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Spatio-temporal tuning of coherent motion evoked responses in 4–6 month old infants and adults

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ABSTRACT

Motion cues provide a rich source of information about translations of the observer through the environment as well as the movements of objects and surfaces. While the direction of motion can be extracted locally these local measurements are, in general, insufficient for determining object and surface motions. To study the development of local and global motion processing mechanisms, we recorded Visual Evoked Potentials (VEPs) in response to dynamic random dot displays that alternated between coherent rotational motion and random motion at 0.8 Hz. We compared the spatio-temporal tuning of the evoked response in 4–6 months old infants to that of adults by recording over a range of dot displacements and temporal update rates. Responses recorded at the frequency of the coherent motion modulation were tuned for displacement at the occipital midline in both adults in infants. Responses at lateral electrodes were tuned for speed in adults, but not in infants. Infant responses were maximal at a larger range of spatial displacement than that of adults. In contrast, responses recorded at the dot-update rate showed a more similar parametric displacement tuning and scalp topography in infants and adults. Taken together, our results suggest that while local motion processing is relatively mature at 4–6 months, global integration mechanisms exhibit significant immaturities at this age.

1. Introduction

Motion sensitivity, like spatial vision, is a fundamental aspect of visual perception. A crude form of direction selectivity can be demonstrated in V1 cells of infant macaques at 1–2 weeks of age (Chino, Smith, Hatta, & Cheng, 1997), in very young visually inexperienced kittens (Hubel & Wiesel, 1963) and in visually naïve ferrets (Li, Van Hooser, Mazurek, White, & Fitzpatrick, 2008). Visual experience with moving contours however is critical for refining and maintaining cortical direction selectivity (Cynader, Berman, & Hein, 1973; Cynader & Chernenko, 1976; Humphrey & Saul, 1998; Humphrey, Saul, & Feidler, 1998; Li, Fitzpatrick, & White, 2006; Li et al., 2008), as is normal binocular interaction (Watanabe et al., 2005).

Assessment of direction selective mechanisms in humans is necessarily more indirect, and different assays suggest different developmental time courses. Directional optokinetic eye movement responses (OKN) can be elicited in newborns (Kremenitzer, Vaughan, Kurtzberg, & Dowling, 1979; Naegele & Held, 1982; Phillips, Finocchio, Ong, & Fuchs, 1997; Volkmann & Dobson, 1976). However, because OKN in primates is controlled by a combination of cortical and subcortical motion systems (Distler, Vital-Durand, Korte, Korbmacher, & Hoffmann, 1999), it is not clear which system is responsible for neonatal OKN. Other directional eye movements can also be elicited near birth in humans (Rosander, 2007), but again the locus of control is uncertain. Using Visual Evoked Potentials (VEPs), (Wattam-Bell, 1991) found evidence for cortical direction selectivity in infants by the age of 10 weeks for a stimulus velocity of 5 deg/s and by the age of 12 weeks for a stimulus velocity of 20 deg/s, suggesting that the development of directionality proceeds from low to high velocities. A more recent VEP study has found that direction-reversal responses appeared in less than 25% of infants under 7 weeks of age, rising to 80% or more at 11–13 weeks (Braddick, Birtles, Wattam-Bell, & Atkinson, 2005). The monocular oscillatory motion VEP displays a directional bias in older infants (Norcia et al., 1991), but not before about one month of age (Birch, Fawcett, & Stager, 2000), suggesting that cortical direction selectivity emerges post-natally in humans. Finally, a number of behavioral preference studies provide evidence for directional motion sensitivity within the first 3 months of life in humans (Braddick, Atkinson, & Wattam-Bell, 2003).

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A common strategy for studying motion selectivity in human is to use population response measures such as fMRI and visual evoked potentials/magnetic fields with experimental designs that contrast responses to coherent versus incoherent motion in dynamic random-dot kinematograms (Aspell, Tanskanen, & Hurlbert, 2005, Braddick, et al., 2001; Braddick, O'Brien, Wattam-Bell, Atkinson & Turner, 2000; Handel, Lutzenberger, Thier, & Haarmeier, 2007; Koyama et al., 2005; Lam et al., 2000; Morrone et al., 2000; Nakamura et al., 2003; Niedeggen & Wist, 1999). Coherent motion displays contain two types of motion signals, a local one involving short-range correlations in the apparent motion of individual dots in the pattern and a global one involving a systematic organization of the local motion vectors into flow fields (Newsome & Pare, 1988). Differential responses to coherent versus incoherent motion displays indicates successful encoding of both the local direction signals as well as their global organization.

Behavioral sensitivity to coherent motion has been demonstrated within the second month of life (Banton & Bertenthal, 1996; Banton, Bertenthal, & Seaks, 1999; Wattam-Bell, 1994, 1996). A longitudinal behavioral study in macaque infants aged between 10 days and 3 years found that coherent motion sensitivity continued to improve up to at least 3 years of age (Kiorpes & Movshon, 2004). The sensitivity of the youngest monkeys was highest at large dot displacements and fast speeds and coherence sensitivity improved for small dot displacements and slow speeds with age. In humans, development of psychophysical sensitivity is incomplete in middle childhood, especially at slow speeds (Atkinson, 2000, Ellemberg et al., 2004; Ellemberg, Lewis, Maurer, Brar, & Brent, 2002).

