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Visually-based temporal distortion in dyslexia

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ABSTRACT

In this study, we show that invisible flicker adaptation reduces the perceived duration of a subsequently viewed stimulus in control subjects, but not in dyslexics. Dyslexics, like controls, show apparent duration compression after 20 Hz flicker and show normal shifts in apparent temporal frequency after adaptation. However a subgroup of the test group, scoring low on both a test of phonological skill (spoonerisms) and a test of literacy (NART), show an apparent temporal expansion after 5 Hz flicker adaptation, a finding not previously seen in controls. Recent studies have linked genes conferring susceptibility to a cluster of language and sensory deficits to anomalous neural migration, providing a tentative biological basis for dyslexia. However it has proved difficult to establish a clear link between sensory deficits and impaired reading. The results presented here point to an abnormal adaptation response within the early precortical stages of the magnocellular pathway, occurring in tandem with a deficit in word-level cognitive processing, providing psychophysical evidence for anomalous cortico-thalamic circuits in dyslexia.

1. Introduction

Dyslexics have been reported as having visual deficits that could contribute to their reading difficulties. Studies employing psychophysical (Cornelissen, Richardson, Mason, Fowler, & Stein, 1995; Lovegrove, Bowling, Badcock, & Blackwood, 1980), fMRI (Ben-Shachar, Dougherty, Deutsch, & Wandell, 2007; Demb, Boynton, & Heeger, 1997; Eden et al., 1996) and anatomical (Livingstone, Rosen, Drislane, & Galaburda, 1991) techniques have ascribed these visual impairments to a deficit in the magnocellular system (Stein, 2001) although the role of the magnocellular system in dyslexia is controversial (Ramus, 2003).

fMRI studies have indicated abnormal responses in dyslexics to motion in the MT/V5 complex (Ben-Shachar et al., 2007; Eden et al., 1996; Eden & Zeffiro, 1998) and V1 (Demb et al., 1997; Demb, Boynton, & Heeger, 1998). Anatomical evidence from post-mortem examinations of the brains of dyslexics (Galaburda & Livingstone, 1993; Livingstone et al., 1991) indicate abnormalities in magnocellular, but not parvocellular layers of the LGN and not in the corresponding input layers of the visual cortex (Jenner, Rosen, & Galaburda, 1999). There is also evidence of greater numbers of ectopias and microgyri, the results of abnormal cell migration, in the left perisylvian cortex of dyslexic brains (Galaburda, LoTurco, Ramus, Fitch, & Rosen, 2006; Galaburda, Sherman, Rosen, Aboitiz, & Geschwind, 1985), which may be the primary cause of the abnormalities seen in the LGN (Galaburda et al., 2006; Ramus, 2004), since male mice with induced microgyria have thalamic abnormalities and concomitant sensory disorders (Galaburda et al., 2006). Despite the anatomical evidence, psychophysical tests of magnocellular function in dyslexia have led to equivocal results (Ramus, 2003). Tasks have been criticised as not isolating magno cells (Skottun, 2000) or, as in the case of motion coherence threshold tasks, requiring high-level extrastriate cortical motion processing (Skottun & Skoyles, 2006) well beyond the point at which magno and parvo streams interact. Although the LGN division has been considered to be a facet of two distinct processing pathways from the retina through the cortex, recent evidence points to a combination of magno and parvo streams as early as the first synapse after the input layers of V1 (Sincich & Horton, 2004). Ideally a psychophysical test of the magnocellular hypothesis should target properties specific to magno cells in the retina and LGN.

Magno cells are tuned to higher temporal frequencies than parvo cells. The high temporal frequency cut-off of cells in the rather heterogeneous koniocellular layers of the LGN tends to be intermediate between parvo and magno cells (Xu, Ichida, Allison, Boyd, & Bonds, 2001). In addition the high temporal frequency cut-off of

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LGN cells is around 20 Hz higher than cells in primary visual cortex (Foster, Gaska, Nagler, & Pollen, 1985; Hawken, Shapley, & Grosof, 1996; Hicks, Lee, & Vidyasagar, 1983). Therefore it is possible to bias processing in favour of the precortical magnocellular pathway by stimulating the visual system with temporal frequencies that are high enough to be beyond the pass-band of typical cortical neurons outside the input layers of V1 (at which point magno and parvo streams may combine) but which would still provide a signal in the LGN (Hawken et al., 1996; Solomon, White, & Martin, 1999). Furthermore, it has been reported that the contrast gain changes resulting from fast and slow adaptation at high temporal frequencies affect magno cells but are absent or nearly so in parvo cells (Benardete & Kaplan, 1999; Shapley & Victor, 1978; Solomon, Peirce, Dhruv, & Lennie, 2004). Specifically, Solomon et al. (2004) have recently reported a slow adaptation effect in which the magno cell response to an 11 Hz drifting grating is reduced after 45 Hz counterphase flicker but not after 1 Hz adaptation. Thus, as they point out, high frequency adaptation can be used to select the magno pathway.

