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Catching Moving Objects: Differential Effects of Background Motion on Action Mode Selection and Movement Control in 6- to 10-Month-Old Infants

ABSTRACT: *In human adults the use of visual information for selecting appropriate modes for action appears to be separate from the use of visual information for the control of movements of which the action is composed (Milner & Goodale, [1995] The visual brain in action; [2008] Neuropsychologia 46:774–785). More specifically, action mode selection primarily relies upon allocentric information, whereas movement control mainly exploits egocentric information. In the present study, we investigated to what degree this division is already present in 6- to 10-month-old infants when reaching for moving objects; that is, whether allocentric information is uniquely exploited for action mode selection (i.e., reaching with one or the other hand) or whether it is also used for movement control (i.e., reaching kinematics). Infants were presented with laterally approaching objects at two speeds (i.e., 20 and 40 cm/s) against a stationary or moving background. Background motion affects allocentric information about the object's velocity relative to its background. Results indicated that object speed constrained both infants' action mode selection and movement control. Importantly, however, the influence of background motion was limited to action mode selection and did not extend to movement control. The findings provide further support for the contention that during early development information usage is—at least to some degree—separated for action mode selection and movement control. © 2015 Wiley Periodicals, Inc.* Dev Psychobiol 57:921–934, 2015.

Keywords: *infant reaching; relative velocity; action mode selection; motor control; two-visual systems model*

INTRODUCTION

Research in adults suggests a division in the human visual system into two functionally and neuro-anatomically separate visual systems: *vision for movement* and *vision for perception* (Goodale & Milner, 1992; 2004; Milner & Goodale, 1995; 2008).[1] Vision for movement is engaged in the online control of movements whereas

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[1]Note that, originally, the "vision for movement" system was termed "vision for action" (Goodale & Milner, 1992). Yet, it is our contention that the term "movement" more directly speaks to the function of the dorsal stream, which yields the control of movements and does not include action mode selection (van Doorn et al., 2007). In addition, it should be noted that the current study only includes behavioral data and does not validate activations in the ventral or dorsal stream. Hence, findings are interpreted within the two-visual systems model on a behavioral level (i.e., exploitation of visual information) and are only suggestive with respect to the underlying neural circuitry.

vision for perception is involved in the perception of objects, events, and situations. Apart from engaging separate cortical areas (i.e., the dorsal and ventral stream, respectively), these systems can be distinguished on a behavioral level by the type of visual information that they preferably exploit (Haffenden & Goodale, 2000; Michaels, 2000; Milner & Goodale, 2008; van der Kamp, Oudejans, & Savelsbergh, 2003). That is, vision for movement mainly, but not exclusively, relies on egocentric (i.e., context-independent) sources of information, whereas vision for perception primarily exploits allocentric (i.e., context-dependent or relative metrics) sources of information. This division in information use becomes evident in the differential effects that visual illusions have on visual perception and movement control (e.g., Aglioti, DeSouza, & Goodale, 1995; Bruno, Bernardis, & Gentilucci, 2008; Ganel, Tanzer, & Goodale, 2008; Stöttinger et al., 2012; Stöttinger, Soder, Pfusterschmied, Wagner, & Perner, 2010). For instance, the perception of the properties of a shaft (e.g., its length) embedded in the Müller–Lyer illusion is clearly affected by the object's visual surroundings (i.e., the tails of the illusion), which underlines that vision for perception uses context-dependent, allocentric information. Yet, when the object is grasped, the unfolding of hand aperture is scaled to the physical size of the object and remains relatively immune to the illusion, demonstrating that vision for movement is primarily reliant upon context-independent, egocentric information (Aglioti et al., 1995; Ganel et al., 2008; Milner & Goodale, 2008; Otto-de Haart, Carey, & Milne, 1999; van Doorn, van der Kamp, & Savelsbergh, 2007). Importantly, it has recently been demonstrated that vision for perception also contributes to the selection of an appropriate mode for action (Milner & Goodale, 2008; van Doorn et al., 2007; van Doorn, van der Kamp, de Wit, & Savelsbergh, 2009). For example, the selection of using one or two hands to grasp relatively large shafts embedded in the Müller–Lyer illusion involved, like the perception of their length, the use of the contextual, allocentric information, suggesting contributions of vision for perception.

Based on Milner and Goodale's framework, van Wermeskerken, van der Kamp, and Savelsbergh (2011) have recently suggested that the developmental trajectories of vision for perception and vision for movement are not necessarily linked to one another. They showed that infants as young as 5 months were able to select adaptive reaching modes (i.e., one- or two-handed reaching) and adjusted their movement kinematics (i.e., the unfolding of bimanual hand aperture) to the size of the object. Yet, and more pertinently, they showed that the age-related changes within these processes did not mutually constrain each other. That is, age-related differences in the selection of a reaching mode that is appropriate for the size of the object did not directly map onto age-related differences in how infants adjusted their reaching to object size and vice versa. This suggests that the developments of vision for perception and vision for movement are (partly) independent. This would be further corroborated if it could be shown that the processes rely on different sources of information. Tentative evidence for this was recently provided by van Wermeskerken and colleagues (van Wermeskerken, van der Kamp, Savelsbergh, & von Hofsten, 2013). In their study, 6- to 7-month-old infants were presented with two objects against a background with a textural gradient, not unlike the Ponzo figure. Against this illusory gradient, adults perceive one object as closer than the other (see Ganel et al., 2008). Van Wermeskerken et al. (2013) reported that infants' reaching kinematics were not affected by the illusory distance information. Presumably, the reaching kinematics were based on nonillusory, egocentric distance information. By contrast, infants more often chose to reach for the apparently closer object, suggesting that the selection of which of the two objects to reach for was clearly influenced by illusory, allocentric information.

Although these studies support the hypothesis of a distinct use of visual information for action mode selection and movement control in early development, it is limited to grasping stationary objects. Hence, the present study aimed at scrutinizing the same distinction, but for a task that also demands adjustments to temporal properties of the objects (i.e., speed) instead of to their spatial aspects only (i.e., size or distance). To this end, infants 6 months and older were presented with a laterally moving object against stationary and moving backgrounds. By moving the background, allocentric sources of information that specify object speed relative to the background are manipulated. In adults, such manipulations typically result in over- or underestimation of object speed depending on the direction of the moving background (see e.g., Smeets & Brenner, 1995). At the same time, however, background motion does not affect the egocentric information sources that specify object speed relative to the infant.

