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A temporal sampling framework for developmental dyslexia

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Neural coding by brain oscillations is a major focus in neuroscience, with important implications for dyslexia research. Here, I argue that an oscillatory 'temporal sampling' framework enables diverse data from developmental dyslexia to be drawn into an integrated theoretical framework. The core deficit in dyslexia is phonological. Temporal sampling of speech by neuroelectric oscillations that encode incoming information at different frequencies could explain the perceptual and phonological difficulties with syllables, rhymes and phonemes found in individuals with dyslexia. A conceptual framework based on oscillations that entrain to sensory input also has implications for other sensory theories of dyslexia, offering opportunities for integrating a diverse and confusing experimental literature.

Dyslexia and auditory neuroscience

Developmental dyslexia affects ~7% of children and is defined as a specific learning difficulty affecting reading and spelling that is not due to low intelligence, poor educational opportunities or overt sensory or neurological damage [1]. Across languages, children with dyslexia have poor phonological processing skills, leading to the dominant phonological core deficit [2] model of this heterogeneous disorder. Here, I propose a novel causal framework for developmental dyslexia, the temporal sampling framework (TSF), which has this phonological model as its focus.

Temporal coding is an important aspect of information coding in the brain [3,4], and temporal coding via the synchronous activity of oscillating networks of neurons at different frequency bands (e.g. Delta, 1.5–4 Hz; Theta, 4–10 Hz; and Gamma, 30–80 Hz [3]) is crucial in the perceptual processing of speech [5]. For example, stimulus-induced modulation ('phase locking') of inherent neural oscillations at specific frequencies is important for syllabic perception (Theta) [5,6] and for prosodic perception (Delta) [7]. The acoustic speech signal can be considered as a summation of several frequency bands fluctuating in intensity (amplitude) over time (the 'amplitude envelope', AE). Neurally, the auditory system codes amplitude modulation in natural sounds both across different frequency channels and on different timescales [8]. The AE can be analysed in terms of its constituent temporal modulation frequencies. The dominant modulation frequencies are ~4–6 Hz, irrespective of the audio frequency band, type of speech or the speaker, reflecting the sequential rate of words and syllables [9]. In auditory cognitive neuroscience, these insights are exploited in multi-time resolution speech-processing models (Box 1) [5,6].

The framework proposed here integrates difficulties in processing the rate of change of amplitude (rise time) at AE onset (found in dyslexia across languages [10–15]) with impaired temporal sampling of input by low-frequency Theta and Delta oscillatory mechanisms. Rise time difficulties suggest impairments in distinguishing the different modulation frequency ranges in speech, perhaps arising

Glossary

Allophone: acoustically different forms of the same phoneme; for example, the sound corresponding to the letter P in the spoken syllables 'spin' and 'pin' is acoustically different, the sound in 'spin' being more like /b/, but both sounds are treated in English as the phoneme /p/.
Amplitude: volume of sound (intensity).
Amplitude envelope (AE): the summation over time of the intensity fluctuations (amplitude modulations) in the different frequency channels in the speech signal.
Formant: a concentration of acoustic energy within a narrow frequency band in the speech signal.
Formant transition duration: the time taken from the mouth obstruction that forms a consonant to the steady position marking the succeeding vowel (usually rapid, <50 ms).
Magnocellular: visual processing pathway containing neurons with large cell bodies, involved in motion perception (also called the dorsal pathway).
Onset/Rime: phonological units created by dividing any syllable at the vowel (*s-eat sw-eet str-eet*).
Phase: the fraction of a wave cycle at a certain frequency that has elapsed relative to an arbitrary point. Phase is a circular measure.
Phase coherence: whether phase is temporally correlated at particular time points at a certain oscillatory frequency. If inter-trial phase coherence is high then phase is correlated at these frequencies.
Phase locking: when the phase of an oscillator signal is tied to the phase or timing of a reference signal. Thought to indicate that neural oscillations are being driven by aspect/s of an external stimulus.
Phoneme: a theoretical unit of sound that distinguishes word meanings, such as CAT–HAT, CAT–COT or CAT–CAP. In practice, phonemes usually correspond to several phonetically distinct sounds so a shorthand for these abstract units is that they correspond to the sounds associated with alphabetic letters.
Phoneme awareness: ability to reflect on the sound units in words that correspond to alphabetic letters, usually measured by oral phoneme elision or Spoonerism tasks (Bob Dylan to Dob Bylan).
Phonetic features: aspects of sound production, such as degree of voicing and nasalization, which distinguish sound elements from each other.
Phonology: the sound system of a particular language.
Rhyme awareness: ability to reflect on rhyme units within words, usually measured by tasks such as same-different judgement (*sign–wine*) or spotting the non-rhyming word in a triple of words (*fat pit cat*).
Syllable: a unit of speech comprising a vowel sound (nucleus) and usually some consonant sound/s preceding the vowel (onset) and/or following it (coda). The most frequent syllable type across languages is a consonant–vowel (e.g. BA).
Syllable awareness: ability to reflect on the syllabic structure of words, usually measured by syllable-counting tasks or same–different judgement tasks.
Syllable stress: the more prominent syllables in the speech stream, which require greater muscular effort by the speaker and usually have greater amplitude, duration and pitch as well as larger rise times.
Temporal fine structure: the rapid oscillations in the speech envelope over time, which contribute primarily to changes in fundamental frequency (F0), harmonics and formant transition.

