit or some other part of the hand to contact the target. In contrast, when they did make prior contact with the underlying table, they were twice as likely to use a pincer digit to contact the target. Such a relationship did not exist in unsighted adults χ^2 (1, $N=215$) = 0.133, $p=0.715$, who very rarely used a pincer digit to contact the target regardless of whether or not they made prior contact with the underlying table. Nor did this relationship exist in sighted adults χ^2 (1, $N=219$) = 2.044, $p=0.153$, who were much more likely to use a pincer digit to contact the target regardless of whether or not they made prior contact with the underlying table. The results of this analysis reveal that, for all participants, contact with the table may often be inevitable, due to the small size of the target, but for infants it is not inconsequential because it appears to enhance their ability to subsequently direct a pincer digit to a nearby visual target.

Discussion

Previous work has not fully clarified the neural and behavioural factors that enable the developmental transition from somatosensory to visual control of the reach and grasp in

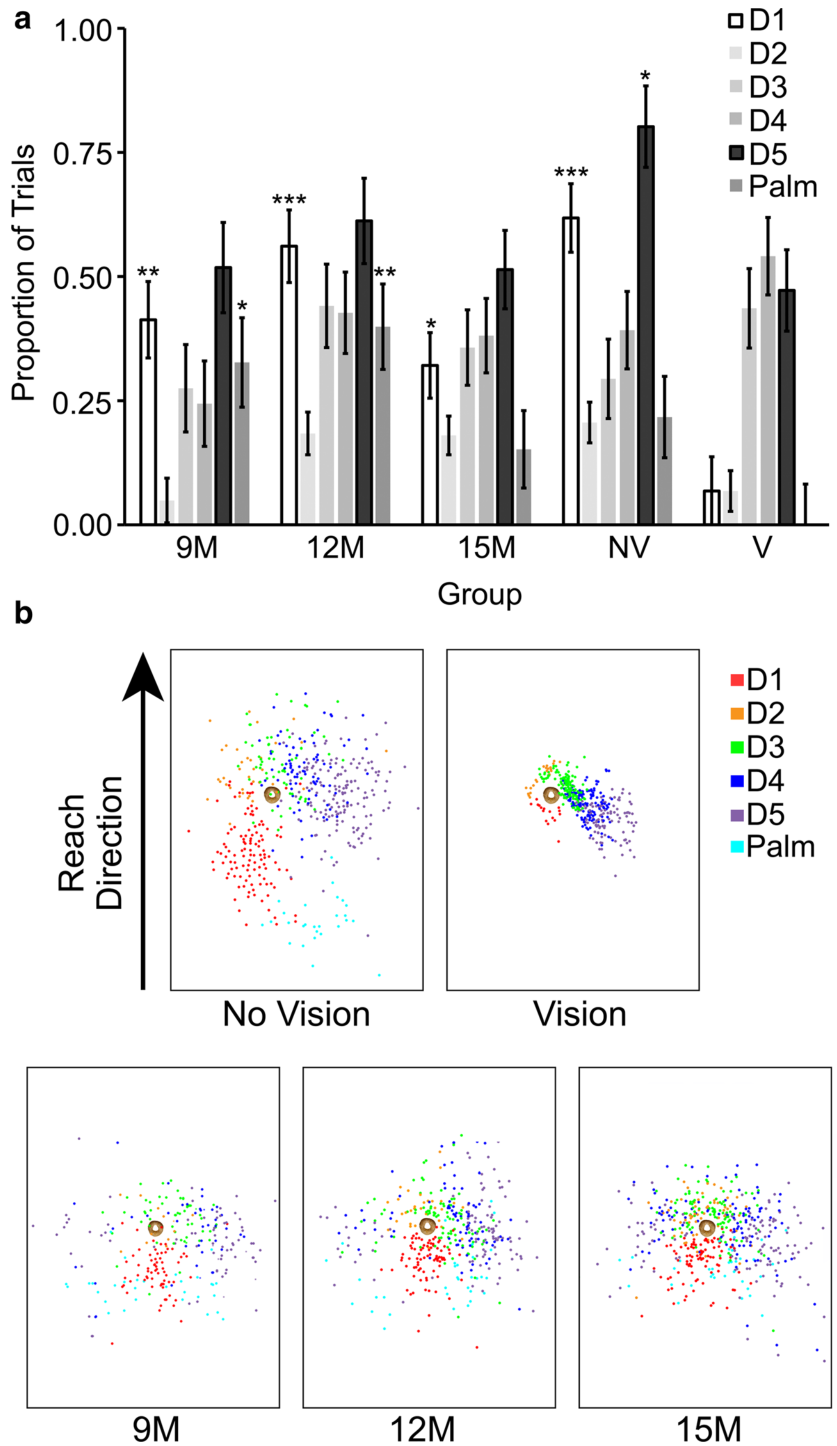

Fig. 8 **a** The proportion of total trials (mean ± SE) that participants used each part of the hand to contact the table and **b** topographical maps illustrating the part of the hand to contact the table and the location of table contact relative to the target for all trials, by all participants, in each group. Infants and unsighted adults tended to contact the table with the thumb and/or pinky finger, whereas sighted adults tended to contact the table with the tips of the middle, ring, and pinky finger. The location of table contact was more variable in infants and unsighted adults compared to sighted adults. D1 = thumb, D2 = index finger, D3 = middle finger, D4 = ring finger, D5 = pinky finger, P = palm. *Significant difference compared to sighted adults (***$p < 0.001$; **$p < 0.001$; *$p < 0.05$)