Previous habituation and preferential looking studies have shown that 1-month-old infants can already exploit allocentric information to perceptually discriminate stimulus motion relative to the static boundaries of the display on which the moving stimuli are shown (Wattam-Bell, 1996), although initially this seems restricted to large velocity differences (i.e., differences in relative velocity of 9 deg/sec). With increasing age,

infants come to discriminate smaller differences in velocity between stimuli and background (i.e., up to 1.2 deg/sec at 4.5 months of age; Aslin & Shea, 1990; Bertenthal & Bradbury, 1992; Dannemiller & Freedland, 1989; for an elaborate overview on the development of infants' use of allocentric information see van Wermeskerken, van der Kamp, & Savelsbergh, 2010). However, whether this allocentric information is also used to guide action mode selection, and perhaps affects movement control as well, has not been investigated so far. Hence, in the present study, 6- to 10-month-old infants were presented with laterally approaching objects that moved at two speeds (20 and 40 cm/s) against a background that was stationary or either moved in the same or opposite direction as the object (at 10 or 30 cm/s for object speeds of 20 and 40 cm/s, respectively).

Thus far, studies on infants' reaching for moving objects have shown that temporal constraints (i.e., object speed in relation to the infants' action capabilities) can affect both infants' action mode selection and control of reaching (e.g., van Hof, van der Kamp, & Savelsbergh, 2008; von Hofsten, 1983). That is, higher object speeds result in smaller time-windows within which the interception can be made successfully. Accordingly, research has shown that more rigorous temporal constraints result in higher peak velocities and shorter movement durations in 4- to 8-month-olds (Out, Savelsbergh, & van Soest, 2001; von Hofsten, 1983). With respect to action mode selection, van Hof and colleagues demonstrated that with higher object speed infants chose to reach with the hand contralateral to the side from which the object approaches (e.g., with the right hand when the object approaches from the left; van Hof, van der Kamp, Caljouw, & Saveslbergh, 2005; see also von Hofsten, 1980). Systematic effects of object speed on the selection of bimanual reaching modes have not been reported. Yet, in these studies only the speed of the object relative to the infant was varied, but not isolated from object speed relative to the background (i.e., egocentric and allocentric information that specify speed co-vary). By introducing background motion, this study examined to what extent background motion affects action mode selection (i.e., reaching with the hand ipsi- or contralateral to side from which the object approaches) and/or the subsequent control of the reaching movements (e.g., movement kinematics such as peak velocity and movement duration). Based upon the two visual systems model, and in line with previous findings (van Wermeskerken et al., 2013), we hypothesized that if early in development infants' use of visual information for action mode selection is indeed functionally distinct from movement control, then background motion (i.e., affecting allocentric but not egocentric information) would primarily affect infants' reaching modes (i.e., more contralateral reaches with apparently higher temporal constraints), but have no effects on the control of the reaching movement. Object speed per se (affecting both egocentric and allocentric information), however, would affect both action mode selection and movement control.

METHODS

Participants

Eleven 6-month-old ($M = 6.0$ months, SD = 0.2 months), fifteen 8-month-old ($M = 8.0$ months, SD = 0.1 months) and ten 10-month-old ($M = 10.0$ months, SD = 0.2 months) healthy full-term infants participated in the study after their parents gave written informed consent. 24 additional infants (12 6-month-olds, 5 8-month-olds, and 7 10-month-olds) were tested but excluded from the analysis because of fussing or crying ($n = 5$), not reaching ($n = 17$), or technical failure ($n = 2$). The local institution's ethical committee approved the experiment.

Apparatus and Task

Infants were seated in an infant chair with adjustable head and trunk supports such that the infants had their trunk straight, head upright, and limbs free to move. The seat was reclined at 18° from the vertical and was positioned in front of a conveyer belt, which was 300 cm long, 6.5 cm wide, and 80 cm high. Objects were attached by the use of a magnet to a holder placed on the conveyer belt. All objects afforded one-handed grasping and consisted of polystyrene, multicolor balls (diameter of 4 cm) or small animal puppets of similar size. The height of the holder and the sagittal (object-infant) distance could be adjusted such that the object moved within arm reach of the infant, resulting in an average distance between the infant's chest and the object of 15–20 cm. The conveyer belt was set in motion by a Galil DMC-700 motion controller, such that the object approached the infant from the left at speeds of 20 or 40 cm/s (i.e., we only presented objects moving from left to right, because including the opposite direction would have led to a doubling of conditions, and may also introduce issues of handedness and reaching proficiency differences between hands [see Fagard, Spelke, & von Hofsten, 2009]). Behind the conveyer belt, a large screen (140×106 cm) was positioned on which a background was projected using a projector (ASK Proxima C250, China; for a schematic representation of the set-up see Fig. 1). The distance between the infant's head and the screen was approximately 44 cm. The background was black with randomly oriented white stripes and was either stationary or moving. In case of a moving background, it moved in the direction opposite to the object (i.e., right to left, resulting in an increase of relative velocity) or in the same direction as the object (i.e., left to right, resulting in a decrease of relative velocity) but 10 cm/s slower than the object. That is, in case of an object velocity of 20 cm/s, the background moved with 10 cm/s; for an object velocity of 40 cm/s, it moved with

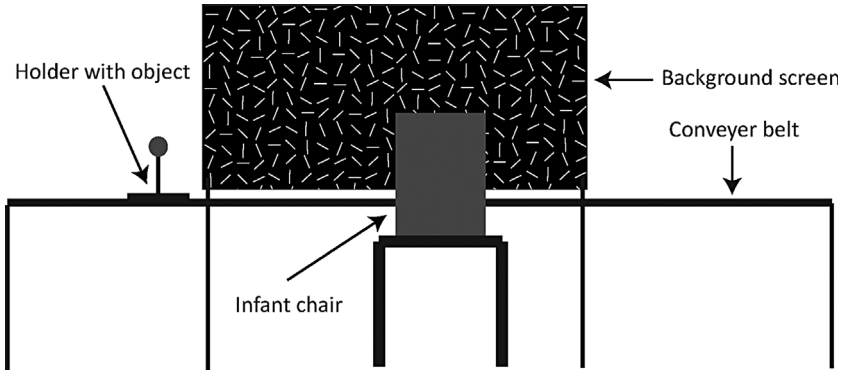

FIGURE 1 View from behind of the experimental set-up.

30 cm/s.[2] The infant chair was positioned to the right of the center of the screen. This ensured that infants had enough time to intercept the object, while the screen still encompassed their entire visual field.