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  doi:10.1016/j.tics.2010.10.001

Box 1. The multi-time resolution model of cortical speech processing (MTRM)

Just as visual input is processed on multiple spatial scales, auditory input is processed on multiple temporal scales. The auditory signal can be fractionated on the basis of both frequency and time, and cochlear mechanisms with respect to coding frequency are well documented. However, the ear is more than a frequency analyser, and energy (amplitude) changes over time provide crucial information, particularly for syllabic segmentation. In the auditory cortex, there is spontaneous neural activity at oscillatory frequencies of 3–6 Hz (Theta) and 28–40 Hz (Gamma) [25] and, by MTRM [6], stimulus-induced modulation of these inherent cortical rhythms is important for speech analysis.

In MTRM, a right-lateralized 'theta sampling network' is preferentially driven by slower temporal rates and codes the lower modulation frequencies in the speech signal [6], enabling temporal integration at the syllable scale. The phase pattern of the Theta band tracks and discriminates spoken sentences, segmenting the incoming speech signal into syllable-sized packets and resetting and sliding to track speech dynamics (e.g. as speech rate varies) [5]. This phase resetting mechanism is thought to be driven by the onsets or edges of sounds (e.g. syllable rise time), and to reflect neural coding of the AE. Other neurofunctional models include low-frequency temporal sampling by Delta oscillators [7].

In MTRM, higher frequency modulations in the signal are coded by a 'Gamma sampling network' that is bilateral and enables temporal integration at the phonetic ('phoneme') scale. The different temporal integration windows used by the different oscillatory networks yield packets of information at different grain sizes (syllable and phoneme) that would (by hypothesis) be one source of phonological learning and that can be matched during lexical access to stored representations in the mental lexicon. Application of this model to dyslexia suggests that impaired syllable-level processing (less efficient Theta phase locking) is accompanied by unimpaired Gamma sampling, resulting in greater weighting of phonetic-feature information in phonological development. Therefore, children with dyslexia might be sensitive to all the phonetic contrasts that are used in human languages as are typically developing infants [31].

Whereas impaired syllable-level processing could explain the impaired development of phonological awareness in developmental dyslexia, enhanced phonetic-level coding could amplify the pervasive difficulty in mapping sounds to letters. For many phonetic continua (e.g. da-ta), there would be more candidate phonemes (e.g. the distinction between/d/,/t^h/and/t/) than letters (D/T) [52].

from inefficient phase locking to these frequency ranges by neuronal oscillations. An important modulation frequency range for speech is 3–10 Hz, where the modulation spectrum peaks, reflecting the underlying syllabic structure of the AE [16]. I argue that an oscillatory perspective can explain why auditory sensory difficulties lead to phonological impairments in dyslexia [and, by extension, specific language impairment (SLI)] and might also enable a systematic approach to integrating other sensory impairments in dyslexia (Table 1). In particular, I propose that a difficulty with slower temporal modulations [in the Theta and Delta range (1.5–10 Hz) [3]] explains difficulties in dyslexia with syllable parsing and perceiving both syllable stress and the phonetic constituents of the syllable. By proposing a specific difficulty with Theta and Delta oscillators, I suggest that auditory rhythmic entrainment is also likely to be impaired. When oscillations entrain to an input rhythm [4], their high excitability phases coincide with events in the stimulus stream, such as syllable onsets in speech. Impairments in auditory entrainment are likely to have consequences for attention and also auditory–visual integration. This novel framework links the sensory and phonological deficits found in dyslexia to recent auditory neuroscience and neurobiological models of speech processing (Box 1).