human infants. This descriptive study used frame-by-frame video analysis to examine the reach and grasp movements of sighted 9M, 12M, and 15M infants, as well as sighted and unsighted adults, to try to identify age-specific behavioural factors that may relate to the development of feedforward visual control of the reach and grasp. The results reveal that infants, like unsighted adults, were highly likely to contact the underlying table before contacting a small precise target. Initial table contact usually involved the tip of the thumb and/or pinky finger, a relatively open and extended hand, and poor reach accuracy. Despite this, infants used a pincer digit, defined as the tip of the index finger or thumb, to subsequently contact the target just as frequently as sighted adults did. Only in infants was this ability related to whether or not they had made prior contact with the underlying table. These results suggest that initial contact with an underlying table or

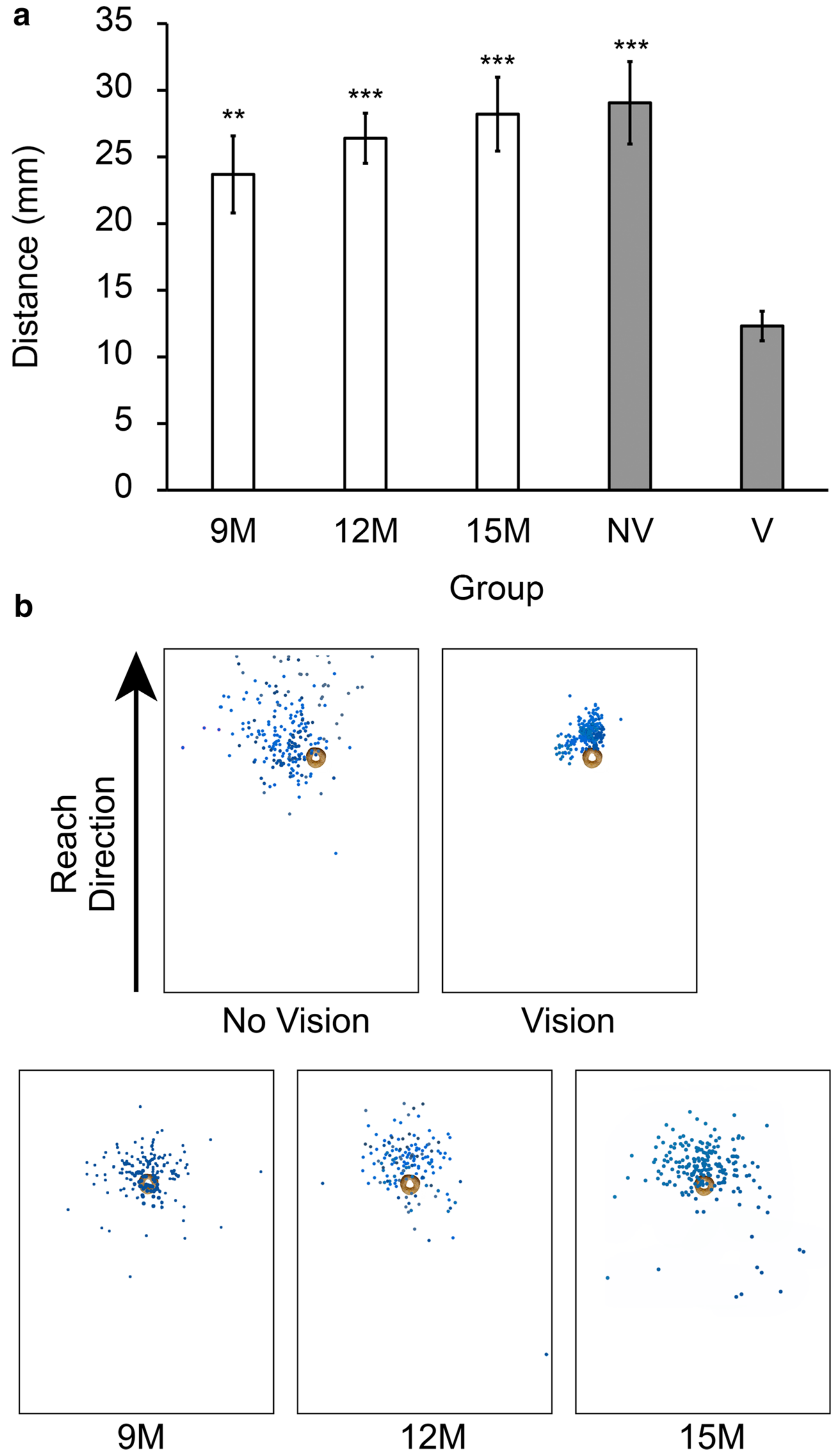

Fig. 9 **a** Reach accuracy (mean ± SE) at the time of table (or target) contact for each group and **b** topographical maps illustrating the location of the tip of the index finger relative to the target at the time of table contact for all trials, by all participants, in each group. Infants and unsighted adults had poorer reach accuracy compared to sighted adults in that they were less accurate at directing the tip of the index finger to the target location by the time they contacted the table. *Significant difference compared to sighted adults (***$p < 0.001$; **$p < 0.001$)

surface may assist infants in using feedforward visual control to direct their digits to a precise nearby target location.

