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Research Article

Increased Response to Altered Auditory Feedback in Dyslexia: A Weaker Sensorimotor Magnet Implied in the Phonological Deficit

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Purpose: The purpose of this study was to examine whether developmental dyslexia (DD) is characterized by deficiencies in speech sensory and motor feedforward and feedback mechanisms, which are involved in the modulation of phonological representations.
Method: A total of 42 adult native speakers of Dutch (22 adults with DD; 20 participants who were typically reading controls) were asked to produce /bep/ while the first formant (F1) of the /e/ was not altered (baseline), increased (ramp), held at maximal perturbation (hold), and not altered again (after-effect). The F1 of the produced utterance was measured for each trial and used for statistical analyses. The measured F1s produced during each phase were entered in a linear mixed-effects model.
Results: Participants with DD adapted more strongly during the ramp phase and returned to baseline to a lesser extent when feedback was back to normal (after-effect phase) when compared with the typically reading group. In this study, a faster deviation from baseline during the ramp phase, a stronger adaptation response during the hold phase, and a slower return to baseline during the after-effect phase were associated with poorer reading and phonological abilities.
Conclusion: The data of the current study are consistent with the notion that the phonological deficit in DD is associated with a weaker sensorimotor magnet for phonological representations.

Developmental dyslexia (DD)—with a prevalence estimate of approximately 7% across languages, a relatively common condition (Goswami, 2015)—is defined as a brain-based difficulty in acquiring fluent word-decoding skills (Lyon, Shaywitz, & Shaywitz, 2003) and interferes considerably with the level and amount of educational and occupational activities (Kutner et al., 2007). Despite adequate general cognitive abilities and appropriate educational opportunities, individuals with DD fail to automate the associations between graphemes and phonemes (Liberman, Shankweiler, & Liberman, 1989). There is considerable consensus that deficits in the development of phonological processing, and specifically the quality of or access to phonological representations, are implicated in DD (Boada & Pennington, 2006; Boets et al., 2013; Sprugevica & Høien, 2003). Notably, these phonological deficits are reported to largely persist into adulthood (Shaywitz et al., 1999; Wilson & Lesaux, 2001). To date, research on phonological abilities in DD has focused predominantly on either speech perception (e.g., Ziegler, Pech-Georgel, George, & Lorenzi, 2009) or production (e.g., Foy & Mann, 2012). Current models of speech production, however, suggest that the interaction between speech perception and production might be crucial in understanding the development of phonological representations (Guenther, Ghosh, & Tourville, 2006; Hickok, Houde, & Rong, 2011). Indeed, poorer performance by individuals with dyslexia on nonword repetition tasks (Messbauer & de Jong, 2003)—an integrated measure of speech perception and production—can be seen as an indication that perception–production interaction might be deficient in DD (Coady & Evans, 2008; Snowling, Chiat, & Hulme, 1991). As such, we propose that studying speech perception and production interaction is

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important in understanding the nature of the phonological deficit in DD and do so in the current study by assessing online adjustments of speech production following altered auditory feedback.

A Phonological Processing Deficit in DD

The evidence for phonological processing deficits in DD comes from a vast number of studies starting in the 1980s (Katz, 1986; Snowling, 1981). In more recent studies, phonological awareness and rapid naming are marked as important predictors of reading acquisition (Thompson et al., 2015; Van der Leij et al., 2013), although the strength of these predictors is reported to vary across orthographies (Caravolas, Lervåg, Defior, Seidlová Málková, & Hulme, 2013; Georgiou, Parrila, & Papadopoulos, 2008; Ziegler et al., 2010; but see Vaessen et al., 2010). Phonological awareness appears to develop on a continuum from being able to segment syllables and detect rhyme to individual sound segmentation and manipulation (Anthony & Francis, 2005). According to segmentation theory, the quality of phonological representations is dependent on this development, and deficient segmentation is associated with reduced reading ability (Metsala & Walley, 1998). In contrast, Elbro and colleagues (Elbro, 1996, 1998; Elbro, Borstrom, & Petersen, 1998) suggested that a lack in distinctness of these representations underlies the phonological deficit in DD. The deficient phonological representations have been described by various classifications such as immature, underspecified, fuzzy, fragile, nonrobust and indistinct, which indicates that the exact nature of the deficit in phonological representations is rather vague (e.g., Boada & Pennington, 2006). Adequate processing of speech input as well as articulatory output representations are implied in the development of phonological representations (Nittrouer, 1996). Consequently, it is often assumed that poor speech perception and production skills underlie the impaired phonological skills in DD (Foy & Mann, 2001, 2012; Mann & Foy, 2007; Preston & Edwards, 2010).

People with DD indeed show deficient abilities in speech perception and production. Many studies on speech perception point to reduced abilities to identify and discriminate between phonemes, both in optimal (De Weirdt, 1988; Godfrey, Syrdal-Lasky, Millay, & Knox, 1981) and in adverse listening conditions (Ziegler, Pech-Georgel, George, Alario, & Lorenzi, 2005; Ziegler et al., 2009). Although many studies focused on deficiencies in perceiving consonants, the perception and production of vowels is also less precisely defined (Bertucci, Hook, Haynes, Macaruso, & Bickley, 2003; Stark & Heinz, 1996). Although a large number of studies showed perception deficits in DD, it should be noted that speech perception deficits were not always found in the majority of people with DD (Manis et al., 1997), not for all phonetic contrasts (Cornelissen, Hansen, Bradley, & Stein, 1996), and not always in silent (Ziegler et al., 2009) or in noise conditions (Hazan, Messaoud-Galusi, & Rosen, 2012; Law, Vandermosten, Ghesquiere, & Wouters, 2014). Although the majority of studies show that people with DD have deficient perceptual abilities, resulting in less precise or degraded phonological representations, another perspective on the perception deficit comes from Serniclaes, Van Heghe, Mousty, Carré, and Sprenger-Charolles (2004). These authors provided evidence that people with DD remain sensitive to allophonic variants within phoneme categories, hence hindering phoneme-level representations from developing adequately (but see Ramus & Szenkovits, 2008). This theory suggests that speech perception is not degraded in DD on an acoustic level, but instead, not adequately attuned to the phonetic contrasts present in the native language. This hypothesis has further been supported using behavioral and neuroimaging measures in children at risk for DD (Noordenbos, Segers, Serniclaes, Mitterer, & Verhoeven, 2012a, 2012b). With regard to speech production, it has been shown that both articulatory skills (Catts, 1986, 1989) and oral motor skills are impaired in people with DD (Malek, Amiri, Hekmati, Pirzadeh, & Gholizadeh, 2013; Smith, Roberts, Lambrecht-Smith, Locke, & Bennett, 2006).