The temporal sampling framework

Although current phonological models of dyslexia are based on deficits in subsyllabic phonology (e.g. awareness of onset-rimes and phonemes, see Glossary), developmental dyslexia also involves impaired syllabic and prosodic perception [17] (Table 1). A general difficulty in distinguishing different modulation frequency ranges, which particularly affects the slower temporal rate in speech processing and tracking of the AE, would affect the efficiency of syllabic segmentation. Rise times are crucial events in the speech signal, as they reflect the patterns of amplitude modulation that facilitate the temporal

Table 1. Cognitive and sensory features of developmental dyslexia[a]

Phonological deficits in dyslexia				
Phonological awareness [30]	Phonological memory [30]	Rapid phonological output [30]	Syllable stress [22]	Prosodic perception [17]
Examples of tasks				
Count syllables: three syllables in oasis	Digit span	Rapid automatised naming (RAN)	Matching multi-syllabic words for stress pattern	DeeDee tasks
Judge rhyme: fit, *cat*, pit	Non-word repetition	RAN colours and RAN objects		
Manipulate sounds: Bob Dylan to Dob Bylan		RAN digits and RAN letters		
Explained by TSF?				
Yes	Yes	Yes	Yes	Yes
Other reported deficits				
Magnocellular function [35,38,39]	Noise exclusion [36]	Sluggish attention shifting [37]	Cerebellar function (balance) [40]	Rhythmic entrainment [19,20]
Consistent with TSF?				
Yes, via AV integration	Yes, via impaired modulations	Yes, via impaired phase locking	Yes, via Kotz's cerebellar model [71]	Yes, via impaired phase locking

[a]Classically, the core cognitive features of developmental dyslexia cluster around word-level phonology (phonological awareness of syllables, onset-rimes and phonemes), phonological memory for sequences of digits or monosyllabic words, and RAN of digits, letters, colours and objects. However, there are also suprasegmental deficits in the perception of prosody and syllable stress. Moreover, deficits in rhythmic entrainment, coherent motion detection (via the Magnocellular pathway), spatial attention, balance and noise exclusion are also reported. The TSF can explain how the difficulties in phonology arise. The TSF is also consistent with several current sensory theories of dyslexia, if some extra assumptions derived from current work on multisensory integration and the role of low frequency modulations are allowed.