Both single-unit recording studies (Duffy & Wurtz, 1995; Heuer & Britten, 2004; Snowden, Treue, & Andersen, 1992; Tanaka & Saito, 1989) and human functional imaging studies (Braddick, O'Brien, Wattam-Bell, Atkinson, & Turner, 2000; Goossens, Dukelow, Menon, Vilis, & van den Berg, 2006; Morrone et al., 2000; Seiffert, Somers, Dale, & Tootell, 2003) indicate that sensitivity to global structure in coherent motion displays is greatest in extra-striate cortical areas. Given the hierarchical nature of the coherent motion stimulus, and the relative specificity of global responses in extra-striate areas, these two responses, one "global" and the other "local" likely reflect different visual processing mechanisms located at different levels in the visual pathway. In our experiment, both the spatial and temporal displacements of the local apparent motion cue were varied parametrically in such a way that we could determine the overall pattern of spatio-temporal dependence of both local responses—those that were time-locked to the dot-update rate (15, 20 or 30 Hz) and global responses—those that were time-locked to the global-update rate (0.8 Hz) at which the directional coherence modulated. More specifically, the stimulus parameters were chosen to provide a strong test of whether the local or global response tuning depended separately on spatial and temporal displacement or on speed. Speed sensitivity is likely to have relevance behaviorally but it is unclear at present whether the evoked response of either adults or infants shows evidence of explicit coding of speed or whether it reflects more basic parameters of spatial and temporal displacement. Moreover, changes in speed sensitivity could occur due to development in spatial or temporal resolution or both.

We find that the infant response to modulations of motion coherence is maximal at larger spatial displacements than that of the adults, consistent with Kiorpes and Movshon's behavioral study in the macaque. We also find that the adult response to coherence modulation is speed-tuned at lateral electrodes. Local motion sensitivity, on the other hand is adult-like in terms of its spatio-temporal tuning. Together our results suggest that the first stages of local motion extraction are relatively mature by 4–6 months, but that significant immaturities are present in the mechanisms, which we presume to lie primarily in extra-striate cortex, that encode the global organization of the local motion vectors.

2. Methods

2.1. Observers

A total of 36 healthy full-term infants between 17–24 weeks of age (mean age: 21 weeks ± 2.3 weeks) and 14 adults with normal or corrected to normal vision between 17 and 53 years of age (mean age: 34 years ± 11 years) participated. The research protocol was approved by the Institutional Review Board of the California Pacific Medical Center and conformed to the tenets of the Declaration of Helsinki. Written informed consent was obtained from the parents of the infants and the adult observers after the VEP recording procedure was explained.

2.2. Stimuli and apparatus

The participants viewed random-dot kinematograms displayed on a color CRT monitor running in monochrome mode (640 × 480 pixel resolution, 120 Hz refresh rate). The active display area was 24° in diameter at a 70 cm viewing distance for both adults and infants. The random-dot kinematograms were composed of 12.4′ white dots (105 cd/m^2) on a black background (5 cd/m^2). Dot density was 10% of the screen area (3 dots/deg). A small fixation mark was presented in the center of the display.

The display alternated between circular coherent motion and incoherent motion at 0.83 Hz, with the direction of coherent motion alternating, e.g., 0.6 s of clockwise motion followed by 0.6 s of random motion, followed by 0.6 s of counter-clockwise motion followed by 0.6 s or random motion, etc. in order to reduce the effects of motion adaptation (see Fig. 1). A full stimulus cycle thus lasted 2.4 s, but the data were averaged across the two directions of motion to yield a single 0.83 Hz cycle of coherent/incoherent alternation. Five stimulus cycles were shown one after the other in a trial lasting 12 s. All dots of both the random and coherent motion displays were updated at 15, 20 or 30 Hz and remained stationary for periods equal to the reciprocal of the update rate. Each dot was displaced by a fixed distance in a given block of trials.

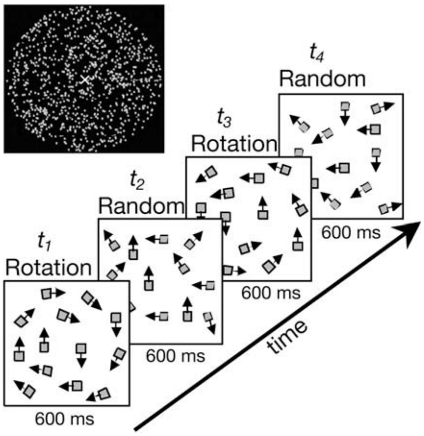

Fig. 1. Schematic illustration of the stimuli. A random-dot kinematogram was used. A full cycle of the stimulus consisted of 0.6 s of circular coherent motion (clockwise) followed by 0.6 s of incoherent motion, followed by 0.6 s of anticlockwise motion, followed by 0.6 s of incoherent motion. The position of individual dots was shifted over a fixed spatial displacement at each temporal update in both coherent and incoherent phases of the display. VEP responses were measured over a wide range of dot displacements (Δx) at three dot-update frequencies ($1/\Delta t$'s of 15, 20 and 30 Hz).