The nature of these phonological deficits is, however, challenged by a series of experiments by Ramus and Szenkovits (2008), suggesting that the phonological deficit is related to the access to, rather than the quality of, phonological representations. The authors claim that the phonological deficit becomes particularly apparent when tasks place strong demands on short-term memory, conscious awareness, and speed, which impedes fluent retrieval, extraction, and manipulation of phonological representations. The same study indicates that individuals with DD are equally unable to discriminate between foreign speech sounds, and hence questions the theory of an allophonic mode of perception in DD (posed by Serniclaes et al., 2004). In addition, neuroimaging findings from Boets and colleagues (2013) report impaired connectivity between frontal and temporal language areas, which hampers “efficient access to otherwise intact representations of speech sounds” (p. 1254). These studies do not reject a phonological deficit in DD, but suggest an alternative formulation of the impairment.

A frequently employed measure in the DD literature that provides an integrated, but nondecomposable, measure of speech perception and production is nonword repetition. Many consider nonword repetition to be primarily a measure of phonological short-term memory (e.g., Ramachandra, Hewitt, & Brackenbury, 2011); however, multiple processes are involved and reflected by nonword repetition. Each of these processes, including auditory processing, phonological processing, phonological storage, speech–motor planning, and speech output (Gathercole, 2006), were found to be related to DD. It can be assumed that poor or inaccessible phonological representations constrain the ability to adequately process the auditory input and produce the auditory output in nonword repetition tasks. Indeed, a deficient ability to repeat nonwords has been reported in a variety of language disorders (e.g., stuttering [Sasisekaran, 2013] and specific-language impairment [Edwards & Lahey, 1998]) and has consistently been shown in people with, or at risk for, DD (Catts, Adlof, Hogan, & Weismer, 2005; de Bree,

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Rispens, & Gerrits, 2007). A recent meta-analysis of the role of nonword repetition in DD also concluded that people with DD perform reliably worse on nonword repetition tasks, with large effect sizes when compared with chronological age-matched controls and small to moderate effects when compared with reading level–matched controls (Melby-Lervåg & Lervåg, 2012).

Current models of speech production suggest that it is not either speech perception or production that is important in the adequate development of phonological representations but that the interaction between perception and production is crucial for this development (Hickok, 2012; Houde & Nagarajan, 2011; Tourville & Guenther, 2011). Speech perception and production have largely been investigated separately in DD, but probing how perception and production interact might be vital in understanding the nature of the phonological deficit in DD. Attempts to study speech perception–production interaction have been made by administering a nonword repetition task in the context of a paired associate learning task, in which the same nonword had to be repeated multiple times. People with DD have been reported to acquire new phonological forms more slowly (Messbauer & de Jong, 2003), particularly in the case of phonologically complex nonwords (Mayringer & Wimmer, 2000). These deficiencies in nonword learning in people with DD could be a result of impairments in speech perception–production interactions, but they do not speak to the mechanism(s) underlying such a deficient interaction. In contrast, studies outside the DD literature have provided testable models about the formation and modulation of phonological representations (Guenther et al., 2006; Hickok et al., 2011) and applying these models to a DD population could potentially help to explain the nature of the phonological deficit.

Phonological Representations and the Role of Altered Auditory Feedback

Neurocomputational models have indicated that the quality of phonological representations depends on the integrity of speech sensory and speech motor feed-forward and feedback mechanisms (Hickok, 2012; Houde & Nagarajan, 2011; Tourville & Guenther, 2011). Two prominent and neurally plausible theories on how phonological representations are formed and adjusted are the Directions Into Velocities of Articulators (Guenther et al., 2006) and State-Feedback Control (Houde & Nagarajan, 2011) models. Although these models differ on some fundamental issues (e.g., whether the dynamics of the articulators are fully taken into account; for more discussion see Houde & Nagarajan, 2011; Riley-Graham, 2011; Tourville & Guenther, 2011), both models adopt a feed-forward trace that maps phonological representations to motor effectors, and a feedback trace that controls whether the sensory consequences of the speech realization match with the predicted sensory consequences. Mismatches are used to adjust the phonological representation. Once adequate feed-forward commands are formed, the inefficient and slow feedback system becomes redundant and will largely disengage (Guenther et al., 2006). Perturbations in auditory feedback induce a conflict between these motoric and sensory traces associated with phonological representations. Villacorta, Perkell, and Guenther (2007) hypothesized that humans use auditory goals in their motor planning. By measuring changes in an individual's speech productions under conditions of altered auditory feedback, we acquire information about an individual's auditory target associated with a particular phonological representation, and his or her ability to adjust his or her speech production to match those auditory goals (Guenther, 2015; Niziolek & Guenther, 2013). As such, this paradigm enables us to quantify aspects of phonological representations.

The presence and quality of auditory feedback during development has indeed been shown to significantly affect skills in speech production. For instance, there is evidence that prelingual deaf children have problems in developing intelligible speech skills (Oller & Eilers, 1988) and that speech production of children with cochlear implants, who receive better auditory input, is often more adequate than that of children with strong hearing loss using hearing aids (Baudonck, Dhooge, D'haeseleer, & Van Lierde, 2010). Several studies have shown that delaying auditory feedback or masking auditory feedback by noise affects speech production both in typical (Amazi & Garber, 1982; Chon, Kraft, Zhang, Loucks, & Ambrose, 2012; Sasisekaran, 2012) and clinical populations (Hudock & Kalinowski, 2014).

