Development of visual-evoked potentials to radially modulated concentric patterns

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The visual processing of radially modulated concentric patterns was studied in human participants, aged 3–22 years, by recording event-related potentials. These stimuli are known to activate the fusiform face area as well as area V4 in normal adults. The electrophysiological data showed a P1 latency that reached a maturation asymptote before 3 years of age, whereas that of N1 and P2 became adultlike by 13 years of age. In addition, the distribution of the P2 component over the scalp was focalized in the primary visual cortex before adolescence and became distributed over the entire brain after adolescence. Radially modulated concentric stimuli thus induce brain activation that is not mature until 13 years of age. *NeuroReport* 16:1753–1756 © 2005 Lippincott Williams & Wilkins.

Keywords: brain development, radially modulated concentric pattern, visual-evoked potentials, visual maturation

Introduction

Using functional magnetic resonance imaging, Wilkinson and colleagues [1] have demonstrated that a continuously changing radially modulated concentric visual pattern (Fig. 1 is similar to their extreme frames) activates area V4 and the fusiform gyrus in adults when compared, for example, with rotating sinusoidal gratings. This finding is consistent with previous psychophysical [2] and physiological [3] data indicating that analysis of concentric and radial structures represents an important aspect of processing at intermediate levels of form vision. Neurophysiological and lesion experiments in monkeys have also shown that, in addition to color, area V4 processes intermediate-level shape information, such as curvature [4].

Such radially modulated patterns are thus complex stimuli inasmuch as they recruit different higher-order brain systems for their analyses. They are also simple as they have well-understood low-level visual properties and are defined by a mere quadruplet of parameters (i.e. average cycles per degree (c/deg), standard deviation of cycles per degree, number of bumps and phase of bumps). These stimuli offer the possibility of studying complex visual processing without sacrificing rigor.

As functional and structural plasticity largely depends on 'critical periods', it is important to establish a timeline to understand the effects of visual input and experience on brain organization. Here, we studied the normal electrophysiological development of the processing of radially modulated concentric stimuli from early childhood to adulthood. Electrophysiological studies bearing on simple visual functions carried out by ourselves [5] and others [6,7] have indicated that, by the age of 5 years, children are essentially adultlike. On the basis of electrophysiological studies on the development of color ([8], but see [9]) and of face processing [10], however, we expected a relatively late maturation of the brain mechanisms responsible for the processing of radially modulated stimuli.

Materials and methods

Fifty-three participants, ranging in age from 3 to 22 years, took part in the experiment. They were healthy and had normal or corrected-to-normal vision. The experiment was conducted with the understanding and the written consent of each participant or their guardian when under the age of 18 years, and the local ethics committee formally approved the experiment.

Participants passively viewed a high contrast sinusoidal concentric grating (0.8 c/deg), subtending a stimulation field of 10 deg^2, with a duration of 500 ms immediately, followed by a similar radially modulated grating with a duration of 500 ms (see Fig. 1). More specifically the radially, modulated pattern comprised five bumps and had an average concentric periodicity of 0.8 c/deg with a standard deviation of 0.071 c/deg. The successive presentations of these two images induce transformational apparent motion. Transformational apparent motion occurs when one shape is suddenly replaced by a different overlapping shape, such that the former appears to undergo a smooth transformation into the latter [11].

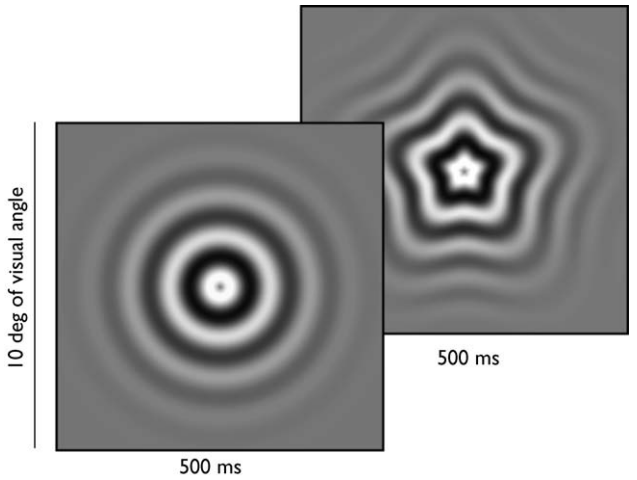

Fig. 1 High contrast (80%) sinusoidal concentric grating (0.8 c/deg), subtending 10 deg^2, followed 500 ms after onset, by a similar radially modulated grating.

