

Neuroplasticity as a Double-edged Sword: Deaf Enhancements and Dyslexic Deficits in Motion Processing

Courtney Stevens and Helen Neville

Abstract

■ We examined the hypothesis that aspects of processing that are most modifiable by experience (i.e., “plastic”) display the most vulnerability in developmental disorders and the most compensatory enhancement after sensory deprivation. A large literature reports that motion processing and magnocellular visual function is selectively deficient in dyslexia. A smaller literature reports enhancements in such functions in deaf individuals. However, studies with dyslexic and deaf individuals have used different experimental paradigms to assess visual function, and no research has yet examined both sides of modifiability (i.e., enhancements and deficits) using the same experimental paradigm. In the present research, visual function was compared in dyslexic ($n = 15$), deaf ($n = 17$), and

control adults by using automated peripheral kinetic and foveal static perimetry. In the kinetic perimetry task, the dyslexic group showed deficits ($p < .003$), whereas the deaf group showed enhancements ($p < .001$) for detecting moving light points in the periphery. In the foveal static perimetry task, neither the dyslexic ($p = .866$) nor the deaf ($p = .632$) group differed significantly from controls in foveal contrast sensitivity thresholds, and no group or individual approached ceiling performance on this task. Taken together, the present data bridge previous literatures and suggest that motion processing tasks are selectively modifiable, either to decrement or enhancement, whereas foveal contrast sensitivity does not differ in dyslexic or deaf groups. ■

INTRODUCTION

In principle, a neural system that is dependent on and modifiable by experience—that is, “plastic”—might be both more vulnerable and more enhanceable compared to a system that is more strongly determined in development. Very little evidence exists on this point. Here we provide evidence on the two sides (or double-edged sword) of neuroplasticity.

Studies of many atypically developing populations indicate that certain aspects of visual processing are altered. For example, motion processing has been shown to be deficient among individuals with dyslexia, autism, or Turner or Williams syndrome (Braddick, Atkinson, & Wattam-Bell, 2003; Spencer et al., 2000; Talcott, Hansen, Assoku, & Stein, 2000; Witton et al., 1998; Atkinson, 1992). By contrast, motion processing is enhanced among congenitally deaf individuals (Bavelier, Tomann, et al., 2000; Neville & Lawson, 1987a). The enhancements and deficits that have been observed do not span the entire visual system, but rather reflect selective modifiability of *subsystems* within vision. Interestingly, whereas the literatures describing selective enhancements and deficits in vision have identified both

a common subset of modifiable visual functions and a common theoretical framework for describing that selectivity, the two literatures have developed largely in parallel, with little cross-referencing between the two. The overarching goal of the present research is to bridge these two literatures by comparing both sides of neural modifiability (i.e., enhancements and deficits) within the same experimental paradigm.

Selective deficits in visual functions have been reported among individuals with developmental disorders including dyslexia, Williams syndrome, Turner syndrome, and autism (Braddick et al., 2003; Spencer et al., 2000; Talcott et al., 2000; Atkinson, 1992). Although each of these developmental disorders has a unique genetic etiology and set of primary markers (e.g., a phonological deficit in dyslexia), there is strong evidence to suggest that at least a subset of individuals with these developmental pathologies also show deficits in certain visual functions.

Studies of both adults and children with dyslexia provide the most extensive evidence for a selective deficit in visual function. Behaviorally, dyslexic individuals show lower sensitivity to detecting coherent motion in random-dot kinetograms (Hansen, Stein, Orde, Winter, & Talcott, 2001; Talcott et al., 2000; Everatt, Bradshaw, & Hibbard, 1999; Cornelissen, Richardson, Mason, Fowler, & Stein, 1995) despite showing normal thresholds for

detecting coherent form in similar arrays of static line segments (Hansen et al., 2001; Talcott et al., 2000). Dyslexic individuals also show higher thresholds for detecting changes in the speed of motion flow fields (Demb, Boynton, Best, & Heeger, 1998), as well as higher critical flicker fusion thresholds for monochromatic, but not isoluminant color, stimuli (Sperling, Lu, Manis, & Seidenberg, 2003). In addition, a wide and somewhat controversial literature indicates that dyslexic individuals show deficits in pattern contrast sensitivity for high-contrast, low-spatial-frequency gratings (Lovegrove, Martin, & Slaghuis, 1986). The behavioral evidence for a visual deficit in dyslexia has been corroborated by recent neuroimaging studies showing decreased (Demb et al., 1998) or even nonsignificant (Eden et al., 1996) activations in motion-sensitive areas (MT/MST) of dyslexic individuals when viewing motion stimuli, although no activation differences are observed when viewing stationary patterns (Eden et al., 1996).

Interestingly, a parallel literature on cross-modal plasticity indicates that congenitally deaf adults show *enhancements* in a remarkably similar subset of visual functions. Behaviorally, deaf individuals are faster and more accurate than hearing individuals at detecting the direction of motion of selectively attended stimuli presented in the peripheral, but not central, visual field (Neville & Lawson, 1987a, 1987b). Deaf individuals also tend to be more accurate at identifying simple geometric shapes presented briefly in the peripheral visual fields (Reynolds, 1993). Analyses of event-related brain potential (ERP) and functional magnetic resonance imaging (fMRI) data also suggest selective enhancements in visual processing. Compared to hearing controls, deaf individuals show an increased N1 amplitude to selectively attended stimuli in the peripheral, but not central, visual field (Neville & Lawson, 1987b; Neville, Schmidt, & Kutas, 1983), as well as shifts in the distribution of later ERP components toward the occipital cortex (Neville & Lawson, 1987b). The increased N1 amplitude has also been observed when deaf participants monitor grayscale low-spatial-frequency gratings that appeared to drift transversely, with greater effects observed for peripheral than for central gratings (Armstrong, Neville, Hillyard, & Mitchell, 2002). That same study found no difference between deaf and hearing individuals when they monitored high-spatial-frequency colored gratings that periodically changed color. Recent neuroimaging studies (Bavelier, Brozinsky, et al., 2001; Bavelier, Tomann, et al., 2000) are consistent with the behavioral and electrophysiological data, showing increased activation in motion-sensitive areas (MT/MST) in deaf compared to hearing participants when monitoring motion flow fields to detect velocity changes. As in previous studies, the effects were observed only for peripheral stimuli.

The selective enhancements observed in deaf individuals for stimuli that are of low spatial frequency, peripheral, or in motion have been attributed to the effects of

auditory deprivation rather than use of a manual-spatial language because the same effects are not seen in hearing native signers (e.g., hearing children of deaf parents) (Bosworth & Dobkins, 2002b; Bavelier, Brozinsky, et al., 2001; Neville & Lawson, 1987c). Specifically, it has been suggested that the selective enhancements could be attributed to possible compensatory hypertrophy of the remaining modalities, recruitment of cortical space typically devoted to the missing modality, changes in polysensory or multimodal cortical and subcortical areas, and/or an increased reliance on peripheral vision for perceiving the environment (Neville & Bavelier, 2002).

It is important to acknowledge that the literature on selective visual system modifiability is not without inconsistencies, either in studies of deaf or in studies of dyslexic individuals (Bosworth & Dobkins, 2002a; Johannes, Kussmaul, Münte, & Mangun, 1996; Cornelissen et al., 1995; Bross, 1979). In large part the inconsistencies could reflect differences in participant selection criteria, specific experimental procedures used, and control group matching. For example, research on visual processing in dyslexia defines dyslexic participants by using diverse selection criteria ranging from self-reported difficulty in reading to more formal criteria of IQ/reading ability discrepancies observed at the time of testing. Similarly, some research on cross-modal plasticity in the deaf has included individuals who became deaf at later ages or due to major illness (e.g., meningitis) in which the central nervous system may also have been affected (noted in Neville & Bavelier, 2001b, 2002). In addition, some studies from both literatures are confounded by use of a control sample with a different sex distribution than the research sample, in some cases despite reports in the same study of sex differences in the visual tasks used (Winner et al., 2001). Indeed, studies of sex differences in visual perception indicate that women perform worse than men on visuospatial tasks (Weiss, Kemmler, Deisenhammer, Fleischhacker, & Delazer, 2003) as well as tasks involving moving stimuli including tests of dynamic visual acuity (Millslagle, 2004), perceived trajectory judgments (Kaiser, Proffitt, & Anderson, 1985), and, for older women, coherent motion detection (Gilmore, Wenk, Naylor, & Stuve, 1992).