The present study used a number of innovative techniques to examine reach accuracy, hand preshaping, table contact, and target contact in both infants and adults. First, while the majority of infant studies use larger acrylic rods or plastic toys as reaching targets, the present study used a small precise target—a single Cheerio. Larger rods or toys can be successfully grasped at a variety of contact points and with a number of different hand configurations whereas reaching to grasp a Cheerio requires great precision in both hand transport and digit shaping. Thus, the present task allowed us to probe the upper limits of the infants' ability to use feedforward visual control to transport and shape their hand to the

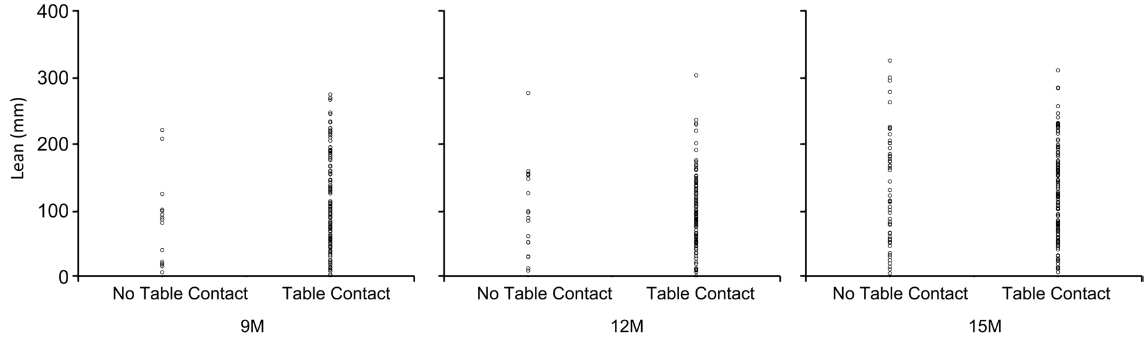

Fig. 10 The relationship between lean and table contact for each group of infants. Each graph illustrates the extent to which an infant leaned forward during a given trial and whether or not they contacted the table before the target on that same trial. The extent to which infants leaned forward on a given trial was unrelated to whether or not they contacted the table before the target on that same trial

small precise target. Second, time-synchronized frame-by-frame video analyses were used to quantify reach and grasp behaviour. This approach allows for a more ethologically valid description of the reach and grasp, as it avoids the attachment of wired kinematic sensors to the hands, which impede somatosensory feedback, perturb natural motor behaviour, and serve as a major distraction, especially in young infants (Domellöf et al. 2007). Third, the behavioural coding system used in the present study produced very high inter-rater reliability, enabling strong confidence in the reproducibility of the results.

Still, some methodological caveats must be noted. Reach accuracy and hand aperture were measured in two dimensions from a single bottom-up view, which is less informative than the three dimensional measures that can be acquired by automated motion tracking technologies. Nonetheless, inspection of the front and side video views verified that the present approach is unlikely to have biased the results in any consistent fashion. Second, infants were more variable than adults in regards to the start position of their hand at the beginning of each reaching trial. Differences in hand start position could increase variability in the time required to establish table contact, target contact, and final grasp of the target in infants. We attempted to minimise this effect by having the experimenter gently guide the infants' hands to their laps at the onset of each reaching trial and were largely successful in doing so. Third, the present study included 9M, 12M, and 15M infants. Yet, previous research has indicated that the transition from somatosensory to visual control is asymmetric with feedforward visual control of the reach maturing between 9 and 12 months, and feedforward visual control of the grasp continuing to mature beyond 24 months of age. Thus, the present study is more likely to have identified factors related to the development of visual control for the reach as compared to the grasp.

Analyses of the temporal organization of the prehensile act revealed that there were no group differences in the amount of time required to contact the table, yet, after table contact, unsighted adults and infants took significantly longer to grasp the target compared to sighted adults. This finding may relate to the early view of Woodworth (1899) and others (Arbib et al. 1985; Jeannerod 1981) that a reaching (or pointing) movement consists of two phases. First, a ballistic, or visually elicited, movement brings the hand to the general location of the target and then a visually controlled corrective movement positions an appropriate part of the hand on the target. In the present study, the moment of table contact may reflect the termination of the visually elicited phase of the reach, which appears to be largely mature by 9 months of age, and the onset of the visually corrected phase of the reach, which involves directing the digits to the target location, followed by grasping of the target. That 9M infants took significantly longer to use a pincer digit to contact the target, but 12M and 15M infants did not, suggests that the visually corrected phase of the reach may not mature until slightly later at 12–15 months. Still, the apparent maturity of this visually corrective movement may depend on whether or not the infant made prior contact with the underlying table. That infants and unsighted adults took longer than sighted adults to grasp the target after contacting it is in agreement with previous literature (Barrett and Needham 2008; Karl and Whishaw 2014; von Hofsten and Rönnqvist 1988; Schum et al. 2011) in suggesting that feedforward visual control of hand preshaping for grasping is not yet mature in 15M infants.