Infants' reaching movements were recorded with a high-speed camera (Basler A602f, Basler AG, Ahrensburg, Germany) that sampled at 100 Hz. A 3-D motion analysis system (Optotrak 3020, Northern Digital Inc., Waterloo, Ontario, Canada) recorded infants' reaching movements with a sampling frequency of 200 Hz. Two pre-calibrated Optotrak camera units were positioned at 2.5 m from the infant on either side of the experimental set-up. The infants wore bracelets with three infrared light-emitting diodes (IREDs) on each wrist to assure that the entire movement could be tracked. An additional IRED was attached to the holder to track the movement of the object. High-speed recordings and the Optotrak system were synchronized by the use of an external trigger, which also controlled object and background motions.

Design and Procedure

Once the infant was seated in the chair, the experimenter adjusted the height of the holder and the distance between the infant and the object. The infant was allowed to grasp and play with the toy attached to the holder, while the experimenter fastened the bracelets with the IREDs to the infant's wrists. The experiment started after moving the holder to the left of the screen and triggering all devices.

During the first up to a maximum of three trials, the object approached the infant from the left with 10 cm/s to familiarize the infant with the experimental set-up. During these trials, the background was stationary. In the case that the infant reached for the moving object on the first familiarization trial, the experiment proceeded to the test trials; otherwise, the infant was presented with a second or third familiarization trial before proceeding to the test trials. During the first nine test trials, the speed of the object was set at 20 cm/s in which each background condition (stationary, moving in the same and opposite direction as the object) was presented three times in random order. Subsequently, object speed was 40 cm/s for nine test trials, presenting each background condition three times in random order. Then, infants were presented with blocks of three test trials in which each background condition was presented once. Infants were alternately presented with a block in which object speed was 20 cm/s and 40 cm/s. The experiment was terminated when the infant consistently refused to reach, got fuzzed, or cried. The experiment lasted about 30 min on average.

Data Analysis

Reaching Mode. Infants' modes of reaching were scored based on the video recordings in combination with the 3-D recordings of the reaching movements (see below). A reach was defined as an arm movement directed towards the object and approaching it within a fist-size distance. In the case reaching kinematics met these criteria, we scored whether the reach was successful (i.e., resulted in contact with the object), and unimanual (i.e., involving one hand) or bimanual (i.e., involving both hands). In addition, the mode of reaching was scored for the unimanual reaches as ipsilateral (i.e., left-handed) or contralateral (i.e., right-handed; bimanual reaches were excluded from analyses).[3] Subsequently, for each infant

[2] In a pilot experiment, these conditions were found to effectively affect adults' ($n = 6$) perception of (relative) object velocity. That is, adults were presented with two events after which they had to verbally judge the velocity of the second object relative to the first object (i.e., "slower", "faster"). The first event consisted of an object that moved laterally with 40 cm/s. The background was either stationary or continuously moved in the same or opposite direction with 30 cm/s. In the second event, an object moved laterally with a velocity varying between 30 and 50 cm/s with intervals of 5 cm/s against a stationary background. In line with previous observations (Smeets & Brenner, 1995), the findings showed that if the background moved in the opposite direction, adults perceived the object as moving faster than if the background was stationary. On the contrary, if the background moved in the same direction, the perceived velocity of the object was lower as compared to when the background was stationary.

[3] We discarded bimanual reaches because our hypotheses are based on changes in infants' propensity to reach with the ipsilateral or contralateral hand in response to higher time constraints.

and each of six object velocity by background conditions the percentage of reaches was computed (i.e., number of trials that yielded a reach) as well as the percentage of unimanual reaches (i.e., number of unimanual reaches relative to the total amount of reaches) and the percentage of ipsilateral reaches (i.e., number of ipsilateral reaches relative to the total amount of unimanual reaches). Percentages of reaches and ipsilateral reaches were used as outcome variables for Generalised Estimated Equations (GEE) models. GEE is equivalent to regression analysis but accounts for repeated observations within participants (Liang & Zeger, 1993). Also, since missing values do not result in suppressing the participant from analyses (e.g., some infants did not perform a unimanual reach in each condition, which would result in missing values for percentage ipsilateral reaches), the number of included participants can be maximized. GEE analyses were conducted using SPSS 20.0 with the correlation structure set to exchangeable. A p-value of $<.05$ was considered significant. A three-step protocol was used for all outcome variables. First, only the primary predictor was included (i.e., velocity or background) in the regression model to assess its unadjusted main effect. Second, age was added to the model to explore whether age would bias the association between velocity/background and the outcome variable (confounding). This second step is reported only in the case that inclusion led to a substantial (i.e., $>10\%$) change in the unadjusted coefficient of velocity/background. The last step consisted of including the interactions between age and velocity/background in the model. Only in case of significant interaction effects, this model is reported.

In order to explore the effects of object velocity on infants' reaching modes (i.e., reaching percentage, percentage of ipsilateral reaches) GEE analyses were conducted that included object velocity, age, and the interaction between these predictor variables in the model. Age and velocity were entered as categorical variables, which enabled us to directly test the differences between the two velocity conditions and the three age groups (the 20 cm/s and 6-month-olds were the reference categories). Only data from the stationary background condition were included.

In a second step, we analyzed the effects of background condition within each velocity condition separately. Background, age, and the interaction between the two variables were included in the model as predictor variables. Age and background were entered as categorical variables with the same direction background condition (i.e., condition in which background moved in the same direction as the object) and 6-month-olds as the reference categories. This allowed us to test the difference between the effects of the background moving in the same and opposite direction as the object. Only data from the moving background conditions were included.

Reaching Kinematics. The 3-D positions of the recorded Optotrak IREDs were filtered with a second-order recursive Butterworth low-pass filter with a cutoff frequency of 10 Hz. For the reaching movements, data of one of the three IREDs with most data across trials were selected for analysis. A least squares method for interpolation was used if the missing data did not exceed 100 ms. Otherwise, the reach was excluded from further analysis (i.e., 13 reaches or 1.2%). Subsequently, initiation and end of the reaching movement was determined using the multiple sources of information method (Schot, Brenner, & Smeets, 2010, see also van Wermeskerken et al., 2011). This method entails that several objective functions together compute the probability that a certain instant is the onset or end of a movement. The instant with the highest probability is considered to reflect movement onset or end. These instants were then confirmed with the video recordings. In the case that the instants were clearly too late or too early, they were adjusted accordingly.

Subsequently, infants' reaching kinematics were analyzed. For each reach we computed (1) movement time (s), (2) peak velocity (cm/s), (3) relative moment of peak velocity, that is, the moment of peak velocity relative to the total duration of the reach (%), and (4) moment of reach onset, that is, the time remaining for the object to reach the body midline at reach initiation (s). For each infant and each of six conditions, averages of these kinematic variables were computed for the unimanual reaches (i.e., ipsilateral and contralateral reaches were collapsed). We then explored which of these outcome variables were constrained by the velocity manipulation (i.e., comparing the 20 cm/s and 40 cm/s object velocity conditions with a stationary background) and then assessed for these variables the effects of background condition (i.e., comparing the moving background conditions) within each velocity condition separately. Similar as for action mode selection, the primary kinematics analyses only encompassed unimanual reaches. Nonetheless, for the interested reader, the kinematics of bimanual reaches are presented in the Appendix.

