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Phonological Decoding and Morpho-Orthographic Decomposition: Complementary Routes During Learning to Read

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Introduction

Visual word recognition is a key component of reading proficiency (Cutting & Scarborough, 2006). In most models of reading acquisition, beginning readers initially have access to the meanings of words by applying spelling-to-sound translation on letters decoded serially (Ehri, 1995; Grainger & Ziegler, 2011; Seymour, 1997; Share, 1995; Ziegler & Goswami, 2005). Each successful decoding through this orthography-phonology-meaning route is assumed to help develop a direct connection between orthography and meaning, which is no longer mediated by using phonological units (Share, 1995). The emergence of a direct orthography-meaning route is thought to support more automatic word recognition processes for more efficient silent reading for meaning (Coltheart et al., 2001; Diependaele et al., 2010; Grainger & Ferrand, 1994; Grainger & Holcomb, 2009; Grainger & Ziegler, 2011; Perry et al., 2007, 2010). As described by Grainger and Ziegler (2011), automatic visual word recognition is achieved principally via the parallel processing of letter identities and their positions thus delegating phonological decoding to a secondary role.

More precisely, Grainger and Ziegler's (2011) dual-route model hypothesized that skilled readers process written words using two types of sublexical orthographic representation. On the one hand, a coarse-grained orthographic code enables flexible letter-position coding, which provides fast access to whole-word orthographic representations. A well-known manifestation of this coarse-grained code is the transposed-letter effect which reflects the tendency of skilled readers to confuse, to a larger extent, a base-word with a transposed-letter nonword (e.g., judge with jugde) than with a replacement-letter nonword (e.g., judge with jupte; see Blythe et al., 2014; Grainger, 2008; Guerrero & Forster, 2008; Perea & Lupker, 2004). In an innovative study, Grainger et al. (2012) investigated the development of the coarse-grained route by comparing the size of the pseudo-homophone (PsH) effect (i.e., participants are more likely to judge that a pseudoword that can be pronounced like a real word is a word, for example,

BRANE can be pronounced to sound like the word BRAIN) and the transposed-letter effect (i.e., participants are more likely to judge that a pseudoword created by the transposition of two letters is a word, such as TALBE derived from the word TABLE) in a lexical decision task. Results showed that children exhibit large PsH effects in Grade 1 (44.61 %), which continuously decreased over reading acquisition (16.07% in Grade 5, and only 4.6% in adults). Interestingly, the transposed-letter effect followed the opposite trajectory with the effect increasing as reading level increased (starting at 8.24% in Grade 1 and reaching its maximum - 12.88% - in Grade 4). These results were interpreted as evidence for a decreased reliance on phonological decoding (the PsH effect) and an increased reliance on the coarse-grained route (the transposed-letter effect) during learning to read.

The present study builds on one additional assumption in the model of Grainger and Ziegler (2011), that the fine-grained code is crucial for precisely encoding not only graphemes but also small morphemic units (i.e., affixes). Morphemes are hypothesized to play a key role in visual word recognition by providing an island of regularity to overcome the arbitrariness of the spelling-meaning relationships (Rastle et al., 2000). Prior research has shown that although children already have awareness for morphological structures in their oral language from a pre-school age (Treiman & Bourassa, 2000; Treiman & Cassar, 1997), it takes many years of reading experience for children to develop the kind of automatic, morphological parsing mechanisms that are characteristic of skilled reading (e.g., Beyersmann et al., 2012, 2021; Dawson et al., 2018, 2021; Hasenäcker et al., 2020; Schiff et al., 2012). In the present study we tested pseudo-morphemic (PsM) nonwords as the morphological equivalent of PsH nonwords. More precisely we used PsM nonwords composed of a real stem and affix such as the English example *farmity* composed of the stem *farm* and the suffix *ity*.