Analyses of table contact revealed that all participants tended to contact the table before the target, with infants and unsighted adults contacting the table significantly more often than sighted adults. For both infants and adults, it is likely that initial contact with the underlying table was often inevitable due to the small size of the target. Had a larger reaching target been used, the precision requirements of the task would have been greatly reduced and it is highly likely that all participants would have been able

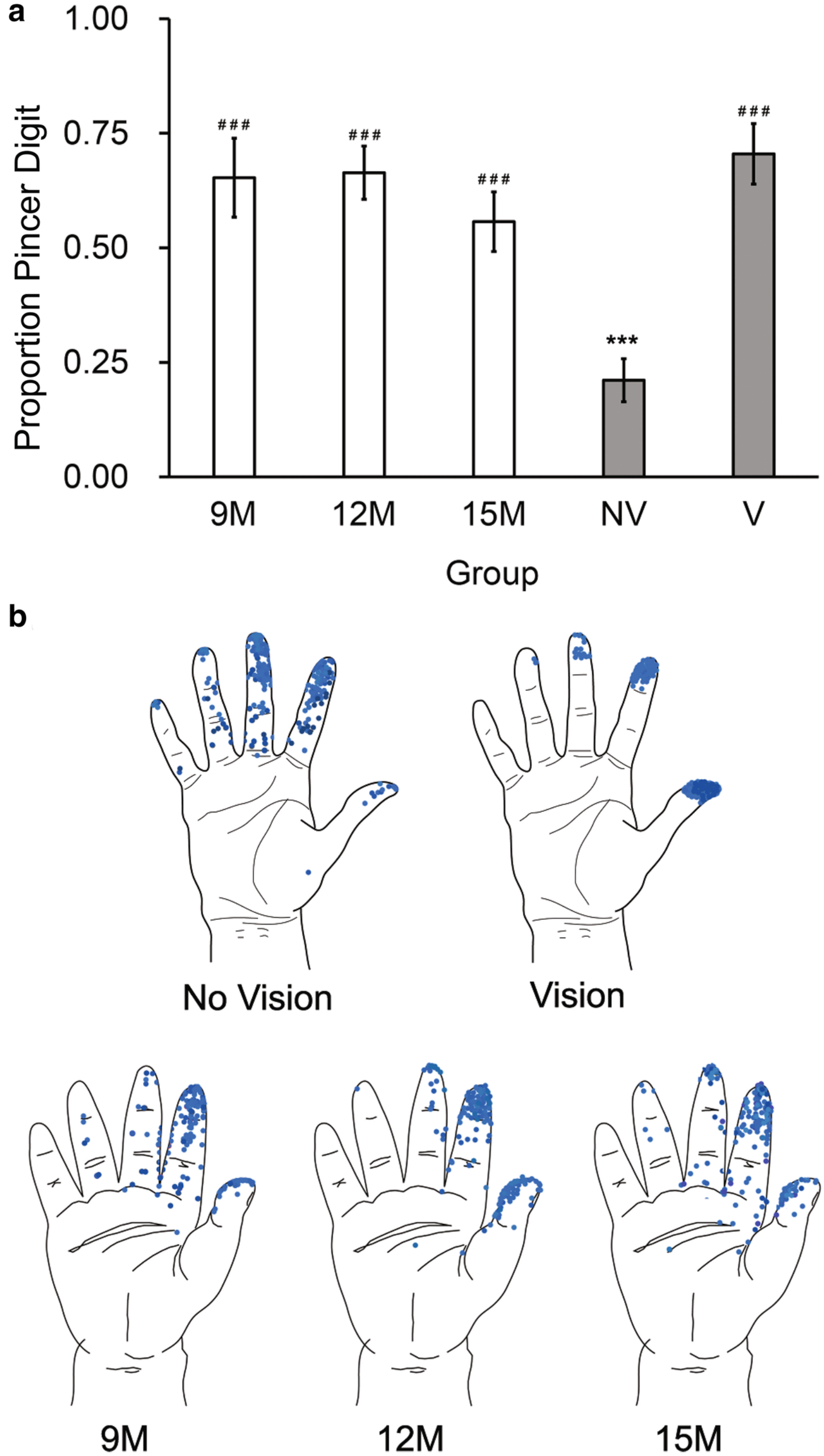

Fig. 11 **a** The proportion of total reach trials (mean ± SE) that a pincer digit, defined as the distal phalange of either the thumb or index finger, was used to make first contact with the target and **b** topographical maps illustrating the part of the hand to make first contact with the target for all trials, by all participants, in each group. Infants were similar to sighted adults in that they were significantly more likely than unsighted adults to use a pincer digit to contact the target. *Significant difference compared to sighted adults. #Significant difference compared to unsighted adults (*** or ###$p < 0.001$)

to successfully contact and grasp the larger target without first touching the table. This is because it is possible to successfully contact and grasp larger targets using much less precise digit-to-target contacts and with less precise grip configurations. In essence, the task is much easier and thus, the need for precise feedforward visual control of the reach and grasp is greatly reduced. The extent to which initial table contact facilitates appropriate digit-to-target contact is almost certainly modulated by target size, task precision, and the extent to which participants are able to use feedforward visual control to guide their reach and grasp movements. Thus, the exact target size and level of task precision required to reveal the relationship between initial table contact and subsequent digit-to-target contact