The stimuli were presented 100 times while an electroencephalogram was recorded. Potentials were recorded from 40 scalp electrodes (10–20 system), referenced to linked earlobes. An electrode between Fz and Cz was used as ground. The sample rate was 1000 Hz. We epoched trials with a window beginning at −100 ms and finishing at 500 ms relative to stimulus onset. Each epoch was averaged and corrected for eye blinks and those with artifacts above 150 μV were discarded. Visual-evoked potentials were averaged from at least 50 trials for each participant. These averaged waveforms were digitally low passed with a cutoff at 30 Hz.

Nine of the participants (aged 5–13 years) did the experiment twice, with a 1-year interval. We expected them to show the trend observed transversally in the 53 participants. Finally, we ran a control experiment with a pattern-reversal grating (0.8 c/deg) on half of the participants.

Results

We first report waveforms from electrode Oz (Fig. 2a and b), because they best illustrate the brain response to our visual stimulation. It has been demonstrated that the amount of activity in the striate cortex (V1) is a good predictor of human awareness to visual motion [12]. As V1 receives back projections from all the extrastriate visual areas, the data gathered at occipital electrodes might reflect higher-order visual activity, especially in components that appear about 150 ms after stimulus onset [13,14].

We used these data to divide participants into six groups approximately of equal size (Fig. 2a). Five age groups were first created by maximizing within-group similarity (Pearson correlation) and minimizing between-group similarity. Within-group similarity was high in all groups except the 11 to 13-year-olds. Cluster analysis was then employed to segregate the waveforms of this critical age group into two homogeneous averages (dashed black lines). The average waveform of participants in one of these two subgroups (long-dashed line) is strikingly similar to that of the 14 to 18-year-old group (green line) and that of adults (blue line).

For each waveform, we computed the latencies of the first three major maxima (P1, N1 and P2) at electrode Oz. These three main components were present in all individual waveforms. All individual components were plotted against age and latency in Fig. 2b (circles, P1; squares, N1 and diamonds, P2). The P1 latencies were remarkably stable across ages (and we showed elsewhere that they are similar as early as 4–6 months postnatally [15]), whereas those of N1 and P2 steadily decrease. The solid gray curves superimposed on the data points are the best linear fits to the logarithm of age.

Nine participants were retested after a period of 1 year (see pairs of points connected by a solid red line in Fig. 2b). As in the transversal data, most exhibited a reduction in the latencies of the components ($P < 0.01$), and the amplitude of this reduction was greatest for the N1 and P2 components ($P < 0.01$).

We have reported the results from only the Oz electrode. The most interesting electrophysiological components, P2 and, to a lesser extent, N1, however, were present at all electrodes usually postulated to be important for this type of stimuli (T5, T6, O1, O2). The brain activity distribution in the six groups is represented in Fig. 3. These cartographic pictures show the brain activation of each group when the waveform reaches the maximal amplitude (maxima ±4 ms) for the three components (P1, N1 and P2). It is clear that P1 is stable across age in terms of both cortical distribution and latency. The cortical distribution of N1 is relatively unchanging across age; it tentatively becomes more anterior in the older participants. Most interestingly, P2 appears to be focalized in posterior areas, possibly the primary visual cortex (V1), before adolescence, and becomes distributed over the entire brain after adolescence.

The results in the control condition with a pattern-reversal grating replicated the results of others (e.g. [5,16,17]). Participants were essentially adultlike by the age of 5 years.

Discussion

The data resulting from this experiment suggest that maturation for concentric radially modulated pattern processing is attained at about 13 years of age. More specifically, between 11 and 13 years of age, the latencies of the N1 and P2 components reached an asymptote. In contrast, responses related to control gratings in the same participants were adultlike at 5 years of age.