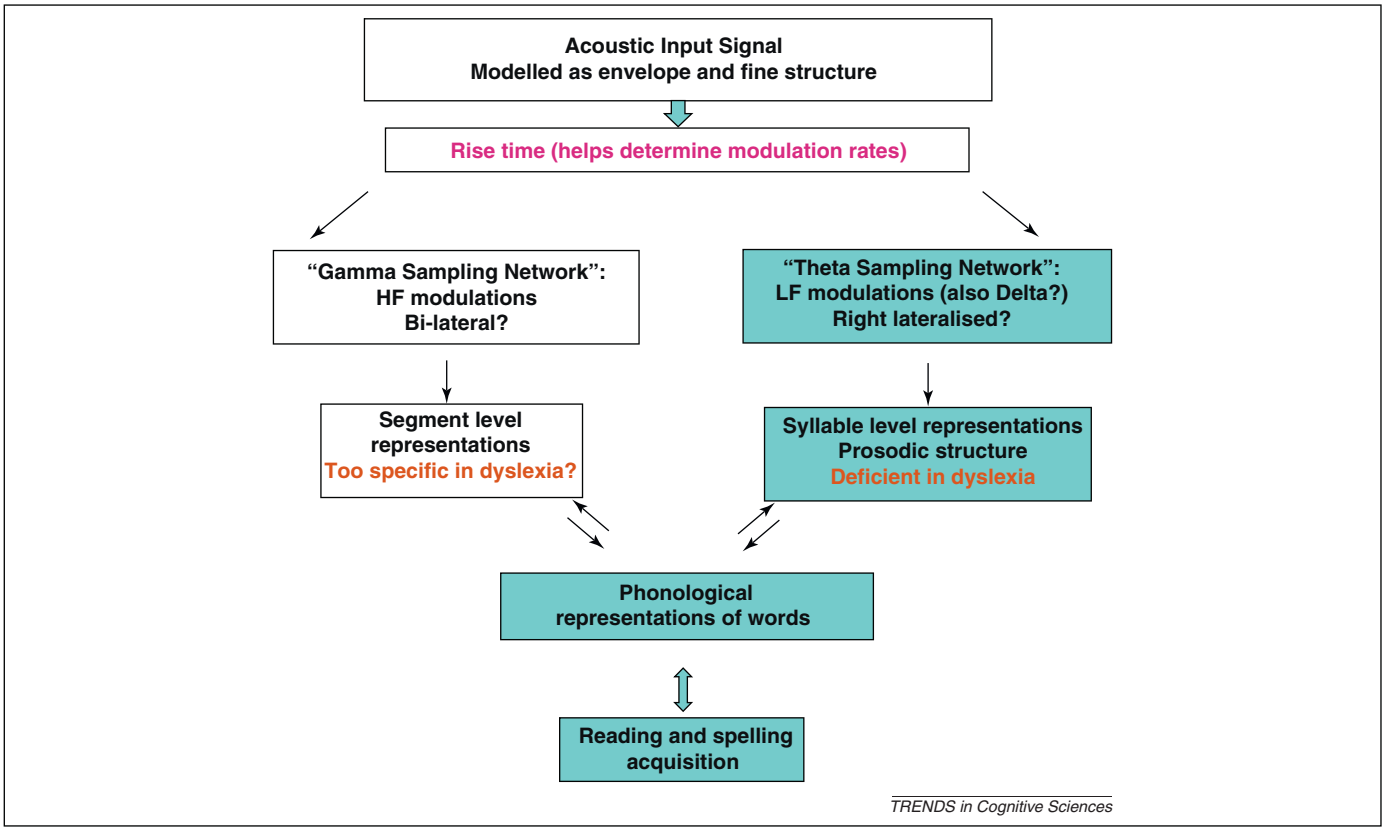

Figure 1. The temporal sampling framework. The TSF assumes a specific dyslexic difficulty with slower temporal modulations, as rise-time perception difficulties in dyslexia involve more extended rise times. As slower modulations are preferentially processed by the right hemisphere, the TSF assumes a right-lateralised impairment in Theta and Delta oscillators. The proposed range of low-frequency modulations processed by the Theta oscillators varies across published studies, but is proposed by Poeppel *et al*. [6] to yield a temporal integration window of ~100–300 ms (approximating the syllable rate). The proposed range for high-frequency modulations also varies across studies, but in [6] yields a temporal integration window of 20– 50 ms, approximating the phonetic rate. According to the TSF, the proposed temporal integration window for syllabic parsing in the right hemisphere might function atypically in dyslexia, yielding the auditory basis of the associated phonological and language deficits (deficits indicated by blue shading).

segmentation of the acoustic signal into syllables. Rise-time discrimination is impaired in dyslexia in English [10], French [11], Hungarian [12], Spanish [13], Chinese [13] and Finnish [14], with conflicting data only for Greek [15] (where control children performed unusually poorly, however). Rise time is a significant predictor of phonological awareness as measured in these languages [e.g. awareness of rhyme ('wine-sign') in English [10], awareness of lexical tone (rising or falling syllable pitch) in Chinese [13]], is almost a significant predictor of phonological awareness in Greek ($p = .06$ [15]) and predicts novel word learning in English [18].

Furthermore, there is evidence of impaired rhythmic entrainment (tapping to a beat) in dyslexia, particularly at 2 Hz [19,20]. Although syllables occur approximately every 200 ms across languages (within the Theta band of 3–10 Hz), linguistic analyses suggest that stressed syllables occur approximately every 500 ms (2 Hz) [21], implicating also Delta band processing. Impairments in perceiving syllable stress have recently been found in dyslexia [22]. Furthermore, children with dyslexia appear to have difficulties in discriminating more extended rise times [23] (e.g. a syllable such as WA has a more extended rise time than does a syllable such as BA). Extended rise times are related mathematically to lower frequency modulations and slower temporal rates. Children with dyslexia also appear to be impaired relative to controls in perceiving speech presented as low frequency modulations (<4 Hz) but not as high frequency modulations (22–40 Hz; U. Goswami *et al.*, unpublished data).

The TSF therefore adapts the multi-time resolution model of Poeppel and colleagues [6] (MTRM) to a syllabic rather than phonemic perspective on phonological development (Figure 1). According to this adaptation of MTRM, the primary neural deficit in dyslexia should be impaired phase locking by (rightward lateralized) Theta (and possibly Delta) oscillatory networks in auditory cortex (impaired temporal processing could also arise from problems lower in the auditory pathway, however, supporting evidence is not yet available). Theta networks enable temporal integration at the syllable rate [5,6] and Delta networks should be important for perceiving prosody [7] (strong versus weak syllabic beats [24]). Impaired Theta mechanisms would also have consequences for phoneme perception. Impaired phase locking by Theta generators might hamper the integration between different acoustic features contributing to the perception of the same phoneme. Alternatively, impaired Theta mechanisms could lead developmentally to a phonological system that is weighed towards the information coded bilaterally by Gamma oscillations, which are analysed by MTRM independently and then bound perceptually with the output from Theta oscillators. Accordingly, phoneme perception could be different in dyslexia. Dyslexic difficulties with rise

time could be a neural marker for the postulated dyslexic difficulty in distinguishing different modulation frequency ranges. If difficulties with lower frequency modulations arise from impaired phase locking by Theta oscillatory networks in the right hemisphere [5,6,7,25,26], this could throw light on atypical right hemisphere activity found in both developmental dyslexia and SLI [27,28].