Table 4 Measures of target contact

Group	Descriptives				Kruskal–Wallis *H* test		
	Median	Mean	SD	SEM	*H*	*df*	*p*
Pincer digit to make target contact[a]					21.803	4	0.001***
9M	0.68	0.65	0.26	0.09			
12M	0.67	0.66	0.18	0.06			
15M	0.62	0.56	0.22	0.06			
NV	0.19	0.21	0.15	0.05			
V	0.77	0.71	0.22	0.07			
Total	0.62	0.55	0.27	0.04			
Hand aperture at target contact (mm)					30.387	4	0.001***
9M	34.89	36.52	8.72	2.89			
12M	36.45	36.13	8.59	2.73			
15M	34.31	34.51	7.67	2.21			
NV	55.38	50.27	14.73	4.43			
V	18.02	18.80	3.52	1.14			
Total	33.91	35.22	13.68	1.86			
Hand aperture at target contact[b]					33.077	4	0.001***
9M	0.43	0.50	0.11	0.04			
12M	0.44	0.42	0.07	0.02			
15M	0.45	0.44	0.10	0.03			
NV	0.34	0.32	0.09	0.03			
V	0.11	0.12	0.02	0.01			
Total	0.38	0.35	0.16	0.02			

***$p < 0.001$

[a]Proportion of trials

[b]Corrected

should be investigated further in future work using larger reaching targets.

While all participants frequently contacted the table before the target, there were important differences in how they contacted the table. Sighted adults initially contacted the table near the target, with the tips of the pinky, ring, and/or middle finger, flexed digits, and high reach accuracy. For sighted adults, contact with the table appeared to be coincidental and to reflect the fact that they had preemptively flexed and preshaped the hand for grasping. In contrast, infants and unsighted adults tended to contact the table with the thumb and/or pinky finger at variable locations farther from the target. Their digits were more open/extended and they were initially less accurate at directing the tip of the index finger to the target location. Together, these results indicate that instead of preshaping the hand prior to table/target contact, infants and unsighted adults tended to pronate an open hand over the general location of the target. While infants and unsighted adults initially contacted the table in a similar way, their reasons for doing so are likely different. Unsighted adults likely contact the table because they lack vision and must rely on somatosensory cues to determine the location of the target. In contrast, infants likely contact the table due to the fact that their postural control, arm and hand control, manual dexterity, as well as visuomanual coordination are not yet mature.

Despite differences in why infants and unsighted adults initially contact the table, the fact that they contact the table in a similar manner is interesting. It has been suggested, that the human reach movement is derived from the evolutionarily earlier movement of forelimb stepping (Gerogopoulos and Grillner 1989; Karl and Whishaw 2013; Sacrey et al. 2009; Whishaw and Karl 2014). Studies comparing the forelimb movements of rodents and humans find that the two movements share a similar kinematic structure (Karl and Whishaw 2013; Sacrey et al. 2009). Both movements are initiated by flexing the elbow and lifting the hand. The digits flex and close as the limb is transported forward, they then open and extend on approach to the target. Finally, the open hand pronates in the lateral to medial direction over the general location of the target. Only when foveal vision is available do humans preshape the hand for grasping during pronation (Karl et al. 2012). That the kinematic structure of the step and reach are similar in rodents, infants, and unsighted adults suggests that infants and unsighted adults may generate an evolutionarily conserved hand shape during the initial visually elicited phase of the reach that reflects the evolutionary history of the forelimb as a stepping effector.