The amplitudes follow a similar developmental trend. Reductions in overall amplitudes with age were observed for all three visual-evoked potential components, as has been demonstrated in previous studies ([9], for instance). These large-scale developmental changes may be driven, in part, by factors such as skull growth and myelination, as well as by perceptual and cognitive development.

The responses related to concentric radially modulated stimuli probably come from different brain structures, especially those implicated in the ventral system, including the neuronal population located in V4. The redistribution of visual processing to different higher-order-sensory and associative areas indeed suggests a more integrated and complex analysis of the visual signal.

A similarly late development of the ventral visual-stream function in humans was observed psychophysically in at least one experiment [18]. Participants between 5 and 30 years of age were asked to identify the location of collinearly

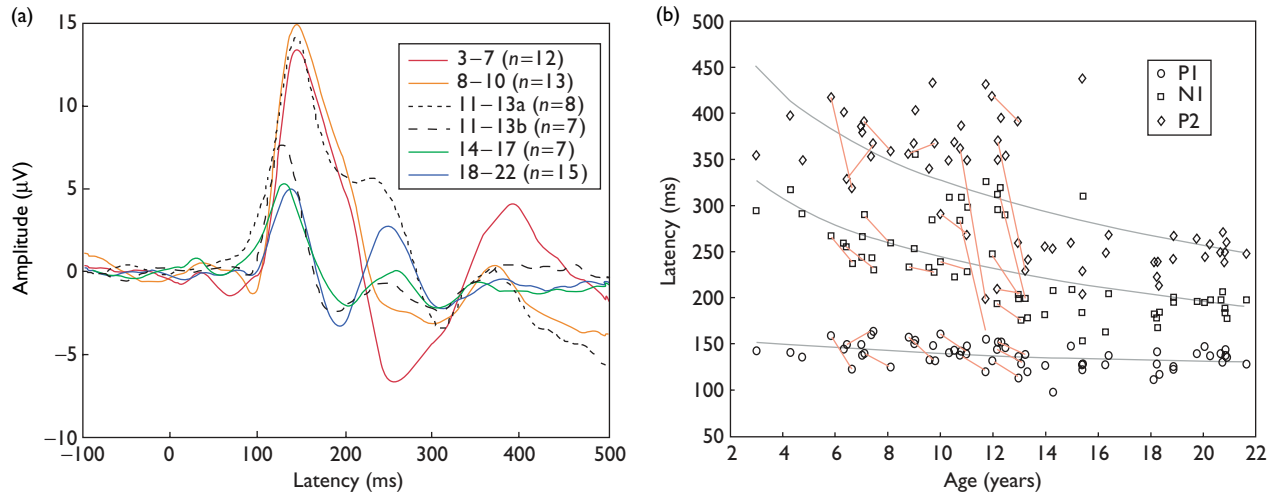

Fig. 2 (a) Average waveforms (μV) of the four age groups shown to be homogeneous (average Pearson r_{3-7}=0.63, r_{8-10}=0.64, r_{14-18}=0.60 and r_{18-22} =0.70). Fuzzy c-means cluster analysis was used to segregate the more heterogeneous waveforms (average Pearson r_{11-13}=0.53) of a fifth age group – the 11 to 13-year-olds – into two homogeneous sets of waveforms (r_{11-13a}=0.69 and r_{11-13b}=0.68); averages of these sets are displayed. (b) Latencies of the first three major components extracted from the waveforms of all 53 participants plotted as a function of age (in years). The solid lines superimposed on the data points are the best linear fits to the logarithm of age (r^2_{P1}=0.87; r^2_{N1}=0.64; and r^2_{P2}=0.61). The solid red lines connecting pairs of data points represent results obtained from the same participants taken 1 year apart.

