

Research Article

EGOCENTRIC ACTION IN EARLY INFANCY:
Spatial Frames of Reference for SaccadesRick O. Gilmore¹ and Mark H. Johnson²¹Carnegie Mellon University and ²MRC Cognitive Development Unit, London

Abstract—The extent to which infants combine visual (*i.e.*, retinal position) and nonvisual (eye or head position) spatial information in planning saccades relates to the issue of what spatial frame or frames of reference influence early visually guided action. We explored this question by testing infants from 4 to 6 months of age on the double-step saccade paradigm, which has shown that adults combine visual and eye position information into an egocentric (head- or trunk-centered) representation of saccade target locations. In contrast, our results imply that infants depend on a simple retinocentric representation at age 4 months, but by 6 months use egocentric representations more often to control saccade planning. Shifts in the representation of visual space for this simple sensorimotor behavior may index maturation in cortical circuitry devoted to visual spatial processing in general.

A central issue in cognitive development concerns the ways in which infants' capacities to understand spatial relationships change early in life. Beginning at the age of about 6 months, looking and reaching behavior becomes gradually less bound by the specific spatial positions of objects relative to the baby's body and more sensitive to the positions of objects and features in the environment that remain stable despite the infant's own movements (Acredolo, 1990; Bremner, 1978). This transition suggests that the way infants represent spatial information—the frame of reference they use for coding location—shifts from being largely egocentric, or body-centered, to being allocentric, or environment-centered. The shift may occur in accord with increasing locomotor skills that afford infants new opportunities to discover stable spatial relationships by active exploration. How infants younger than 6 months understand spatial relationships and what role in spatial cognition patterns of postnatal brain development might play have remained largely unexplored questions.

Adults' spatial processing appears to employ multiple frames of reference or coordinate systems for coding the positions of stimuli in the environment (Stein, 1992). Retinal-, head-, trunk-, arm-, and even object-centered representations have been shown to have neurophysiological (Andersen, Snyder, Li, & Striccanne, 1993; Graziano, Yap, & Gross, 1994; Olson & Gettner, 1995) and behavioral (Abrams & Dobkin, 1994; Behrmann & Tipper, 1994; Posner & Cohen, 1984; Tipper, Driver, & Weaver, 1991) correlates. Most current accounts of spatial processing in the brain accord a special role to the extrastriate regions of the cortex, especially the parietal lobe. However, behavioral, neuroimaging, and neuroanatomical evidence has indicated that for some visually guided actions, such as saccades, there is a shift from predominantly subcortical to predominantly cortical control over the first few months of life (Atkinson, 1984; Braddick et al., 1992; Bronson, 1974; Chugani & Phelps, 1986; Johnson, 1990). This view

remains controversial (Slater, Morison, & Somers, 1988), but it suggests that young infants' and adults' spatial representations may differ in fundamental ways. Because vision is the dominant modality for spatial perception in primates, and because shifts of gaze are among infants' first exploratory actions, we asked what spatial information guides babies' shifts of gaze.

Adults appear to use both retinal and eye position information in planning sequences of saccades to targets that flash in the dark. In the double-step saccade paradigm (Becker & Jurgens, 1979; Hallett & Lightstone, 1976), participants are instructed to make saccades to sequences of two visual cues flashed briefly in a dark visual field, the second stimulus appears and disappears shortly before or during the first saccade. Observers cannot use retinal position relative to the fovea to plan a response to the second target because the saccade to the first stimulus shifts the center of gaze, and with it, the second target's position relative to the fovea. Accordingly, to make accurate saccades to the locations of both targets, subjects must plan the saccade to the second target by combining retinal and eye position signals (Dasnoville, Schlag, & Schlag-Rey, 1993; Hallett & Lightstone, 1976). Adults make accurate saccades to both targets in many circumstances, suggesting that the mature oculomotor system represents saccadic target locations by systematically combining retinal position and eye position into a head-centered representation of visual space that remains stable across eye movements.

The integration of visual and nonvisual spatial information appears to depend on processing in the cerebral cortex. Neurophysiological studies in awake behaving monkeys have indicated that cells in eye movement regions of the parietal cortex respond to combinations of retinal, eye, and head position in a manner consistent with a distributed coding of visual space in head- or body-based *egocentric* coordinates (Andersen et al., 1993; Zipser & Andersen, 1988). These findings contrast with those from cells in the superior colliculus, a subcortical structure involved in visual orienting, which appear to code for saccades within an eye-based or *retinocentric* frame of reference (Schlag-Rey, Schlag, & Shook, 1989).