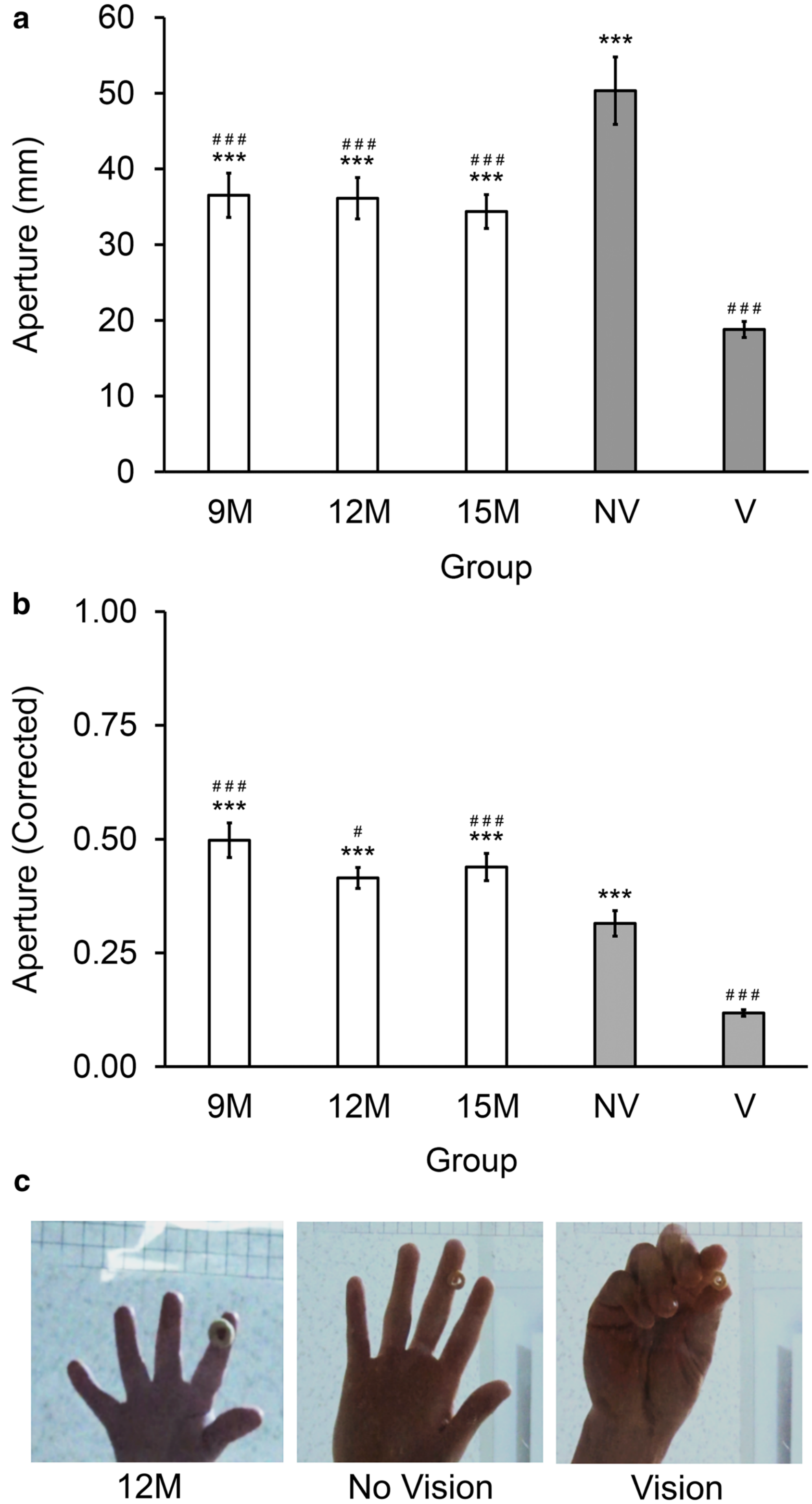

Fig. 12 Aperture (mean ± SE) at the time of target contact for each group **a** in millimetres and **b** as a proportion of maximum hand aperture as well as **c** representative still frames illustrating hand aperture at the time of target contact for a 12-month-old infant, unsighted adult, and sighted adult. Infants and unsighted adults tended to contact the target with a large hand aperture whereas sighted adults did so with a small aperture. *Significant difference compared to sighted adults. #Significant difference compared to unsighted adults (*** or ###$p<0.001$; ** or ##$p<0.01$; * or #$p<0.05$)

Interestingly, adult primates with lesions to primary visual cortex (V1) also produce reach movements that are kinematically similar to those described above for infants and unsighted adults (e.g., Whishaw et al. 2016). These are likely enabled by subcortical visual pathways that bypass V1 by projecting from the lateral geniculate nucleus or pulvinar directly to dorsal stream area MT. Primate studies indicate that these subcotical visual inputs to area MT are more

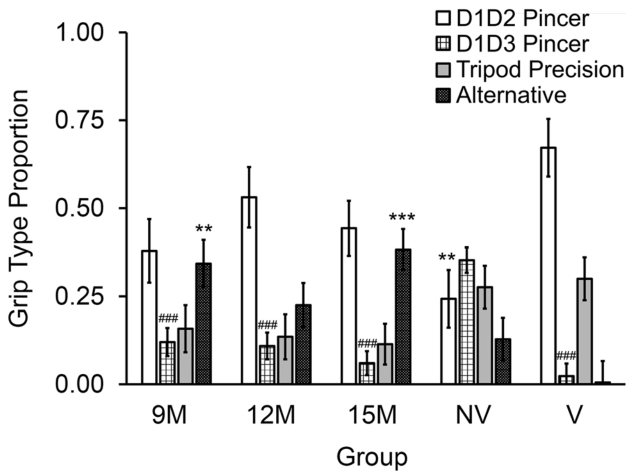

Fig. 13 The proportion of total reaches (mean ± SE) that participants used a D1D2 pincer, D1D3 pincer, tripod, or alternative grip to acquire the target. Infants were more similar to sighted adults in that they tended to use a D1D2 pincer grip to acquire the target; however, when they didn't, they tended to use an alternative grip, which sighted adults never did. *Significant difference compared to sighted adults. #Significant difference compared to unsighted adults (*** or ###$p < 0.001$; ** or ##$p < 0.01$)

prominent during early development than those projecting from V1 (Bourne and Morrone 2017; Mundinano et al. 2017, 2018; Turner et al. 2017; Warner et al. 2012). Thus, they may be at least partially responsible for mediating the initial visually elicited phase of the reach movement that transports the hand to the general location of the target in 9- to 15-month-old human infants.