A variety of different tasks have been used to tease apart the different component processes involved in reading PsM nonwords, such as masked priming (e.g., Beyersmann et al.,

2015; Hasenäcker et al., 2016, 2020), lexical decision (e.g., Casalis et al., 2015; Dawson et al., 2018; Hasenäcker et al., 2017; Quémart et al., 2012) and reading aloud (Colé et al., 2012; Mousikou et al., 2020). What is typically seen in unprimed lexical decision, which was the task of choice in the current study, is a stepwise pattern showing that it is harder to reject a nonword when it is exhaustively decomposable into two morphemic subunits (*farmity*: i.e., PsM nonwords) than nonwords containing just one embedded morpheme (e.g., *farm* in *farmald* or *ity* in *falmity*), which in turn are harder to reject than non-morphemic control items (*falmald*). This so-called morpheme interference effect (Crepaldi et al., 2010; Taft & Forster, 1975) has been observed in mid-primary school children (in Italian: Burani et al., 2002; in French: Casalis et al., 2015; Quémart et al., 2012; in English: Dawson et al., 2018), with a tendency of becoming more robust throughout reading development (Dawson et al., 2018).

A related approach was used by Hasenäcker and Schroeder (2017) to investigate the developmental trajectory of the use of syllabic structure and morphological structure during learning to read. In a lexical decision task in German, the functional units of mono- and multi-morphemic words and nonwords were highlighted using a colon (:), and their position either respected syllable or morpheme boundaries. For example, the word FAHRER was disrupted at the syllable boundary (FAH:RER) in the syllable-congruent condition and the morpheme boundary (FAHR:ER) in the syllable-incongruent/morpheme-congruent condition. Results showed that children rely on different functional units over reading development. On the one hand, second graders showed a preference for syllabic units regardless of lexicality or morphological complexity. On the other hand, fourth graders exhibited the same reliance on syllabic units except for multi-morphemic nonwords, which were harder to reject when the presentation format highlighted morphological units (HELB:ER) rather than syllabic units (HEL:BER). Interestingly, the emphasis on either syllabic or morphological units no longer affected adult word recognition performance. These results are consistent with the hypothesis

that phonological processes (influenced by syllabic structure) have an early influence, whereas morphological processing requires more reading experience.

The present study builds on this prior theoretical and empirical work in an investigation of the time-course of phonological and morphological processes during reading acquisition in three groups of developing readers (from Grade 1 to Grade 5) and one group of adults. To this end, we investigated the learning trajectory of PsH and PsM interference effects following the same experimental design as used by Grainger et al. (2012), but this time replacing the transposed-letter nonwords with PsM nonwords. We predicted that phonological effects (i.e., PsH interference) should be strong for novice readers and then gradually diminish as reading expertise increases, which means that novice readers will be more likely to judge a pseudo-homophone non-word as a real word. On the other hand, we expected morphological effects (i.e., PsM interference) to take longer to emerge and gradually increase as reading expertise increases, which means that skilled readers will be more likely to judge a pseudo-morphemic non-word as a real word. Although we instructed our participants to respond as rapidly as possible (in order to increase error rates), given the large variability in response times in young readers (e.g., Grainger et al., 2012) we used error rates supplemented with signal detection theory to analyze our results.

Methods

Participants

One hundred and ninety-four children from public elementary schools were tested at the end of their school year in May: 36 were 1st Graders, 49 were 3rd Graders, and 59 were 5th Graders. All participants were native French speakers with normal or corrected-to-normal vision. Informed consent was provided by the participant's caregivers prior to experimentation. Ethical approval for this study was granted by the *Comité de Protection des Personnes* SUD-EST IV (No. 17/051). The experiment was performed in accordance with relevant guidelines and regulations and in accordance with the Declaration of Helsinki. An additional group of 50 adult students was tested at the University of Lyon. They were between 18- and 30-years age (mean age = 22 years and 11 months, SD = 2 years and 11 months). All participants were pre-tested for their reading fluency using a French standardized test (Lefavrais, 2005)

Design and Stimuli

Thirty base-words (mean word frequency per million = 172.32, SD = 209.60) were used to construct 120 nonwords divided into four conditions: 30 pseudo-homophones (PsH), 30 pseudo-homophone controls (PsHc), 30 pseudo-morphemes (PsM), and 30 pseudo-morpheme controls (PsMc). Base-word frequencies were obtained from the Manulex database (Lété et al., 2004). All base-words occurred in Grade 1 texts in the Manulex corpus, meaning that these words are regularly encountered by beginning readers¹.

Pseudo-homophone nonwords

¹ The mean word frequency per million for selected-based words was 172 (SD = 210); therefore, they could be considered highly frequent in the children's corpus. The detailed word frequency values for each base word are available in the online supplementary material.