If young infants' saccades are dominated by subcortical circuitry, then frames of reference that depend on cortical processing may not influence saccade planning early in life. Instead, the retinocentric representation characteristic of the subcortical pathway may dominate young infants' orienting. In turn, gradual maturation of cortical spatial-processing mechanisms over the first several months of life (Johnson, 1990) might gradually make available more stable egocentric representations in older infants. To test this hypothesis, we tested infants between 4 and 6 months on two versions of the double-step saccade paradigm.

EXPERIMENT 1

When infants maintain fixation throughout the presentation of two visual targets in a double-step display, they are presented with potentially conflicting sources of information (see Figs 1a and 1b). A

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retinocentric representation of each target's position consists of the distances and directions relative to the center of the retina or fovea at the time the targets are shown, but ignores eye position, an egocentric representation consists of the distance and direction of the targets from the center of the head (or trunk) and is stable across eye movements. If subjects used retinocentric information in planning saccades, they would simply make a response to each target equal to that target's position relative to the fovea at the time it was viewed. So a retinocentric sequence of saccades would consist of two saccades that followed each other sequentially, each equal in length to the retinal position vector of its target. In contrast, an egocentric sequence would consist of a saccade to the first target, then a saccade to the second

Experiment 1 examined the frequency of spontaneous retino- and egocentric saccade sequences in 4- to 6-month-old infants presented with this type of display.

Method

Twelve 4-month-old (range 122–137 days, $M = 129$, 5 female, 7 male) and thirteen 6-month-old (range 182–196 days, $M = 189$, 7 female, 6 male) full-term healthy human infants participated. Five additional 4-month-olds and two 6-month olds were tested but eliminated from the analyses because they did not make a codable response on at least half of the presented trials.

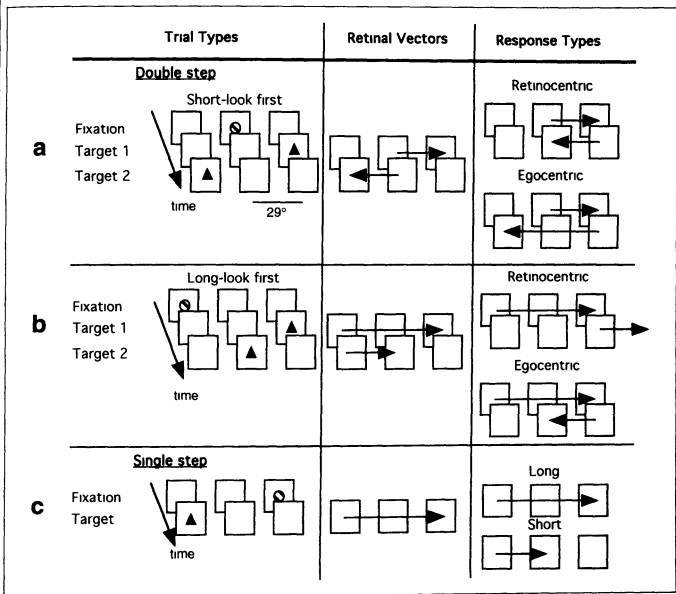


Fig. 1 Stimulus sequences and coding classifications for the experimental and control trials in Experiments 1 and 2. The first column depicts the display sequence. The second column indicates the retinal vectors of the targets relative to fixation. The third column depicts the critical saccade patterns of interest. Participants in Experiment 1 viewed trials from the patterns depicted in (a) and (c). The experimental group in Experiment 2 viewed trials chosen from (a), (b), and (c).

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Each participant was seated in an infant seat 50 cm from the center of three 13-in color computer monitors. The room lights were dimmed, but not extinguished, in order to maintain the infant's cooperation and to provide sufficient illumination for the video camera. The experimenter recorded the infant's eyes and head on videotape at 30 frames/s while a microcomputer generated stimuli. Each trial began with a fixation display consisting of a sequence of geometric shapes (5° in width) and auditory tones (440–880 Hz). A single randomly selected tone sounded simultaneously with the appearance of each shape in the fixation sequence. Tones were generated by a speaker located behind the testing screen. The display attracted the infant's attention to the center of a single screen prior to the presentation of the subsequent targets.