Analyses of target contact revealed that despite differences in how infants and sighted adults contacted the table, infants used a pincer digit, defined as the tip of the index finger or thumb, to contact the target just as frequently as sighted adults did. Only in infants was the tendency to contact the target with one of these digits related to whether or not they had made prior contact with the underlying table. This suggests that after infants contact the table they are better able to direct their digits toward the precise location of a nearby visual target. There are two possible ways that this may be accomplished. First, infants may compare the kinesthetically felt position of their hand with the seen location of the target to direct their digit towards the target. Alternatively, infants may use vision to compare the seen location of their hand with the seen location of the target to accomplish the same outcome. Schlesinger and Parisi (2001) suggest that early development of crude reaching movements involves coordinating the felt location of the arm with the seen location of the target, and that this coordination is refined and reinforced when the hand makes tactile contact with the target. However, they predict that as reaching becomes more skilled, precise vision will play an increased role in aligning the seen location of the hand with the seen location of the target. Future experiments should aim to determine which of these two possibilities most likely mediates increased digit-to-target accuracy after table contact in 9- to 15-month-old human infants.

Analyses of final grasp revealed that even though infants were more likely to use the tip of the index finger or thumb to contact the Cheerio if they had first contacted the table, this did not translate into increased use of D1D2 pincer grips. Review of the video record revealed that infants often looked away from the target as soon as they contacted it and, thus, completed the majority of the grasp under purely somatosensory control. This is not unlike healthy sighted adults (Sacrey and Whishaw 2012); but, because infants and sighted adults contacted the table differently—infants were more likely to contact the table with their thumb and with a larger index-thumb aperture—the way that infants contacted the table may have hindered their ability to subsequently form a D1D2 pincer grip on the target and increased their reliance on alternative grips.

The present study is descriptive in nature and has identified that 9- to 15-month-old infants are more likely to use a pincer digit, defined as the tip of the index finger or thumb, to contact a precise visible target if they first make contact with an underlying surface. Additional studies in our laboratory have aimed to determine whether or not this relationship is causal by comparing infants reaching for Cheerios located on a table versus a narrow pedestal, in which all tactile and physical support from the underlying table is removed (Karl et al. 2017). In this follow-up study, infants were less likely to use the tip of the index finger or thumb to contact the Cheerio when it was located on top of a narrow pedestal. This suggests that contact with the underlying table does somehow enhance the infant's ability to direct their index finger and/or thumb towards a precise visual target. Additional studies are needed to determine why this is the case. Thus, it is useful to consider potential neural and behavioural factors that might contribute to the current findings so that they might be investigated in future research.

First, gross motor abilities, such as postural and upper limb control, are not yet mature in 9- to 15-month-old infants. Thus, infants may have difficulties directing the hand towards the target and may initially contact the underlying table near the target. This could allow the infant to stabilize the weight of their body and arm on their hand, as well as stabilize the position of their hand near the target. Stabilization of the hand near the target would reduce the complexity of the task by reducing the number of degrees of freedom that the infant needs to actively control when trying to contact the target. This may free up the majority of their attention and effort to direct the pincer digits towards the target, resulting in more accurate digit-to-target contact as compared to when no physical support of the hand, arm, or

Table 5 Measures of final grasp

Group	Descriptives				Kruskal–Wallis *H* test		
	Median	Mean	SD	SEM	*H*	*df*	*p*
D1D2 final grip[a]					11	4	0.027*
9M	0.38	0.38	0.21	0.07			
12M	0.45	0.53	0.32	0.10			
15M	0.42	0.44	0.20	0.06			
NV	0.20	0.24	0.18	0.06			
V	0.80	0.67	0.38	0.11			
Total	0.40	0.45	0.30	0.04			
D1D3 final grip[a]					23.423	4	0.001***
9M	0.11	0.12	0.09	0.03			
12M	0.07	0.11	0.12	0.04			
15M	0.05	0.60	0.06	0.02			
NV	0.40	0.35	0.20	0.06			
V	0.00	0.02	0.06	0.02			
Total	0.07	0.13	0.16	0.02			
Tripod final grip[a]					7.852	4	0.097
9M	0.05	0.16	0.19	0.06			
12M	0.12	0.13	0.12	0.04			
15M	0.07	0.11	0.13	0.04			
NV	0.25	0.28	0.16	0.05			
V	0.20	0.30	0.33	0.10			
Total	0.13	0.20	0.21	0.03			
Alternative final grip[a]					24.264	4	0.001***
9M	0.33	0.34	0.31	0.10			
12M	0.22	0.23	0.18	0.06			
15M	0.27	0.38	0.26	0.07			
NV	0.10	0.13	0.11	0.03			
V	0.00	0.00	0.02	0.00			
Total	0.17	0.21	0.24	0.03			

$*p < 0.05$, $***p < 0.001$

[a]Proportion of total trials

body is available. Still, the results of the present study reveal that infants contacted the table before the target regardless of whether or not they leaned forward during their reach attempt. In addition, review of the video record revealed that infants appeared to use their non-reaching hand to support their upper body weight. Thus, it seems that infants do not necessarily contact the table to counteract immature postural mechanisms or to support body and upper limb weight, but future experiments should aim to further clarify these issues.

