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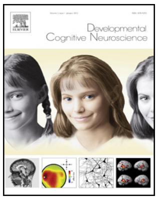

Averaging, not internal noise, limits the development of coherent motion processing

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ABSTRACT

The development of motion processing is a critical part of visual development, allowing children to interact with moving objects and navigate within a dynamic environment. However, global motion processing, which requires pooling motion information across space, develops late, reaching adult-like levels only by mid-to-late childhood. The reasons underlying this protracted development are not yet fully understood. In this study, we sought to determine whether the development of motion coherence sensitivity is limited by internal noise (i.e., imprecision in estimating the directions of individual elements) and/or global pooling across local estimates. To this end, we presented equivalent noise direction discrimination tasks and motion coherence tasks at both slow (1.5°/s) and fast (6°/s) speeds to children aged 5, 7, 9 and 11 years, and adults. We show that, as children get older, their levels of internal noise reduce, and they are able to average across more local motion estimates. Regression analyses indicated, however, that age-related improvements in coherent motion perception are driven solely by improvements in averaging and not by reductions in internal noise. Our results suggest that the development of coherent motion sensitivity is primarily limited by developmental changes within brain regions involved in integrating motion signals (e.g., MT/V5).

1. Introduction

The processing of motion is a critical part of visual development, allowing children to track moving objects with their eyes, to reach for and grasp objects that are in motion, and to navigate within a dynamic world. Motion processing contributes to a range of elementary visual functions including the segmentation of scenes into different objects and surfaces, the perception of depth, the registration of trajectories and the identification of objects. Often, it is important to combine motion information across space, for example in order to determine the overall direction of a flock of birds, each of which will be following a different motion trajectory. This ability – termed *global motion processing* – is typically tested experimentally using the motion coherence paradigm (Newsome and Paré, 1988), which requires observers to judge the direction of coherently moving dots in the presence of randomly moving noise dots.

Given the importance of motion processing in visual development, it is perhaps unsurprising that some aspects of motion processing (e.g., directional selectivity) develop

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early in life (Wattam-Bell, 1991, 1992; see Braddick et al., 2003, for review). However, other types of visual motion processing follow a protracted development and only reach adult-like levels by mid-to-late childhood. For example, the minimum speed required to support perception of motion-defined form and the maximum displacement supporting perception of movement mature by around 7–8 years (Hayward et al., 2011; Parrish et al., 2005), motion coherence thresholds reach adult-like levels between 10 and 14 years (Gunn et al., 2002; Hadad et al., 2011) and speed discrimination abilities are not yet fully adult-like by 11 years (Manning et al., 2012). Such motion processing abilities rely primarily on the dorsal pathway (Milner and Goodale, 1995), which originates from motion-sensitive neurons in area V1, and projects to extrastriate areas including MT/V5. While neurons in V1 can signal the presence of local motion (Hubel and Wiesel, 1962), neurons in V5 play a key role in global motion processing, as they have larger receptive fields capable of integrating inputs from V1 (Mikami et al., 1986).

Adult studies of visual motion processing suggest the existence of at least two distinct systems tuned to different ranges of speed (Burr et al., 1998; Edwards et al., 1998; Thompson et al., 2006; also see review by Burr and Thompson, 2011), which may follow different developmental trajectories in the maturing brain. Hayward et al. (2011) reported greater immaturity in sensitivity to coherent motion at the slowest speed tested (0.1°/s) compared to faster speeds of 0.9 and 5°/s. Also, in a speed discrimination task, Manning et al. (2012) reported a more gradual development of thresholds for slow (1.5°/s) than fast (6°/s) speeds. However, Hadad et al. (2011) did not find different rates of development for motion coherence thresholds measured with random dot stimuli moving at 4°/s and 18°/s. Together, this research suggests that motion processing for intermediate and fast speeds may follow similar rates of development, but that processing of much slower speeds (e.g., 0.1 and 1.5°/s) may develop more slowly.

Global motion processing abilities in childhood are generally thought to be limited by poor integration of local motion cues over space (e.g., Ahmed et al., 2005; Hadad et al., 2011; Manning et al., 2012). Such integration is believed to occur in higher-order areas of the motion processing hierarchy, such as in area MT/V5 (Born and Tootell, 1992; Britten et al., 1992). Yet performance on tasks traditionally used to assess global motion processing (i.e., motion coherence paradigms; Newsome and Paré, 1988) is not limited *solely* by global integration. Such tasks are likely limited not only by an observer's ability to globally pool the motion of individual dots across space, but also by their ability to estimate the local motion direction of each dot (Barlow and Tripathy, 1997), and by their ability to segment the signal dots from the masking noise (Dakin et al., 2005; Tibber et al., 2014; Webster et al., 2011).

Increased neural variability would lead to imprecision in estimating individual dot directions, which, when pooled, could lead to elevated motion coherence thresholds. This neural variability has been termed 'internal noise', and has many potential sources, including photon noise, variability in the firing of action potentials, and variability in synaptic transmission (Faisal et al., 2008). Through development, neurons in area V1 undergo extensive synaptic pruning (Garey and de Courten, 1983; Huttenlocher et al., 1982; Huttenlocher and de Courten, 1987), and the bandwidths of direction-selective cells reduce with age (at least in the primate brain, Hatta et al., 1998). It is possible that such developmental changes might be manifest as reduced internal noise with age.

The traditional motion coherence paradigm cannot distinguish between local and global limits to motion perception and has hence obscured our understanding of what limits global motion processing during development (and in a variety of neurodevelopmental disorders; Dakin and Frith, 2005). To address this issue, the current study used the equivalent noise paradigm (Barlow, 1956; Pelli, 1990) to determine whether local or global processing limits motion coherence sensitivity in development. The equivalent noise paradigm is based on comparing human performance to that of an ideal observer that is limited both by additive internal noise and by how completely it samples the information available from the stimulus (Pelli, 1990). When equivalent noise analysis is applied to direction discrimination (Dakin et al., 2005), *internal noise* maps onto the precision with which individual motion directions are estimated and *sampling* represents an estimate of the effective number of local motion directions that are globally pooled (or averaged). Whereas motion coherence stimuli contain both signal dots and randomly moving noise dots, equivalent noise stimuli contain dots whose directions (on any one trial) are sampled from a single Gaussian distribution (Dakin et al., 2005). The standard deviation of this distribution is varied across conditions, in order to manipulate the level of stimulus variability (or 'external noise'; see Fig. 1A).

In the equivalent noise task, the observer is asked to discriminate the mean direction of dots, and the performance measure is the smallest difference in direction from a fixed reference direction (e.g., upwards) that observers can reliably report. With no directional variance (i.e., when the standard deviation is 0° and all elements move in the same direction), the observer's performance is limited both by internal noise and sampling. Consequently, small amounts of extra external noise have little effect on thresholds, as it is swamped by the observer's own internal noise. However, as the level of external noise is increased, a point is reached where the external noise exceeds the internal noise inherent in the system, and thresholds start to increase with the addition of further external noise. An equivalent noise function can be fit to these data to derive estimates of the individual's internal noise and sampling (see Fig. 1A).

As thresholds are measured across a range of external noise levels, the equivalent noise method typically requires several thousand trials, making it unsuitable for investigating the visual abilities of children, who may get bored and become inattentive. However, a more efficient equivalent noise procedure has been developed, which provides reliable estimates of internal noise and sampling in fewer than 100 trials (Tibber et al., 2014). In this novel method, two highly informative points on the equivalent noise function are probed (see grey line, Fig. 1B). In one condition