With regard to DD, reading under conditions in which auditory feedback was masked (by playing familiar tunes over headphones; Breznitz, 1997) or in which the participants' pitch was shifted (Carter, Rastatter, Walker, & O'Brien, 2009; Rastatter, Barrow, & Stuart, 2007) significantly increased reading accuracy, fluency, and comprehension in both children and adults with DD. Although these studies show that people with DD process auditory feedback differently—which apparently impedes reading—they are not informative as to the mechanism behind this difference. Manipulating auditory feedback on a trial-by-trial basis can be seen as promising in this respect because it allows us to examine how auditory feedback is implicated in adjusting phonological representations dynamically (MacDonald, Johnson, Forsythe, Plante, & Munhall, 2012; Villacorta et al., 2007).

Studies in which *formants*—spectral peaks in the sound system—are manipulated and fed back in real time may provide better insight into the mechanisms of adjusting phonological representations. In classical studies it has been found that formants largely determine the identity of vowels and that manipulating the first formant (F1) can cause one vowel to sound like another (Delattre, Liberman, Cooper, & Gerstman, 1952). Formant adaptation studies generally consist of a baseline phase in which the normal distribution of the participants' formant production is measured. This phase is followed by a ramp and hold phase in which one or more formants are gradually adapted (either increased or decreased) over trials and fed back in real time. The last phase consists of trials without altered feedback to measure whether the participants' response returned to baseline. It has been found that participants usually adapt to the auditory

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perturbation by shifting their formant production in the opposite direction of the manipulation (Houde & Jordan, 1998, 2002; MacDonald et al., 2012; Purcell & Munhall, 2006; Villacorta et al., 2007). There is evidence that participants are able to modify their response to correct for multiple auditory transformations and that the modification of a phoneme tends to generalize across different words (Rochet-Capellan & Ostry, 2011). These production changes are strong enough to be partly retained when feedback is blocked by noise (Houde & Jordan, 2002). When feedback is back to normal, the return to baseline was found to be gradual and not dependent on the number of trials of maximal perturbation (Purcell & Munhall, 2006; Villacorta et al., 2007). Another important issue related to the amount of adaptation is whether the auditory perturbation changes the phoneme identity or varies only on a subphonemic level. Near and across-phoneme boundary perturbation has been reported to result in stronger adaptation (Niziolek & Guenther, 2013). Niziolek and Guenther (2013) report these effects in the context of the native language magnet theory (also known as the perceptual magnet theory; Feldman, Griffiths, & Morgan, 2009; Kuhl, 1991). Its core claim is that a phonetic category prototype functions as an attractor (i.e., magnet) that warps the psychoacoustic space, resulting in poorer discriminability for neighboring stimuli near the category prototype (i.e., a narrower space) and better discriminability farther away from the prototype (i.e., a stretched space). Perturbations in the auditory signal are hence expected to elicit a stronger response when the presented auditory stimulus is farther away from the phonemic category prototype.

It should be noted, however, that the amount of adaptation in the studies varies widely across individuals, and several accounts exist for this variability. For instance, Burnett and colleagues (Burnett, Freedland, Larson, & Hain, 1998; Burnett, Senner, & Larson, 1997) reported that some participants changed their formant production in the direction of the adaptation. It was suggested that these participants might use an external auditory reference for adequate formant frequencies, rather than an internally set reference (Burnett et al., 1998). Alternatively, Lametti, Nasir, and Ostry (2012) showed that individuals differ in their preferential reliance on auditory or somatosensory feedback, which could well explain why some individuals do and some do not adapt under conditions of altered auditory feedback. This variability in response is certainly not unique to speech perception–production interaction. For instance, the McGurk effect, a traditional measure of audiovisual integration and well known in the DD field, shows a dramatic diversity of responses both across individuals and across used stimuli (Mallick, Magnotti, & Beauchamp, 2015).

The aforementioned studies show how auditory feedback affects speech production in the typical population. Studies on these formant adaptation effects in clinical disorders are scarce. Using simulations, Civier, Tasko, and Guenther (2010) showed that stuttering may be caused by deficits in speech feed-forward and feedback mechanisms (as explicated in the Directions Into Velocities of Articulators model). Their study suggests that stutterers rely too heavily on the auditory feedback trace to control speech and hence are more sensitive to changes in auditory feedback. Another relevant clinical group concerns specific language impairment (SLI), which shares many characteristics with DD, including a phonological processing deficit (Bishop & Snowling, 2004; Edwards & Lahey, 1998). In a small case-control comparison, it was found that children with SLI showed more adaptation than their typically developing peers when the frequency of the F1 of a vowel was altered, and furthermore did not fully return to baseline when feedback was back to normal (Holmes, 2012). To date, however, no attempt has been made to examine whether DD is characterized by differences in response to this altered auditory feedback to shed light on the nature of the phonological deficit.

Present Study

The present study aimed to gain better insight into the nature of the phonological deficit in DD by examining the ability to modulate existing phonological representations in adults with DD and participants who were typically reading (TR) controls. If the phonological deficit in DD is characterized by deficiencies in speech perception–production interaction, individuals with DD should adjust their productions differently when auditory feedback (i.e., speech perception) is manipulated.

To assess these speech feed-forward and feedback mechanisms, we used an altered auditory feedback design (Houde & Jordan, 1998; Purcell & Munhall, 2006; Rochet-Capellan & Ostry, 2011), changing the perception of the F1 of the vowel in the participants' production of the word /bep/. After a first phase, during which the F1 of the /e/ was not altered (i.e., baseline), the frequency of the F1 gradually was increased during the second phase (ramp) and was held at maximal perturbation in the third phase (hold). Last, the manipulation was switched off, and the frequency of the F1 fed back to the participant was unchanged from their production for the last phase of the experiment (after-effect). Typically, participants will respond to the manipulation by adjusting the frequency of the F1 of their productions in the opposite direction. Changes in formant production in response to alterations in auditory feedback are indicative of how perceiving auditory manipulations interacts with producing speech. Differences in the amount of adaptation between individuals with DD and typical readers could be caused by several different factors. For instance, both stronger and weaker adaptation during the ramp phase could be purely related to perceptual deficiencies in DD (allophonic perception or degraded perception, respectively), but also to motor impairments (e.g., unstable or rigid motor commands). The pattern of the responses to the different phases of feedback, however, could clarify whether DD is characterized best by a perceptual deficit, a motor deficit, or a deficient interaction between perception and production.

