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Brief article

Body-centered representations for visually-guided action emerge during early infancy

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Abstract

The nature of the spatial representations that underlie simple visually guided actions early in life were investigated through the application of a ‘double-step’ saccade paradigm to 3- and 7-month-old infants. Saccades in the older infants, like those observed in adults, were executed within body-centered spatial coordinates that take into account the effects of intervening eye movements. In contrast, younger infants tended to respond according to the targets’ retinocentric locations and did not incorporate the effects of displacements caused by previous saccades. These results indicate that, contrary to prevailing views, body-centered representations for action are not present from birth but emerge, probably through experience, over the first few months of life. © 1997 Elsevier Science B.V.

Keywords: Eye movements; Double-step saccade paradigm; Body-centered representations

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1. Introduction

A central question in cognitive development concerns the nature of the mental representations that guide and regulate action, and how these change with age. Previous research indicates that infants initially specify spatial locations using body-centered coordinates then gradually shift to using environment-centered representations. However, it is not known whether body-centered representations for

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action are prespecified and present from birth, or whether they emerge gradually over the first year from an even more primitive coordinate system. In the present study, we examine this issue by examining the coordinate system, or frame of reference, used by 3- and 7-month-old infants to plan saccadic eye movements in a double-step paradigm.

Developmental studies have indicated that infants of 6 months old and older search for hidden objects using information about target locations that is defined relative to the current position of the body (Piaget and Inhelder, 1948; Acredolo, 1990; Reiser, 1979; Tyler and McKenzie, 1990). The ability to combine body-centered information with the effects of body movements or the configuration of landmarks develops gradually throughout the first several years of life (Hermer and Spelke, 1994). However, the representations utilized for action planning in infants younger than 6 months have remained largely unexplored, despite the fact that this is a period of dramatic change in infants' perceptual and motor skills and in the brain systems which underlie them (Atkinson, 1984; Bronson, 1974, 1982; Johnson, 1990).

Since gaze shifts are among infants' first exploratory actions, we investigated

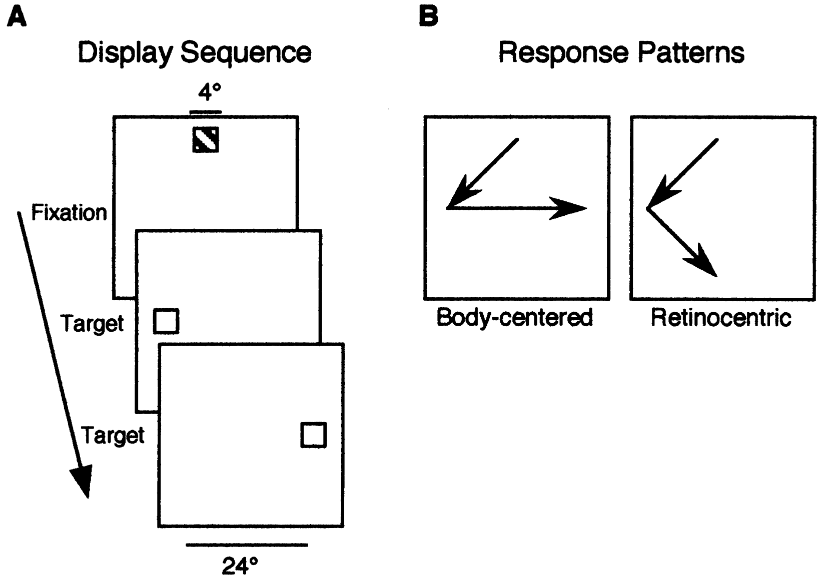


Fig. 1. Design of infant double-step saccade experiment. (A) A trial began with the presentation of a fixation stimulus consisting of a sequence of colored shapes which was followed by the brief appearance of two identical targets that flashed sequentially. Fixation and target positions varied in a pseudo-random order. (B) Two types of responses were of critical concern: a body-centered sequence consisting of two saccades, the first saccade to the first target, and the second saccade to the second target; and a retinocentric sequence consisting of two saccades, the first to the first target, and the second equivalent to the position of the second target relative to the fovea at the time it was initially presented. In the situation depicted here, the second target appeared below and to the right of fixation, so a retinocentric second saccade would be directed below and to the right of the endpoint of the first saccade.