Perhaps most importantly, studies with dyslexic participants are particularly vulnerable to confounds due to the high comorbidity of dyslexia with other developmental disorders, most notably attention deficit hyperactivity disorder (American Psychiatric Association, 2000). It is troubling that despite this known comorbidity, few studies on visual deficits in dyslexia report whether the dyslexic or control participants had clinical attention deficits or took psychoactive medications (e.g., ritalin), which may affect response times, cerebral blood flow (i.e., fMRI activation patterns), neuronal timing (i.e., ERP latencies), and overall performance in the visual tasks assessed. One computer simulation (Stuart, McAnally, & Castles, 2001) of generalized and

sporadic inattention suggests that discrepant findings in contrast sensitivity studies with dyslexics could be related to unmeasured attention deficits in the dyslexic samples.

Finally, experiential factors, including video game use (Green & Bavelier, 2003) and sports participation (Berg & Killian, 1995), are related to enhanced visual perception and attention. However, no study of visual differences in deaf or dyslexic participants has examined or controlled for these possible sources of bias. Taken together, these limitations underscore the importance of careful subject selection of research groups and well-matched control groups for any comparisons made.

Theoretical Framework

A common theoretical framework has been invoked by studies of both deaf and dyslexic individuals to explain the selectivity of the visual system modifiability observed. Specifically, both literatures have suggested that visual functions that show modifiability map onto the magnocellular pathway, the dorsal visual pathway, or both, whereas those aspects of visual processing that appear stable across populations map onto the parvocellular pathway, the ventral visual pathway, or both. Distinctions between these main processing pathways have been supported by several lines of anatomical, physiological, and behavioral evidence, with differentiation of the two pathways beginning in the retinal ganglion cells and lateral geniculate nucleus (LGN) and continuing, although to a lesser extent, at the cortical level (Yabuta & Callaway, 1998; Sawatari & Callaway, 1996; Ungerleider & Haxby, 1994; Zeki et al., 1991; Deyoe & Van Essen, 1988; Livingstone & Hubel, 1988).

The dorsal pathway, which projects from V1 to the parietal lobe and includes extrastriate areas including MT and MST, receives input primarily from magnocellular layers of the LGN, whereas the ventral pathway, which projects from V1 toward the temporal lobe, receives input from both magnocellular and parvocellular layers of the LGN (Yabuta & Callaway, 1998; Ungerleider & Haxby, 1994; Merigan & Maunsell, 1993; Livingstone & Hubel, 1988). Although there is overlap and interconnectivity of the two processing streams, particularly in extrastriate regions, the two pathways are specialized for different types of visual processing. For example, M cells and cortical areas associated with the dorsal pathway are primarily implicated in processing of stimuli that are peripheral, of low spatial frequency, in motion, or require faster transmission velocities. By contrast, P cells and ventral pathway regions are primarily implicated in the processing and analysis of fine detail, including color, form, texture, and central visual field stimuli (Bavelier, Brozinsky, et al., 2001; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1999; Ungerleider & Haxby, 1994; Baizer, Ungerleider, & Desimone, 1991; Zeki et al., 1991; Merigan & Maunsell, 1990; Schiller,

Logothetis, & Charles, 1990; Merigan, 1989; Livingstone & Hubel, 1988; Schiller & Malpeli, 1978).

Within the literature on deficits in dyslexia, this explanation has been formalized as the magnocellular deficit hypothesis (Stein & Talcott, 1999), which suggests that deficits in magnocellular pathways in the visual and auditory systems may make it difficult for children to process the rapid formant transitions that distinguish different speech sounds. In support of this hypothesis, postmortem autopsies suggest that among dyslexic individuals, magnocells in the LGN are smaller and more disorganized than in controls, although no abnormalities are observed in the parvocellular layers of the LGN in dyslexic individuals (Livingstone, Rosen, Drislane, & Galaburda, 1991). Similarly, abnormalities have also been observed in the magnocells in the medial geniculate nucleus of dyslexic individuals (Galaburda, Menard, & Rosen, 1994). Within the literature on enhancements in the deaf, the hypothesis also has been considered, with emphasis placed on the possibly greater modifiability within the cortical dorsal processing stream, including motion processing areas MT/MST (Bavelier & Neville, 2002; Neville & Bavelier, 2001a).

Limitations of Previous Work

Despite the striking similarity in both the visual functions showing modifiability and the theoretical accounts reported in the literature on deafness and dyslexia, the two literatures have developed largely in parallel, with little cross-referencing between the two. Furthermore, each literature has used a unique set of paradigms to assess visual function, making post hoc comparisons difficult. Although it is tempting to compare across the two literatures, more direct evidence for the comparability of the enhancements and deficits observed is needed. Such evidence would be important in determining whether the enhancements and deficits observed in previous studies may reflect two sides (i.e., enhancements and deficits) of the same phenomenon, for example, selective magnocellular and/or dorsal pathway modifiability. To the extent that the two literatures do describe a common phenomenon, bridging the literatures should provide a first step toward synthesizing the data on selective visual enhancements and deficits and, more generally, understanding the conditions that confer more or less neuroplasticity on neural systems and subsystems. Similarly, to the extent that the two literatures do *not* describe a common phenomenon, bridging the literatures should be useful in understanding how different underlying mechanisms can give rise to similar profiles of selective modifiability.

A separate issue concerns the selection of specific paradigms to measure visual processing. Although only a subset of visual functions show modifiability between groups, previous paradigms have been criticized on the grounds that the tasks used are confounded by

differences in attentional or cognitive demands. Specifically, tasks that have shown group differences, which are often labeled as dorsal or M pathway tasks, typically are more complex compared to tasks in which no group differences emerge and participants perform at or near ceiling levels (Neville & Lawson, 1987b). As such, it is possible that any differences previously observed in dorsal or M pathway tasks reflect more general cognitive or attentional differences between groups, rather a selective visual difference per se. Alternatively, it is possible that the visual differences observed in special populations are not specific to the dorsal pathway tasks, but simply have not been detected in other tasks because all groups are performing at or near ceiling level.

Recent evidence has partially addressed this criticism by creating tasks to assess the M and P pathways that use identical task structure. One study recorded ERPs while deaf and hearing adults monitored visual gratings designed to activate either the magnocellular or parvocellular layers of the LGN. In this study, despite identical task structure, group differences in the N1 were observed only for the gratings designed to activate the magnocellular layers of the LGN (Armstrong et al., 2002). Similarly, a recent study (Sperling et al., 2003) of dyslexic individuals assessed the flicker threshold for detecting “phantom contours” created by alternating dot images defined with either black and white dots (designed to activate the magnocellular system) or isoluminant red and green dots (designed to activate the parvocellular system). Compared to controls, the dyslexic individuals showed deficits only in the magnocellular version of the task.

These studies provide valuable evidence that the group differences previously observed are not artifacts of the different task structure used, but instead reflect a selective modifiability of magnocellular and/or dorsal pathway processing. However, the studies do not address the most controversial class of evidence from previous studies. Specifically, it is the complexity of *motion processing* tasks in previous studies, which require global processing or two-alternative forced-choice decisions, that have been the most widely criticized. Further studies using less complex motion detection tasks will help clarify whether the selective modifiability observed in motion processing tasks could be attributed to more general aspects of motion processing paradigms (e.g., attention). In addition, a more difficult task of central visual field processing, in which no group or individual performs at ceiling level, could provide a stronger test of whether group differences are present in a central visual field task.

Overview of the Current Study

The present research included three main goals. The first goal was to test motion processing in deaf and dyslexic adults by using a simple detection paradigm. A

second goal was to test central visual field processing in deaf and dyslexic adults by using a more difficult task in which no group or individual approaches ceiling performance. The third, overarching goal was to bridge the two sizable literatures on selective visual system differences among deaf and dyslexic individuals in order to better understand the conditions that give rise to selective modifiability of neural systems and subsystems.

To address these three goals, groups of deaf ($n = 17$) and dyslexic ($n = 15$) adults were compared to matched controls on tasks designed to assess motion processing and central visual field contrast sensitivity. A Zeiss-Humphrey Field Analyzer (HFA) was used to collect standard automated peripheral kinetic and static visual perimetry data, which are both simple detection tasks. The HFA contains a spherical testing bowl that allows presentation of static or moving light stimuli across the entire monocular visual field, extending over 60° in the azimuth and vertical dimensions. In the kinetic perimetry task, participants pressed a button upon detecting a small, white light moving from any direction in the periphery toward the center of vision. In accord with the previous literature, it was predicted that the deaf would perform better (i.e., detect the points of light sooner) and the dyslexic group would perform worse (i.e., detect the points of light later) relative to matched controls. In the static perimetry task, participants pressed a button upon detecting a small point of white light projected briefly in the fovea. Thresholds for contrast sensitivity measured the minimum light brightness required for participants to report seeing the light point 50% of the time. It was predicted that even in a central visual field task in which no group or individual approached ceiling performance, no group differences would be apparent.