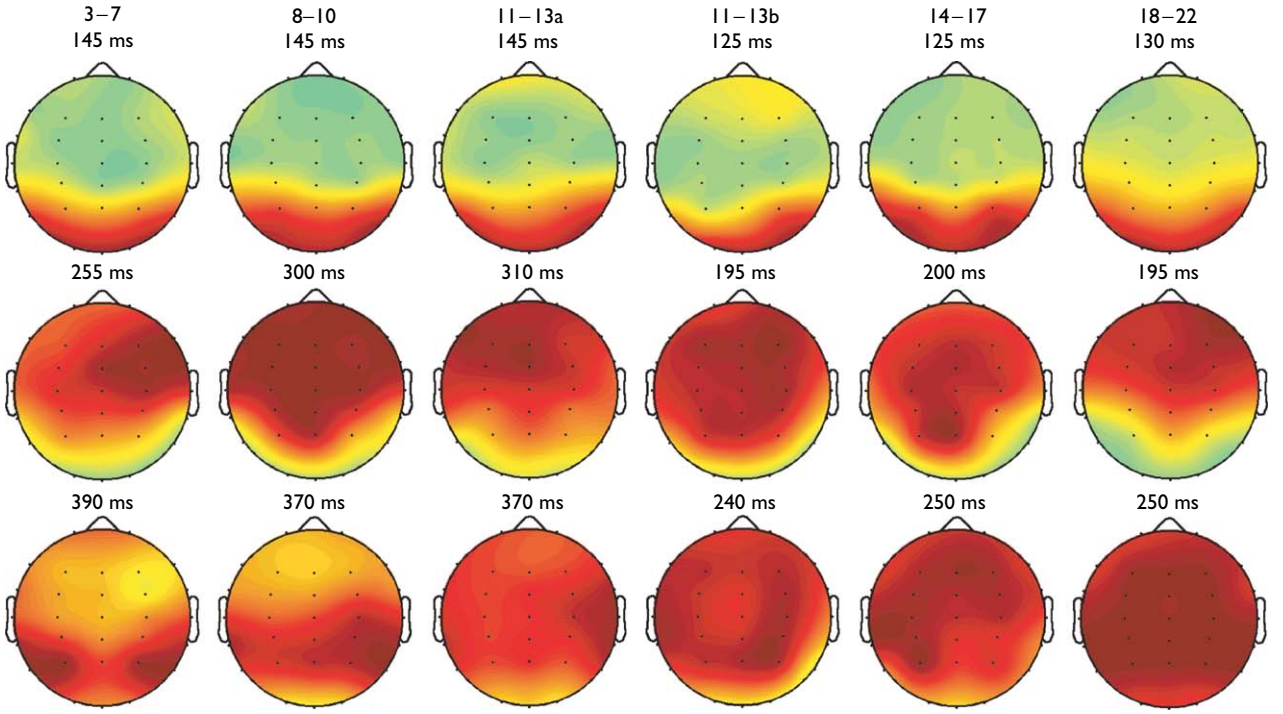

Fig. 3 Topographic maps at the maximum amplitude of the P1 (top row), N1 (middle row) and P2 (bottom row) for the six groups. We normalized within electrodes instead of normalizing between electrodes in order to clearly demonstrate the polarization of each electrode relative to its own signal.

aligned Gabor patches against a background of randomly oriented and positioned Gabor patches. A significant improvement in performance was observed between 5 and 14 years of age.

The results are in accordance with previous anatomical findings as well. It has been shown that the number of synapses in the primary visual cortex peaks between 8 months and 2 years of age, and then decreases until it reaches an asymptote around 11 years of age [19]. In visual associative areas, synaptic pruning extends to early adulthood [20]. Similarly, myelinization continues into early adulthood, with the longest period of myelinization occurring in the frontal and higher-order brain regions [21,22].

Finally, magnetic resonance imaging [23] and functional magnetic resonance imaging [24] investigations have demonstrated a functional maturation sequence that begins with the primary sensory cortex and terminates with the

superior temporal cortex, which contains associative areas that integrate information from several sensory modalities. Maturation of these higher-order brain regions seems to reach an asymptote during adolescence, years after changes in the primary visual cortex, which occur during infancy.

Conclusion

The present study demonstrated late brain maturation in the processing of concentric radially modulated patterns. The continuity in the changes occurring until about 13 years of age suggests snapshots of a unique mechanism taken at different stages of maturation rather than pictures of altogether different mechanisms.

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