Figure 1 depicts the sequence of visual stimuli infants observed in both this and the subsequent experiment. In the double-step trials for Experiment 1 (see Fig. 1a), the fixation appeared in the center of the middle monitor until a computer key press terminated it and the accompanying tones. Then two 5° triangular-shaped target stimuli 200 ms in duration appeared in the center of the left and right screens (29° from fixation), one following the other, with an interstimulus interval of less than 33 ms. In the single-step trials (Fig. 1c), the fixation appeared on the right- or left-side monitor, and after the key press, a single 200-ms target appeared on the monitor opposite the side of fixation. A 1,500-ms interval during which no visual or auditory stimuli were presented followed each trial. There were 32 double-step trials, 16 each of the left-right and right-left target sequences, and 12 single-step trials, 6 each of left- and right-side single targets. Trials were run during a single testing session in a pseudorandom order fixed for all subjects.

A trained coder analyzed videotape records off-line by noting the start time (in frames) and endpoint (left, center, or right screen) of both the first and the second saccades. If the subject failed to make a saccade or looked away from the display during the interval before the next fixation, the look was coded as invalid. Reliability in coding, assessed by a second coder's assessments of 20% of total trials, was high ($\kappa = .85$ and $.81$ for the first and second saccades, respectively).

We did not analyze trials in which babies (a) made a sequence of two saccades beginning with a response toward the second target (other sequence), (b) made only one saccade to either target (one look), or (c) did not make a saccade (invalid). We selected for detailed analysis those double-step trials in which infants made a valid sequence consisting of two looks: the first toward the first target and the second toward one of the other screens (see Fig. 1a, column 3). Retinocentric and egocentric position information for the second target differs only when a saccade sequence begins after the second target has disappeared. So, these sequences were further classified into two groups according to the start time of the first saccade in the sequence relative to the second target's offset. Sequences that began before the second target's offset were grouped into one category, sequences that began after the second target's offset were grouped into a second category. In the latter group, sequences were categorized as *retinocentric* if the second saccade ended at the midpoint of the center screen, and *egocentric* if it ended at the midpoint of the lateral screen where the second target had appeared (see Fig. 1a, columns 2 and 3). We computed an egocentric preference score for each subject equal to the number of egocentric sequences divided by the sum of egocentric and retinocentric sequences. The propensity to make long saccades (see Fig. 1c, column 3) was assessed by performance on the

single-step trials, for which we computed the proportion of responses that ended at the target location (*long looks*) relative to those that ended in the center screen (*short looks*). Raw percentage scores were subjected to a log transform to stabilize variance prior to conducting statistical tests, but for clarity we report untransformed scores.

Results

Table 1 shows the distribution of responses. Four-month-olds made fewer valid sequences as a proportion of total double-step trials than 6-month-olds (.27 vs .49) and had more invalid trials (.25 vs .09). But the fraction of trials in which infants spontaneously made sequences of saccades compares favorably with the behavior of 5- to 6-year-old participants who made valid sequences to double-step saccade targets on 40% to 50% of trials after receiving instructions to make saccades to all observed target shifts (Groll & Ross, 1982).

Of the double-step trials, 110 (4-month-olds: 1–11 trials/infant, $M = 3.9$, 6-month-olds: 1–10 trials/infant, $M = 4.9$) met the criteria for an analysis of retino- and egocentric response patterns. Four-month-olds made more retinocentric sequences than egocentric ones (mean egocentric preference score = 28, $SE = .09$), whereas 6-month-olds made more egocentric sequences (mean egocentric preference score = 75, $SE = .07$), $t(23) = 4.42$, $p < .001$ (see Fig. 2). A comparison of the total number of egocentric and retinocentric responses pooled across subjects confirmed that 4-month-old infants made significantly fewer egocentric responses overall than 6-month-olds, $\chi^2(1, N = 110) = 23.4$, $p < .0001$. A comparison of the mean proportions of long looks relative to short ones in the single-step trials (4 months: $M = 51$, $SE = 10$, 6 months: $M = 71$, $SE = 06$) reached marginal significance, $t(23) = 1.81$, $p < .09$. However, infants who made long looks on 5 or more of the single-step trials ($N = 8$ for 4-month-olds, $N = 11$ for 6-month-olds) still showed a significant age difference in the proportion of egocentric looks, $t(17) = 3.89$, $p < .001$. Further, performance on single-step trials did not predict the proportion of egocentric responses in a simple regression model, $F(1, 22) < 0.0001$, $n.s.$

Discussion

Four-month-old infants made more saccade sequences based on retinocentric information and fewer sequences based on egocentric

Table 1 Experiment 1 Distribution of responses

Type of response	Mean proportion of trials	
	4-month-olds	6-month-olds
Double-target trials		
Valid sequence	27 (.06)	49 (.06)
Other sequence	07 (.02)	08 (.02)
One look	41 (.25)	34 (.05)
Invalid	25 (.05)	09 (.02)
Single-target trials		
Long look	25 (.06)	51 (.07)
Short look	30 (.09)	18 (.07)
Invalid	45 (.07)	31 (.06)

Note: Standard errors are shown in parentheses.