RESULTS

Static Perimetry

Prior to data analysis, subjects with excessive fixation losses, false positives, or false negatives as defined by standard testing requirements were removed from analysis. For the deaf versus hearing comparison, four subject pairs were removed, leaving data available from 13 subject pairs. For the dyslexic versus nondyslexic comparison, data from all 15 subject pairs were available for analysis. The control groups matched their respective research samples in terms of age, sex, handedness, familial socioeconomic status (SES), years of education, video game use, and sports participation, as shown in Table 1.

For each group, the mean threshold value was calculated for the fovea by averaging the 20 threshold values output by the perimeter for each subject. Data were analyzed using *t* tests applied separately to the deaf versus hearing and dyslexic versus nondyslexic data.

Table 1. Demographic Characteristics of Participant Groups for Static Perimetry Analysis

	<i>Deaf</i>	<i>Hearing</i>	<i>p</i>	<i>Dyslexic</i>	<i>Nondyslexic</i>	<i>p</i>
<i>n</i>	13	13	–	15	15	–
Age, <i>M (SD)</i> (years)	32.0 (10.0)	32.2 (10.8)	.96	29.1 (11.4)	29.7 (11.4)	.89
Age range (years)	22–48	21–50	–	18–51	18–50	–
No. of women	11	9	.64	6	6	–
No. right-handed	13	13	–	13	13	–
Years of education, <i>M (SD)</i>	14.3 (2.2)	14.8 (1.5)	.54	14.7 (2.4)	14.1 (1.4)	.42
SES, ^a <i>M (SD)</i>	46.0 (9.6)	46.8 (13.7)	.86	55.4 (8.5)	51.4 (12.8)	.28
Video game use, ^b <i>M (SD)</i>	1.2 (2.1)	2.6 (6.0)	.41	1.4 (2.7)	2.0 (3.8)	.54
Sports participation (no. sports played) ^c	4	2	.64	8	6	.46

^aSocioeconomic status (SES) measured by using the Hollingshead Index of Social Status.

^bVideo game use measured in hours per week. There were still no significant differences between groups if video game use was assessed in hours per month or in terms of use/nonuse.

^cSports participation was measured by asking participants whether they regularly played sports (yes/no responses). There were still no significant differences between groups if sports participation was coded as the number of sports participants played.

Dyslexic versus Nondyslexic

There was no significant difference in foveal contrast sensitivity thresholds between the dyslexic and nondyslexic group, $t(14) < 1$, $p = .866$, mean contrast sensitivity for dyslexic group = 33.3 dB ($SE = .25$), mean contrast sensitivity for nondyslexic control group = 33.4 dB ($SE = .34$), as shown in Table 2. No group or individual approached ceiling performance on this task, which would have been a threshold of 51 dB.

Deaf versus Hearing

There was no significant difference in foveal contrast sensitivity thresholds between the deaf and hearing groups, $t(12) < 1$, $p = .632$, mean contrast sensitivity for deaf group = 32.8 dB ($SE = .53$), mean contrast sensitivity for

hearing control group = 33.2 dB ($SE = .40$), as shown in Table 2. No group or individual approached ceiling performance on this task, which would have been a threshold of 51 dB.

Kinetic Perimetry

Prior to data analysis, extreme outliers were identified and removed from each data set separately. This accounted for less than 1% of the total observations. Due to technical error, data were not available from one subject pair in the dyslexic group comparison. The control groups matched their respective research samples in terms of age, gender, handedness, familial SES, years of education, video game use, and sports participation, as shown in Table 3.

Using the remaining data points, we calculated the visible surface area for detecting motion separately for each group by using the formula for spherical triangles, surface area = $R^2[(A + B + C) - \pi]$, where R is the radius of the testing bowl and A , B , and C are the angle measurements of the three vertices projected against the viewing surface, which could be calculated by using the initial angle output by the perimeter (Weisstein, 1999; Harris & Stocker, 1998). This resulted in a set of 14 surface area means for each subject group, one for each of the seven sectors (defined by any two adjacent meridians) at the two brightness levels tested. Analyses conducted on the raw angle measurements output from the perimeter were nearly identical to those reported below.

Data were analyzed by using the SAS Mixed Procedure, which was applied separately to data from the deaf versus hearing and dyslexic versus nondyslexic data sets. The SAS Mixed Procedure is designed to analyze repeated measures data by accounting for the correlation

Table 2. Means and Standard Errors for Static and Kinetic Perimetry Tasks

	<i>Static Perimetry</i> (foveal contrast threshold), mean (SE)	<i>p</i>	<i>Kinetic Perimetry</i> (surface area for detecting motion), mean (SE)	<i>p</i>
Deaf	32.8 (.53)		196 (6.5)	
Deaf control	33.2 (.40)	.632	180 (6.5)	<.001
Dyslexic	33.3 (.25)		192 (6.4)	
Dyslexic control	33.4 (.34)	.866	202 (6.4)	<.003

Static perimetry means measured in decibel attenuation from a maximum light intensity of 10,000 apostils. Kinetic perimetry mean visible sector surface area measured in square centimeters.

Table 3. Demographic Characteristics of Participant Groups for Kinetic Perimetry Analysis

	<i>Deaf</i>	<i>Hearing</i>	<i>p</i>	<i>Dyslexic</i>	<i>Nondyslexic</i>	<i>p</i>
<i>n</i>	17	17	–	14	14	–
Age, <i>M</i> (<i>SD</i>) (years)	32.0 (9.93)	32.12 (10.31)	.97	27.9 (10.7)	28.3 (10.5)	.90
Age range (years)	22–49	21–50	–	18–51	18–50	–
No. of women	13	13	–	6	5	.70
No. right-handed	17	17	–	12	12	–
Years of education, <i>M</i> (<i>SD</i>)	14.06 (2.19)	14.82 (1.67)	.26	14.9 (2.4)	14.1 (1.5)	.75
SES, ^a <i>M</i> (<i>SD</i>)	44.29 (11.64)	43.53 (13.94)	.86	54.6 (8.2)	53.4 (10.5)	.74
Video game use, ^b <i>M</i> (<i>SD</i>)	1.35 (2.5)	3.12 (6.0)	.27	.57 (.5)	.57 (.5)	–
Sports participation (no. sports played) ^c	6	2	.22	8	6	.45

^aSocioeconomic status (SES) measured by using the Hollingshead Index of Social Status.

^bVideo game use measured in hours per week. There were still no significant differences between groups if video game use was assessed in hours per month or in terms of use/nonuse.

^cSports participation was measured by asking participants whether they regularly played sports (yes/no responses). There were still no significant differences between groups if sports participation was coded as the number of sports participants played.

between levels of the within-subject factors. Because it uses a likelihood-based estimation method rather than a method of moments, sums of squares and mean squares are not computed. As such, subject pairs with missing observations on one of the values are not excluded from analysis (Wolfinger & Change, 1995), and reported means represent the expected value at the mean age of participants.

The dependent variable in the model was visible surface area for detecting motion. The independent variables included group (research/control), brightness (15/20 dB), and sector (1–7, each representing a triangular area shown in Figure 1). Age was entered as a covariate in the model.

Dyslexic versus Nondyslexic

As predicted, the dyslexic group had a significantly smaller field of view for detecting motion: main effect of group, $F(1,358) = 9.16, p < .003$ (Figure 2A). The dyslexic group had a mean visible sector surface area of 192 cm^2 ($SE = 6.4$), whereas the nondyslexic control group had a mean visible sector surface area of 202 cm^2 ($SE = 6.4$), as shown in Table 2. However, the main effect of group differed as a function of sector: interaction of group and sector, $F(6,353) = 2.48, p < .023$. Simple effects tests for the effect of group at each sector indicated that the dyslexic group showed smaller fields of view only in two lower visual field sectors: Sector 5, $t(354) = 3.46, p < .001$; Sector 6, $t(354) = 3.26, p = .001$; all other sectors, $p > .4$. In addition, a trend toward a significant interaction between group and brightness, $F(1,353) = 2.89, p < .1$, suggested the smaller field of view for detecting motion observed in the dyslexic group may vary as a function of the stimulus brightness. Simple

effects tests for the effect of group at each brightness indicated that the main effect of group was driven largely by significant differences at the dimmer, 20-dB brightness level, $t(356) = 3.35, p < .001$, rather than the 15-dB brightness level, $t(356) < 1, p = .345$.