The hypothesized overreliance on auditory feedback in stuttering (Civier et al., 2010) as well as the stronger response to altered feedback in SLI (Holmes, 2012) led us to expect a stronger response to altered auditory feedback

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in adults with DD during the ramp and hold phase. This would also be in line with the allophonic mode of perception in DD proposed by Serniclaes and colleagues (2004). In contrast, a reduced response to altered feedback in the ramp and hold phase, we think, would be consistent with the "phonological access" deficit (Boets et al., 2013; Ramus & Szenkovits, 2008, p. 137). The expectations for the aftereffect phase were harder to explicate on these accounts. If DD is indeed characterized by an overreliance on auditory feedback or an allophonic perception mode, a stronger return to baseline might be expected. Nonetheless, children with SLI did not return to baseline to the same extent as typically developing controls (Holmes, 2012), and there may be parallels in DD. This pattern of responses would fit with a more general hypothesis predicated on the notion that, irrespective of the mechanism, phonological representations in DD are of lower quality and may act as weaker attractors (Anderson, Morgan, & White, 2003; Baker, Trofimovich, Mack, & Flege, 2002) or perceptual magnets (Iverson & Kuhl, 2000; Kuhl, 1991). On that notion we might expect stronger adaptation and weaker de-adaptation in DD. In addition to examining these group responses, we explored whether individual differences in the response to altered auditory feedback were associated with phonological and reading abilities. Given our assumption that this response taps into aspects of phonological representations that are relevant to reading, we expected this to be the case.

Methods

Participants

A total of 20 TR university students (14 women, six men; $M_{\text{age}} = 22.32$ years; $SD_{\text{age}} = 2.7$ years) and 22 university students with DD (17 women, five men; $M_{\text{age}} = 23.13$ years; $SD_{\text{age}} = 2.7$ years) were included in this study. All participants were native Dutch speakers. Participants were approached via email as they took part in earlier studies in our lab and had consented to be contacted in this manner. As part of these earlier studies, participants were recently (<12 months) characterized in terms of reading and phonological awareness. All participants received course credits or monetary compensation for participation.

To be included in the DD group, participants had to be officially diagnosed and perform below the 30th percentile on reading accuracy or below the 30th percentile on reading time. TR students were required to perform above these thresholds. In addition, all participants passed the hearing screening, perceiving pure tones presented at less than 30 dB at 250 Hz, 500 kHz, 1 kHz, 2 kHz, and 4 kHz in both ears. One participant was excluded because of a cold, which significantly affected speech production. Participant characteristics are provided in Table 1.

Materials

Reading

To assess reading ability, all participants were asked to read aloud a 582-word text, a subtest of a standardized Dutch test battery for the diagnosis of DD in adolescents and adults (Test voor gevorderd Lezen en Schrijven [Test for advanced reading and writing], Depessemier & Andries, 2009). Guttman split-half reliability for reading accuracy and reading time was adequate (.77 and .90, respectively). The text was divided into paragraphs, and the number of phonologically complex and unfamiliar words increased for each paragraph to evoke reading errors. The produced reading was recorded to optimize scoring accuracy. Omissions, additions, replacements, and inversions were counted as errors and were carefully determined by listening to the recorded audiofiles. Norm scores from the manual were used to calculate percentiles to determine whether the participants fulfilled the inclusion criteria. The raw test scores for the number of errors and the time to complete the task (in seconds) were used for all statistical analyses.

Phonological Awareness

Phonological awareness was measured using the phonological reversal task from the same test battery (Test voor gevorderd Lezen en Schrijven [De Pessemier & Andries, 2009]). The reliability of this task had been calculated at $r = .90$ (Guttman split-half reliability). In each trial, two audio-recorded items were presented to the participant who was asked to indicate (yes-no) whether the second item was the phonological reverse of the first. A next trial was started after the experimenter pressed the button to continue. The task started with six practice trials during which feedback was provided. The experimental part consisted of 20 items for which accuracy per item and total duration for all items was registered. Total number correct (accuracy) and the time to complete the task (in seconds) are reported.

Altered Auditory Feedback Task

In the altered auditory feedback task, participants were asked to produce the word /bep/ when a specific blue cartoon figure popped up on the screen. In case of other cartoon figures, participants were asked to remain silent. The blue figure appeared in ±70% of the presentations, and speech was automatically recorded for 2 s to capture the /bep/ production. Participants were explicitly instructed to say nothing else than /bep/ until the experiment was finished. A total number of 95 productions were collected for each participant. The participants' speech production was manipulated and fed back in real time with approximately 10 ms of delay.

To ensure that the participants perceived the altered signal instead of their own voice, the speech signal was amplified and accompanied by 70 dB of pink noise. The pink noise further reduced the perception of the air and bone conduction of the produced signal. The experiment consisted of four phases. The first phase (baseline) consisted of 30 trials during which feedback was not altered. The second phase (ramp) consisted of 25 trials during which frequency of the F1 of the speech production was gradually and imperceptibly shifted until a maximal increase of approximately 30% was reached. The third phase (hold) consisted of 25 trials during which the F1 was maximally

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Table 1. Participant characteristics for the readers with developmental dyslexia (DD) and the typically reading (TR) controls.

Characteristic	TR, *n* = 19 *M*	TR, *n* = 19 *SD*	DD, *n* = 22 *M*	DD, *n* = 22 *SD*	Significance *t* or *U* test
Reading (errors)	8.63	4.46	16.68	7.05	$t = 4.288^{**}$
Reading (time)[a]	243.74	8.99	303.41	27.90	$U = 2.0^{**}$
Phonological awareness (accuracy)	16.89	2.16	17.18	1.99	$t = -0.443$
Phonological awareness (time)[a]	97.58	17.64	123.68	32.79	$U = 87.5^{*}$

Note. *M* = mean; *SD* = standard deviation.

[a]Mann–Whitney *U* test as the distribution in the DD group was nonparametrical.

$^{*}p < .01$. $^{**}p < .001$.

altered. The last phase (after-effect) consisted of 15 trials during which the altered feedback was completely shut off.