Adaptation of magno cells could have multiple perceptual consequences. Recently we have shown that adaptation to a 20 Hz visual flicker results in an apparent temporal compression of subsecond intervals of 10 Hz flicker placed in the adapted retinal location. Compression after adaptation to 5 Hz was small or absent. These temporal effects are independent of the orientation of the adaptor, consistent with a precortical locus (Johnston, Arnold, & Nishida, 2006). It has previously been reported that dyslexics are impaired on a temporal duration discrimination task (Nicolson, Fawcett, & Dean, 1995) although a recent study failed to replicate this observation (Ramus, Pidgeon, & Frith, 2003). In our case we are interested not in temporal discrimination, a measure of subjects' precision, but in perceived duration – a temporal illusion. We hypothesized that if dyslexics have a magnocellular deficit then the changes in temporal duration judgement, we have previously attributed to adaptation of the magno pathway, may not occur at the high temporal frequencies that selectively adapt magno cells.

2. Methods

We investigated the influence of spatially localised flicker adaptation on time perception. In Experiment 1, we measured the perceived duration of a visual stimulus after adapting to an invisible flicker in normal subjects. In Experiments 2 and 3, dyslexics and normal controls judged the duration (Experiment 2) or temporal frequency (Experiment 3) of visual stimuli after adapting, in separate sessions, to a 0, 5, 20 or 60 Hz flicker.

2.1. Subjects

Five adult subjects (four males, one female) aged between 19 and 30, with normal or corrected to normal vision, participated in Experiment 1. Eleven developmental dyslexic subjects (six males and five females) and 10 control (five males and five females) subjects, who had no reported reading difficulties, participated in Experiments 2 and 3. The dyslexic subjects were all recruited from the UCL Dyslexia Assessment and Support Centre (DASC). They had all been assessed by the Centre and judged to be deserving of extra time in university examinations on account of their disability. The criteria used by DASC in their assessment are those published in the DfES Working Group Guidelines (2005)[1]: a history of difficulty with the acquisition of literacy skills; persisting difficulty with reading, writing and expression; evidence of an underlying cognitive defect such as phonological awareness; exclusion of other factors such as sensor impairment or educational opportunities and any discrepancy between underlying ability and attainment was also taken as supporting evidence. All of the first four criteria need to be met for a dyslexia diagnosis and the 5th criterion is generally met by university students. Some students arrive at UCL with an existing post-16 assessment and some arriving with a pre-16 assessment require a top-up assessment. All students who present with dyslexia are interviewed and tested by DASC. The great majority are given a full assessment in order to determine the level of disability and appropriate time concession. The full assessment utilises a battery of psychometric tests including WRAT4 reading and spelling; prose reading (oral and silent) and handwriting speed; TOWRE words and non-words; digit span; digit and letter naming; spoonerisms; précis and WASI vocabulary, similarity and matrices. DASC then makes a clinical judgement about the existence and severity of the deficit in each case. Later we recruited additional controls from the normal student population and dyslexic subjects from DASC making 17 dyslexic and 16 controls in total, with the dyslexic group consisting of nine male and eight female subjects aged between 18 and 29 and the non-dyslexic group consisting of six male and ten female aged between 20 and 28. Post-hoc tests showed the groups were matched for age and for IQ (Tables 1 and 2).

[1] DfES: SpLD Working Group 2005/DfES Guidelines http://www.dfes.gov.uk/studentsupport/uploads/SPLDG%20Final%20report%20rev.doc.

2.2. Psychometric tests

All subjects completed three psychometric tests: the National Adult Reading Test (NART), the spoonerisms test from the Phonological Assessment Battery (Frederickson, Frith, & Reason, 1997) and a short test from the Ravens Advanced Progressive Matrices (APM) collection (Raven, Raven, & Court, 1998). The NART (Nelson, 1983) was used to test for literacy. It is comprised of a series of 50 irregular words increasing in difficulty. The subject is asked to read out the words as they thought they should be pronounced and the number of words mispronounced are recorded. Since all the words are irregular it assessed reading ability via the lexical route. The spoonerisms test was used to identify dyslexics with poor phonological skills. The test consisted of two parts, each with a time limit of 3 min. In the first part the subject was given a word and a sound, and was asked to replace the first sound of the word with the new sound given. In the second part two words were given and the subject was asked to swap round the first sounds of each word (e.g. Ben found→Fen bound). Each part had three practice questions followed by 10 test questions, and the number of correct responses was recorded. The final test, the APM test, tested for intelligence, and consisted of 12 different patterns. Each pattern had a piece missing and the subject was required to pick, out of 8 possibilities, which would be the best fit in terms of the continuity of the pattern. This test had a time limit of 10 minutes and again the number of correct responses was recorded. For each test the subject was asked to work as quickly and as accurately as possible, and the time taken to complete each test was recorded. The spoonerisms test and the NART were used to define a subgroup (9 subjects) of dyslexics who scored poorly on either or both of these psychometric tests.