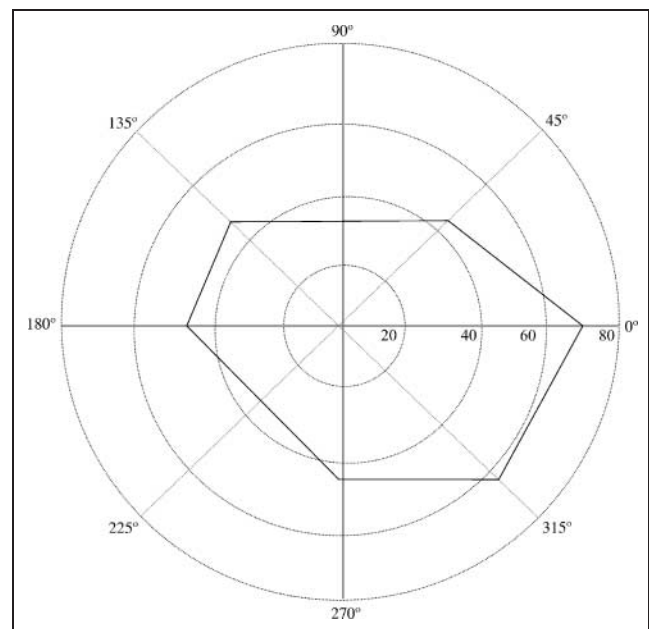


Figure 1. 2-D representation of a peripheral kinetic perimetry isopter. Numbers around the circle's periphery denote the meridians (in degrees) along which moving points of light could travel. Numbers along the horizontal axis indicate the visual angle (in degrees) for positions along each concentric ring. Sectors were numbered counterclockwise around the meridian beginning with Sector 1 from 0° to 45°, Sector 2 from 45° to 90°, and so forth. Sector 5 ranged from 180° to 270° because the lower nasal meridian was not tested.

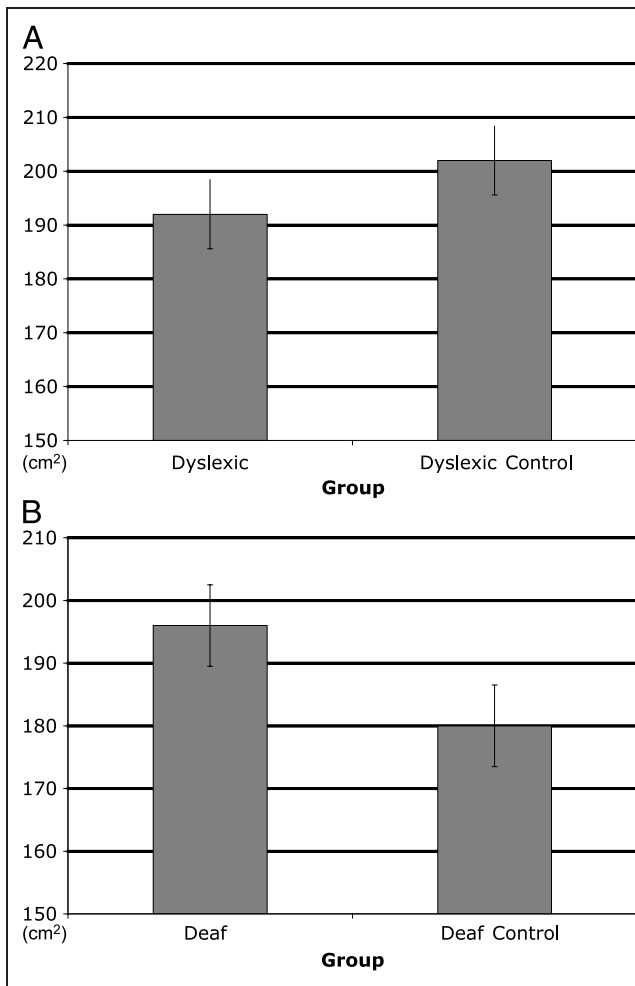


Figure 2. Mean visible sector surface area for detecting motion. (A) Dyslexic versus nondyslexic group. (B) Deaf versus hearing group.

Across both groups, visible surface area was larger for the brighter, 15-dB stimuli, compared to the 20-dB stimuli: main effect of brightness, $F(1,353) = 964.31$, $p < .001$. Across both groups, there was also a significant effect of sector: main effect of sector, $F(6,353) = 240.41$, $p < .001$, reflecting that temporal sectors had larger areas than more nasal sectors. In addition, there was a significant interaction between sector and brightness, $F(6,353) = 20.48$, $p < .001$, reflecting the larger decrease in surface area for more temporal compared to nasal sectors as stimuli brightness decreased.

Deaf versus Hearing

As predicted, the deaf group had a significantly larger field of view for detecting motion: main effect of group, $F(1,440) = 17.41$, $p < .001$ (Figure 2B). The deaf group had a mean visible sector surface area of 196 cm^2 ($SE = 6.5$), whereas the hearing control group had a mean visible sector surface area of 180 cm^2 ($SE = 6.5$), as shown in Table 2. No other effects involving group were significant in the deaf versus hearing comparison, indi-

cating that the enhancement observed in the deaf did not vary as a function of stimulus brightness or sector tested.

Across both groups, visible surface area was larger for the brighter, 15-dB stimuli, compared to the 20-dB stimuli: main effect of brightness, $F(1,440) = 910.55$, $p < .001$. Across both groups, there was also a significant effect of sector: main effect of sector, $F(6,440) = 179.36$, $p < .001$, reflecting that temporal sectors had larger areas than more nasal sectors. In addition, there was a significant interaction between sector and brightness, $F(6,440) = 16.44$, $p < .001$, reflecting the larger decrease in surface area for more temporal compared to nasal sectors with decreases in stimulus brightness.

Comparison of Control Groups

To explore the apparent differences in performance between the deaf (primarily women) and dyslexic (primarily men) control groups, a separate analysis of the combined control group of 23 subjects was conducted that indicated men showed larger areas for detecting motion than women: main effect of sex, $F(1,301) = 47.1$, $p < .001$. Men were also more likely to report regularly playing sports than did women (Fisher's exact test, $p < .02$). Five of nine men reported regularly playing sports, whereas only 1 of 14 women reported regular sports play. Men also reported participating in a greater number of sports activities than women, $t(21) = 2.42$, $p < .03$. Men reported playing an average of 1.33 sports ($SD = 1.73$), whereas women reported playing an average of .14 sports ($SD = .54$). The familial SES of the male participants was higher than the SES for the female participants, $t(21) = 2.40$, $p < .03$, male mean SES 55.2 (10.6), female mean SES 42.0 (14.0). Male and female participants in the control groups did not differ in any of the other background variables assessed including age, handedness, video game use, or years of education.

To determine whether there was a relationship between reading measures and visible surface area in the control participants, partial correlations were computed that controlled for the effects of age and sex. None of the three reading measures correlated significantly with visible surface area (all $p > .3$).

DISCUSSION

The present research represents a first attempt to bridge two sizable literatures on selective visual system differences among deaf and dyslexic individuals. Groups of deaf and dyslexic individuals were compared to control groups on tasks designed to assess motion processing and central visual field contrast sensitivity. By using the same experimental paradigm, both enhancements and deficits in motion processing were observed among deaf

and dyslexic research groups, respectively. In contrast, no group differences were apparent in the static perimetry task that tested central visual contrast sensitivity, although no group or individual approached ceiling performance on this task. Taken together, the present data suggest that foveal contrast sensitivity does not differ in deaf or dyslexic groups, whereas motion processing is selectively modifiable and can display either vulnerability or enhancement.

Results from the static perimetry task indicated that neither the deaf nor dyslexic group differed from controls in foveal contrast sensitivity. More importantly, unlike previous tasks of central visual field function, no group or individual approached ceiling performance on this task (i.e., no group or individual approached the maximum threshold of 51 dB). This reinforces previous studies (e.g., Neville & Lawson, 1987b) showing no difference in atypically developing populations for central visual field tasks. Work in animals indicates that the central visual field is most strongly represented in parvocellular layers of the LGN, whereas the peripheral visual field is most strongly represented in the magnocellular layers (Baizer et al., 1991; Schiller et al., 1990). The present results provide a more rigorous test of central visual field, and, by extension, parvocellular differences in either deaf or dyslexic adults.