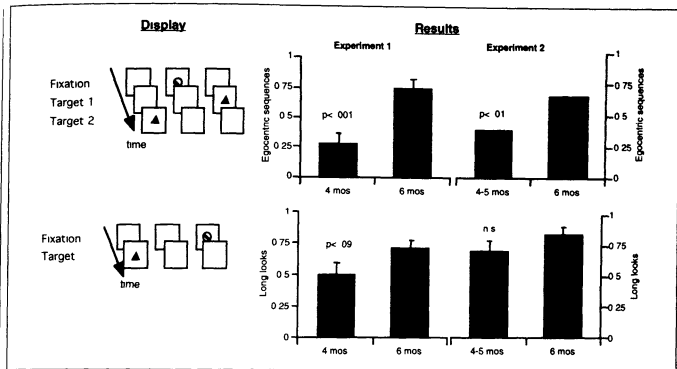


Fig 2 Combined results for short-look-first (top) and single-step (bottom) trials in Experiments 1 and 2. For Experiment 1, we report the mean proportions of egocentric saccades, egocentric/(egocentric + retinocentric). For Experiment 2, we report the relative proportion of egocentric sequences pooled across subjects within a group, total egocentric/(total egocentric + total retinocentric), because of insufficiently large sample sizes for group comparisons based on individual averages. For the single-step trials in both experiments, we report the mean proportions of successful long looks, long/(long + short).

information than did 6-month-olds. This finding suggests that the younger infants less reliably integrated retinal and eye position information necessary for a head-centered representation, but instead relied more frequently on the retinocentric positions of the targets in planning saccades to them. An alternative explanation is that the younger infants were merely less likely to make the long saccade required for an egocentric response. But differences between the 4- and 6-month-olds in the mean proportion of successful long saccades reached only marginal significance, and success in generating long saccades to a single target did not predict the extent of orienting to egocentric target locations. We propose that cortical circuitry is required to integrate the components of head-centered spatial representations (retinal and eye positions), and that continuing development in these systems between ages 4 and 6 months accounts for the observed behavioral shift.

EXPERIMENT 2

We conducted a second experiment designed to replicate the results and rule out several alternative accounts: (a) that age differences in the ability to make long eye movements explain the egocentric shift, (b) that the younger infants were employing some simple strategy, such as "return to center," or (c) that the infants' responses did not reflect processing of both targets. In Experiment 2, infants in one group saw both single-step and double-step trials designed so that the fixation stimulus appeared in all three screen positions, making it difficult to predict the next fixation or target position. The addition of a new double-step pattern was designed to elicit sequences with long

initial saccades. A second group of subjects saw only single targets. The performance of this group provided a measure of the prevalence of sequences and single saccades when only a single target was processed.

Method

Seventeen 4- to 5-month-old (range 123–167 days, $M = 136$, 11 female, 6 male) and seventeen 6-month-old (range 180–198 days, $M = 190$, 7 female, 10 male) healthy human infants participated in an experimental group. Nine 4-month-old (range 124–135 days, $M = 129$, 5 female, 4 male) and eight 6-month-old (range 182–192 days, $M = 185$, 5 female, 3 male) infants participated in a separate control group. Four additional 4- to 5-month-olds and one 6-month-old were tested but not included in the analyses because they did not make a codable response on at least half of the presented trials.

Two flat rectangular shapes the same size and color as the computer monitors were attached to an apparatus similar to that used in Experiment 1 at positions to the far left and far right of the horizontal monitor array. These figures created the illusion that there were additional computer monitors at the periphery, and made any contribution of object- or scene-based information roughly equivalent for the five spatial locations where subjects might direct their saccades. The procedures were similar to those for Experiment 1. The experimental group observed 36 trials in total, 30 with double targets and 6 with only a single target, run in a pseudorandom order equivalent for all subjects. Twenty-four instances of a new double-step trial type (see

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Fig 1b) were included. These long-look-first trials presented the fixation stimulus on the left- or right-side monitor, then displayed targets first opposite the fixation point and then on the central screen. Pilot testing had indicated that subjects rarely made a saccade to the more distant first target unless it appeared for a longer time period than the closer second target. Therefore, we increased the duration of the first target to 250 ms and decreased the duration of the second to 150 ms in order to elicit more initial saccades to the first target. Six double-step trials with the same timing regime, but appearing in the spatial pattern of Experiment 1 (Fig 1a), were also included. The single-step trials (Fig 1c) were identical to those from Experiment 1 except for the duration of the target (250 ms).