A developmental perspective

As both dyslexia and SLI are developmental disorders of learning, the phonological deficits in these disorders, according to the TSF, must arise because basic auditory processing is atypical from birth. Indeed, human infants show syllabic sensitivity as neonates [29], using rhythmic cues to segment syllables and words from the acoustic signal to build a lexicon of spoken word forms. Deficiencies in processing low-frequency modulations in infancy would reduce rhythmic sensitivity and impair phonological development. Syllable awareness is also primary in early childhood, as phonological awareness (the ability to recognise and manipulate phonological units in words) follows a developmental sequence across languages, from syllable to onset-rime to (once reading is taught) phoneme [30]. Audio-visual learning in infancy also supports a syllabic focus [31] as, similar to syllabic rhythms, natural mandibular cycles occur at ~4 Hz [32]. Hence, low-frequency information in visual input supports syllable perception [26]. Impaired processing of low-frequency modulations in infancy would affect auditory–visual integration ('speech reading'), further affecting phonological development. The experience of making sounds (talking) is also important for the quality of the phonological representations developed by the child. This would implicate motor processes [33] and, by the MTRM, an important developmental role for right superior temporal gyrus (STG, thought to be crucial in prosodic analysis) [6].

Interestingly, a recent report implicates right STG as a key neural structure related to the genetics of developmental dyslexia (Black *et al.*, unpublished data), and a study of two- and three-year-olds at genetic risk for dyslexia showed that those children who later had reading difficulties also had speech-timing difficulties, producing significantly fewer syllables per second (4.8 at age 3 compared to 7.1 for non-risk children) and pausing for longer between articulations [34]. Furthermore, the spontaneous oscillatory neural activity at both Theta and Gamma frequencies demonstrated in auditory cortex by Giraud and colleagues (Box 1) is correlated with spontaneous activity in visual and premotor regions [25]. It is thus possible that inefficient phase locking in auditory cortex has associated effects on the development of visual and motor processing and could also be the source of some of the observed visual, motor and attentional difficulties in developmental dyslexia [35–40]. For example, according to dynamic attending theory [41], stimulus discrimination is enhanced when an auditory event is anticipated at a regular and predictable rhythmic rate, narrowing the window of attention. As rhythmic entrainment is impaired in dyslexia (and, by hypothesis, is governed by neural phase locking), difficulties in forming an internal representation of rhythmic timing might have knock-on effects for the development of visual attention [38], auditory–visual integration, sluggish attention shifting [37] and cerebellar function [40].

Predictions from the TSF

The TSF makes several novel predictions about sensory, cognitive and behavioural deficits in dyslexia, some of which have been previously been explored and some of which can be evaluated using data from other research perspectives [22]. In particular, the postulated rise-time deficits can explain a host of seemingly disparate perceptual and linguistic deficits. For example, rise time is a crucial cue to the perception of syllable stress and also to rhythmic timing [42]; therefore, both should be impaired in dyslexia. In speech, rhythm depends on the motor constraints inherent in producing syllables, with long and short, or stressed and unstressed, syllables following each other (metrical structure: alternating strong and weak beats). These intensity fluctuations vary in rise time, hence rise-time deficits might also cause difficulties in perceiving metrical structure. Here, I discuss recent evidence for prosodic, syllable stress and metrical perceptual deficits in dyslexia, as well as evidence of difficulties in rhythmic entrainment at syllable-relevant rates. I also mention preliminary evidence for impaired neural phase locking.

Language development: prosody and syllable stress

With respect to prosodic perception, dyslexic impairment is found in reiterative speech tasks, in which strong syllables are replaced by the syllable 'DEE' and weak syllables by 'dee' (hence Casablanca becomes DEEdeeDEEdee, Kitzen, unpublished data). In a version for children [17], significant dyslexic impairments were found in recognising pictures of famous people spoken in 'DeeDees' (Harry Potter as DEEdeeDEEdee). Individual differences were predicted by rise-time discrimination. The perception of syllable stress has also been measured directly [22]. Adults with dyslexia were asked to judge whether two four-syllable words were stressed in the same way (e.g. *maternity ridiculous*). They showed significant impairments, and individual differences were predicted by rise-time discrimination rather than by other auditory measures (frequency or intensity discrimination). The imitation of weak–strong or strong–weak syllable stress is also impaired in children with dyslexia (Huss and Goswami, unpublished data).

Rhythmic timing: auditory entrainment and musical meter

With respect to rhythmic timing, Wolff has long argued for a difficulty in dyslexia in finger-tapping tasks [43]. In a recent study, it was demonstrated that keeping time with a metronome beat by finger tapping (rhythmic entrainment) was impaired at syllable-relevant rates in developmental dyslexia (particularly 500 ms) [19,20]. Both adults and children with dyslexia were impaired at keeping time with a beat at 2 Hz (500 ms); children were also impaired at 2.5 Hz (400 ms) but not at 1.5 Hz (666 ms [19]). By contrast, adults were impaired compared with controls at 1.5 Hz but not at 2.5 Hz [20]. For both children and adults, individual differences in rhythmic entrainment

were predicted by rise-time discrimination. A metrical musical task has also been developed in which short 'tunes' are presented to children, each tune comprising three repetitions of phrases of two to five notes, with downbeat on the first, second or third note [44]. For half of the trials, the meter was disrupted by making the note carrying the downbeat slightly longer in a second repetition of the tune. Children with dyslexia were impaired in detecting whether metrical structure was the same or different, and rise-time discrimination, rather than duration discrimination, predicted individual differences.