In contrast, as predicted, the dyslexic participants showed smaller areas for detecting moving stimuli (i.e., deficits), whereas the deaf participants showed larger areas for detecting moving stimuli (i.e., enhancements). The criteria employed for inclusion in this research precluded the possibility that the motion processing differences observed in deaf and dyslexic adults could be explained by attendant neurological disorders, comorbid clinical attention deficits, or use of psychoactive medications. Matching of the control groups for each research sample further indicates that the results cannot be explained by differences in age, sex, familial SES, sports participation, or video game experience.

For the dyslexic group, the reduction in visible surface area for detecting motion was greatest in the lower visual field. Past work with deaf participants has also suggested that enhancements in visual processing may be larger in the inferior visual field (Bosworth & Dobkins, 2002b), although this relationship was not observed in the current study. Interestingly, work by Previc (1990) suggests that the lower visual field is more strongly represented in the M or dorsal pathway, which is consistent with the greater differences observed in the inferior visual field reported in some studies of plasticity in deaf or dyslexic individuals. The visual field differences suggest that future studies should examine whether overall group differences are largest or only present in a particular eccentricity or location of the visual field.

Although no differences were observed between groups as a function of right or left visual field (LVF) position, this may have been an artifact of the right

monocular testing procedure used. Past research indicates anomalous visual field asymmetries in both deaf and dyslexic individuals. Relative to controls, dyslexic individuals show an LVF mini-neglect (Facoetti & Molteni, 2001; Hari, Renvall, & Tanskanen, 2001; Facoetti & Turatto, 2000). In contrast, early signers (whether deaf or hearing) show a right visual field (RVF) bias in tasks where nonsigners show either no bias or an LVF bias (Bosworth & Dobkins, 2002b; Neville & Lawson, 1987c). As the monocular visual field is asymmetrical, the testing method in the present study reduced the size of the left (nasal) visual field. Although deaf enhancements and dyslexic deficits were observed, the testing method could have biased the results in favor of a finding an advantage in the deaf participants and against finding a disadvantage in the dyslexic participants. The method also limited the extent to which LVF and RVF differences could be assessed in the groups. A more full characterization of the visual field would be available if both the left and right eye (and subsequently the full left and right visual fields) had been tested.

In some previous studies of cross-modal plasticity (Bosworth & Dobkins, 2002a, 2002b; Bavelier, Brozinsky, et al., 2001; Neville & Lawson, 1987c), hearing native signers have been included to determine whether the effects observed in deaf adults could be attributed to use of a manual–spatial language. These studies have found that the enhancements in motion processing and visual attention are only found in deaf signers (Bosworth & Dobkins, 2002a; Bavelier, Brozinsky, et al., 2001; Neville & Lawson, 1987c), whereas differences in hemispheric asymmetries are observed in both hearing and deaf signers (Bosworth & Dobkins, 2002b; Bavelier, Brozinsky, et al., 2001; Neville & Lawson, 1987c). On this basis, it seems likely that the motion processing advantages observed in the deaf participants on the present study are the result of deafness, rather than use of a manual–spatial language. However, because neither hearing native signers nor deaf orally raised participants were included, it cannot be unequivocally determined whether the deaf enhancements in the current motion detection task were due to exposure to American Sign Language (ASL) or deafness.

It is also interesting to consider whether the deficits observed in the dyslexic group can be attributed to poor reading or dyslexia per se. Although the question cannot be answered directly, two lines of evidence suggest that the motion processing deficits observed in dyslexic individuals are not a consequence of poor reading. First, in an analysis of the control group, the partial correlation between reading measures and visible surface area was not significant, suggesting no relationship between reading ability and motion detection. Second, although deaf individuals typically show below age-appropriate reading levels (Dyer, MacSweeney, Szczerbinski, Green, & Campbell, 2003; Conrad, 1979), they also consistently show enhanced motion processing (e.g., Bavelier,

Brozinsky, et al., 2001; Neville & Lawson, 1987b). Unfortunately, reading measures were not taken on the deaf participants in the current study, so their reading performance cannot be compared directly to that of the dyslexic group.

The paradigm used in the present research represents a departure from previous paradigms to assess motion, which have been criticized as being unnecessarily complicated. Paradigms used in previous studies certainly tap motion processing, but may show group differences as a result of cognitive or attentional differences between groups. Indeed, some researchers have proposed that group differences might only emerge for more complex, cognitively demanding motion detection tasks where attention can play a role (Proksch & Bavelier, 2002). Although a visual perception study can never completely remove the attentional component, the kinetic perimetry task used in the present study was comparatively simple, with participants detecting single points of moving light. Yet, even when this “simple” motion detection task was used, group differences in motion processing reported in previous literature (Bavelier, Tomann, et al., 2000; Talcott et al., 2000; Cornelissen et al., 1995) persisted. The present results suggest that both deaf and dyslexic individuals show differences in motion processing, even for simple stimuli, and suggest the need for further studies in this area.

Although the motion processing task used here did not specifically manipulate attention, all participants in the present study also completed a modified version of the Attention Network Task (ANT) (Fan, McCandliss, Sommer, Raz, & Posner, 2002) to test for possible group differences in the alerting or exogenous orienting networks of attention. Results from the ANT indicated that neither the deaf nor the dyslexic sample differed from control groups in either the alerting or the exogenous orienting of visual attention (Darves, Rueda, Stevens, Marrocco, & Neville, 2003). More importantly, variations of the ANT task showed no group differences even when stimuli were presented in the peripheral visual field (15°) or when moving stimuli were used (Darves et al., 2003). Comparisons of group reaction times in the attention experiment also indicate that the differences in motion processing cannot be explained by overall group differences in reaction times. Finally, although past work has shown that at least some dyslexic individuals show larger visual crowding effects than controls (Atkinson, 1991), this is unlikely to account for the present results because dyslexic individuals did not show deficits in the most crowded environment (i.e., in the foveal static perimetry task). However, it should be noted in the present study that visual crowding was not assessed directly.

Although the deaf and dyslexic groups cannot be compared directly on the motion task due to differences in demographic characteristics, a separate analysis was conducted on the combined control group to examine pos-

sible effects of sex on the results. This analysis indicated that sex does have an effect on the size of the surface area for detecting motion, with men showing larger areas for detecting motion (i.e., better performance) than women. The effect of sex likely accounts for the apparent differences in surface area measures between the control groups used for the dyslexic (primarily male) versus deaf (primarily female) sample. It also underscores the importance of matching control and research samples for sex in future studies of visual differences.

Within the literature on sex differences in perception, an emerging hypothesis suggests a male bias for processing motion or M-pathway stimuli (Lephart, 2005; Alexander, 2003). This possibility is supported by sex differences observed in anatomical studies of the visual pathway (Salyer, Lund, Fleming, Lephart, & Horvath, 2001; Juraska, 1991), imaging studies of visual processing (Kaufmann, Elbel, Gössl, Pütz, & Auer, 2001, p. 36), and behavioral studies of movement and movement-related object preference in children (Iijima, Arisaka, Minamoto, & Arai, 2001), neonates (Connellan, Baron-Cohen, Wheelwright, Batki, & Ahluwalia, 2000), and non-human primates (Alexander & Hines, 2002). The male bias for processing M-pathway stimuli has been linked to sex hormones (Iijima et al., 2001; Salyer et al., 2001). The sex differences observed in the present study are consistent with this hypothesis. However, it is important to note that the male advantage observed in the kinetic perimetry task may be related to experiential factors, including sports participation. In the present study, men were more likely than women to report regular sports participation and also reported engaging in a greater number of different sports activities. Past work using the same kinetic perimetry paradigm showed that college-level female athletes have larger areas of motion detection than female nonathletes (Berg & Killian, 1995).

