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Motion- and orientation-specific cortical responses in infancy

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Abstract

During the first 3 months, infants develop visual evoked potential (VEP) responses that are signatures of cortical orientation-selectivity and directional motion selectivity (Braddick, O. J., Wattam-Bell, J., & Atkinson, J. (1986). Orientation-specific cortical responses develop in early infancy. *Nature, London, 320*, 617–619; Wattam-Bell, J. (1991). Development of motion-specific cortical responses in infancy. *Vision Research, 31*, 287–297). This study compared these responses directly in the same infants, to investigate whether the later appearance of direction selectivity was intrinsic, or a function of the spatio-temporal characteristics of the stimuli used. Steady-state orientation-reversal (OR-) VEPs and direction-reversal (DR-) VEPs were recorded in infants aged 4–18 weeks. DR-VEPs were elicited with random pixel patterns and with gratings spatially similar to those used for OR-VEPs, at velocities of 5.5 and 11 deg/s, and reversal rates of 2 and 4 reversals/s. Infants throughout the age range showed significant responses to orientation-reversal. Direction-reversal responses appeared in less than 25% of infants under 7 weeks of age, rising to 80% or more at 11–13 weeks, whether tested with dots or gratings and for both speeds and reversal rates. However, 2 reversals/s elicits the DR-VEP on average about 2 weeks earlier than 4 reversal/s stimulation. We conclude that human cortical direction selectivity develops separately from orientation-selectivity and emerges at a later age, even with tests that are designed to optimise the former.

Keywords: Visual evoked potentials; Motion; Orientation; Visual development; Infant

1. Introduction

Neurons in primary visual cortex show stimulus selectivity in a number of ways—for example, selective responses to particular values of orientation, direction of motion, and binocular disparity. During the early months of life, human infants begin to show properties of visual processing that indicate the development of these selective cortical responses (Atkinson, 2000; Braddick, Atkinson, & Wattam-Bell, 1989). However, the signatures of the different forms of cortical selectivity do not necessarily emerge at the same time. In particular, the behavioural and neural responses indicative of orientation selectivity (Atkinson, Hood, Wattam-Bell, Anker, & Tricklebank, 1988; Braddick, 1993; Braddick, Wattam-Bell, & Atkinson, 1986; Hood, Atkinson, Braddick, & Wattam-Bell, 1992), have been detected earlier in infancy than the corresponding responses that reflect cortical processing of motion direction (Wattam-Bell, 1991, 1994, 1996a, 1996b). This developmental sequence, if correct, has important implications for understanding how the characteristic connectivity of human visual cortex becomes established, and what visual information is available to infants at the early stages in development of systems for visual perception, object recognition, and spatial cognition.

However, the stimulus parameters used to test these two cortical properties have differed in various ways, and there has not so far been any direct comparison of orientation and motion selectivity in the same individual

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infants. The work reported here was designed to make such a comparison, and as far as possible to exclude the effects of incidental differences between the stimuli used to test orientation and direction selectivity.

Direction and orientation selectivity are often found together as properties of the same cortical neurons. However, they provide the precursors of what are considered as distinct major processing streams. Responses to oriented contour elements in area V1 provide the earliest kind of shape-selective activity, and so serve as the basis for object- and pattern-selectivity found in extrastriate and temporal-lobe areas of the ventral cortical processing stream (Ungerleider & Mishkin, 1982). In contrast, directionally selective signals in V1 are routed to V5 (MT) and areas of the dorsal stream that are believed to be responsible for the visual control of spatially directed actions (Glickstein & May, 1982; Milner & Goodale, 1995; Mishkin, Ungerleider, & Macko, 1983). A secure knowledge of how these properties develop is therefore a necessary underpinning for understanding the broader developmental sequence of ventral and dorsal stream function.

The present study used analogous methods for analysing both forms of selectivity. In each case, a visual evoked potential (VEP) signal was detected, time locked to a reversal of orientation or direction, respectively. In each method, these changes are embedded in a sequence of stimulus transitions, designed to control for spatio-temporal changes which are associated with the orientation or direction change but are not themselves diagnostic of an orientation- or direction-selective response. Both methods have been well-established in previous work with normally developing and at-risk infants (Braddick, 1993; Braddick et al., 1986; Mercuri et al., 1998; Wattam-Bell, 1991). As previously applied, the methods differ in the spatial characteristics of the display (random pixel patterns for direction, grating patterns for orientation). In this study, we test whether this is a critical difference by testing direction-selective responses with gratings similar to those used in orientation-reversal testing. We also examine whether the later onset of direction-selective responses might be a consequence of the temporal frequencies used in the test.

2. Subjects

Healthy full-term infants aged between 5 and 18 weeks postterm and born within 14 days of their due date were recruited from volunteer families. The subjects showed no strabismus or significant refractive error. A total of 121 infants participated. They were tested with various combinations of conditions in the same session, which serve as the basis for Comparisons 1, 2, and 3 below. Table 1 presents the number of infants participating in each comparison. Data from a session with a particular infant can contribute to more than one of these Comparisons: 21 infants contributed to both Comparisons 1 and 2, and 35 infants contributed to both Comparisons 1 and 3; 10 infants completed only one condition so their results are included in the general analysis of motion responses only (Fig. 7).

The various comparisons are reported for data divided into five age groups, as shown in Table 1. A number of infants attended for repeat visits, with an interval of 2 weeks or longer, and provided data that could be included in more than one age group, as described under 'subjects' for each comparison.

3. Comparison 1: Orientation- vs direction-selective responses

3.1. Stimuli

The orientation-reversal stimulus was similar to that used previously by Braddick et al. (1986) and Mercuri et al. (1998) except that the stimuli were high contrast sine wave (rather than square-wave) gratings, of spatial frequency 0.3 c/deg, presented on a computer monitor at a 40 cm viewing distance from the infant's eyes. The stimulus sequence consisted of changes in orientation of the grating pattern between 45° and 135° at a rate of 4 reversals/s. These orientation changes will be accompanied by local luminance changes, wherever a dark region in the 45° grating pattern is replaced by a light region in the 135° grating, or vice versa. To isolate orientation-specific responses, the orientation reversals

Table 1
Infants in each age group participating in the various comparisons

Group age range (weeks)	Comparison 1		Comparison 2		Comparison 3		Overall direction-reversal test	
	N	Mean age (SD)	*N*	Mean age (SD)	*N*	Mean age (SD)	*N*	Mean age (SD)
5–7	21	6.0 (0.5)	2	7.2 (1.1)	11	6.2 (0.4)	22	6.0 (0.6)
7–9	21	7.7 (0.5)	6		11	7.9 (0.4)	24	7.9 (0.5)
9–11	24	9.9 (0.5)	13	9.9 (0.5)	12	10.0 (0.5)	32	9.8 (0.5)
11–13	28	11.9 (0.5)	10	11.7 (0.7)	18	11.9 (0.5)	37	11.8 (0.6)
13–18	21	15.2 (1.7)	20	15.6 (1.6)	8	16.3 (1.4)	41	15.7 (1.8)

Note. In each comparison, some infants participated in more than one age group—see text for details.