Phase locking and low-frequency modulations

Regarding sensory and neural deficits, the TSF predicts reduced perceptual sensitivity to amplitude modulation and to frequency modulation at lower rates, and possibly (via MTRM) atypical right-hemisphere processing of low-frequency modulations [5–7]. Envelope-following difficulties dependent on impaired phase locking should also be found. Temporal modulation transfer functions to AM noise are indeed impaired in both adults [45] and children [46] with dyslexia, with particular insensitivity for children at 4 Hz (the lowest frequency measured in adults was 10 Hz). Frequency modulation detection is also impaired in dyslexic children at slower rates [39] (2 Hz but not 240 Hz) and, in typically developing children, the threshold for detecting 2-Hz FM predicts reading and spelling skills [47]. EEG recordings with adults with dyslexia have shown significantly smaller amplitude modulation following auditory evoked responses compared with controls [48]. For children, a recent EEG study assessed phase locking to speech by cross-correlating the response in temporal electrodes with the broadband envelope of a sentence [49]. Impaired phase locking was found in poor readers. The timing of phase locking for each hemisphere also differed by reading skill. Whereas typically developing readers had earlier right-hemisphere responses, poor readers had earlier left-hemisphere responses, and cortical asymmetry predicted 50% of unique variance in phonological skills. In studies where intelligibility of syllables presented as envelope speech has been assessed, children with dyslexia show clear impairments [50]. These findings are all consistent with the TSF. Finally, in a recent EEG study exploring auditory rhythmic entrainment in dyslexia (Soltész *et al.*, unpublished data), atypical phase locking was found at lower frequencies (0.5–4 Hz, within Delta and Theta bands) to a 2-Hz rhythmic stimulus stream in dyslexia. This implicates Delta and Theta mechanisms in dyslexia; in addition, whereas Theta oscillations track syllable-level information [5], Delta oscillations have been proposed to encode metric foot and phrase-level information [7], also areas of linguistic difficulty in dyslexia [51].

Phonetic representation: different in dyslexia?

One attractive and provocative feature of the TSF is that it places perceptual deficits at the level of the syllable rather than of the phoneme. For phonemes, the closest acoustic correlates are phonetic features, and children with dyslexia can be more sensitive to allophonic variation (phonetic variation within phoneme categories) than are typically developing children [52]. Atypical phonetic-level perception would have serious consequences for establishing grapheme–phoneme correspondences [52]. Consistent with this view, neural integration between letters and sounds (e.g. indexed by neural activation when letters and sounds mismatch, as in E and /a/) is reduced in dyslexia [53]. Making a phonetic discrimination between the syllables BA and WA on the basis of formant transition duration is significantly enhanced in dyslexia [23]; discriminating BA from WA on the basis of rise time is significantly impaired in the same children [23]. The TSF proposes that fast rate processing (Gamma sampling of the speech signal) is preserved in dyslexia, possibly resulting in greater weight being accorded to sensory feature-level cues and enhancing perception of formant transitions (Figure 1).

There are also relevant data from auditory brainstem studies. When a syllable is spoken, certain harmonics are boosted depending on the vowel. The brainstem frequency following response (FFR) reflects neural phase locking to these harmonics, and brainstem timing is poorer in poor readers [54]. Additionally, the FFR to repetition of the same syllable (DA) versus variants of the syllable created by varying different features [e.g. DA with high pitch; DA with dipping pitch; long DA; and different voice onset time (hence TA)] differs between typically developing and dyslexic readers [55]. Typical readers show larger amplitudes to repetition of the same syllable in the formant transition region of the FFR (7–60 ms). By contrast, dyslexic readers show larger FFR amplitudes to the variants of the syllable over this range, suggestive of increased sensitivity to fine-grained (allophonic) information.

The temporal sampling framework and other sensory theories

As noted earlier, there are many sensory deficits in dyslexia (see Table 1 for examples). Theories of attention difficulties in dyslexia [37] fit the TSF, as attention is enhanced when stimuli arrive in phase with neural oscillations [26]. Impaired phase locking in dyslexia could explain the atypical visual and auditory cueing effects that underpin sluggish attention-shifting theory [37]. Theories based on magnocellular dysfunction [35] have suffered from inconsistent data [56]. Researchers now propose either broader dorsal stream deficits affecting visuo-spatial attention [38], or difficulties in the detection of dynamic visual (and auditory) events [39]. Regarding the former, deficits that are observed in visual crowding (when visual features such as letters are jumbled together perceptually) are insufficient to explain the degree of reading impairment shown by children with dyslexia [57]. Regarding the latter, difficulties in dynamic sensory sensitivity are consistent with the TSF if the neural coding of lower frequency information (perhaps spatial as well as temporal) is primarily impaired. However, neither visual dorsal stream deficits nor attention deficits are specific to developmental dyslexia, weakening recent claims that they represent the primary impairment [38]. Dorsal stream deficits occur in many other developmental learning difficulties, including autism [58] (where recoding print to sound can be enhanced, as in hyperlexia) and dyscalculia [59] (where reading can be normal), as do attention deficits (notably attention deficit hyperactivity disorder, where reading can