To the best of our knowledge, this study represents the first demonstration of both sides of visual system modifiability (i.e., enhancements and deficits) using the same experimental paradigm. Over the past 30 years, the literature on selective visual system enhancements in deaf individuals has developed largely in parallel to the literature on selective visual system deficits in certain developmental pathologies, including dyslexia, autism, and Turner's and Williams syndromes, although the two literatures both invoke the notion of a selectively modifiable magnocellular and/or dorsal pathway to explain the specificity of group differences observed. An important implication of the present research is the possibility of bridging these two related literatures. To the extent that both literatures are describing the common phenomenon of selective magnocellular and/or dorsal pathway modifiability, combining the two literatures could add to our understanding of the conditions that give rise to dorsal pathway enhancements and deficits. This is not to say that the underlying causes of selective enhancements and deficits are necessarily the same. Indeed, the

genetic and environmental effects of deafness and dyslexia are markedly different, and no attempt is being made here to equate the two. However, the common outcome of motion processing modifiability may reflect a more general susceptibility of the M or dorsal pathway, including motion processing, to aberrant developmental experience.

Several differences between the visual pathways support the idea that the M or dorsal pathway might be more developmentally modifiable, either to enhancement or decrement. For example, anatomical studies suggest that connections within the parvocellular layers of the LGN are more highly genetically specified, whereas connections within the magnocellular layers are believed to contain redundancies that can be shaped by experience over a longer developmental time course (Chalupa & Dreher, 1991). Molecular differences have also been observed between the two visual pathways, with the dorsal pathway containing a greater concentration of the Cat-301 antigen, a molecule hypothesized to play a role in stabilizing synaptic connections via experience-dependent plasticity (Deyoe, Hockfield, Garren, & Van Essen, 1990). In addition, there is considerable, although not unequivocal, evidence indicating that the dorsal pathway matures more slowly than the ventral pathway (Coch, Skendzel, Grossi, & Neville, 2005; Mitchell & Neville, 2004; Hollants-Gilhuijs, Ruijter, & Spekrijse, 1998a, 1998b). This could render the dorsal pathway more vulnerable to the effects of aberrant experience that can lead either to enhanced or to deficient processing.

Conclusions

In summary, the present research, using the same experimental paradigm, demonstrated enhancements in motion processing among deaf individuals and deficits among dyslexic individuals. In contrast, neither the deaf nor the dyslexic groups differed from controls on a measure of foveal contrast sensitivity thresholds in which neither group approached ceiling performance. This suggests that the findings of selective modifiability of motion processing, either to enhancement or to decrement, may arise from the same underlying mechanisms, possibly mapping to the M or dorsal pathway. Future research should continue to assess whether these two sides of neural modifiability can be explained by similar mechanisms and within a common theoretical framework.

METHODS

Subjects

Seventeen deaf and 15 dyslexic adults participated. Because the deaf and dyslexic samples differed in demographic characteristics, two control groups were needed.

From a pool of 23 control participants, separate control groups were selected for the deaf and dyslexic samples to match on the dimensions of sex, age, and handedness (Oldfield, 1979). Nine control participants (five women) were used as controls for both the deaf and dyslexic samples. All participants had normal or corrected-to-normal vision and were prescreened to exclude individuals taking psychoactive medications or diagnosed with an attention deficit disorder. Each deaf and dyslexic participant was assigned a specific age-matched control to account partially for the large intragroup variability caused by the expanded age range of the sample.

Post hoc analyses also indicated that the control groups did not differ from their respective research samples in video game use, sports participation, years of education, or SES (Hollingshead, 1975), as shown in Tables 1 and 3. Video game use was assessed by asking participants whether they regularly played video games (use/nonuse) and to indicate the amount of time spent playing video games on a weekly and monthly basis. Very few participants reported playing the first-person shooter games associated with enhancements in visual attention (Cohen, Green, & Bavelier, 2005; Green & Bavelier, 2003). Sports participation was assessed by asking participants whether they regularly played any sports (e.g., soccer, football) and to list all sports in which they participated. Tables 1 and 3 present descriptive information on all groups, as well as the results of significance tests for differences between the research samples and their respective control groups. Differences in sex, video game use, and sports participation were analyzed by χ^2 tests of independence or Fischer's exact tests, as appropriate. All other variables were analyzed by using independent sample *t* tests.

A separate set of analyses compared the two control groups to one another. The relationship between control group (deaf control vs. dyslexic control) and sex was significant, $\chi^2(1, n = 32) = 4.39, p < .04$. The dyslexic control group was primarily male, whereas the deaf control group was primarily female, as shown in Tables 1 and 3. The dyslexic control group also tended to report playing a greater number of sports than the deaf control group, $t(30) = -1.885, p < .07$, dyslexic control mean = .4 (.51) sports, deaf control mean = .12 (.33) sports. The relationship between control group and sports use was just above a statistical trend, Fischer's exact test, $p = .106$. There were no significant differences between the two control groups in age, handedness, SES, years of education, or video game use.

Deaf participants were recruited through contacts in the local deaf community. All deaf participants reported a congenital, severe-profound degree of deafness. The most commonly reported cause of deafness was genetic, in which the cochlea fails to develop fully during prenatal development. Deaf participants were prescreened to exclude individuals with etiologies involving illness (e.g., spinal meningitis, high fever, rubella) in which the

central nervous system may have been affected. All deaf participants used ASL.

Dyslexic participants were recruited through referrals from local universities' disability services offices, postings on the Oregon Dyslexia Association Web site, and advertisements in local newspapers. Participants were pre-screened and included on the basis of previous testing history for dyslexia/specific reading impairment. In addition, the dyslexic group performed significantly worse than the dyslexic control group on three behavioral language assessments administered at the time of the data collection, including the Word Attack subtest of the Woodcock–Johnson Educational Battery, and the Reading and Spelling subtests of the Wide Range Achievement Test, Revised Third Edition (WRAT-3), as shown in Table 4.

Apparatus

Visual fields were assessed with the Zeiss-Humphrey (San Leandro, CA) Field Analyzer II, Model 750, which is standard ophthalmology equipment for performing automated static and kinetic visual perimetry. The curved testing bowl is illuminated at 31.5 apostils (ASB), and static or moving target light points of varying sizes and light intensities can be presented across the entire monocular visual field. A gaze tracker and display screen on the side of the perimeter allow the technician to monitor eye fixation throughout the experiment.

Standard automated static perimetry was conducted on the macula, extending 2° around fixation in any direction. A total of 20 small (4-mm diameter) points of white light were projected one at a time against the white background. Stimulus intensities were measured in decibel attenuation from a maximum intensity of 10,000 ASB (0 dB) to a minimum intensity of 0.08 ASB (51 dB). Each stimulus appeared for 200 msec.

Participants fixated centrally and pressed a small, handheld button upon seeing a white point of light appear. A stair-step bracketing algorithm standard to the perimeter identified the participant's contrast threshold sensitivity, defined as the light intensity (in decibels) at which the participant reported seeing the stimulus 50% of the time. Several locations were tested in a cycle. The

amount of time between light presentations was varied to reduce predictability and typically lasted approximately 1–2 sec. Fixation losses, false positives, and false negatives were tracked automatically by the perimeter according to standard methods.

In the kinetic perimetry task, participants fixated a central dot and pressed a handheld button whenever they saw a small (1 mm), white light moving from the periphery toward the center of vision. The light points moved at a velocity of 4° per second along meridians occurring every 45°, as shown in Figure 1. Meridians tested were 0°, 45°, 90°, 135°, 180°, 270°, and 315° (the 225° meridian was excluded because pilot testing revealed nasal occlusion at the periphery). The perimeter automatically recorded the point, in degrees from center, at which the participant reported seeing the moving light. Stimuli were presented at both 15 and 20 dB. The experimenter monitored gaze fixation during kinetic perimetry throughout the task using the machine-mounted eye camera. In cases of visible eye movement, the test results were cancelled and the task restarted.

Procedure

The order of the static and kinetic perimetry tasks was counterbalanced across subjects. Participants received instructions either verbally (hearing participants) or in ASL (deaf participants). The left eye was patched, and right monocular testing was completed.

Before the static perimetry task, participants were instructed to fixate the central orange light and push a button each time they saw a small, white point of light anywhere in their visual field. The fixation point remained present throughout testing. Participants were encouraged to respond only when they were certain they had seen a point of light. Participants were also encouraged to pause the machine at any time by pushing and holding down the response button if they began to feel fatigued. A practice session was provided before testing.

Before the kinetic perimetry task, participants were instructed to look straight ahead at the central fixation light and press a handheld button whenever they saw a small, white light traveling from any direction in the periphery toward the center of vision. The fixation point remained present throughout testing. Participants were encouraged to push the button only when they were sure they saw a moving white dot. A practice session was provided before testing.