2.3. Apparatus

Stimuli were displayed in a darkened room on a Clinton Monoray screen, equipped with a fast phosphor, which had a resolution of 800 × 600 pixels and a refresh rate of either 100 Hz (50 Hz adaptation) or 120 Hz (60 Hz adaptation). It was driven by a VSG 2/5 visual stimulus generator (Cambridge Research Systems).

2.4. Procedure

In Experiment 1, subjects had to compare the duration of a flickering Gaussian comparison stimulus against a standard. An adapting flicker was displayed on one side of fixation (centred 2.2° of visual angle to the left of a central fixation point) for 20 s with 10 s top-up adaptation between trials. The temporal frequency of the adapting flicker was just above the flicker fusion threshold that was individually determined for each subject before starting the experiment. The threshold value was 50 Hz for two subjects (AB, RJ) and 60 Hz for three subjects (AA, AK, JW). The Michelson luminance contrast of the flicker was also adjusted individually (AA = 95%; AB = 68%; AK = 96%; JW = 92%; RJ = 69%) to make sure that the adaptor was invisible. After the adaptation phase, the comparison and the standard were displayed sequentially (the order of presentation was randomized). The duration of the standard stimulus (displayed in the same spatial position as the adapting flicker) was fixed across trials (500 ms). The duration of the comparison stimulus (shown on the unadapted side) was varied in seven steps between 350 and 700 ms. The temporal frequency was set to 10 Hz and the luminance contrast to 100% for both standard and comparison. At the end of each test trial, subjects were asked to report which of the two stimulus intervals was perceived to be briefer. Subjects were instructed to keep fixation on the centre of the monitor for the whole duration of the experimental session. For each subject, a psychometric function indicating the percentage of trials in which the standard was judged as shorter than the comparison was determined. Each data point was the average of 20 repetitions. All the subjects were also tested in a control condition without adaptation.

In Experiment 2, the procedure we used to measure perceived duration in dyslexic and control subjects was the same as in Experiment 1, except that the frequency of the adapting flicker could be 0, 5, 20 or 60 Hz and the duration of the comparison stimulus was varied between 100 and 1000 ms. Michelson contrast was 100%. In this experiment the highest frequency shown was 60 Hz. We did not measure the flicker fusion frequency (FFF) for each subject individually to keep testing time within bounds but 60 Hz was close to or above the FFF for all subjects, particularly after a period of adaptation. Each data point on the psychometric function was the average of 10 trials.

In Experiment 3, subjects were asked to judge temporal frequency, instead of duration, after flicker adaptation. Otherwise the adapting frequencies and the procedure were the same as in Experiment 2. The temporal frequency of the standard

Table 1
Average score of the dyslexic and control groups on the psychometric tests for the sample in Experiments 2 and 3 (Fig. 2)

	n	Spoonerisms score (%)	NART score (%)	SN index	APM score (%)
Controls	10	99.7 ± 0.9	77.8 ± 3.0	89.5 ± 1.4	95.8 ± 7.2
Dyslexics	11	84.3 ± 11.5	58.7 ± 4.1	72.9 ± 3.3	88.8 ± 14.1
Independent samples test value		$U = 6.5$	$t = 3.7$	$U = 9$	$t = 1.3$
p		<0.001	0.002	0.001	0.201

stimulus was fixed (10 Hz) across trials. The temporal frequency of the comparison stimulus was varied between 2 and 18 Hz in seven steps. The duration of both standard and comparison was fixed (500 ms). At the end of each test trial, subjects reported which of the two stimuli they perceived to be flickering at a lower frequency. Psychometric functions were determined for each subject and each data point on the psychometric function was the average of 10 trials.