Pseudo-homophones (PsH) were obtained by substituting one grapheme of the base-word by another one of the same length associated with the same phonological representation (e.g., base-word: *visage*, PsH: *visaje*). The substitutions were made according to substitution rules described by Farioli et al. (2011). Then, pseudo-homophone controls (PsHc) were obtained according to the same principle but by using a grapheme that differs from the original phonological representation (base-word: *visage*, PsHc: *visape*). Thus, pseudo-homophones were not associated with a valid orthographic representation stored in the lexicon (*visaje* is an incorrect spelling in French), while pseudo-homophone controls had both incorrect orthographic and phonological representations. Pseudo-homophones and their controls were matched on number of syllables, number of letters, orthographic similarity (as measured by the Orthographic Levenshtein Distance 20; Yarkoni et al., 2008), the mean consistency of grapho-phonological associations as computed on words in ManulexInfra (Peereman et al., 2007), and bigram frequency.

Pseudo-morphemic nonwords

Pseudo-morphemic (PsM) nonwords were obtained by adding an existing legal French suffix to the base-word (base-word: *visage*, PsM: *visageable*). Then, pseudo-morphemic nonword controls (PsMc) were obtained according to the same principle but by adding a non-affix ending of the same length and of the same number of syllables as the suffix ending (base-word: *visage*, PsMc: *visagealle*). Non-morphological endings were obtained by substituting one letters of the suffix in the PsM condition to have a high degree of orthographic overlap between PsM and PsMc nonwords. PsM and PsMc nonwords were matched on number of syllables, numbers of letters, orthographic similarity, and bigram frequency.

Filler words

For the purpose of the lexical decision task, 120 words were selected from the Manulex database (Lété et al., 2004). Half were high-frequency words (mean word frequency per million = 136.24, SD = 243.20) and the other half were low-frequency words (mean word frequency per million = 4.08, SD = 7.07). For each frequency class, half of the words were mono-morphemic, and the other half were morphologically complex. Thus, we obtained: 30 high-frequency monomorphemic words, 30 low-frequency monomorphemic words, 30 high-frequency morphologically complex words, and 30 low-frequency morphologically complex words. Filler words were matched with the critical nonword stimuli on length in letters and number of syllables. The complete set of stimuli are available in the Supplemental Materials.

Procedure and apparatus

Participants were seated in front of a 14-inch laptop computer running *OpenSesame* software (Mathôt et al., 2012) at a viewing distance of approximately 60 cm. The stimuli were displayed in black lowercase in 24-point Courier font on a gray background with a resolution of 1280 x 720 px. Participants were tested in groups of two. The main experiment (lexical decision) lasted around 20-minutes.

Each trial began with a fixation cross for 1000 ms. Then, the fixation cross was replaced by a target stimulus at the center of the screen until the participant's response. Participants were instructed to decide as quickly and as accurately as possible using the "M" key if the stimulus was a legal French word and the "Q" key otherwise on an AZERTY keyboard where the Q and M keys occupy the left and right extremes of the central row of letters (for left-handed participants the response keys were reversed). Stimuli were divided into five counterbalanced blocks of 24 experimental trials. Blocks and trials within blocks were presented in a randomized order. A practice block of 24 trials was also presented before experimental blocks. To avoid fatigue, a break was offered between each block.

Children were tested in groups of four to six by three experimenters in the same room. The lexical decision task was explained by an experimenter who gave the children examples of words and nonwords written on paper and asked them to respond together and orally if the letter string was a word or a nonword. The experimenter let the children express their opinion before providing the correct response. Examples were given until the experimenter believed that children had correctly understood the lexical decision task. During the practice trials, experimenters carefully controlled children's seating position and their correct use of the keyboard.

Results

The final data set retained for analysis consisted of 23,280 observations. As acknowledged by Grainger et al. (2012), the high percentage of errors for young readers in most developmental studies on reading acquisition makes the use of reaction time data unreliable². Analyses reported below were therefore only performed on the error data. We completed the error rate analyses with a signal detection analysis.

Error data analyses

Error data were analyzed using generalized linear mixed effects (lme4 package in R, version 1.1.31; Bates et al., 2015). The GLME analysis was conducted using Group (Grade 1, Grade 3, Grade 5, and Adults), Type of Manipulation (pseudo-homophone vs. pseudo-morpheme) and, Type of Condition (experimental vs. control) as fixed factors. The maximal random structure model that successfully converged was used. We tested the significance of the effects using Type III sum of squares and χ^2 Wald tests. Post-hoc contrasts were calculated using the emmeans package (Lenth, 2023). Full model outputs are given in the Online Supplemental Materials.