Equipment. A microphone (e835 FX; Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) was placed in close proximity to the mouth and participants wore a headphone (HD360 Pro; Sennheiser Electronic GmbH & Co. KG). The produced speech was amplified using the microphone preamplifier (Tube UltraGain MIC100, Behringer GmbH, Kirchardt, Germany) and split into two streams. In one stream, the F1 was altered by a sound signal processor (VoiceOne; TC Helicon Vocal Technologies, Victoria, British Columbia, Canada). The signal in the other stream was unaltered. Using analog filters (852; Wavetek, San Diego, CA), we applied a low-pass filter on the altered stream (<1 kHz; F1 of /e/ is below 1 kHz) and a high pass filter (>1 kHz) on the unaltered stream. The sound signal processor was controlled via midi in an external audio device (Roland UA-25 EX, Hamamatsu, Japan). Because the sound signal processor takes approximately 10 ms to alter the signal, the high-frequency stream was delayed by 10 ms using an audio delay box (DataVideo AD100; Datavideo Technologies Europe BV, Utrecht, the Netherlands). Finally, the two streams and the noise signal were mixed (Skytec STM3004; Skytronic Ltd, Manchester, UK) and amplified through a headphone amplifier (HA400, Behringer GmbH).

Procedure

Informed consent was signed after the participants arrived at the lab. Participants were then positioned in front of the microphone and a monitor. Subsequently, the amplification of the signal was increased as much as was still comfortable for the participant. The noise volume always remained at 70 dB. All participants started with a 15-trial practice block and when everything was clear, progressed to the experimental items. After the experiment, participants were asked whether they noted anything special during the experiment, and if not, more specifically, whether they noted anything remarkable about the sound. In case both answers were negative, we explained exactly what we did and asked whether the participant now recognized the manipulation. None of the participants confirmed to be aware of or recognized the manipulation. Participants left after a short debriefing.

Analyses

Given the considerable variability in the amount of adaptation observed across individuals, as well as the assumed fundamentally different underlying mechanisms of the presence or absence of the typical adaptation response (Burnett et al., 1997; Lametti et al., 2012), we first examined whether a similar number of people with DD and TR controls showed the typical adaptation response when the frequency of the F1 was altered. Then, using the data from these adapters only, we asked whether people with DD differed from TR controls in the magnitude of adaptation for the distinct phases of the experiment.

The F1s were calculated using linear predictive coding (Rabiner & Schafer, 1978) in Matlab 2014 (The MathWorks Inc., Natick, MA) after the first author manually indicated the center of each vowel. Outlying formants (>3 *SD,* calculated per phase) were removed from all of the analyses. We then determined for each participant whether the response should be classified as an adapting or a nonadapting response to the feedback alteration. This was determined by comparing the F1 frequency during the hold phase with the baseline phase (one-sided *t* test; $\alpha = .05$). The typical response is a significant depression of F1 in the produced vowel sound in response to the manipulation of F1 increase. We categorized participants who showed this typical adaptive behavior as adapters. Nonadapters were participants who either did not respond to the perturbation at all (possibly as a result of relying more heavily on somatosensory feedback [see Lametti et al., 2012]) or followed the manipulation in the same direction (possibly as a result of external auditory goals [see Burnett et al., 1997, 1998]). Independent *t* tests analyses were performed to ensure that the frequency and variability of the baseline F1 productions were comparable across the TR and DD groups. In addition, independent *t* tests were run to ensure that behavioral measures (reading and phonological awareness) did not relate to (non-)adapting to the manipulation. Chi-square tests were performed to ensure the number of adapters between groups as well as the gender distribution within groups were

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comparable. All further analyses were performed on adapters only.

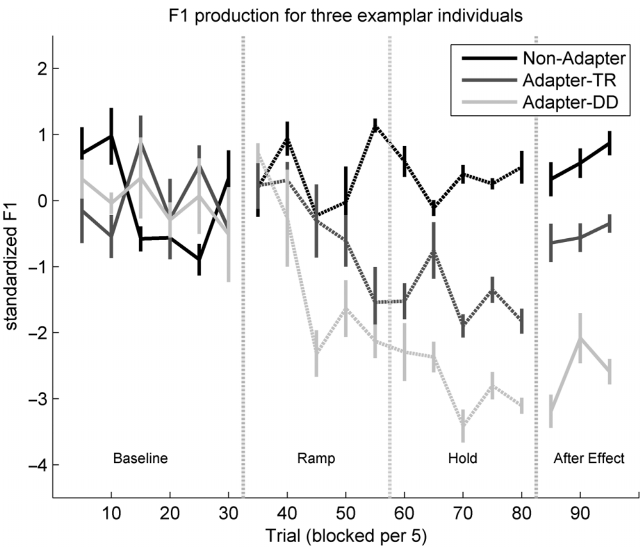
We performed linear mixed effects modeling only using the lmer function of the lme4 package (Bates, Maechler, Bolker, & Walker, 2014) in R (R Core Team, 2014) on the raw F1 scores per feedback phase with gender, trial, phase of feedback, and group (i.e., DD vs. TR) as fixed factors. Gender was added to the models because formant frequencies are reported to be systematically lower in men (Peterson & Barney, 1952). The feedback phase is entered as a fixed factor, rather than an interval variable, to allow differentiating between the absence of altered feedback in the baseline and after-effect phase. The best model fit was obtained by conduction analyses of variance on sequential models, starting from simple (by entering main effects) and gradually moving to complex models (by entering different interaction effects). Standardized F1 scores (by using the average and standard deviation of the baseline phase) were only used for graphical purposes and correlational analyses.

Exploratory correlational analyses were performed to relate individual differences in response to altered auditory feedback to differences in phonological and reading abilities, both within and across groups. Particularly important in studying the robustness of phonological representations is how fast participants deviate from baseline (calculated using the slope in the ramp phase), how much participants ultimately adjust (calculated using the mean standardized frequency of the F1 during the hold phase), and how fast participants return to baseline (calculated using the slope in the after-effect phase). The slopes were calculated, for these correlational analyses only, by dividing the difference between the average of the first and last five trials of a phase by the total number of trials in that phase.