3. Results

3.1. Experiment 1: invisible flicker adaptation reduces the perceived duration of a visual stimulus

We determined whether control subjects show temporal duration compression after adaptation to invisible flicker. We chose an adaptor that was slightly above the flicker fusion frequency limit because this is a key perceptual boundary which occurs between the frequencies that, in the macaque, would be high enough to obviate a significant cortical response but low enough to still generate neural responses in the LGN (Hawken et al., 1996). Subjects were presented with a central fixation point and an adapting stimulus, placed lateral to fixation, consisting of an invisibly flickering Gaussian pattern in a yellow square on a black background (Fig. 1A). After a period of adaptation, two flickering Gaussian patterns (10 Hz) were shown sequentially, on the adapted and unadapted sides. We asked subjects to report which stimulus appeared to be briefer. The duration of the standard stimulus (10 Hz), displayed on the adapted side of fixation, was fixed at 500 ms, while the duration of the comparison, displayed on the unadapted side, was varied systematically to generate a psychometric function. The point of subjective equality (the 50% point of the psychometric function) provided an estimate of the perceived duration of the standard stimulus after adaptation. The experimental condition was compared against a control condition, in which a static yellow patch, identical in appearance to the adaptor was displayed in its place. We found that, after adapting to invisible flicker, the perceived duration of the stimulus displayed in the same retinal location as the invisible adaptor was significantly reduced (Fig. 1B) in comparison to the baseline condition. All the subjects showed the same pattern of results. Psychometric functions collapsed over subjects are shown in Fig. 1C. Individual psychometric functions are shown in the Supplementary material.

The existence of apparent temporal compression for invisible flicker, in a paradigm which exploits an adaptation effect only

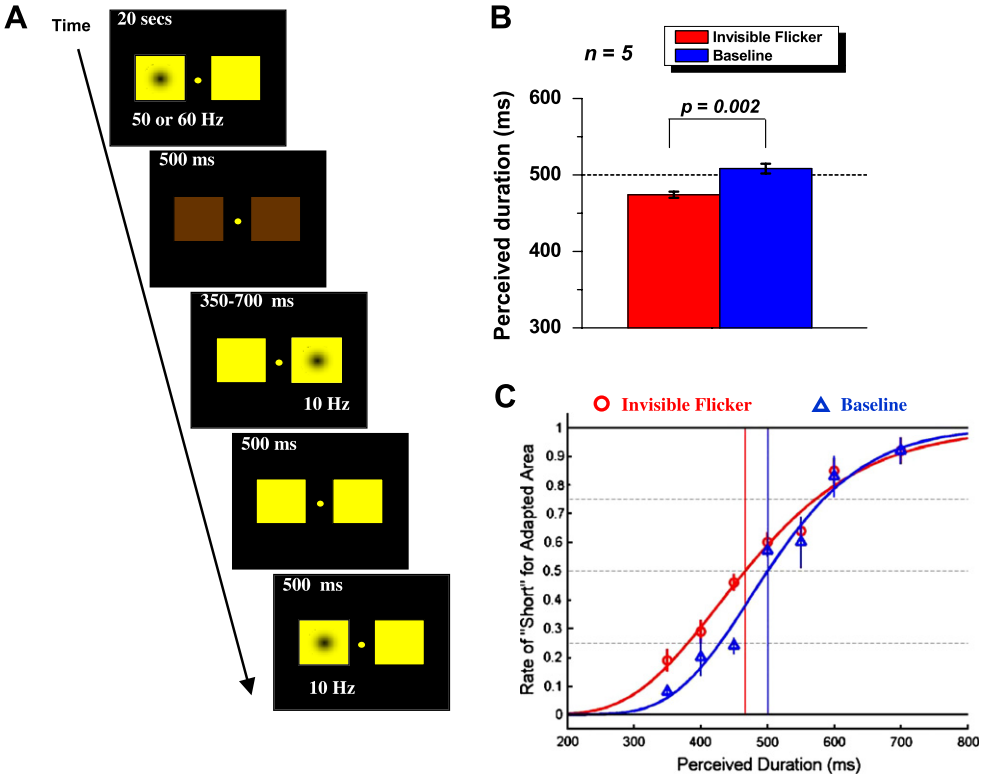

Fig. 1. (A) Time course of the flicker adaptation experiment: an initial period containing a flickering Gaussian pattern (the adaptor) was followed by a standard and a comparison flicker that were displayed sequentially in the same and in the opposite spatial position to the adaptor respectively. Subjects were asked to report which test interval appeared briefer (perceived duration) or (in a separate experiment) which appeared to be flickering at a lower rate. (B) Perceived duration of a 500 ms flickering Gaussian after adaptation to an invisible flicker (flicker fusion frequency was determined individually) and in a control condition where no adaptation was presented. Each point is the average measured over five subjects. Error bars indicate ±1 standard error. (C) Average psychometric functions (for the invisible flicker and the control condition) obtained by collapsing the data from all the five subjects for each duration of the comparison stimulus. Standard errors and points of subjective equality are reported for both curves.