be intact [60]). By contrast, rise-time deficits are found wherever there are phonological difficulties (e.g. in SLI [61,62]), and are also found in compensated adult dyslexics [63], suggesting a specific sensory deficit that does not resolve itself over developmental time. Worse sensory function in the presence of noise is also consistent [36,50] (noise will affect temporal modulations).

It was recently proposed that children with dyslexia have difficulties in forming perceptual anchors [64] [benefitting from repetition of the same sensory reference stimulus (anchor) across trials]. However, such a broad deficit would have implications for cognitive development outside the language and/or reading sphere and has failed to be supported by specific tests [65]. Similarly, rapid auditory processing (RAP) deficit theory [66] (which proposed specific difficulties in processing brief, rapidly successive acoustic changes) has also failed to be supported by several studies [67]. RAP theory proposed that impaired discrimination of formant transitions affected phonetic perception. However, stretching the formant transitions in syllables (or stretching the syllables in time) does not improve syllable perception in dyslexia, a necessary corollary of RAP [68]. Furthermore, FastForwardR, an auditory training programme based on slowing down speech by 50%, also amplified the amplitude modulations between 3 and 30 Hz in the narrowband filtered signal [68]. Therefore, the amplitude modulation amplification might be more potent in contributing to training effects. Finally, several of these theories have been proposed as alternatives to the phonological core deficit model, treating the pervasive and well-documented phonological difficulties found across languages as incidental rather than causal in dyslexia [38]. An advantage of the TSF is that it places impaired phonology at the heart of this specific learning difficulty.

Concluding remarks

The TSF proposes a specific deficit in dyslexia with low-frequency phase locking mechanisms in auditory cortex, which is argued to have an impact on phonological development. The proposed auditory phase locking deficit might also have implications for the efficient functioning of other sensory systems. Being able to define the core neural deficit(s) underlying dyslexia will improve the efficacy of educational interventions. The TSF suggests a novel focus on the syllable in educational interventions, incorporating direct tuition about speech prosody. Interventions based on rhythm and music might also offer benefits for children with developmental dyslexia, as the dyslexic brain is 'in tune but out of time' [62]. Perceiving melody is not dependent on rhythm, as demonstrated in a model of acoustic analysis [69] derived from amusic (tone-deaf) patients (Figure 2). The acoustic parameters that are preserved in amusia are impaired in dyslexia, whereas sensitivity to lower frequency modulations is preserved in amusia [70] and impaired in dyslexia. As rhythm and meter are more overt in music than in language, it might be that remediation based on music and rhythm (ideally multi-modal), such as matching syllable patterning to metrical structure in music (singing), and playing instruments or moving in time with rhythms or rhythmic language (e.g. metrical poetry), will impact