Results

Our first research question concerned the number of people showing the typical adaptation response to altered auditory feedback. There was considerable variability in response to the manipulation: A total of 25 (61%) participants (12 TR [63%]; 13 DD [59%]) showed the typical adaptation response (decreasing F1 in response to an increased F1 during altered auditory feedback), whereas 16 (39%) participants (7 TR [37%]; 9 DD [41%]) did not. The total number of adapters and nonadapters did not significantly differ between groups (χ^2 = .071, p = .790). Figure 1 shows individual examples from the different phases of the experiment for a nonadapting individual with DD, a typical-reading individual, and an individual with DD. Independent t tests showed that the adapters and nonadapters did not significantly differ on the reading and phonological tests (all p values >.08). Also, the gender distribution within groups was not significantly different between adapters and nonadapters for the TR group (χ^2 = .022, p = .882), nor for the DD group (χ^2 = .087, p = .769).

Figure 1. Examples of the responses of a nonadapting individual with developmental dyslexia (DD), a participant who was a typically reading (TR) control, and a participant with DD. F1 = first formant.



Our second research question focused on the frequency of F1 productions across the different phases of the experiment for the adapters only (as shown in Figure 1), for which we performed linear mixed-effects modeling. Group (TR vs. DD), trial, gender (male vs. female), and phase of feedback (baseline, ramp, hold, after-effect) were entered as fixed factors. As random effects, participants were added, along with by-participant slope adjustments for feedback phase and trial (Barr, Levy, Scheepers, & Tily, 2013). The best model fit was obtained by likelihood ratio tests using the maximum likelihood criterion. Satterthwaite approximations were used to estimate p values within the model (Kuznetsova, Brockhoff, & Christensen, 2015). The resulting model had gender and a Feedback × Trial and a Feedback × Group interaction entered as fixed factors in the model. This model was significantly better than a model with gender and trial plus a Feedback × Group interaction (p < .001) and better than a model with gender, group, and a Feedback × Trial interaction (p < .001). Adding three-way or four-way interactions did not significantly improve the model fit.

In accordance with the expectations, women had a significantly higher F1 production than men (β = 132.66, SE = 21.021, p < .001), and F1 production was significantly decreased in the hold phase (β = −22.30, SE = 6.011, p < .001) and after-effect phase (β = −24.49, SE = 6.052, p < .001). Trial had a small but significant effect on F1 production (β = −0.29, SE = .111, p < .01). No main effects were found for group, DD versus TR (β = −27.80, SE = 19.567, p = .168), and for the ramp phase (β = −1.54, SE = 4.007, p = .702). Significant Feedback × Trial interactions were found for the ramp phase (β = −0.66, SE = .159, p < .001) and the after-effect phase (β = 1.56, SE = .289, p < .001), but not for the hold phase (β = −.25, SE = .159, p =.123). Interestingly, a stronger decrease in F1 frequency during the ramp phase (β = −9.67, SE = 4.63, p = .047), and a weaker increase of F1 frequency during the after-effect phase

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($\beta = -20.30$, *SE* = 7.55, $p = .013$) was revealed for the DD group when compared with the TR group, whereas no significant group difference was observed during the hold phase ($\beta = -9.86$, *SE* = 7.754, $p = .215$). Including the nonadapters yielded an insignificant model, possibly because of the increased variance, but the general pattern remained the same for the after-effect. Importantly, the frequency of F1 productions during the baseline phase also did not differ between the TR group ($M_{\text{F1}} = 664.90$ Hz; $SD_{\text{F1}} = 70.08$) and the DD group ($M_{\text{F1}} = 694.95$; $SD_{\text{F1}} = 76.96$), $t(23) = -1.018$; $p = .319$. Similarly, no significant difference in the variability of the productions between groups during the baseline was observed (TR: $M_{\text{SD\_F1}} = 20.23$; $SD_{\text{SD\_F1}} = 8.33$; DD: $M_{\text{SD\_F1}} = 20.32$; $SD_{\text{SD\_F1}} = 6.67$), $t(23) = -.704$; $p = .489$. All coefficients of the final model are summarized in Table 2 and the results are displayed in Figure 2.

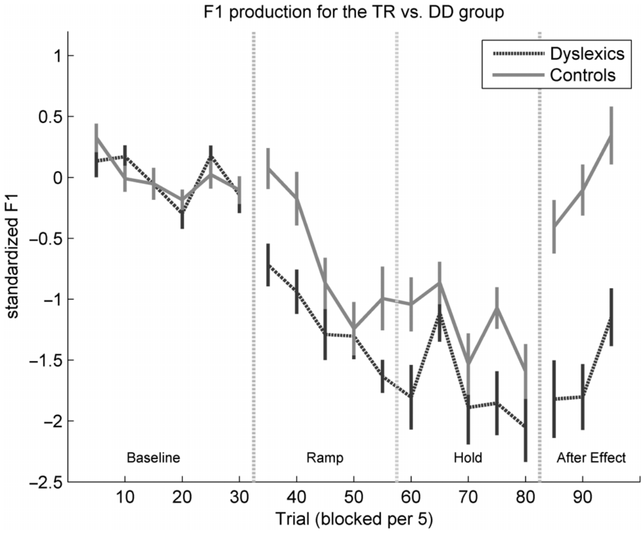
To address our third research question, we performed a number of exploratory correlation analyses to investigate whether the slope and magnitude of the standardized response to the manipulation related to performance on reading and phonological awareness tasks. The slope of the response during the ramp and after-effect phase and the averaged response during the maximally altered feedback signal were correlated with the reading and phonological awareness scores for the sample as a whole, and for the DD and TR groups separately. The sample as a whole showed a significant correlation between the average frequency of the F1 during the hold phase and the number of reading errors made ($r = -.45$, $p = .022$). A stronger response to the manipulation was related to more reading errors (see Figure 3a). The DD group showed significant correlations between the slope in the ramp phase and phonological awareness accuracy ($r = .57$, $p = .044$; see Figure 3b), and between the slope in the after-effect phase and the number of reading errors ($r = -.64$, $p = .019$; see Figure 3c) and reading time ($r = -.71$, $p = .007$; see Figure 3d). A steeper slope away from baseline in the ramp phase and a shallow slope toward baseline in the after-effect phase were thus associated with poorer phonological and reading abilities in the DD group. The control group did not show any significant correlations.

Table 2. The fixed-effects coefficients of the final model (Gender + Feedback × Trial + Feedback × Group).