which sources of information guide babies' saccadic eye movements. This question has been explored in adults and older children using the double-step saccade paradigm (Becker and Jürgens, 1979; Hallett and Lightstone, 1976; Aslin and Shea, 1987; Findlay, 1982; Honda, 1989; Groll and Ross, 1982). Participants are instructed to look at sequences of visual targets that flash briefly in a dark visual field; the second stimulus appears and disappears before or during the response to the first stimulus (Fig. 1A). The position of a target relative to the fovea, that is, its retinocentric position, is sufficient for planning a response to the first, but not the second target. This is because the first eye movement shifts the center of gaze, and with it, the second target's position on the retina (see Fig. 1B). Accordingly, to make an accurate sequence of saccades, participants in the double-step paradigm must incorporate additional, non-retinal, information, such as eye or head position, in planning their eye movements. Adults and school children make accurate saccades to both targets in many circumstances (Becker and Jürgens, 1979; Hallett and Lightstone, 1976; Aslin and Shea, 1987; Findlay, 1982; Honda, 1989; Groll and Ross, 1982). This suggests that the mature oculomotor system does not represent visual target locations in retinocentric coordinates. Instead, adults use either head-centered representations, which combine retinal position with signals specifying eye position (Andersen et al., 1993; Mays and Sparks, 1980; Freedman et al., 1996; Guitton et al., 1990), or eye-centered representations, which incorporate the effects of planned eye movements (Duhamel et al., 1992, 1993; Goldberg and Colby, 1992; Dassonville et al., 1992). For the purposes of this paper, we call spatial representations of saccade targets that incorporate both retinal and extraretinal, eye or head position, information, body-centered.

We used the double-step saccade paradigm to investigate whether infants are guided by adult-like body-centered spatial representations from birth or whether these emerge during the first months of life. Specifically, we asked at what age infants would take into account the displacement caused by the first saccade in planning their second response. For several reasons, we predicted that young infants tested in the double-step paradigm would show more retinocentric sequences and fewer body-centered sequences when compared with older children or adults. Body-centered representations for action have been linked to neural networks in the parietal and frontal cortex (Andersen et al., 1993; Duhamel et al., 1992, 1993; Goldberg and Colby, 1992; Graziano et al., 1994; Stein, 1992). However, behavioral, neuroimaging, and neuroanatomical evidence suggests that eye movement control shifts from predominantly subcortical to predominantly cortical sources over the first few months of life (Atkinson, 1984; Bronson, 1974, 1982; Johnson, 1990). Consequently, young infants' spatial representations may differ from the adult in fundamental ways. This is because the integration of retinal and extraretinal (eye or head position) information depends upon cortical processing mechanisms which develop slowly, and mature saccade planning may require extensive periods of postnatal calibration between the retinal and eye position signals that contribute to saccade motor commands (Aslin, 1993).

In an earlier study, we used a one-dimensional version of the double-step paradigm with infants to produce preliminary evidence consistent with the above hypothesis in infants from 4 to 6 months old (Gilmore and Johnson, 1997). However, the one-dimensional procedure, and our particular implementation of it for use with infants, allowed for a number of alternative hypotheses. Specifically, the one-dimensional version suffered from alternative explanations in terms of (1) the possibility of infants learning sequences of looking patterns, (2) the possible use of object-centered cues due to the stimuli appearing on three screens, and (3) longer saccades were required for egocentric responses than retinocentric. All of these alternatives are eliminated by the present two-dimensional double-step procedure.

2. Methods

We recorded on videotape the spontaneous eye movements of separate groups of 3- ($n = 13$) and 7- ($n = 12$) month-old infants who observed double-step visual events as depicted in Fig. 1A. Infants sat in a car seat 50 cm from a 51 cm color computer monitor controlled by a microcomputer. Infant head movements were limited by padding, but the head was unrestrained in order to maintain babies' cooperation. In each trial, a fixation stimulus appeared in one of four positions on the screen (up, down, left or right). Following a computer key press that terminated the fixation stimulus, two targets appeared on the screen, one following the other, with no period of overlap. Fixation and target patterns were chosen randomly from a subset of high contrast designs each presented at 4° in width. Pairs of targets appeared opposite one another, e.g. above right and below right of fixation, and at a distance of 17° from the middle of the fixation point. There were eight combinations of fixation-target sequences presented once in a balanced pseudorandom order within a single block of trials. There were six blocks presented in a continuous fashion without interruption for a total of 48 trials per infant. Target durations were selected to maximize the number of trials in which babies' made sequences of saccades. Based on pilot testing, we chose durations of 175/125 ms for the 3-month-old group and 125/100 ms for the 7-month-old group. However, to ensure that retinal and eye position information were completely separated, we did not include in our analyses those trials (3-month-old, 11% of total; 7-month-old, 2% of total) in which participants made their first saccade prior to the offset of the second target. A 1.5 s response interval followed each double-step trial.