Prior to the analyses, we excluded two participants (one adult and one 5th Graders) with a reading level exceeding +/- 2.5 SD from the mean of their group. In addition, four items were removed after data collection because of material defects³. The analyses revealed significant main effects of Group ($\chi^2 = 156.99, p < .001$), Type of Manipulation ($\chi^2 = 34.52, p < .001$), and

² In our experiment, the pseudo-homophone condition elicited more than 50% of the errors, which makes the use of reaction times less reliable (see also (Goswami et al., 2001) for another example).

³ The pseudo-homophone control "cuje" built on the base-word "cage" was not built on a single substituting operation based on the critical grapheme "g." Hence, we took the decision to remove all items associated with the base-word "cage" : caje, cuje, cagitude, cagitude.

Type of Condition ($\chi^2 = 111.83, p < .001$). Most importantly, the three-way interaction between Type of Condition, Type of Manipulation and Group was significant ($\chi^2 = 124.14, p < .001$). This three-way interaction reflects the distinct learning trajectories for pseudo-homophone and pseudo-morpheme effects. The pseudo-homophone effect decreased with age and was no longer significant in Adults ($\Delta ER = 2.67\%, z = 1.88, p = .060$), which highlights the fact that more skilled readers are less likely to judge a pseudo-homophone as a real word. On the contrary, the pseudo-morpheme effect, which was already significant in Grade 1 ($\Delta ER = 3.29\%, z = 2.04, p = .042$) increased with age, which highlights the fact that more skilled readers are more likely to judge a pseudo-morphemic non-word as a real word. (see planned comparison and effect sizes reported in Table 1).

Table 1.

Mean percentage of error for pseudo-homophones (PsH), pseudo-morphemes (PsM), and their respective controls (PsHc, PsMc) across participant groups (standard errors in parentheses). The difference between PsH and controls reflects the size of the pseudo-homophone effect, whereas the difference between PsM and controls reflects the size of the pseudo-morpheme effect. The significance (p-value computed with emmeans package) and the effect size (Cohen's d) of these differences were also reported.

Condition	Group			
	Grade 1	Grade 3	Grade 5	Adults
PsH	74.71 (3.66)	54.82 (3.25)	33.47 (1.55)	7.74 (.64)
PsHc	31.90 (3.21)	25.19 (3.56)	11.47 1.39	5.07 (.83)
Difference	42.81	29.63	22.00	2.67
p	<.001	<.001	<.001	.060
d	2.22	1.79	1.65	.45
PsM	30.01 (3.28)	30.26 (3.20)	17.90 (1.64)	12.74 (1.74)

PsMc	26.72 (3.66)	22.10 (3.25)	9.93 (1.55)	2.96 (.64)
Difference	3.29	8.16	7.97	9.78
<i>p</i>	.042	<.001	<.001	<.001
<i>d</i>	.43	.74	.97	1.96

Signal Detection Theory Analysis

We conducted a Signal Detection Theory (SDT; Swets et al., 1961) analysis to ensure that the different learning trajectories for pseudo-homophone and pseudo-morpheme effects were not due to a shift in the strategy used by participants to complete the lexical decision task, and more precisely, to possible changes in response bias across grades. Although the proportion of correct responses is affected by both sensitivity (i.e., the difficulty in discriminating words from pseudowords) and bias (i.e., the extent to which one response is more probable than another), SDT provides two distinct measures for these components. Crucially, for the present purposes, the sensitivity measure (d') provided by SDT provides a measure of participants' accuracy in classifying pseudo-homophones and pseudo-morphemes as pseudowords while controlling for response bias. Thus, accuracy data were used to calculate sensitivity (d') based on the percentage of hits (correct rejection of pseudowords – the critical stimuli in our experiment) and false alarms (incorrect classification of words as pseudowords). Sensitivity (d') was analyzed using an ANOVA based on the same factorial design as used in the mixed model analysis: Group (Grade 1, Grade 3, Grade 5, and Adults) as a between-participants factor, and Type of Manipulation (pseudo-homophone vs. pseudo-morpheme) and Type of Condition (experimental vs. control) as within-participant factors. Post-hoc contrasts were calculated using the emmeans package (version 1.8.4.1; Lenth, 2023).