Fixed effect	β	*SE*	*p*
Intercept	569.78	21.198	<.001
Gender, females	132.66	21.021	<.001
Group, DD	27.80	19.567	.168
Trial	−0.29	0.111	<.01
Feedback ramp	−1.54	4.007	.702
Feedback hold	−22.30	6.011	<.001
Feedback after-effect	−24.49	6.052	<.001
Feedback Ramp × Trial	−0.66	0.159	<.001
Feedback Hold × Trial	−0.25	0.159	.123
Feedback After-Effect × Trial	1.56	0.289	<.001
Feedback Ramp × DD	−9.67	4.629	.047
Feedback Hold × DD	−9.86	7.754	.215
Feedback After-Effect × Trial	−20.30	7.55	.013

Note. DD = developmental dyslexia; *SE* = standard error.

Figure 2. The adapted responses to the altered auditory feedback during the course of the experiment for adults with developmental dyslexia (DD; dashed line) and typically reading (TR; continuous line) controls. Plotted is the average frequency of the first formant (F1) per group, averaged per five trials. Error bars represent ± 1 standard error.



Discussion

In this study, we examined speech feed-forward and feedback mechanisms—assumed to be critical for the formation and adjustment of phonological representations—in adults with DD and TR controls using an altered auditory feedback paradigm. We found that about 61% of all participants showed the typical adaptation response to the F1 increase in the altered feedback phase. The number of adapters and nonadapters did not significantly differ between the two groups, and this could not be explained by differences in behavioral abilities or gender distribution. Furthermore, it was evidenced that people with DD adapted stronger in the ramp phase and returned to baseline to a lesser extent when feedback was back to normal when compared with the TR group. Finally, exploratory correlational analyses showed that a faster deviation from baseline during the ramp phase, stronger adapting response during the hold phase, and a slower return to baseline during the after-effect phase were associated with poorer reading and phonological abilities.

This finding, that DD is related to stronger adaptation under conditions of altered feedback and to weaker de-adaptation when feedback is back to normal, is not fully explained by the allophonic theory of speech perception in DD discussed in the introduction. This view predicts that individuals with DD are (unconsciously) more sensitive to acoustic variation within a phoneme category. This explanation fits with the stronger adaptation we found in the

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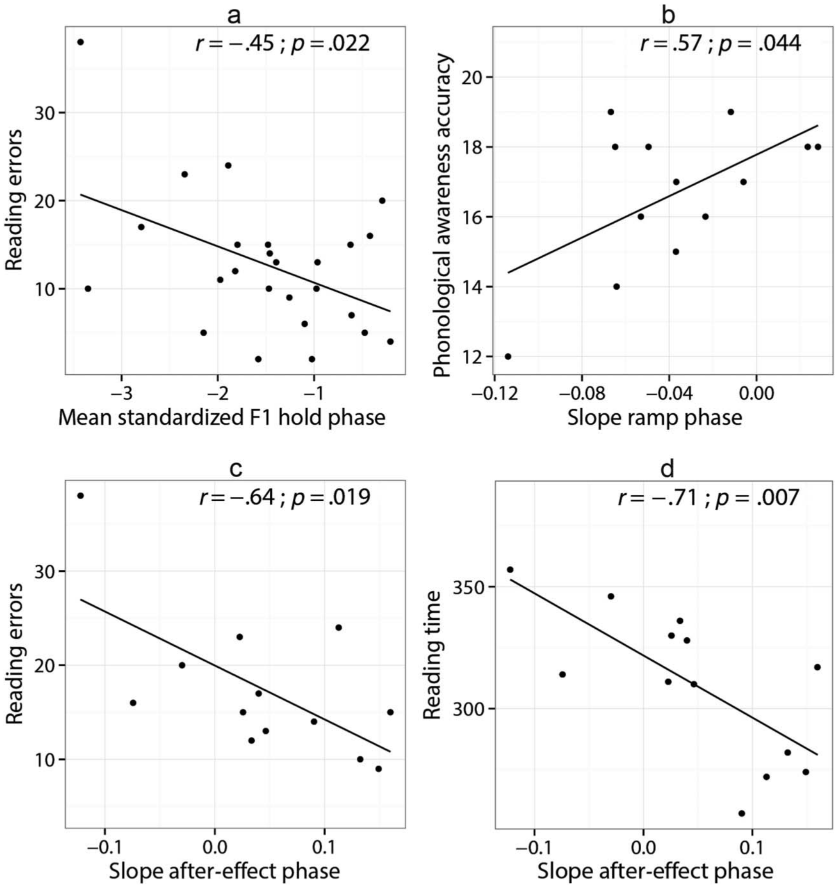
Figure 3. Correlations between (a) the averaged response during the hold phase and reading errors for the whole sample (N = 25) and the slope in the ramp phase and phonological awareness accuracy (b), the slope in the after-effect phase with reading errors (c) and reading time (d) for the developmental dyslexia (DD) group only (n = 13). F1 = first formant.



ramp phase because the perturbation in this study remained within a phoneme category. Arguing against this explanation is the lack of a significant difference between groups for the hold phase. If individuals with DD have an allophonic mode of speech perception, a large difference should be present also for the hold phase. Even more important, we think that this explanation predicts a stronger return to baseline for the people with DD, whereas the opposite was found. The stronger response to altered auditory feedback in the ramp phase is at least partially consistent with an overreliance on auditory feedback, another model discussed earlier. This interpretation corresponds to neurocomputational models showing that stuttering, reported to share characteristics with DD (Malek et al., 2013), is characterized by a bias toward feedback control (Civier et al., 2010). This overreliance, however, on auditory feedback could also not explain the weak de-adaptation in DD in the after-effect phase.

In addition, the current study does not support the claim that the phonological deficit should be reformulated as entirely a deficit in access to phonological representations, as proposed by Ramus and Szenkovits (2008) and Boets et al. (2013). First, Ramus and Szenkovits (2008) claimed that the phonological deficit becomes apparent when tasks place a strong demand on short-term memory, conscious awareness, and speed. The task employed in this study requires very minimal short-term memory, has no time constraints, and the evoked response, when present, remained completely unconscious for all participants. Second, if there is an (unconscious) impaired access to phonological representations, individuals with DD should be less susceptible to alterations in feedback in this perception and production task, whereas the opposite is found for the ramp phase and no differences were found in the hold phase. This study shows in a novel way that the quality of the representations themselves is impaired in DD. Again, although deficits in access and retrieval are characteristics of DD as Ramus and Szenkovits suggest (2008), these findings also suggest suboptimal phonological representations given the full set of findings.