reported to occur in LGN magno cells, in combination with previous evidence of insensitivity to orientation differences between test and adaptation for both changes in apparent temporal frequency and duration (Johnston et al., 2006), strongly supports a subcortical magnocellular location for the duration adaptation effect. Interestingly, Burr, Tozzi, and Morrone (2007) have reported that flicker induced temporal compression has a head-centred (and likely parietal) component. They associate a retinocentric component with a change in apparent temporal frequency. Our previous and current experiments do not distinguish between craniotopic and retinotopic adaptation, however we have shown changes in apparent duration for test stimuli matched in terms of apparent temporal frequency (Johnston et al., 2006) and here we show further dissociations between temporal frequency adaptation and the duration effect. Temporal perception is also altered around the time of a saccade (Morrone, Ross, & Burr, 2005). This apparent temporal compression has been linked to spatial remapping in the parietal cortex after saccades. However, note, saccades are also associated with neural suppression (Burr, Morrone, & Ross, 1994; Johnston et al., 2006; Terao, Watanabe, Yagi, & Nishida, 2008) which is thought to be confined to the magnocellular stream.

3.2. Experiment 2: dyslexics do not show the effect of invisible flicker on apparent duration

To investigate the effect of visual flicker adaptation on duration perception in dyslexic observers, we measured perceived duration in both dyslexic and control subjects using the previously described task (Fig. 1A), but with a wider range of adapting temporal frequencies (0, 5, 20 or 60 Hz). In this experiment the high frequency adaptor was set at 60 Hz for all subjects. An ANOVA revealed a significant effect of adaptation frequency ($p < 0.001$, $F = 12.13$, df = 3) and group ($p = 0.033$, $F = 5.34$, df=1). The statistical analysis was performed on log transformed data to improve the fit to the normal distribution. The controls showed a significantly greater compression ($p = 0.013$, df = 18) than the dyslexics for the 60 Hz adaptor (Fig. 2A). We also found a reduction in the perceived duration after 60 Hz adaptation, as compared to the static adaptation baseline ($p = 0.041$, df = 17) and 500 ms ($p = 0.012$, df = 8) for control subjects. There was no effect of 60 Hz adaptation for dyslexic subjects. However both dyslexics ($p = 0.027$, df = 10) and controls ($p = 0.015$, df = 9) showed a decrease in apparent duration, compared to baseline (0 Hz), after 20 Hz flicker adaptation for a 10 Hz visual test stimulus displayed subsequently in the same spatial position, while 5 Hz flicker adaptation had little effect (Fig. 2A), in agreement with previous reports (Johnston et al., 2006). No significant difference in the perceived duration for dyslexics and controls was observed in the baseline, 5 or 20 Hz conditions, demonstrating that inattention on the part of the dyslexics (Stuart, McAnally, & Castles, 2001) cannot account for the effect we observed. The adaptation was always in the left visual field and there have been reports of deficient orientation of attention to the left field in dyslexics as evidenced by slower reaction times (Facoetti, Turatto, Lorusso, & Mascetti, 2001), however, again, the lack of a difference between dyslexics and controls in the baseline, 5 or 20 Hz conditions indicates that any lack of attention to the left visual field is not critical here. Clearly the difference between dyslexics and controls in the 60 Hz adaptation condition does not simply reflect a general bias in the dyslexics group in favour of longer intervals. Statistical analysis of the slopes of the psychometric functions in the duration task showed no statistically significant difference between dyslexics and controls apart from in the 5 Hz condition in which the dyslexic group showed poorer duration discrimination ($p = 0.037$, df = 19).

3.3. Experiment 3: dyslexics show a normal temporal frequency shift

In order to see if the observed difference between dyslexics and controls in the duration experiment is mediated by a difference in perceived temporal frequency (Kanai, Paffen, Hogendoorn, & Verstraten, 2006), we measured the apparent flickering frequency of a standard stimulus (10 Hz) after adaptation to a 0, 5, 20 or 60 Hz flicker for the same subjects used in the duration experiment. A control condition with no adaptation was also included. For both dyslexics and controls, 60 Hz adaptation has no effect on the apparent frequency of the test flicker, whereas 20 Hz adaptation reduced it and 5 Hz increased it (Fig. 2B). ANOVA revealed an effect of adaptation frequency ($p < 0.001$, $F = 31.13$, df = 3) but no effect of group and no interaction. The statistical analysis was performed in log transformed data to improve the fit to the normal distribution. These data are consistent with the previously reported dissociation between the effects of visual flicker adaptation on apparent duration and apparent temporal frequency (Johnston et al., 2006) as is the fact that 60 Hz adaptation affected controls but not the dyslexic group in the duration task whereas there were no differences in the temporal frequency task. The lack of a difference between the groups in the temporal frequency task shows that the dyslexic deficit affects neural mechanisms that are specifically involved in determining the duration of a visual stimulus. There is not a general deficit in temporal perception.