As for the reaching modes, GEE analyses were conducted to assess effects of object velocity manipulation on infants' reaching kinematics. To this end, separate GEE analyses were performed for each reaching kinematic (i.e., movement duration, peak velocity, relative moment of peak velocity, and moment of reach onset) as outcome variable. Velocity and age were included as categorical predictor variables and only the stationary background conditions were included. The 20 cm/s velocity condition and the 6-month-old infants served as reference categories.

In a second step, we analyzed the effects of background condition within each velocity condition separately, but to reduce the number of statistical tests, only the kinematic variables that were significantly affected by the object velocity manipulation were analyzed. Age and background were entered as categorical variables with the same direction background condition and 6-month-olds as reference categories. Only data from the moving background conditions were included.

Results

The 36 infants received a total of 1,163 trials during which 1,061 (91.2%) reaches were performed that resulted 822 times (77.5%) in contact with the object. About half of the reaches ($n = 503$, 47.4%) were unimanual of which 42.9% ($n = 216$) were with the ipsilateral hand. As can be seen in Table 1, infants of

Table 1. Mean and Standard Deviation (and Percentages) of the Number of Trials, Reaches, Unimanual Reaches, Ipsilateral Reaches, and Contacts for Each Age Group

	6 months ($n = 11$)	8 months ($n = 15$)	10 months ($n = 10$)
#Trials	30.5 ± 5.1	32.7 ± 3.7	33.7 ± 7.5
#Reaches	28.0 ± 5.4 (91.8%)	29.6 ± 6.5 (89.8%)	30.9 ± 6.2 (92.3%)
#Unimanual reach	10.4 ± 3.6 (37.5%)	14.33 ± 8.6 (49.8%)	17.4 ± 5.4 (57.0%)
#Ipsilateral reach	4.5 ± 4.2 (38.0%)	5.2 ± 6.2 (39.2%)	8.9 ± 7.7 (50.7%)
#Contact	22.2 ± 5.3 (78.9%)	22.5 ± 8.4 (73.9%)	24.1 ± 6.3 (78.4%)
#Ipsilateral contact	3.5 ± 3.5 (80.8%)	4.0 ± 5.4 (66.7%)	7.7 ± 6.6 (82.7%)
#Contralateral contact	3.7 ± 2.3 (62.5%)	5.1 ± 4.9 (55.9%)	6.3 ± 5.7 (71.8%)

different ages reached equally often, were equally successful in contacting the object, and reached equally often unimanually and with the ipsilateral hand (separate One-Way ANOVA's on frequencies and percentages; p's $\geq .059$).

Reaching Modes

To explore the effects of object velocity and background manipulations on infants' reaching behaviors, separate GEE's were conducted on the percentage of reaches and percentage of ipsilateral reaches, respectively.

Effects of Object Velocity on Infants Reaching Modes. We first explored the effects of object velocity on infants' propensity to perform a reach (i.e., percentage of reaches). To this end, only the stationary background conditions were included in the model (see Fig. 2). This did not reveal any significant effects, indicating that the object velocity did not affect whether or not the infants performed a reaching action ($p = .678$). This did not change when including age (p's $\geq .678$) and the interactions between age and object velocity in the model (p's $\geq .607$). Hence, 6- to 10-month-old infants' propensity to reach was not constrained by manipulation of object velocity.

A similar analysis was conducted with the percentage of ipsilateral reaches as outcome variable (note that two infants were excluded, since they only performed bimanual reaches in both velocity conditions with a stationary background, $n = 34$). Previous work suggested that infants more often select the contralateral hand when object velocity increases (van Hof et al., 2005). A first analysis, including only velocity (Eq. 1.1,

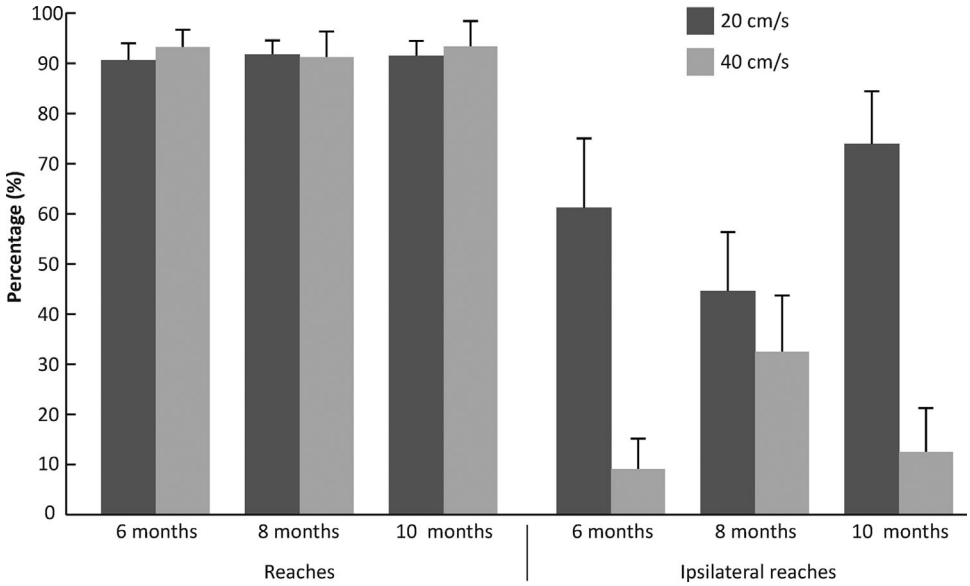

FIGURE 2 Mean percentages of reaches and reaches with the ipsilateral hand for each age group and each velocity condition. Error bars represent standard error of the mean.