The control group observed 36 single-step trials in which the fixation appeared on either the left, center, or right screen, followed by a target (250 ms) on one of the other screens. The fixation and target positions were presented in a balanced pseudorandom order fixed for all subjects.

Data collection and coding procedures were similar to those in Experiment 1. Videotapes were recorded at 50 half-frames/s. Figure 1b depicts the scheme for coding the new long-look-first trial type. For the control group, which viewed only a single target on each trial, we determined where the second target would have been located in the equivalent double-step trial. Then, single saccades and sequences of saccades were classified accordingly. If a baby made a first saccade toward the target and a second saccade toward the retinocentric or egocentric screen location of the second target on the equivalent double-step trial, the sequence was coded as valid.

Results

Table 2 shows the distribution of responses for infants in both groups. The data from the experimental group indicate that valid sequences in the long-look-first condition were rare at both ages despite the timing manipulation. The most frequent response was a single saccade to the second target—the one nearer the fixation point. In the short-look-first trials, valid sequences were observed at frequencies comparable to those for the first study. The total number of valid experimental sequences was 63 in the long-look-first condition (4–5 months 0–4 trials/infant, $M = 1.9$, 6 months 0–8 trials/infant, $M = 2.4$) and 84 in the short-look-first condition (4–5 months 0–7 trials/infant, $M = 1.3$, 6 months 1–6 trials/infant, $M = 3.1$). The small sample sizes made it necessary to loosen the strict timing criterion used in the first experiment by including sequences that began during the second target's appearance, and to analyze the responses pooled across subjects in each age group. Overall, the younger infants made significantly fewer egocentric responses than the older infants in the short-look-first trials, $\chi^2(1, N = 84) = 7.73, p < .01$, but the two groups did not differ in the proportion of egocentric responses in the long-look-first trials, $\chi^2(1, N = 63) = 2.54, p > .10$. A similar pattern was obtained with the more restricted sample of saccades that occurred only after the presentation of the second target. There were no statistically significant age differences in the mean proportion of long looks in the control trials (4–5 months $M = .70, SE = .07$, 6 months $M = .84, SE = .05$).

The results from the control group showed that there were minimal age differences overall, that valid sequences constituted a small proportion of total trials (4-month-olds $M = .12$, 6-month-olds $M = .05$), and that the most common response was a single saccade to the first target (4-month-olds $M = .49$, 6-month-olds $M = .47$).

Table 2 Experiment 2 Distribution of responses

Type of response	Mean proportion of trials	
	4- to 5-month-olds	6-month-olds
Experimental group		
<u>Short-look-first trials</u>		
Valid sequence	36 (.06)	59 (.06)
Other sequence	05 (.03)	06 (.03)
One look	41 (.05)	26 (.09)
Invalid	18 (.06)	09 (.04)
<u>Long-look-first trials</u>		
Valid sequence	05 (.02)	09 (.03)
Other sequence	13 (.02)	10 (.02)
One look	58 (.05)	70 (.03)
Invalid	24 (.06)	11 (.03)
<u>Single-target trials</u>		
Long look	43 (.06)	61 (.06)
Short look	16 (.03)	13 (.05)
Invalid	41 (.06)	26 (.05)
Control group		
<u>Single-target trials</u>		
Valid sequence	12 (.04)	05 (.02)
Other sequence	07 (.04)	06 (.03)
One look	49 (.08)	47 (.06)
Invalid	32 (.06)	42 (.07)

Note: Standard errors are shown in parentheses. The control group consisted of 4-month-old infants only.