3.4. Some dyslexics show an increase in apparent duration after low frequency adaptation

The trend towards an increase in perceived duration after 5 Hz adaptation in the dyslexic group compared to controls (Fig. 2A;

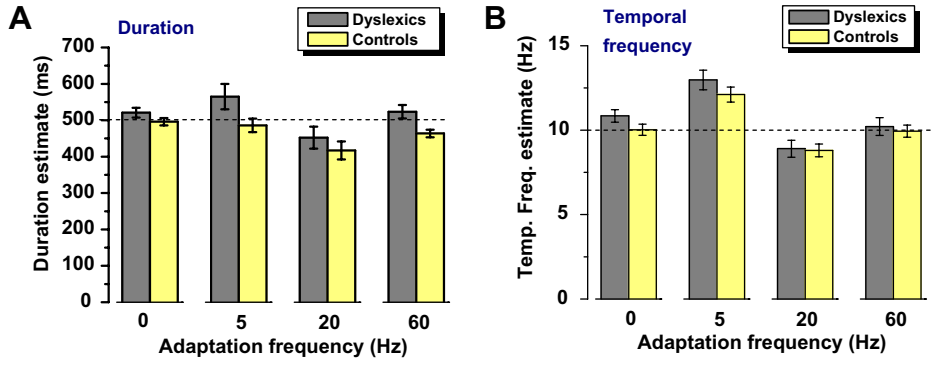

Fig. 2. (A) Duration estimate of a 500 ms flickering Gaussian stimulus after adaptation to a 5, 20, 60 Hz flicker and in a control condition (0 Hz) for a group of 11 dyslexics and a group of 10 controls. Error bars show ±1 standard error. (B) Temporal frequency estimate of a 10 Hz flicker after adapting to a 5, 20 and 60 Hz flicker and in a control condition (0 Hz) for a group of 12 dyslexics and a group of 10 controls. Error bars show ±1 standard error.

$p = 0.061$, df = 19) was intriguing since we had not observed any evidence for a perceived temporal expansion in our previous work. The heterogeneity of the dyslexic population (Castles & Coltheart, 1993) has often been cited as the reason for the heterogeneity of their performance in visual tasks (Stein & Walsh, 1997). Subdividing the dyslexics into different groups according to their results on psychometric tests has led to a significant difference in visual performance between subgroups in some cases (Borsting et al., 1996), but not others (Williams, Stuart, Castles, & McAnally, 2003). We recruited additional subjects in order to increase the statistical power and to investigate potential correlations. Within our group of dyslexics, we then isolated a subsample of subjects with either poor phonological skills and poor reading or both on the basis of their poor performance in the spoonerisms test and the NART (Fig. 3) and we compared their performance in the duration task with that of the control subjects. First, although the spoonerisms test is a test of phonological skill and the NART is composed of irregular words performance on the two tasks is correlated (Fig. 3; $r = 0.49$, $p < 0.004$) reflecting general problems with word-level cognitive processing. Most subjects were high on both or low on both. However, university students clearly have developed compensatory strategies to reduce the effects of their disability. The spoonerisms test is thought of as a good means of detecting dyslexia in high performing populations like university undergraduates. Some dyslexics with poor phonological skill may compensate by reading by the lexical route and having an enhanced vocabulary, leading to a high score on the NART. Others with somewhat better phonological skills may nevertheless have avoided reading complex material due to their disability leading to poor scores on the NART. Combining the spoonerism and NART into a single index incorporates both these types of individuals. Fig. 3 indicates subjects selected by the criterion that they had a low spoonerisms/NART index calculated as the geometric mean of their scores on the two tests expressed as percentages. Post-hoc tests showed dyslexics and controls differed in their NART and spoonerism scores but not in IQ (Table 2). We show in Fig. 4 that, after 5 Hz flicker adaptation, the average perceived duration in the low SN group was significantly higher ($F = 5.35$, $p = 0.011$) than both the control subjects (Tukey HSD, $p = 0.011$) and the other dyslexic group (Tukey HSD, $p = 0.047$). No significant difference between the groups was observed for the other adaptation conditions, including the 60 Hz condition, probably due to the larger variance in the estimate of the mean in the dyslexic sub groups. Interestingly, when we included all the subjects that participated in the duration experiment the spoonerisms/NART index (SNI) significantly correlated ($r = -0.41$; $p = 0.018$) with the expansion in perceived duration (Fig. 4B) – the lower the scores, the higher the apparent expansion. The correlation was still significant with the outlier (SNI = 72.64, duration estimate = 826.8) removed ($r = -0.44$; $p = 0.013$) and for the spoonerisms test ($r = -0.37$; $p = 0.036$) but not the NART ($r = -0.33$; $p = 0.061$) in isolation, indicating a stronger link between the 5 Hz expansion and poor phonological skill. We did not find a significant correlation between size of the temporal frequency shift in Experiment 3 and the SNI ($r = -0.203$; $p = 0.38$). There was no correlation ($r = -0.076$; $p = 0.68$) between the 5 Hz effect size and IQ.