As noted in the introduction, there are models that may be more parsimonious here. Thus, it may be that the current results fit best with the framework of the native language magnet theory (Kuhl, 1991; Feldman et al., 2009;

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Guenther & Gjaja, 1996), which claims that a phonetic category prototype functions as a perceptual magnet, resulting in poorer discriminability for neighboring stimuli close to the prototype. Importantly, a recent update of the theory (native language magnet theory–expanded; Kuhl et al., 2008) argues for a strong interaction between the perceptually formed representations and their associated speech production traces. According to Kuhl and colleagues (2008) the development of motor commands is based on vocal imitation and experience with language. The results of articulatory movements are related to acquired auditory targets that yield a learned mapping between the auditory and articulatory targets. Deficiencies in the perceptual warping of the acoustic space hamper this mapping and could hence affect the adequacy of both the feedback and feed-forward system. As such it might be more appropriate to conceptualize the magnet as a sensorimotor magnet rather than purely a perceptual magnet. Recently, Niziolek and Guenther (2013) provided evidence that the response to altered auditory feedback is significantly influenced by the perceptual magnet effect, with responses up to three times bigger for near-phoneme boundary compared to near-phoneme center perturbation. The results of the current study suggest that the phonological deficit in DD is associated with a weaker magnet (i.e., deficient warping), which makes it easier for individuals with DD to be moved away from the prototype (hence, stronger adaptation) and harder to return to baseline (hence, weaker de-adaptation). In addition, a weaker magnet in DD does not necessarily suggest a difference in the hold phase of the current experiment, which is in correspondence with the results of this study. Once the magnet loses its attracting influence on the perception and production of the utterance, all individuals plateaued at a similar amount of adaptation for both groups. An alternative account for the nonsignificant difference during the hold phase is that the phonological adaptation has not reached its maximum. Lametti, Rochet-Capellan, Neufeld, Shiller, and Ostry (2014) showed that individuals continue to adapt for at least 200 trials. Interestingly, this weaker magnet theory not only offers an explanation for why individuals with DD perform more poorly on speech identification tasks (for instance, during speech-in-noise tasks; Ziegler et al., 2009), but also why individuals with DD perform better at discriminating stimuli in conditions where phonemic categories are weakly perceptible (Serniclaes et al., 2004). Forming stable grapheme–phoneme associations is a crucial step in reading development (Puolakanaho et al., 2007) and a weaker magnet could hinder the formation of these associations. Specifically, if a grapheme is coupled to a variant sensorimotor target (i.e., less strongly attracted to the center of a phoneme category) the grapheme–phoneme association will be noisier and hence less efficient.

A number of steps should be undertaken in future research to further support this finding and to disentangle the contribution of the different explanations. First, the current study applied altered auditory feedback only and approximately 39% of the participants did not show the typical adaptation response. Although this percentage of nonadapters is not abnormal (e.g., Lametti et al., 2012; Ito, Coppola, & Ostry, 2016), a relatively high number of participants had to be excluded from the analyses. This might affect the generalizability of the findings to the DD population as a whole. Nonetheless, because nonadapters are equally distributed across groups, the nonadapting response seems not to be related to DD. The adaptation applied in this study was in the direction of a nonexisting vowel in the Dutch language and we believe this could (partly) explain the percentage of nonresponders. Including altered somatosensory feedback as a condition would likely allow analyzing the response for almost all participants (Lametti et al., 2012). Moreover, it will also indicate whether the current results are restricted to the auditory modality or extend to somatosensory feedback. The latter has been suggested for stuttering (Civier et al., 2010) but needs more thorough examination.

Second, it is important to note that in our study the perturbation of auditory feedback did not cross a phoneme boundary. The manipulation increased the F1 of the /e/ vowel in the direction of the English /ae/ vowel, which does not exist in Dutch. Crossing phoneme boundaries not only increases the magnitude of the response (Niziolek & Guenther, 2013) but also would allow us to elucidate on both the weaker magnet hypothesis and the allophonic perception theory of DD (Serniclaes et al., 2004). Future studies could include both within and across phoneme boundary perturbations. A larger difference in adaptation between DD and TR groups for the within-phoneme boundary manipulation as compared to the across-boundary manipulation during a ramp phase could be taken as corroborating evidence for an allophonic perception mode. The native language magnet hypothesis suggests that at a certain point after crossing the phoneme boundary, the altered percept should be attracted to the other phoneme and this probably results in stronger compensation. A relatively stronger response for a perturbation crossing a phoneme boundary in the TR group when compared with the DD group could be taken as supporting evidence for the weaker magnet in DD. In addition, and to more explicitly examine the complementarity of or contradiction between these different characterizations of the phonological deficit, future studies should include measures that directly assess the allophonic mode of perception and of phonological access.

Third, as expected, individual differences in phonological and reading abilities were associated with the response to altered auditory feedback. A stronger response was found to be associated with poorer phonological and reading skills. In this study, we did not include established and explicit measures of speech perception, speech production, or nonword repetition. Relating these measures to the response to altered auditory feedback could further elucidate on speech perception–production interaction impairments in DD and could clarify the nature of the phonological deficit.

Last, individual differences in the direction and magnitude of the effect should also be examined across different

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developmental phases. The present results are obtained in an adult population. Nonetheless, the speech perception–production interaction is thought to be particularly crucial in early development in which phonological representations are formed and established. Similar studies should be conducted in several childhood populations (e.g., typical, at risk for DD, before and after literacy instruction, etc.) to see whether, when, and how speech feed-forward and feedback mechanisms are involved in the adequate development of phonological representations.

To our knowledge, this is the first study that explicitly investigates whether and how speech perception–production interaction is malfunctioning in DD. We reported that people with DD adapted more strongly in response to altered auditory feedback and de-adapted more weakly when feedback was back to normal and that individual differences in this response were associated with phonological and reading abilities in adults with DD. We interpret these results as evidence for a weaker magnet in DD that is reflected in weaker sensorimotor attraction to the center of the phoneme category. Although it is clear that much work is needed to establish this finding in different populations with improved methodologies, this study opens a promising new line of research into the origins of DD.

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