Discussion

The results replicate the findings from Experiment 1 (see Fig 2). Four- to five-month-old infants made more retinocentric and fewer egocentric sequences of saccades than did their 6-month-old counterparts, and there were no statistically significant differences in the relative frequency of long looks in the control trials. The results from the long-look-first condition indicate that in some circumstances, egocentric position information can reliably guide the saccades of younger infants, but small sample sizes make this conclusion tentative. The results obtained rule out an explanation based on simple response strategies because unlike in Experiment 1, no fixation position occurred more often than any other. Further, the results from the control group show that in the absence of a second target, infants make more single saccades and many fewer sequences. Thus, the sequences observed in the double-step trials appear to reflect processing of both targets.

GENERAL DISCUSSION

In two separate experiments, we observed that 4- to 5-month-olds more often rely on retinal position in planning sequences of saccades, but can integrate retinal and eye position information to plan saccades in egocentric coordinates in some circumstances. By the time infants are 6 months old, egocentric information dominates. The systematic integration of retinal and eye position information is strongly associated with processing in the parietal cortex. We suggest that the gradual emergence of adultlike saccade behavior results from the development of spatial-processing circuits in these parts of the cerebral cortex. The

general view that subcortical circuitry dominates the orienting responses of young infants until cortical mechanisms mature sufficiently to influence saccades is reinforced by recent evidence that the extent of retinal vector averaging, a marker for collicular function, declines in infants between 2 and 6 months of age (Johnson, Gilmore, Tucker, & Minister, 1996).

Evidence from visual anatomy may also provide some insight into the absence of age differences in the long-look-first condition. In these trials, both targets appeared in the same visual hemifield, whereas in the short-look-first trials, the targets appeared in opposite hemifields. The anatomy of retinal projections to the cortex ensures that information from a given hemifield is largely isolated to the hemisphere contralateral to the stimulus early in visual processing. Determining whether mechanisms that integrate spatial information between the cortical hemispheres develop more slowly than those that integrate information within them will require further research.

We have argued that the frame of reference infants use for coding visual space shifts from an eye-centered, or retinocentric, form early in life to the mature head-centered, or egocentric, form by 6 months. An alternative description of mature saccade planning proposes that saccade targets are coded in retinocentric coordinates that shift dynamically in accord with planned or actual eye movements (Duhamel, Colby, & Goldberg, 1993). Patterns of adult saccade errors under certain double-step timing regimes suggest that the internal eye position signal used to compute target locations is updated over time (Dassonville et al., 1993), and neurons that show this property of dynamic updating have been found in the same posterior parietal regions thought to compute head-, trunk-, and other body-centered representations (Duhamel et al., 1993). Whether adult saccades are planned by computing target locations using a dynamically updating retinocentric map or stable egocentric coordinates is unresolved, but the functional consequences and neural mechanisms appear to be the same. As a result, we cannot rule out the possibility that retinocentric information dominates saccades produced by the youngest infants not because they lack egocentric representations for action, but because the cortical representation of eye position is either inaccurate or slowly updated.

Other visually guided behaviors that appear to demand sophisticated, body-centered spatial frames of reference also appear in the same time period as the emergence of egocentric representations for saccades—for example, anticipatory reaching toward moving objects (von Hofsten, 1980) and successful reaching to a sounding object in the dark (Clifton, Muir, Ashmead, & Clarkson, 1993). We note that the onset of accurate auditory localization has also been attributed to the emergence of cortical processing (Muir, Clifton, & Clarkson, 1989). The reliable use of visual scene or landmark information emerges much later in the 1st year, however (Acquadro, 1990; Bremner, 1978). This suggests that there may be a sequence in the development of spatial frames of reference from the simplest based on the natural geometry of the sense organ (e.g., retina or skin surface) to the more complex centered on some part of the body or even objects in the environment. These more complex frames require the integration of multiple sources of spatial information for which the postnatal development of cortical circuitry may be essential.

Of course, these preliminary studies leave several issues unresolved. The experiments were carried out in dimmed light, but not complete darkness as in the original double-step experiments, meaning that improved abilities to use object-based spatial information in

planning saccades could have contributed to the observed shift. Nevertheless, the available evidence suggests that these processes also involve cortical processing at higher levels of the oculomotor system (Behrmann & Tipper, 1994; Olson & Gettner, 1995). Further, infants' head positions were limited by padding, but not fixed in space. As a result, we cannot determine the potentially separate contribution of head- or trunk-centered coordinate representations.

These experiments indicate that the double-step saccade paradigm is a useful method for exploring changes in the nature of the representations that control visually guided actions over the first several months of life. The development of an egocentric frame of reference for visually guided saccades from a more primitive, earlier emerging, retinocentric representation may index the emergence of cortical spatial-processing systems in the infant brain.

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