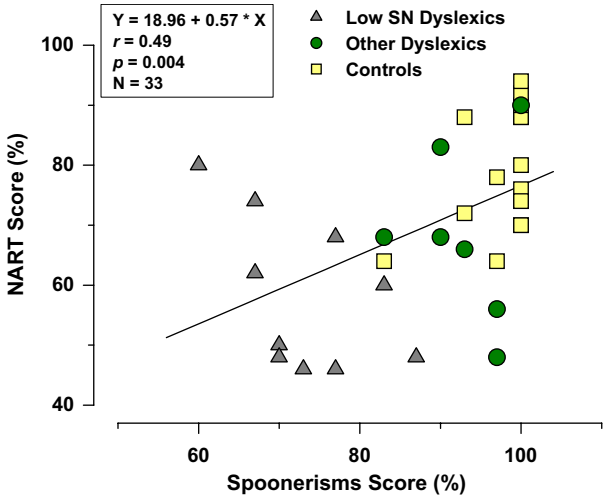

Fig. 3. The subject selected for the low SNI dyslexic group (Fig. 4) scored low on both the spoonerism and NART tests and are plotted as grey triangles. Note there is some overprinting in this figure.

4. Discussion

Psychophysical tests of the magnocellular hypothesis have been compromised by reasonable doubts as to whether the stimuli used selectively target the magnocellular system. The reduction in perceived duration after invisible adaptation is a strong indication that the temporal compression effect is a result of changes in the magno pathway of the retina and LGN. In Experiment 1 we chose an adaptor that was just above the flicker fusion frequency limit and therefore appeared as a steady pattern. The FFF threshold can be considered a functional marker. However the relationship between neural processing and awareness is complex. The sensitivity of the visual system can be reduced after adaptation to perceptually invisible flicker (Shady, MacLeod, & Fisher, 2004) including chromatic flicker. Solomon et al. (2004 point out the adaptation to luminance flicker in this study could be mediated by magno cells in the retina and LGN. Invisibility of the adaptor itself does not guarantee adaptation effects are limited to subcortical regions. For chromatic stimuli, functional imaging shows that a number of brain areas including V1 distinguish between invisible flicker and non-flickering controls (Jiang, Zhou, & He, 2007) and a number of cortical areas, although not V1 in this case, can distinguish between consciously perceived flicker and periods of flicker invisibility induced by the same 30 Hz luminance modulation (Carmel, Lavie, & Rees, 2006). In both these cases flicker frequency was well below the 60 Hz luminance flicker used here and therefore it is not clear that there is a reliable cortical response to 60 Hz flicker. Cortical cells can phase lock to invisible flicker at monitor frequencies (50, 60 Hz) and above (Gur & Snodderly, 1997; Williams, Mechler, Gordon, Shapley, & Hawken, 2004). Interestingly, entrainment (tendency for a spike to occur in phase with the driving stimulus irrespective of firing rate) was most prevalent in the magnocellular recipient layer 4Cα (Williams et al., 2004). However the capacity for entrainment was found to be independent of the preferred temporal frequency of the cells and is therefore dissociated from the information processing function of the cell.

Time perception can be influenced by attention (Tse, Intriligator, Rivest, & Cavanagh, 2004), however attention to the adaptor cannot be critical factor here since for invisible flicker the location of the adaptor could not be determined. Also the fact that 20 Hz adaptation provides a much larger duration adaptation effect than 5 Hz adaptation, even when the tests have been perceptually matched (Johnston et al., 2006) cannot be explained in terms of differences in attention to the 10 Hz test patterns.

The duration compression can be distinguished from changes in perceived temporal frequency. Controls show a duration effect at 60 Hz without a concomitant change in perceived temporal frequency and the dyslexic group did not differ from controls in the size of their temporal frequency shift after adaptation although they did differ in their perception of duration.