The sensitivity analysis was coherent with the error rate analysis, showing significant main effects of Group ($F(3, 188) = 100.61, p < .001$), Type of Manipulation ($F(1, 188) = 100.80, p < .001$), and Type of Condition ($F(1, 188) = 334.71, p < .001$). Most importantly, the three-way interaction between the Type of Condition, Type of Manipulation and Group was also significant ($F(3, 188) = 24.94, p < .001$). Decomposition of this three-way interaction revealed only one significant divergence with respect to the error rate analysis. When this dependent measure was controlled for response bias (i.e., using d'), the pseudo-morpheme effect increased with age, but it became significant only in Grade 3 ($\Delta ER = -.5, t = 5.72, p < .001$). The trajectory of the pseudo-homophone effect remained unchanged. All the planned comparisons are presented in Table 2.

Table 2.

Sensitivity (d') measures for pseudo-homophones (PsH), pseudo-morphemes (PsM), and their respective controls (PsHc, PsMc) across participant groups (standard errors in parentheses). The difference between PsH and controls reflects the size of the pseudo-homophone effect, whereas the difference between PsM and controls reflects the size of the pseudo-morpheme effect. The significance (p -value computed using the emmeans package) of these differences is also reported.

Condition	Group			
	Grade 1	Grade 3	Grade 5	Adults
PsH	-.16 (.11)	.96 (.15)	1.93 (.13)	3.39 (.09)
PsHc	1.18 (.14)	2.00 (.16)	2.72 (.10)	3.60 (.10)
Difference	-1.34	-1.04	-0.79	-0.21
p	<.001	<.001	<.001	.917
PsM	1.16 (.14)	1.68 (.15)	2.37 (.09)	3.22 (.09)

PsMc	<i>1.32</i> (.18)	<i>2.18</i> (.17)	<i>3.14</i> (.12)	<i>3.97</i> (.08)
Difference	-.16	-.5	-.77	-.75
<i>p</i>	.973	<.001	<.001	<.001

Discussion

The present study investigated the learning trajectory of phonological and morphological processes during reading acquisition, with children in grades 1, 3 and 5, and adults. We did so by examining error rates in a lexical decision task to two types of nonword and their corresponding controls all derived from the same base-word (VISAGE in these examples): 1) pseudo-homophone (PsH) nonwords that can be pronounced like a real word (e.g., *visaje*) and the corresponding orthographic controls (e.g., *visape*); 2) pseudo-morphemic (PsM) nonwords that are formed by an illegal combination of a legal stem and suffix (e.g., *visageable*) and the corresponding controls where the suffix ending was changed to a non-suffix ending (e.g., *visagealle*). The results showed that the PsH interference effect (i.e., pseudo homophone nonwords elicited more errors than their orthographic controls) decreased during reading acquisition and was non-significant in adults. On the other hand, the PsM interference effect (i.e., pseudo-morphemic nonwords elicited more errors than their orthographic controls) increased during reading acquisition and was larger in adults. Crucially, a signal detection analysis of the present data revealed practically the same pattern of results with the measure of sensitivity (d') that controls for potential response biases.

These findings align well with previous work on the learning trajectories of the role of phonology and morphology when learning to read. More specifically, the PsH effect shown in our study showed the same learning trajectory as reported by Grainger et al. (2012) and therefore further confirms the importance of phonological decoding during the early stages of reading acquisition. The progressive decrease of phonological decoding marks its gradual replacement by a process that enables a more efficient access to meaning from print (Grainger et al., 2012; Wesseling & Reitsma, 2000). Although part of this more efficient reading route involves direct access to meaning from orthographic representations, a key role is also played by morpho-orthographic representations (e.g., Grainger, 2018). This increasing reliance on

morphological processing during reading development has been documented in numerous developmental studies (Burani et al., 2002; Casalis et al., 2015; Dawson et al., 2018; Quémart et al., 2012). A more surprising result is the small but significant PsM effect on error rates observed in Grade 1. Indeed, on the basis of prior work we expected the PsM effect to occur later. However, this prior work tested older children (mostly from Grade 3). Our results therefore suggest that including younger children in these studies is necessary in order to provide a complete developmental picture of PsM effects. Nevertheless, the PsM effect observed in Grade 1 should be interpreted with caution since it was not significant in the signal detection analysis. This discrepancy could be due to the smaller sample size of Grade 1 children compared to the sample size of other groups, which are close to meeting the recommendation of Brysbaert and Stevens (2018).