A second possibility is that contact with the underlying table might encourage the infant to visually orient towards the nearby target, which could in turn increase the accuracy with which they are able to direct their pincer digits toward the target. This idea is based on the observation by Corbetta et al. (2014) that when young infants first begin to reach for distal objects they learn to direct their visual attention to where their hand is when it makes tactile contact with an object rather than the other way around. Our general observations suggest that this is unlikely with the older 9- to 15-month-old infants tested in the present study as they tended to visually fixate on the target prior to contacting it, but future eye-tracking studies could determine the full extent to which this mechanism might contribute to the present results.

Another possibility is that when an infant contacts the underlying table his/her ability to use vision to process the structural features of the nearby target, and to subsequently act on it, may be enhanced. A number of studies have recently shown that visual processing of an object is enhanced if that object is located near the hands in what is known as peri-hand space (e.g., Brockmole et al. 2013; Brown et al. 2015; Brozzoli et al. 2014; Kao and Goodale 2009; Perry and Fallah 2017). Enhanced visual processing of targets in peri-hand space is proposed to depend on previous experience (Brown and Goodale 2013) and to be mediated by subcortical visual pathways that bypass V1,

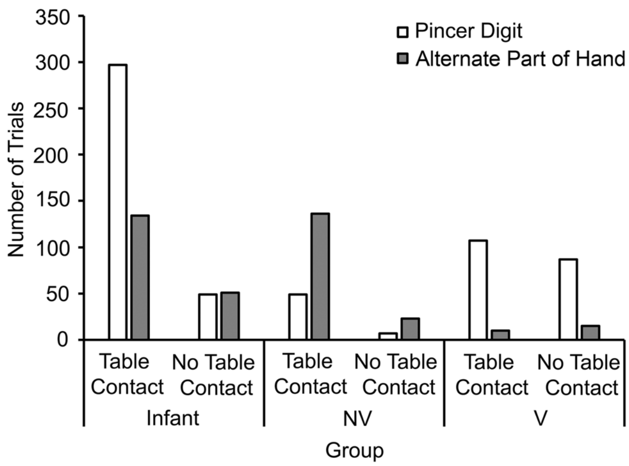

Fig. 14 The relationship between Table Contact and Target Contact. Each graph illustrates the total number of trials that participants initially contacted the table and then used a pincer digit [either the tip of the index finger or thumb (white bar)], or an alternate part of the hand (grey bar), to contact the target; as well as the total number of trials that participants did not contact the target and then used either a pincer digit [the index finger or thumb (white bar)], or an alternate part of the hand (grey bar), to contact the target. Note: only on trials where infants first made initial contact with the underlying table were they more likely to subsequently use a pincer digit to contact the target

including those that are prominent during early development and project directly from the pulvinar to dorsal stream area MT (Brown et al. 2008; Goodhew et al. 2015; Goodhew and Clarke 2016; Gozli et al. 2012; Mundinano et al. 2018; Taylor et al. 2014). From a developmental perspective (e.g., see Thelen and Smith 1994; Edelman 1993), when an infant first begins to reach for precise visual targets, an initially crude and visually elicited reach movement enabled by this subcortical visual pathway would be sufficient to bring the hand to the general location of the target, establish contact between the hand and an underlying surface, and activate parietofrontal brain areas involved in processing the proprioceptive, tactile, and motor signals associated with that movement. This would in turn lead to the activation of recurrent neural pathways that project from the parietofrontal areas back to the slower maturing early extrastriate visual areas, thereby helping to sharpen the visual tuning of these neurons (Perry et al. 2015) to both the infant's hand and the nearby target. This coordinated activity in the parietofrontal and extrastriate cortices could help the infant to align both the seen and felt position of her hand with the seen position of the target, ultimately enhancing her ability to bring the tip of her digits into contact with the target. In other words, initial tactile contact with the underlying table may physically stabilize the infant's arm and hand near the target, but in addition, it may help to fully activate peri-hand space mechanisms in the parietofrontal and extrastriate cortices that appear to play an important role in enabling precise feedforward visual control of reach and grasp movements in adulthood.

In conclusion, the present results support the postulate of Multiple Motor Channel theory that the reach and grasp are separate movements and that feedforward visual control of the two movements develops at different rates. The initial phase of the reach appears to be visually elicited, largely mature by 9 months of age, and may be at least partially mediated by an earlier maturing subcortical visual pathway from the pulvinar to dorsal stream area MT. The precise terminal phase of the reach appears to depend on feedforward visual control that enables the infant to match the seen/felt position of her fingertip with the visual location of the target. While 9- to 15-month-old infants can apparently achieve this, their ability to do so is likely enhanced if they make prior contact with an underlying surface. Finally, feedforward visual control of hand preshaping for the grasp is not yet mature at 15 months of age. Contact with an underlying table or surface could enhance the infant's ability to direct their digits to a precise nearby target by stabilizing the hand near the target, re-directing visual attention towards the target, and/or fully activating peri-hand space mechanisms, all of which would assist the infant in aligning the seen/felt position of the hand with the seen position of the target. Regardless of the extent to which each of these factors may contribute, contact with an underlying surface seems to increase the number of times that an infant experiences a desirable reach outcome (appropriate digit-to-target contact), which is likely to lead to further refinement and reinforcement of both the neural and behavioural events that enabled that successful reach movement in the first place.

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