Acknowledgments

Research was supported by NIH NIDCD grant DC00128 to H. N. and an NSF Graduate Research Fellowship to C. S. The field analyzer was provided on courtesy loan from Zeiss-Humphrey Medical Systems. We thank R. High and E. Stevens for assistance.

Table 4. Mean Performance Scores on Language Measures for Dyslexic and Dyslexic Control Groups

Test	Dyslexic	Dyslexic control	<i>p</i>
Woodcock–Johnson Word Attack, <i>M (SD)</i>	91.53 (9.93)	106.53 (6.72)	<.001
WRAT-3 Spelling, <i>M (SD)</i>	95.20 (12.17)	110.53 (4.47)	<.001
WRAT-3 Reading, <i>M (SD)</i>	98.93 (10.18)	112.13 (7.70)	<.001

WRAT-3 = Wide Range Achievement Test, Revised Third Edition.

Reprint requests should be sent to Courtney Darves Stevens, 1227 University of Oregon, Eugene, OR 97403, or via e-mail: courtney@uoregon.edu.

REFERENCES

- Alexander, G. (2003). An evolutionary perspective of sex-typed toy preferences: Pink, blue, and the brain. *Archives of Sexual Behavior, 32*, 7–14.
- Alexander, G., & Hines, M. (2002). Sex differences in response to children's toys in nonhuman primates (*Cercopithecus aethiops sabaeus*). *Evolution and Human Behavior, 23*, 467–479.
- American Psychiatric Association. (2000). *Diagnostic and statistical manual of mental disorders* (Revised 4th ed.). Washington, DC: APA.
- Armstrong, B. A., Neville, H. J., Hillyard, S. A., & Mitchell, T. V. (2002). Auditory deprivation affects processing of motion, but not color. *Cognitive Brain Research, 14*, 422–434.
- Atkinson, J. (1991). Review of human visual development: Crowding and dyslexia. In J. R. Cronly-Dillon & J. Stein (Eds.), *Vision and visual dysfunction: Vol. 13, Vision and visual dyslexia* (pp. 44–57). Boca Raton, FL: CRC Press.
- Atkinson, J. (1992). Early visual development: Differential functioning of parvocellular and magnocellular pathways. *Eye, 6*, 129–135.
- Baizer, J. S., Ungerleider, L. G., & Desimone, R. (1991). Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. *Journal of Neuroscience, 11*, 168–190.
- Bavelier, D., Brozinsky, C., Tomann, A., Mitchell, T., Corina, D., & Liu, G. (2001). Impact of early deafness and early exposure to sign language on the cerebral organization for motion processing. *Journal of Neuroscience, 21*, 8931–8942.
- Bavelier, D., & Neville, H. J. (2002). Cross-modal plasticity: Where and how? *Nature Reviews Neuroscience, 3*, 443–452.
- Bavelier, D., Tomann, A., Hutton, C., Mitchell, T., Corina, D., Liu, G., & Neville, H. (2000). Visual attention to the periphery is enhanced in congenitally deaf individuals. *Journal of Neuroscience, 20*, 1–6.
- Berg, W., & Killian, S. (1995). Size of the visual field in collegiate fast-pitch softball players and nonathletes. *Perceptual and Motor Skills, 81*, 1307–1312.
- Bosworth, R. G., & Dobkins, K. R. (2002a). The effects of spatial attention on motion processing in deaf signers, hearing signers, and hearing nonsigners. *Brain and Cognition, 49*, 152–169.
- Bosworth, R. G., & Dobkins, K. R. (2002b). Visual field asymmetries for motion processing in deaf and hearing signers. *Brain and Cognition, 49*, 170–181.
- Braddick, O., Atkinson, J., & Wattam-Bell, J. (2003). Normal and anomalous development of visual motion processing: Motion coherence and 'dorsal stream vulnerability.' *Neuropsychologia, 41*, 1769–1784.
- Bross, M. (1979). Residual sensory capacities of the deaf: A signal detection analysis of a visual discrimination task. *Perceptual and Motor Skills, 48*, 187–194.
- Chalupa, L. M., & Dreher, B. (1991). High precision systems require high precision "blueprints": A new view regarding the formation of connections in the mammalian visual system. *Journal of Cognitive Neuroscience, 3*, 209–219.
- Coch, D., Skendzel, W., Grossi, G., & Neville, H. (2005). Motion and color processing in school-age children and adults: An ERP study. *Developmental Science, 8*, 372–386.
- Cohen, J., Green, C., & Bavelier, D. (2005, April). *Training visual attention with video games: Are all games created equal?* Presented at the 12th Annual Meeting of the Cognitive Neuroscience Society, New York, NY.
- Connellan, J., Baron-Cohen, S., Wheelwright, S., Batki, A., & Ahluwalia, J. (2000). Sex differences in human neonatal social perception. *Infant Behavior and Development, 23*, 113–118.
- Conrad, R. (1979). *The deaf school child*. London: Harper & Row.
- Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1999). Attentional modulation of neural processing of shape, color, and velocity in humans. *Science, 248*, 1556–1559.
- Cornelissen, P., Richardson, A., Mason, A., Fowler, S., & Stein, J. (1995). Contrast sensitivity and coherent motion detection measured at photopic luminance levels in dyslexics and controls. *Vision Research, 35*, 1483–1494.
- Darves, C., Rueda, M. R., Stevens, E., Marrocco, R., & Neville, H. (2003). Attentional network differences among deaf, dyslexic, and control adults. *Society for Neuroscience Abstracts* [Online], Program No. 515.24.
- Demb, J. B., Boynton, G. M., Best, M., & Heeger, D. J. (1998). Psychophysical evidence for a magnocellular pathway deficit in dyslexia. *Vision Research, 38*, 1555–1559.
- Deyoe, E. A., Hockfield, S., Garren, H., & Van Essen, D. C. (1990). Antibody labeling of functional subdivisions in visual cortex: Cat-301 immunoreactivity in striate and extrastriate cortex of the macaque monkey. *Visual Neuroscience, 5*, 67–81.
- Deyoe, E. A., & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neurosciences, 11*, 219–226.
- Dyer, A., MacSweeney, M., Szczerbinski, M., Green, L., & Campbell, R. (2003). Predictors of reading delay in deaf adolescents: The relative contributions of rapid automatized naming speed and phonological awareness and decoding. *Journal of Deaf Studies and Deaf Education, 8*, 215–229.
- Eden, G. F., VanMeter, J. W., Rumsey, J. M., Maisog, J. M., Woods, R. P., & Zeffiro, T. A. (1996). Abnormal processing of visual motion in dyslexia revealed by functional brain imaging. *Nature, 382*, 66–69.
- Everatt, J., Bradshaw, M. F., & Hibbard, P. B. (1999). Visual processing and dyslexia. *Perception, 28*, 243–254.
- Facoetti, A., & Molteni, M. (2001). The gradient of visual attention in developmental dyslexia. *Neuropsychologia, 39*, 352–357.
- Facoetti, A., & Turatto, M. (2000). Asymmetrical visual fields distribution of attention in dyslexic children: A neuropsychological study. *Neuroscience Letters, 290*, 216–218.
- Fan, J., McCandliss, B. D., Sommer, T., Raz, A., & Posner, M. I. (2002). Testing the efficiency and independence of attentional networks. *Journal of Cognitive Neuroscience, 14*, 340–347.
- Galaburda, A., Menard, M., & Rosen, G. (1994). Evidence for aberrant auditory anatomy in developmental dyslexia. *Proceedings of the National Academy of Sciences, U.S.A., 91*, 8010–8013.
- Gilmore, G., Wenk, H., Naylor, L., & Stuve, T. (1992). Motion perception and aging. *Psychology and Aging, 7*, 654–660.
- Green, C., & Bavelier, D. (2003). Action video game modifies visual attention. *Nature, 423*, 534–537.
- Hansen, P. C., Stein, J. F., Orde, S. R., Winter, J. L., & Talcott, J. B. (2001). Are dyslexics' visual deficits limited to measures of dorsal stream function? *NeuroReport, 12*, 1527–1530.