The key result of the present study, however, is the demonstration of these opposing learning patterns in the same participants (children in grades 1, 3, and 5, and one group of adults). The decreasing effect of phonological processing and the increasing effect of morphological processing across these four groups is likely due to the development of their language skills and their increasing exposure to written language. At the early stages of reading development, children rely heavily on phonological processing, which involves recognizing and manipulating the sounds of language (Castles et al., 2018). As children become more proficient readers, they start to rely more on the orthographic analysis of meaningful units of language, such as prefixes, suffixes, and stem morphemes (Rastle, 2019). This shift in processing strategies may be due to the fact that children's language skills are rapidly developing as they are exposed to more complex vocabulary and sentence structures. Recognizing the morphological structure of words helps children derive meaning from unfamiliar words. Morphological processing therefore represents the perfect tool to decompose unfamiliar words into smaller, familiar morphemic chunks (Beyersmann et al., 2021). For

example, Hasenäcker et al. (2017) reported that German speaking children with a high vocabulary level benefitted earlier (i.e., Grade 2) and from various types of morphological structure (compounds, suffixed and prefixed words) compared to children with a lower vocabulary level. For children with a low vocabulary level, the presence of a suffix or a prefix was found to be detrimental for word recognition. This is in line with the hypothesis that, as readers become more experienced, they rely more on lexical and morphological processing, which involves accessing the meaning of words and morphemes directly from whole-word and morpheme representations in long-term memory (Beyersmann et al., 2012; Beyersmann & Grainger, 2023; Grainger & Beyersmann, 2017). This not only explains the increased reliance on morphological segmentation, but also explains why more experienced readers are less likely to rely solely on phonological processing when recognizing words, which is consistent with the present findings. However, it should be acknowledged that the present study did not assess children's vocabulary knowledge nor their prior knowledge of the base-words used to generate the PsH and PsM nonwords. We did select the base-words on the basis that they should be known by Grade 1 children according to Manulex (Lété et al., 2004). Nevertheless, the prior knowledge of these base-words in the sample of children that we tested was not assessed. Therefore, one important addition for future work on this topic is to pretest the participants on their ability to read the base-words used to generated the critical nonword stimuli.

The present study points to the general interest, for future research, of studying pseudo-homophone and pseudo-morpheme effects in order to better understand the development of reading skills in children. It is possible that learning to read in highly productive morphemic languages may involve an even greater reliance on morphological representations relative to non-morphological phonological representations (i.e., phonemes and possibly syllables). Indeed, Finnish children appear to show greater reliance on morphemic compared to syllabic

processing, even in a silent reading task (Häikiö & Vainio, 2018). Finnish first- and second-grade children read sentences with embedded inflected target words that had either syllable-congruent or syllable-incongruent hyphenation, while their eye-movements were registered. The study found that Finnish children in Grades 1 and 2 relied more on inflectional morphemes than syllables in their reading, suggesting that morphological processing plays an important role in the acquisition of Finnish reading skills. As an agglutinative language, Finnish clearly has a rich inflectional morphology, which therefore provides an interesting contrast to the current findings in French. Cross-linguistic studies therefore offer an important avenue for future research on the evolution of phonological and morphological processing during reading development.

Conclusions

The present study investigated the use of phonological decoding and morpho-orthographic decomposition strategies during the course of learning to read. French speaking children would appear to use both strategies in the initial stages of learning to read. After that, phonological decoding becomes less important and eventually had a non-significant impact on the performance of adult participants in the present study (at least for the measure used in the present study), while the impact of morphological decomposition increased. This demonstrates how different sublexical representations are used to read words during learning to read silently for meaning, and how their impact changes over the course of learning.

Data availability

All data, materials, and code are available at the Open Science Framework

(https://osf.io/n7qjk/?view_only=7b16a2e5d1034fbeb9c13dfc57c7e391)

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Author contributions

Conceived and designed the experiment: BB, EC, EL, BL. Performed the experiment: BB, EL. Analyzed the data: BB, EL. Wrote the manuscript: EB, BB, EC, JG, EL, BL.
BB and EL contributed equally to this work.

Competing interests

The author(s) declare that there are no potential conflicts of interest with respect to the research, authorship, and/or publication this article.

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