After the testing session, coders (blind as to trial type) determined start times and endpoints (one of nine screen locations on a 3 × 3 grid) of the first and second saccades from PAL format (50 half frames/s) videotapes of the babies' heads and eyes. If the baby was judged not to be looking at fixation during the presentation of the targets, failed to disengage from the fixation, looked away from the display, or the experimenter terminated a trial due to infant fussiness, that trial or look within the trial was coded as invalid. Valid eye movements that began less than 200 ms following the termination of a preceding look were coded as a correction of the previous response, and not a separate saccade. If the two coders disagreed on either the direction or start time for a saccade, a third coder reviewed the trial independently and rejected the assessment of one or both of the other coders. Based on this procedure, two of three coders agreed on 99% of all responses observed in babies from both age groups. Videotape measures of this type have been shown to have sufficient accuracy in comparison with electro-oculogram data (Tucker et al., 1996). Our analysis focused on infants' sequences of two eye movement in which the first saccade was toward the first target. In these circumstances, the endpoint of the second saccade indicated whether retinocentric or body-centered information influenced the response (Fig. 1B).

3. Results

Table 1 summarizes the mean number of trials collected per infant in the critical categories of interest. Unlike older children and adults, infants could not be verbally instructed to make eye movements to the targets; nevertheless, both age groups responded with spontaneous saccades to one of the nine screen locations on the majority of trials (3-month-old, mean 31/48; 7-month-old, mean 38/48), and in frequencies comparable with those of school children (Groll and Ross, 1982). Fig. 2A summarizes the mean distribution of initial saccades for each age group. Most initial saccades were toward the first target, and these responses were, not surprisingly, initiated more rapidly than those to the second target or other screen locations. As Table 1 indicates, on trials where babies made an initial saccade to the first target, both age groups often made a valid second saccade to one of the screen locations (3-month-old, mean 9/15 trials; 7-month-old, mean 15/22). Fig. 2B shows the distribution of these second looks. After determining that there were no notable differences between response patterns based on the location of the fixation or position of the targets, we pooled the data from all display conditions. We then summed each individuals' responses toward each location across the age groups to compute a total distribution for each group. The proportion of retinocentric second looks out of total second looks was larger in 3-month-old infants, chi-square (1, n = 303) = 26.1, $P < 0.0001$, and the proportion of body-centered second looks was larger in older infants, chi-square (1, n = 303) = 12.2, $P < 0.0001$. To verify that pooling data across infants did not result in bias due to a single individual's performance, we also computed mean proportions of retino- and body-centered looks for

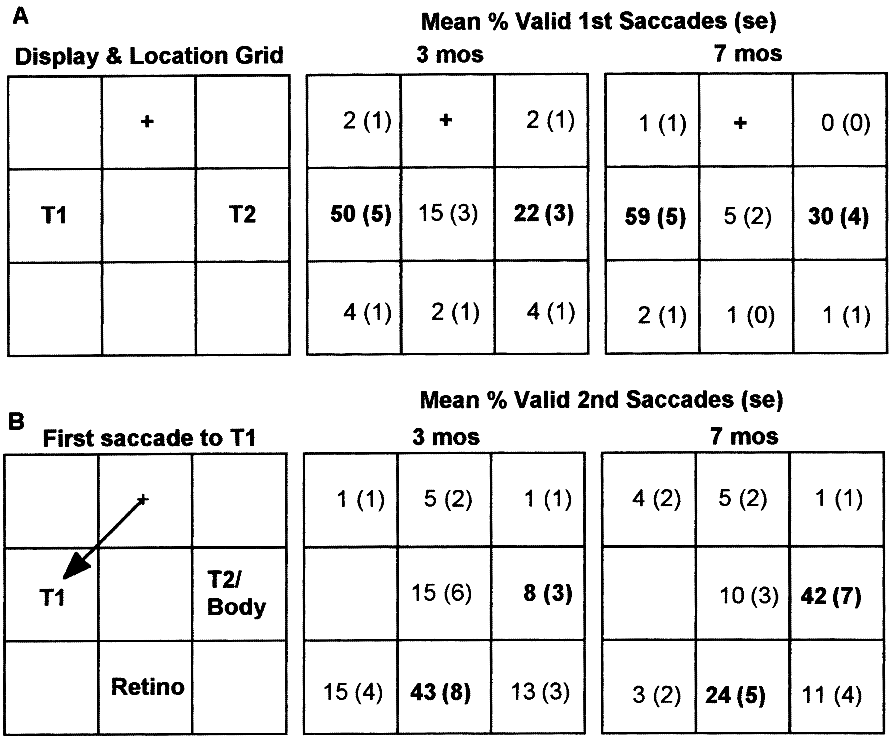
Table 1
Mean number of trials observed per infant