- Hari, R., Renvall, H., & Tanskanen, T. (2001). Left minineglect in dyslexic adults. *Brain and Cognition*, *124*, 1373–1380.
- Harris, J. W., & Stocker, H. (1998). General spherical triangle. In *Handbook of mathematics and computational science* (pp. 106–111). New York: Springer-Verlag.
- Hollants-Gilhuijs, M. A. M., Ruijter, J. M., & Spekreijse, H. (1998a). Visual half-field development in children: Detection of colour-contrast-defined forms. *Vision Research*, *38*, 645–649.
- Hollants-Gilhuijs, M. A. M., Ruijter, J. M., & Spekreijse, H. (1998b). Visual half-field development in children: Detection of motion-defined forms. *Vision Research*, *38*, 651–657.
- Hollingshead, A. B. (1975). *Four factor index of social status*. Unpublished manuscript.
- Iijima, M., Arisaka, O., Minamoto, F., & Arai, Y. (2001). Sex differences in children's free drawings: A study on girls with congenital adrenal hyperplasia. *Hormones and Behavior*, *40*, 99–104.
- Johannes, S., Kussmaul, C. L., Münte, T. F., & Mangun, G. R. (1996). Developmental dyslexia: Passive visual stimulation provides no evidence for a magnocellular processing defect. *Neuropsychologia*, *34*, 1123–1127.
- Juraska, J. (1991). Sex differences in "cognitive" regions of the rat brain. *Psychoneuroendocrinology*, *16*, 105–119.
- Kaiser, M., Proffitt, D., & Anderson, K. (1985). Judgments of natural and anomalous trajectories in the presence and absence of motion. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *11*, 795–803.
- Kaufmann, C., Elbel, G., Gössl, C., Pütz, B., & Auer, D. (2001). Frequency dependence and gender effects in visual cortical regions involved in temporal frequency dependent pattern processing. *Human Brain Mapping*, *14*, 28–38.
- Lephart, E. (2005, August). Sex differences in sensation and perception: Visual. In L. Sax (Chair), *Sex differences in sensation and perception*. Symposium conducted at the 2005 American Psychological Association Annual Convention, Washington, DC.
- Livingstone, M. S., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, *240*, 740–749.
- Livingstone, M. S., Rosen, G. D., Drislane, F. W., & Galaburda, A. M. (1991). Physiological and anatomical evidence for a magnocellular defect in developmental dyslexia. *Proceedings of the National Academy of Sciences, U.S.A.*, *88*, 7942–7947.
- Lovegrove, W., Martin, F., & Slaghuis, W. (1986). A theoretical and experimental case for a visual deficit in specific reading disability. *Cognitive Neuropsychology*, *3*, 225–267.
- Merigan, W. H. (1989). Chromatic and achromatic vision of macaques: Role of the P pathway. *Journal of Neuroscience*, *9*, 776–783.
- Merigan, W. H., & Maunsell, J. (1990). Macaque vision after magnocellular lateral geniculate lesions. *Visual Neuroscience*, *5*, 347–352.
- Merigan, W. H., & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.
- Millsagle, D. (2004). Coincidence anticipation and dynamic visual acuity in young adolescents. *Perceptual and Motor Skills*, *99*, 1147–1156.
- Mitchell, T., & Neville, H. (2004). Asynchronies in the development of electrophysiological responses to motion and color. *Journal of Cognitive Neuroscience*, *16*, 1363–1374.
- Neville, H., & Bavelier, D. (2001a). Effects of auditory and visual deprivation on human brain development. *Clinical Neuroscience Research*, *1*, 248–257.
- Neville, H., & Bavelier, D. (2001b). Variability in developmental plasticity. In J. L. McClelland & R. S. Siegler (Eds.), *Mechanisms of cognitive development: Behavioral and neural perspectives* (pp. 271–287). Mahwah, NJ: Erlbaum.
- Neville, H., & Bavelier, D. (2002). Cross-modal plasticity: Where and how? *Nature Reviews Neuroscience*, *3*, 443–452.
- Neville, H., & Lawson, D. (1987a). Attention to central and peripheral visual space in a movement detection task: An event-related potential and behavioral study. I. Normal hearing adults. *Brain Research*, *405*, 253–267.
- Neville, H., & Lawson, D. (1987b). Attention to central and peripheral visual space in a movement detection task: An event-related potential and behavioral study. II. Congenitally deaf adults. *Brain Research*, *405*, 268–283.
- Neville, H., & Lawson, D. (1987c). Attention to central and peripheral visual space in a movement detection task: An event-related potential and behavioral study. III. Separate effects of auditory deprivation and acquisition of a visual language. *Brain Research*, *405*, 284–294.
- Neville, H., Schmidt, A., & Kutas, M. (1983). Altered visual-evoked potentials in congenitally deaf adults. *Brain Research*, *266*, 127–132.
- Oldfield, R. (1979). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, *9*, 97–113.
- Previc, F. (1990). Functional specialization in the lower and upper visual fields in humans: Its ecological origins and neurophysiological implications. *Behavioral and Brain Sciences*, *13*, 519–575.
- Proksch, J., & Bavelier, D. (2002). Changes in the spatial distribution of visual attention after early deafness. *Journal of Cognitive Neuroscience*, *14*, 687–701.
- Reynolds, H. N. (1993). Effects of foveal stimulation of peripheral visual processing and laterality in deaf and hearing subjects. *American Journal of Psychology*, *106*, 523–540.
- Salyer, D., Lund, T., Fleming, D., Lephart, E., & Horvath, T. (2001). Sexual dimorphism and aromatase in the rat retina. *Developmental Brain Research*, *126*, 131–136.
- Sawatari, A., & Callaway, E. M. (1996). Convergence of magno- and parvocellular pathways in layer 4B of macaque primary visual cortex. *Nature*, *380*, 68–70.
- Schiller, P. H., Logothetis, N. K., & Charles, E. R. (1990). Functions of the colour-opponent and broad-band channels of the visual system. *Nature*, *343*, 68–70.
- Schiller, P. H., & Malpeli, J. G. (1978). Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey. *Journal of Neurophysiology*, *41*, 788–797.
- Spencer, J., O'Brien, J., Riggs, K., Braddick, O., Atkinson, J., & Wattam-Bell, J. (2000). Motion processing in autism: Evidence for a dorsal stream deficiency. *NeuroReport*, *11*, 2765–2767.
- Sperling, A. J., Lu, Z.-L., Manis, F. R., & Seidenberg, M. S. (2003). Selective magnocellular deficits in dyslexia: A "phantom contour" study. *Neuropsychologia*, *41*, 1422–1429.
- Stein, J., & Talcott, J. B. (1999). Impaired neuronal timing in developmental dyslexia: The magnocellular deficit hypothesis. *Dyslexia*, *5*, 59–77.
- Stuart, G., McAnally, K., & Castles, A. (2001). Can contrast sensitivity functions in dyslexia be explained by inattention rather than a magnocellular deficit? *Vision Research*, *41*, 3205–3211.

- Talcott, J. B., Hansen, P. C., Assoku, E. L., & Stein, J. F. (2000). Visual motion sensitivity in dyslexia: Evidence for temporal and energy integration deficits. *Neuropsychologia*, *38*, 935–943.
- Ungerleider, L. G., & Haxby, J. V. (1994). 'What' and 'where' in the human brain. *Current Opinion in Neurobiology*, *4*, 157–165.
- Weiss, E., Kemmler, G., Deisenhammer, E., Fleischhacker, W., & Delazer, M. (2003). Sex differences in cognitive functions. *Personality and Individual Differences*, *35*, 863–875.
- Weisstein, E. W. (1999). *Spherical triangle*. Available: <http://mathworld.wolfram.com/SphericalTriangle.html>. Retrieved March 25, 2004.
- Winner, E., von Karolyi, C., Malinsky, D., French, L., Seliger, C., Ross, E., & Weber, C. (2001). Dyslexia and visual–spatial talents: Compensation vs. deficit model. *Brain and Language*, *76*, 81–110.
- Witton, C., Talcott, J. B., Hansen, P. C., Richardson, A. J., Griffiths, T. D., Rees, A., Stein, J. F., & Green, G. G. R. (1998). Sensitivity to dynamic auditory and visual stimuli predicts nonword reading ability in both dyslexic and normal readers. *Current Biology*, *8*, 791–797.
- Wolfinger, R., & Change, M. (1995). Comparing the SAS GLM and mixed procedures for repeated measures. *Proceedings of the Twentieth Annual SAS Users Group Conference* (pp. 1–11). Cary, NC: SAS Institute, Inc.
- Yabuta, N. H., & Callaway, E. M. (1998). Functional streams and local connections in layer 4C neurons in primary visual cortex of the macaque monkey. *Journal of Neuroscience*, *18*, 9489–9499.
- Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. J. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience*, *11*, 641–649.