Table 2. Results of the GEE Regression Analyses by Which the Percentage of Ipsilateral Reaches Was Predicted as Function of Velocity or Background Manipulation

	Eq.	Dep. Variable		Coefficient	SE	95% CI Lower	95% CI Upper	*p*-value
Effects of Velocity (Background = stationary)	1.1	% Ipsilateral reach	Constant	58.6	7.0	45.0	72.2	<.001
			Velocity	−37.9	7.1	−51.8	−24.0	<.001
	1.2	% Ipsilateral reach	Constant	59.8	12.7	34.9	84.8	<.001
			Velocity	−50.7	11.1	−72.6	−28.9	<.001
			Age 6–8	−14.6	16.9	−47.7	18.4	.386
			Age 6–10	14.0	16.2	−17.8	45.7	.388
			Vel –8	40.9	15.1	11.3	70.5	.007
			Vel –10	−6.4	14.5	−34.9	22.0	.695
Effects of Background (Object Velocity = 20 cm/s)	2.1	% Ipsilateral reach	Constant	50.4	7.6	35.4	65.4	<.001
			Background	2.1	7.0	−11.6	15.7	.768
	2.2	% Ipsilateral reach	Constant	55.1	13.4	28.9	81.3	<.001
			Background	1.8	7.0	−11.9	15.5	.796
			Age 6–8	−17.4	15.6	−48.0	13.2	.265
			Age 6–10	9.6	17.8	−25.3	44.5	.589
Effects of Background (Object Velocity = 40 cm/s)	3.1	% Ipsilateral reach	Constant	29.1	7.5	14.5	43.8	<.001
			Background	3.7	3.3	−2.7	10.1	.258
	3.2	% Ipsilateral reach	Constant	13.6	11.9	−9.6	36.9	.251
			Background	16.7	6.4	4.1	29.3	.009
			Age 6–8	19.7	17.0	−13.5	53.0	.244
			Age 6–10	24.2	18.1	−11.4	59.7	.182
			Background –8	−17.3	8.0	−32.9	−1.6	.030
			Background –10	−19.8	7.1	−33.6	−6.0	.005

Table 2)[4] indeed revealed that infants were less inclined (i.e., approx. 40% decrease) to perform a reach with the ipsilateral hand with an increase in velocity. Including age in the analysis revealed that age did not bias the association between velocity and ipsilateral reaching (i.e., change in the coefficient when including age <10%). Yet, when also including the interaction between object velocity and age in the GEE model, it was found that the 8-month-olds were less affected by the increase in velocity than the 6-month-olds, that is, 8-month-olds showed a smaller decline in ipsilateral reaching (i.e., decline of 9.8%) as compared to the 6-month-olds (i.e., decline of 50.7%) when object velocity increased from 20 to 40 cm/s (see significant interaction term in Eq. 1.2, Table 2).

Effects of Background Motion on Infants Reaching Modes. In a subsequent step, we analyzed the effects of background motion (same vs. opposite direction) on reaching with the ipsilateral hand for each velocity condition separately (see Fig. 3; $n = 36$). For the 20 cm/s velocity condition, this revealed no effects of background (Eq. 2.1, Table 2), also not when age ($p = .796$) was included, although this resulted in a substantial change in the velocity coefficient (i.e., >10%; see main effect of background in Eq. 2.2, Table 2). No significant interactions were revealed when including the interactions between object velocity and age (p's $\geq .064$).

For the 40 cm/s velocity condition, there was no effect of background manipulation on the occurrence of reaches with the ipsilateral hand ($p = .258$, see Eq. 3.1,

[4] Equation 1.2 (see Table 2) may be interpreted as 6-month-old infants reaching with the ipsilateral hand 59.8% of the unimanual reaches when object velocity is 20 cm/s (i.e., Constant in the model). 8-month-olds reach 14.6% less with the ipsilateral hand than the 6-month-olds at an object speed of 20 cm/s (i.e., term Age 6–8 in the model; 45.2%) and 10-month-olds reach 14.0% more with the ipsilateral hand than the 6-month-olds (i.e., term Age 6–10 in the model; 73.8%). An object velocity of 40 cm/s yields a decrease in ipsilateral reaches by 50.7% as compared to an object velocity of 20 cm/s for 6-month-old infants (i.e., term Velocity in the model; 9.1%). This effect was significantly different for the 8-month-olds who also showed a decrease in ipsilateral reaching from 20 to 40 cm/s but less so than the 6-month-olds (i.e., $-50.7\% + 40.9\% = -9.8\%$, resulting in a total percentage of 35.4% of ipsilateral reaches for the 8-month-olds at an object velocity of 40 cm/s; term Vel –8 in the model). Lastly, the 10-month-olds had a somewhat (but not significant) larger decline in ipsilateral reaching from 20 to 40 cm/s object velocity than the 6-month-olds (i.e., $-50.7–6.4\% = -57.1\%$, resulting in a total percentage of 16.7% ipsilateral reaching for the 10-month-olds at an object velocity of 40 cm/s; term Vel –10 in the model). Because we aim to reveal *qualitative* rather than *quantitative* effects of the experimental manipulations on infants' reaching behavior, we have restricted our interpretations to qualitative changes in infants' reaching behavior indicated by the GEE equations.

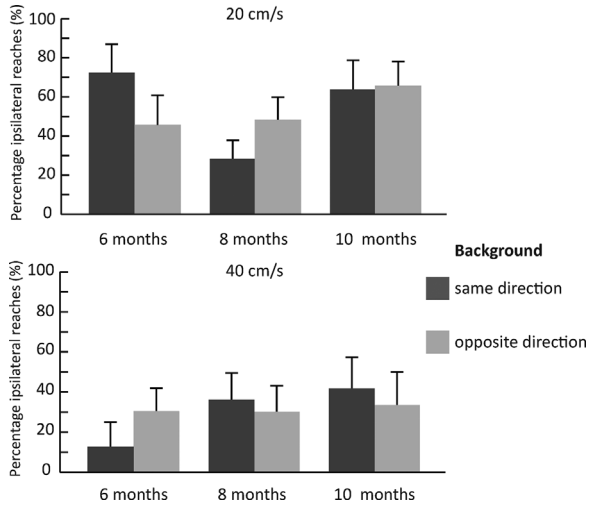

FIGURE 3 Mean percentages of ipsilateral reaches for each age group and each background condition presented per velocity condition. Error bars represent standard error of the mean.

Table 2; note that two infants were excluded because they did not perform a unimanual reach in either background motion condition, $n = 34$). In addition, entering age in the GEE model did not reveal a substantial change in the velocity coefficient. Yet, including the interaction between age and background in the model revealed a significant interaction. These findings show that the 6-month-old infants, contrary to what was anticipated, were inclined to reach more with the ipsilateral hand, in the case that the background moved in the opposite direction ($p = .009$; Eq. 3.2, effect of background). This effect was reversed for the 8-month-olds ($p = .030$) and 10-month-olds ($p = .005$); they performed more reaches with the contralateral hand in the case that the background moved in opposite direction (Eq. 3.2, Table 2, see significant interaction terms).