Table 2
Average score of the dyslexic and control groups on the psychometric tests for the larger sample used in Figs. 3 and 4

	n	Spoonerisms score (%)	NART score (%)	SN index	APM score (%)
Low SN Dyslexics	10	73.1 ± 2.5	58.2 ± 3.9	66.6 ± 1.6	88.4 ± 4.0
Other dyslexics	7	92.9 ± 2.2	68.4 ± 5.5	81.9 ± 2.6	88.1 ± 6.8
Controls	16	97.7 ± 1.1	78.9 ± 2.5	88.9 ± 1.5	97.4 ± 1.5
One-way ANOVA		$F = 48.7$	$F = 10.3$	$F = 47.4$	$F = 2.3$
p		<0.001	<0.001	<0.001	0.115

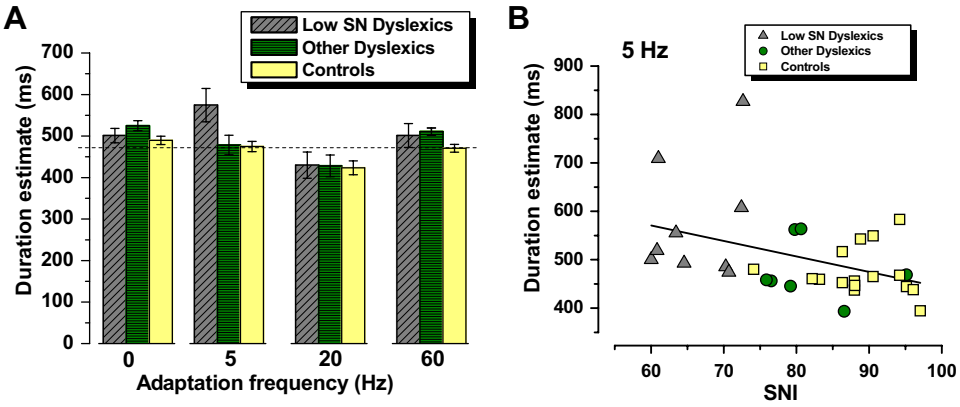

Fig. 4. (A) The duration data of control subjects are compared to a subgroup of ten low SN dyslexics and seven other dyslexics. Error bars show ±1 standard error. (B) Linear regression of the duration estimates after a 5 Hz adaptation on the geometric mean of the spoonerisms and the NART test scores (spoonerism NART Index, SNI). All subjects apart from those participating in Experiment 1 are included in the graph.

The dyslexic group, like controls, show an apparent temporal compression for 20 Hz adaptation, thus compression *per se* does not distinguish the groups. Primate physiology indicates that fast and slow contrast gain changes after adaptation to flicker occur in the magnocellular pathway but are absent or small in the parvocellular pathway. The lack of 60 Hz effect in the dyslexic group indicates an abnormal response of these cells to adaptation and is consistent with earlier reports of a lowering of the flicker fusion frequency in dyslexia (Martin & Lovegrove, 1987; Talcott et al., 1998).

Some dyslexics show an increase in perceived duration after 5 Hz adaptation a finding not seen with controls. There are a number of possible mechanisms. Magno cells in normal monkeys do not show much long term adaptation at low temporal frequency (Solomon et al., 2004). However it is possible that the shifts in temporal tuning of magno cells after high temporal frequency adaptation are reversed with 5 Hz adaptation in dyslexics. Alternatively there may be a greater degree of adaptation in parvo cells in dyslexics. Another possibility that cannot be excluded is that because dyslexics' temporal discrimination is poor they respond on the basis of changes in apparent temporal frequency in place of apparent duration.

Whatever the cause this perceptual effect it is inversely correlated with our SN index but also with poor performance in the spoonerisms test alone. Thus the size of the illusion is predicted by the degree of phonological impairment in addition to the general impairment indicated by the SNI. Interestingly, a recent fMRI study (Ben-Shachar et al., 2007) also reports a correlation between a visual measure, contrast responsivity in the MT+ complex, and phonological skill in children. White et al. (2006) in a substantive review of the role of sensory-motor impairments in dyslexia found that phonological tests were the best indicator of literacy skill. Audio and motor skill was not found to predict phonological skill but a visual stress measure did seem to account for the difficulties of a small number of dyslexic independently of phonological skill. Current views are that there is a group of dyslexics with a visual sensory disorder but these form a small separate group to those with a phonological impairment (White et al., 2006) or that there is a primary cortical disorder in the perisylvian cortex, an area associated with phonological processing, which can have a secondary effect on magnocellular processing in the LGN (Galaburda et al., 2006; Ramus, 2004). The correlation between spoonerism scores and a temporal frequency-based adaptation of duration perception provides a clear link between perceptual and phonological skill deficits in dyslexia. A link between such disparate cognitive functions supports a distributed model of neural abnormality in dyslexia.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2008.04.029.

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