	Total trials	Valid 1st	1st = T1	Valid 2nd	2nd retino	2nd body-ctr
3-month-old	48	31 (6)	15 (5)	9 (4)	5 (4)	1 (1)
7-month-old	48	38 (7)	22 (8)	15 (8)	4 (4)	6 (5)

Standard deviations are noted in parentheses. 'Valid 1st' refers to those trials in which infants looked to one of the nine screen locations after the offset of the second target. '1st = T1' refers to those first saccades that were directed toward the first target. 'Valid 2nd' refers to those trials in which infants looked first to the first target, then made a second look to one of the nine screen locations.

those babies who made at least three second looks (3-month-old, $n = 13$; 7-month-old, $n = 11$) and then (arcsine) transformed these scores to stabilize the variance. Three-month-olds made more retinocentric saccades on average, $t(22) = 2.01$, $P = 0.057$, and 7-month-olds more body-centered saccades, $t(22) = 5.03$, $P > 0.0001$.

Thus, 3-month-old babies most often planned saccades according to the retinocentric coordinates of the targets, and did not appear to take into account the effect of eye movements in planning their second saccades. In contrast, 7-month-olds most often planned saccades which took eye movements into account, and much less often planned saccades based solely on retinocentric information. There were no age differences in the distribution of sequences that began with an initial look toward screen locations other than to the first target. Consequently, the period between 3 and 7 months consists of a shift in the dominant spatial representation for saccades from retinocentric to body-centered.



	+	
T1		T2

2 (1)	+	2 (1)
50 (5)	15 (3)	**22 (3)**
4 (1)	2 (1)	4 (1)

1 (1)	+	0 (0)
59 (5)	5 (2)	**30 (4)**
2 (1)	1 (0)	1 (1)

	+	
T1		T2/ Body
	Retino	

1 (1)	5 (2)	1 (1)
	15 (6)	**8 (3)**
15 (4)	**43 (8)**	13 (3)

4 (2)	5 (2)	1 (1)
	10 (3)	**42 (7)**
3 (2)	**24 (5)**	11 (4)

Fig. 2. Results of first saccades and the second saccades that followed an initial look to the first target (T1). (A) The mean proportions of valid first saccades to each screen location indicate that most responses were directed toward either the first (T1) or second target (T2), highlighted in boldface. (B) The mean proportions of valid second saccades, following a first look toward T1, indicate that most second responses were directed toward either the retinocentric (Retino) location or that of the second target (T2/Body). These locations are highlighted in boldface.

4. Discussion

Because the systematic integration of retinal and body position or movement information is associated with processing in the parietal lobe, we suggest that the gradual emergence of adult-like saccade sequences results from the experience-dependent development of spatial processing circuits in this part of the cerebral cortex. The general view that subcortical circuitry dominates the orienting responses of young infants until cortical mechanisms develop sufficiently is reinforced by several recent lines of evidence (Atkinson, 1984; Bronson, 1974, 1982; Johnson, 1990; Johnson et al., 1996; Gilmore and Johnson, 1997). However, our data cannot rule out the possibility that gradual development in subcortical components of the oculomotor system could contribute to the observed shift in representation (Mays and Sparks 1980; Freedman et al., 1996; Guitton et al., 1990; Knudsen and Brainard, 1991). Because head movements were neither eliminated entirely, nor systematically varied, we also cannot distinguish between the possibly separate influence of head- or trunk-centered coordinates in planning body-centered saccades.

The gradual emergence of body-centered representations for the control of saccades during the first half-year of life is consistent with the development of other visually-guided behaviors that emerge between 3 and 7 months, and which presumably also depend on multimodal, body-centered representations of space: anticipatory reaching toward moving objects and the accurate localization of sounds (von Hofsten, 1990; Clifton et al., 1993; Muir et al., 1989). Consequently, while eye-, head-, trunk-, arm-, and even object-based representations underlie mature visually-guided action, far simpler frames of reference may be most influential early in life. These primitive, but functional mappings between sensory systems and motor commands provide young animals with rudimentary abilities to explore the environment and to acquire patterns of correspondence between visual and non-visual sources of spatial information. As a result, the development of mature spatial representations for visually-guided action may follow a sequence from retina- to body- to environment-centered coordinates in the first several months of life. These increasingly complex mappings are embodied in neural, presumably cortical, circuitry devoted to action planning which undergoes gradual experience-dependent postnatal development.

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