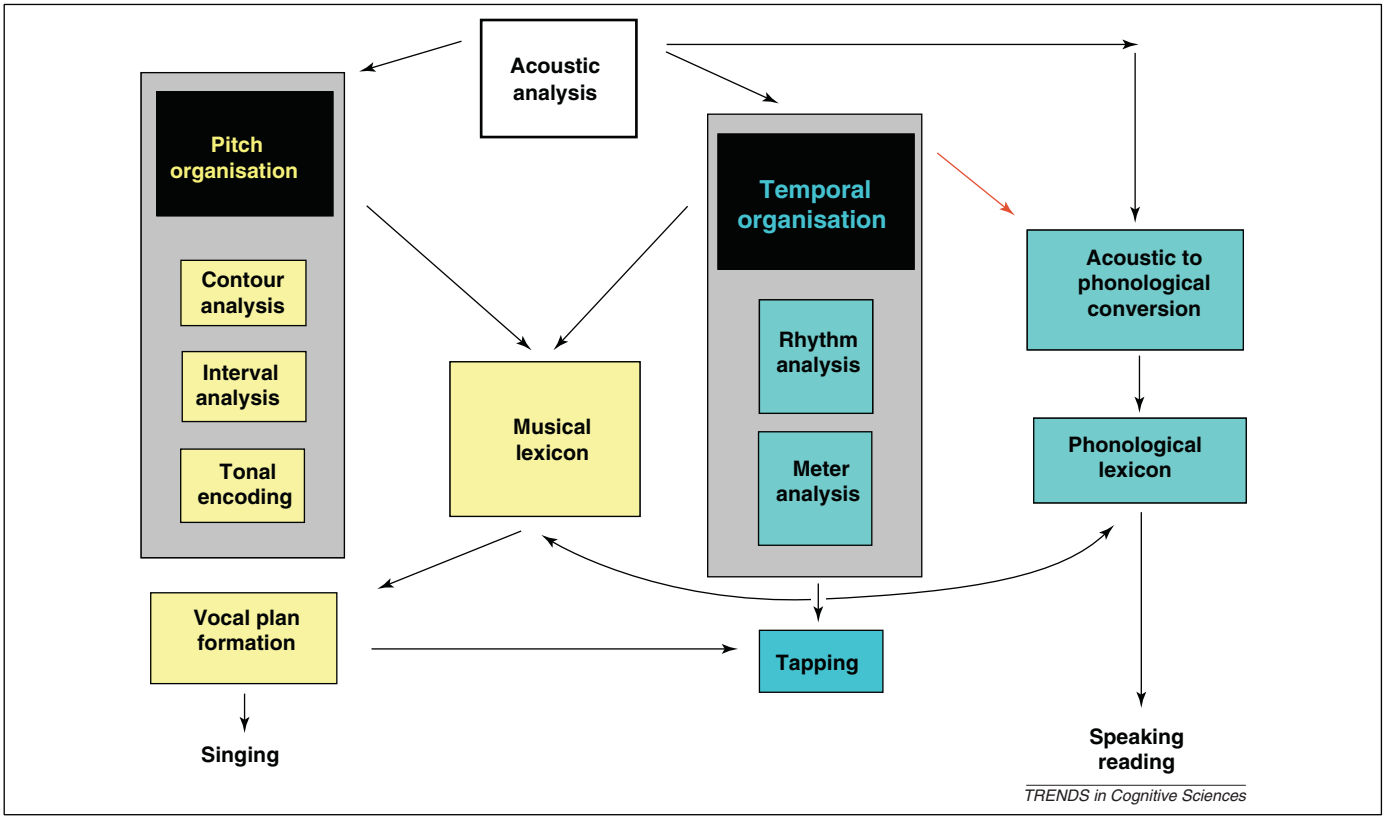

Figure 2. Components of music and language processing. A model of how acoustic analysis of pitch versus rhythm might contribute to language versus musical processing, based on the modular framework of Peretz and Coltheart [69]. The skills preserved in amusia yet impaired in dyslexia are shown in blue. The skills impaired in amusia are shown in yellow. Although developmental disorders of learning are not modular, the framework is useful for supporting the view that musical remediation of dyslexia via training in rhythm and meter might improve phonological development and processing of low-frequency modulations.

Box 2. Questions for future research

The TSF makes several predictions about acoustic processing in dyslexia that can be tested empirically:

- If the key integration windows in speech do correspond to the time frames of Gamma, Theta and Delta oscillations, is it possible to show that the dyslexic brain is unimpaired at sampling auditory signals at faster oscillatory rates such as Gamma, while simultaneously showing impairments at slower oscillatory rates such as Theta and Delta?
- Is it possible to find empirical evidence that perception of temporal fine structure is unimpaired in dyslexia, complemented by evidence that envelope perception is impaired, using the same stimuli (e.g. auditory chimera)?
- Is there a consistent right-hemisphere impairment in key language (temporal) areas, such as STS and STG, in dyslexia and, if so, how does the left hemisphere process stimuli for which the right hemisphere shows processing inefficiencies? Is there left-hemisphere compensation or atypical processing in both hemispheres?
- Is it possible to devise experimental techniques to investigate whether children with dyslexia perceive all the phonetic contrasts in human languages, as young infants do? Is it possible to predict the phonetic contrasts that are likely to be most affected in dyslexic perception based on current evidence for the role of low-frequency modulations in phoneme recognition?
- Is it possible to make predictions about which aspects of language processing should be preserved in dyslexia? For example, as TSF does not accord a key role to frequency perception, is perception of emotional prosody (which relies on F0) preserved whereas perception of intonational patterning (linked to rise time) is impaired?

phonology and language development, for example via subcortical structures such as the cerebellum [71]. Traditional educational practices, such as learning metrical poetry and singing nursery rhymes, might also entrain the Theta and Delta oscillatory networks that are (by hypothesis) impaired in dyslexia. Such interventions could begin very young, long before literacy tuition [72]. Furthermore, exploring how neuronal oscillations code key sensory parameters might be of utility for educational neuroscience beyond dyslexia; for example, in explaining the co-morbidities that are characteristic of developmental disorders of learning [73] (see also Box 2 for a list of outstanding questions).

Acknowledgements

I thank David Poeppel, Steven Greenberg and Ian Winter for many helpful discussions during the development of this framework, and Vicky Leong, Denes Szücs and Martina Huss for their comments. U.G. is supported by a Major Research Fellowship from the Leverhulme Trust and funding from the Medical Research Council (G0400574).

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