Together, these findings indicate that background motion did influence infants' selection to reach with either the ipsilateral or contralateral hand. The effects were more pronounced among the 8- and 10-month-olds and with more demanding time constraints (i.e., 40 cm/s). Except for the 6-month-olds, the background motion effects were in line with the use of allocentric information, that is, apparently higher object velocities evoked more contralateral reaches and vice-versa.

Reaching Kinematics

Similar to the previous section, we first analyzed the effects of object velocity on infants' unimanual reaching kinematics for the stationary background conditions only (see Fig. 4; $n = 34$; see also Appendix, which reports the kinematics of both the unimanual and bimanual reaches). This revealed that an increase in object velocity yielded neither changes in peak velocity ($p = .479$, Eq. 4.2), nor in the relative moment at which peak velocity occurred ($p = .190$, Eq. 4.3). Yet, an increase in object velocity did result in a decrease in movement time (see Eq. 4.1 in Table 3) and a decrease in moment of reach onset (see Eq. 4.4 in Table 3). Including age in these four GEE models did not result in any substantial changes in the velocity coefficient. Also, including the interactions between age and velocity in the models did not show significant

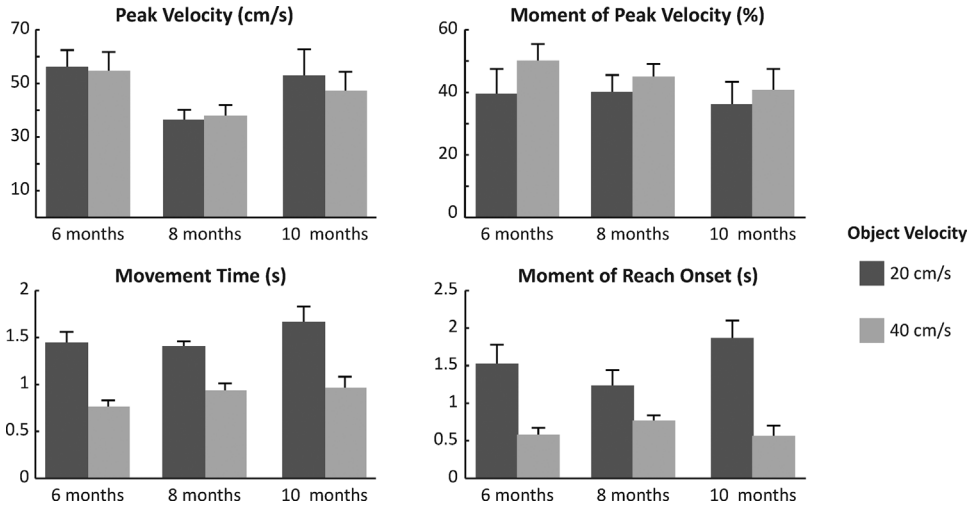

FIGURE 4 Infants' reaching kinematics as function of object velocity (i.e., background was stationary). Error bars represent standard error of the mean.

Table 3. Results of the GEE Regression Analyses by Which the Reaching Kinematics Were Predicted as Function of Velocity Manipulation

	Eq.	Dep. Variable		Coefficient	SE	95% CI Lower	95% CI Upper	*p-value*
Effects of Velocity (Background = stationary)	4.1	Movement time (s)	Constant	1.5	0.07	1.37	1.63	<.001
			Velocity	−0.61	0.08	−0.76	−0.47	<.001
	4.2	Peak velocity (cm/s)	Constant	47.73	4.05	39.80	55.67	<.001
			Velocity	−2.44	3.45	−9.21	4.32	.479
	4.3	Rel. Moment of Peak Velocity (%)	Constant	38.6	3.8	31.3	46.0	<.001
			Velocity	6.7	5.1	−3.3	16.8	.190
	4.4	Reach onset (s)	Constant	1.51	0.14	1.24	1.78	<.001
			Velocity	−0.86	0.15	−1.15	−0.58	<.001

interactions (p's $\geq .093$). Hence, the effects of object velocity on all kinematic outcomes were not affected by the infants' age.

In order to assess the effects of background motion on infants' unimanual reaching kinematics, GEE analyses were performed with movement time or moment of reach onset as outcome variable, since the other kinematic variables were not affected by object velocity (see Fig. 5). In line with the reaching mode analyses, GEE analyses were performed for each object velocity separately ($n = 36$ for 20 cm/s and $n = 34$ for 40 cm/s). For both object velocities, the analyses with movement time as outcome variable and background as predictor variable did not reveal a significant effect (p's $\geq .304$, see Eq. 5.1 and 6.1 in Table 4). Including age in the model did not substantially change the association between background and movement time for both object velocities. Including the interactions between background and age also did not reveal any consistent effects of background on infants' movement times (p's $\geq .178$). The analysis for an object velocity of 40 cm/s did not yield any effects (p's $\geq .227$, for the overall effect of background see Eq. 6.1 in Table 4).

The second analysis with moment of reach onset as outcome variable and background as predictor variable did not reveal any significant effects of background on infants' reaching onset for either object velocity (both p's $\geq .556$, see Eq. 5.2.1 and 6.2.1 in Table 4). Although including age did result in a better estimation of the background coefficient (i.e., >10% change; see Eq. 5.2.2 and Eq. 6.2.2 in Table 4) in the model, it did not yield any significant effects of background (20 cm/s: $p = .919$; 40 cm/s: $p = .606$). Including the interactions between background and age did not reveal any significant interaction effects (20 cm/s: p's $\geq .222$; 40 cm/s: p's $\geq .519$).

Together, these findings indicate that while object velocity affected infants' timing of the reach (i.e., reach onset) and movement times, these variables were not affected by background manipulations.

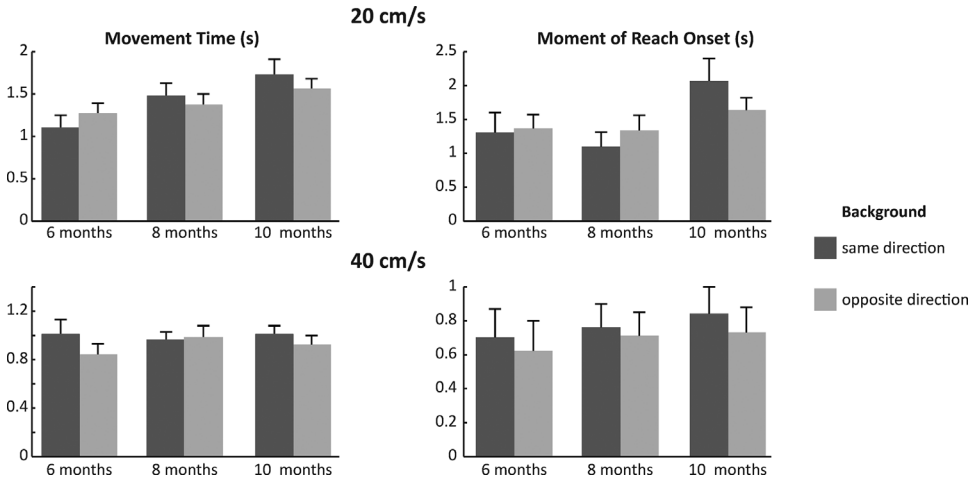

FIGURE 5 Infants' reaching kinematics as function of object velocity (upper: 20 cm/s, lower: 40 cm/s) and background condition. Left panel displays movement time, the right panel displays moment of reach onset. Error bars represent standard error of the mean.

Table 4. Results of the GEE Regression Analyses by Which the Reaching Kinematics Were Predicted as Function of Background Manipulation

						95% CI		
	Eq.	Dep. Variable		Coefficient	SE	Lower	Upper	*p-value*
Effects of Background (Object velocity = 20 cm/s)	5.1	Movement time (s)	Constant	1.45	0.10	1.25	1.64	<.001
			Background	−0.05	0.12	−0.29	0.19	.699
	5.2.1	Reach onset (s)	Constant	1.42	0.17	1.09	1.75	<.001
			Background	0.022	0.18	−0.33	0.37	.903
	5.2.2	Reach onset (s)	Constant	1.31	0.20	0.93	1.70	<.001
			Background	0.018	0.18	−0.33	0.37	.919
			Age 6–8	−0.10	0.23	−0.54	0.35	.676
			Age 6–10	0.54	0.29	−0.02	1.1	.058
Effects of Background (Object velocity = 40 cm/s)	6.1	Movement time (s)	Constant	0.96	0.05	0.89	1.06	<.001
			Background	−0.06	0.06	−0.17	0.05	.304
	6.2.1	Reach onset (s)	Constant	0.73	0.09	0.56	0.89	<.001
			Background	−0.043	0.07	−0.19	0.10	.556
	6.2.2	Reach onset (s)	Constant	0.65	0.15	0.36	0.93	<.001
			Background	−0.037	0.07	−0.18	0.10	.606
			Age 6–8	0.10	0.19	−0.26	0.47	.577
			Age 6–10	0.12	0.20	−0.28	0.51	.564

Discussion

Consistent with the two-visual systems model, adult research suggests a separation in information use for action mode selection and movement control (e.g., Crajé, van der Kamp, & Steenbergen, 2008; Dijkerman, McIntosh, Schindler, Nijboer, & Milner, 2009; van Doorn et al., 2007, 2009). More specifically, movement control mainly exploits egocentric sources of information, whereas action mode selection is primarily reliant on allocentric sources of information (Michaels, 2000; Milner & Goodale, 2008; van der Kamp et al., 2003). Recent studies suggest that action mode selection and movement control are also likely to be independent and to rely on different sources of information from 5 to 6 months onwards (van Wermeskerken et al., 2011, 2013). That is, in line with adult research, 6-month-olds were found to primarily rely on allocentric sources of information for action selection and mainly exploited egocentric sources of information for movement control. Yet, these studies are limited to grasping stationary objects. Therefore, the aim of the present study was to scrutinize this distinction for moving objects, which also demands adjustments to temporal properties of the objects (i.e., speed) instead of only to their spatial aspects (i.e., size or distance). To this end, 6- to 10-month-old infants were presented with laterally approaching objects at two speeds (i.e., 20 and 40 cm/s) that moved against a stationary or moving background. Background motion alters allocentric information that specifies the velocity of the object relative to the background. We hypothesized that if infants' use of visual information is indeed functionally separated for action mode selection and movement control, background motion should affect infants' reaching mode, but have no effect on movement control.

We will first discuss the general effects of time constraints (i.e., object speed) and the additional effects of background motion on infants' action selection and movement control. Subsequently, the theoretical consequences of the present findings will be discussed in the context of the two-visual systems model.

Effects of Time Constraints on Action Selection and Movement Control

Contrary to previous research, infants' propensity to reach was not affected by an increase in time constraints (e.g., van Hof et al., 2008; von Hofsten, 1983; von Hofsten & Lindhagen, 1979). One explanation for this finding might be the relatively low object speeds used in the current study as compared to other studies (i.e., 40 cm/s as compared to speeds exceeding 1 m/s in van Hof et al., 2008). Yet, and most importantly, infants did adjust their action modes and reaching kinematics to the time constraints imposed by object speed, which is in line with previous observations (van Hof et al., 2005; van Hof et al., 2008; von Hofsten, 1980,1983). More specifically, the higher the time constraints (i.e., higher object speed), the more the infants were inclined to reach with the hand contralateral to the side from which the object approached that allows more time to

intercept the object as compared to reaching with the hand ipsilateral to the approaching objects. Yet, infants' reaching capabilities improve with age, and hence, the effects of time constraints may change with age or reaching proficiency (see e.g., Fagard et al., 2009; van Hof et al., 2008). Accordingly, the percentage of reaches with the ipsilateral hand was not significantly reduced for the higher object velocity among the 8-month-old infants (see also van Hof et al., 2005). However, we note that the reduction in ipsilateral reaching at higher speeds was seen again at 10 months.

Reaching kinematics also showed clear and systematic adjustments to different time constraints induced by object velocity. In line with previous findings (e.g., von Hofsten, 1983), a higher object velocity resulted in shorter movement durations and adjustments in moment of reaching onset. More specifically, infants initiated their reaches at different moments of reaching onset (i.e., time to contact) with reaches being initiated at shorter times to contact when time constraints were high. This suggests that infants used a distance strategy in which the reach is initiated with the object at a constant distance from the interception point. This is in contrast with previous findings that report that, unlike younger infants, infants aged 8 months normally time their reaching movements at a constant time before the object reaches the interception (i.e., which is consistent with the use of tau; van Hof et al., 2008). Such time strategy is more adaptive, because it is fitting irrespective of object speed, while with a distance strategy, infants tend to be late with high object speeds. Yet, when time constraints are relatively low, as is the case in the current study, a distance strategy can also suffice (Kayed & van der Meer, 2000; van Hof et al., 2008).

Effects of Background Motion on Infants' Action Mode Selection and Movement Control

The background motion, which alters allocentric information about the object's velocity relative to its background while leaving egocentric information about object velocity relative to the infant unaltered, affected only infants' action mode selection.[5] Yet, it should be noted that these effects seemed far less pronounced than the effects of manipulating object velocity itself (i.e., time constraints). In particular, background motion affected the use of the contralateral (i.e., right) hand versus the ipsilateral (i.e., left) hand. This effect of background motion became only apparent when the time constraints relative to the reaching capabilities of the infant were highest (i.e., object speed of 40 cm/s). However, effects of background motion were mediated by age, suggesting that infants' reaching capabilities also constrained action mode selection. As such, action mode selection of the 8 and 10-month-olds was consistent with the use of relative velocity information, i.e., using the contralateral hand more often in case that the background moved in opposite direction (i.e., higher relative velocity). By contrast, the effects of background motion on 6-month-olds' action mode were opposite. Although clearly affected, the direction of these effects is not consistent with the use of relative velocity information; perhaps these infants were simply distracted by the background motion implying that at 6 months allocentric information plays a different role, if any, for action mode selection. Indeed, the observation that effects of background motion (i.e., allocentric information) were less pronounced than effects of increasing time constraints (i.e., egocentric information), may suggest that action mode selection does not exclusively exploit allocentric information but probably, and maybe even more strongly, also relies on egocentric information—at least when temporal constraints are involved.

With respect to infants' movement control, the kinematic variables that were significantly affected by object speed remained unaffected by the background motion. More specifically, movement duration and moment of reach onset were not significantly constrained by changes in relative velocity.

Together, the present findings suggest that in early development movement control is primarily constrained by egocentric information (i.e., object speed) and remains unaffected by allocentric information (i.e., background motion) that specifies the velocity of the object relative to its surroundings. The selection of action mode, however, is *not only* affected by egocentric information (which is perhaps its main source of information) but also systematically exploits allocentric information.

Theoretical Implications

To date, several authors have alluded to an early dissociation or different developmental trajectories of the use of visual information for ventral system's functions (i.e., visual perception and action mode

[5] This manipulation might have also induced ego motion, which occurs when optic flow does not match true self-motion (e.g., Gibson, 1979/1986), which causes the percept of motion. Although adults did not report this phenomenon when being presented with the current set-up (see footnote 3), infants might have encountered ego motion during the experiment. Given that their reaching propensity did not decrease as a function of an increase in object velocity and background velocity, we deem it unlikely that the possible perception of ego motion affected the current results.

selection) and dorsal system's functions (i.e., movement control; e.g., Atkinson, 2000; Bertenthal, 1996; van der Kamp & Savelsbergh, 2000, 2002). A recent series of studies indeed suggests that the developments of visual perception and movement control are dissociated and follow their own developmental trajectories (e.g., Babinsky, Braddick, & Atkinson, 2012; DeLoache, Uttal, & Rosengren, 2004; Newman, Atkinson, & Braddick, 2001; Street, James, Jones & Smith, 2011; van Wermeskerken et al., 2013). The current findings are partly supportive for this contention. In line with van Wermeskerken et al. (2013), the current findings suggest that action mode selection systematically exploits allocentric sources of information (i.e., object velocity relative to the surroundings), while movement control remains unaffected by allocentric information and is solely reliant upon egocentric sources of information (i.e., object velocity relative to the actor). Yet, and in line with previous findings on intercepting moving objects (van Hof et al., 2005), action mode selection was mainly constrained by manipulations in egocentric information (i.e., object speed). In terms of the two-visual systems model (Milner & Goodale, 1995, 2008), this provides further evidence that the use of visual information, at least when it comes to allocentric sources of information, is functionally differentiated at 8 to 10 months of age. More specifically, exploitation of allocentric information is restricted to action mode selection, while egocentric information has its biggest role in movement control. However, the finding that at 6 months action mode selection was not in accordance with the use of allocentric information suggests that the dissociation is weak or nonexistent. This perhaps reflects that the development of the use visual information for, on the one hand, action mode selection (and visual perception), and on the other hand, movement control is not fully differentiated at this age. In broader context, this raises issues about the age at which differentiation in information usage first starts, and how this changes with age, also after 10 months. Another important topic for further research is to what degree learning on short time scales (e.g., within an experimental sessions) affect the differential use of visual information (see e.g., Johnson & Shuwairi, 2009; Rakison & Krogh, 2011).

To conclude, the present study was the first to demonstrate that, when reaching for moving objects, 8- to 10-month-old infants' use of visual information of action selection and movement control is differentiated, and therefore lends further support for the two-visual systems model (Milner & Goodale, 1995, 2008). More specifically, the use of allocentric information is limited to action mode selection. By contrast, egocentric information is exploited for both movement control and action mode selection, which suggests that the division is not complete in infants aged 6 to 10 months.

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APPENDIX

A considerable amount of reaches were classified as bimanual (i.e., approx. 52% of all reaches). For theoretical reasons, we were mainly interested in changes in unimanual reaching. Nonetheless, in order to portray infants' reaching kinematics fully, Table A1 describes the kinematics of both the unimanual and bimanual reaches as function of age and object velocity (stationary background; see also Fig. 4).

Table A1. Descriptive Statistics of the Kinematic Variables of the Unimanual and Bimanual Reaches as a Function of Age and Object Velocity

		Unimanual Reaches			Bimanual Reaches		
	Kinematic variable	6 months	8 months	10 months	6 months	8 months	10 months
20 cm/s	Peak velocity (cm/s)	56.09 (19.08)	36.29 (13.44)	52.84 (31.20)	46.86 (14.16)	33.98 (9.42)	36.75 (12.43)
	Rel moment of peak velocity (%)	39.49 (24.0)	40.02 (19.18)	36.06 (23.13)	43.87 (11.98)	39.79 (6.85)	28.78 (10.88)
	Movement time (s)	1.44 (0.37)	1.40 (0.22)	1.66 (0.52)	1.31 (0.23)	1.41 (0.33)	1.45 (0.29)
	Reach onset (s)	1.52 (0.77)	1.23 (0.73)	1.86 (0.72)	1.17 (0.27)	1.27 (0.47)	1.07 (0.17)
40 cm/s	Peak velocity (cm/s)	54.55 (23.99)	37.77 (14.22)	46.99 (20.71)	41.87 (13.27)	42.14 (10.98)	45.117 (14.44)
	Rel moment of peak velocity (%)	50.06 (17.95)	44.96 (14.20)	40.71 (19.06)	47.20 (12.48)	54.33 (17.01)	44.24 (15.29)
	Movement time (s)	0.76 (0.22)	0.93 (0.28)	0.96 (0.33)	0.93 (0.18)	0.92 (0.20)	1.02 (0.10)
	Reach onset (s)	0.57 (0.32)	0.76 (0.28)	0.56 (0.36)	0.76 (0.26)	0.76 (0.24)	0.78 (0.18)