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Transposed-Letter Effects Reveal Orthographic Processing in Baboons

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In a recent study (Grainger, Dufau, Montant, Ziegler, & Fagot, 2012), we successfully trained baboons to discriminate a large number of visually presented real English words from nonsense words. However, our findings showed that baboons did not just learn words by heart: They performed well above chance on novel words they had never seen before. To explain this finding, we argued that baboons likely use an orthographic code based on frequently occurring letter combinations and their relative positions; such information could be used to distinguish the novel words from nonwords. However, it is possible that the baboons were learning visual, not orthographic, patterns and that visual rather than orthographic similarities across stimuli were driving the reported effects.

Our goal in the present study was to further investigate the nature of the information used by baboons to discriminate words from nonwords. To do so, we retested the monkeys used in our previous study to see whether they would show transposed-letter effects. Transposed-letter effects are considered to be the hallmark of orthographic processing (Grainger, 2008). They reflect the finding that nonwords created by transposing the letters of real words, such as *caniso* (derived from *casino*), are more likely to be misclassified as words than are nonsense control words, such as *caviro* (Andrews, 1996; Chambers, 1979; Perea & Lupker, 2004). State-of-the-art word-recognition models show that flexible orthographic coding is needed to account for this effect (Davis, 2010; Gomez, Ratcliff, & Perea, 2008; Whitney, 2001). Thus, in the present study, transposed-letter effects served as a marker for such flexible orthographic processing. To test a possible visual account of word/nonword discrimination performance in monkeys, we contrasted transposed-letter effects with effects of visual similarity. If baboons use a truly orthographic code, they should show effects of the former but not of the latter.

The data were obtained from 6 guinea baboons (*Papio papio*; 3 females, 3 males) who participated in the word-learning experiment used in our previous study (Grainger et al., 2012). The baboons had free access to computerized operant-conditioning test systems with touch screens (for details, see Video S1 and Supplemental Method and Results in the Supplemental Material available online). The baboons had to select an oval shape when the sample was a word and a cross shape when it was a nonword. The experiment started right after completion of the learning experiment described in Grainger et al. (2012) with no additional training between the two studies.

Each test block in the present study contained 50 known words (randomly selected from the pool of words that the monkey had learned) and 50 nonwords. In each of the 10 blocks, 8 standard nonwords were replaced by 8 critical nonwords that were reinforced as nonwords. The 80 nonwords in the critical-item set consisted of 20 transposed-letter, 20 double-substitution, 20 visually similar, and 20 visually dissimilar nonwords. The test material was constructed individually for each monkey on the basis of the words it had learned. Transposed-letter nonwords were created by inverting the middle letters of words (e.g., DONE → DNOE). The control items, the so-called double-substitution nonwords (cf. Perea & Lupker, 2004), were created by replacing the two middle letters with letters from the same category (i.e., vowels or consonants; e.g., DONE → DAGE). Visually similar and visually dissimilar nonwords were created by replacing either the second or the third letter of a previously learned word with a visually similar or dissimilar letter, respectively (e.g., visually similar: DONE → DQNE; visually dissimilar: DONE → DFNE). For additional information on

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stimuli, vocabulary size, and the procedure, see Supplemental Method and Results.

Results are shown in Figure 1a (individual data can be found in Table S1 in Supplemental Method and Results). There was a clear transposed-letter effect: Transposed-letter nonwords generated significantly more "word" classifications (i.e., false-positive responses) than double-substitution nonwords did, $F(1, 5) = 7.35$, $p < .05$, $\eta_p^2 = .59$. In contrast, there was no effect of visual similarity, $F(1, 5) = 0.039$, $p > .85$, $\eta_p^2 = .008$. To further investigate the nature of the transposed-letter effect, we computed linear regressions for three variables that might predict the size of the transposed-letter effect: vocabulary size, nonword accuracy, and word accuracy. Although no significant correlations were found for vocabulary size ($R^2 = .08$, $p > .50$) and nonword accuracy ($R^2 = .01$, $p > .80$), overall word accuracy correlated significantly with the size of the transposed-letter effect: The higher a monkey's accuracy on words, the stronger the transposed-letter effect ($R^2 = .68$, $p < .05$; see Fig. 1b). If word accuracy is taken as a measure of the strength of orthographic representations, the finding that monkeys with stronger orthographic representations show stronger transposed-letter effects is consistent with human data showing that transposed-letter effects are stronger for nonwords derived from high-frequency words than from low-frequency words (O'Connor & Forster, 1981).

In sum, word/nonword discrimination performance of monkeys is sensitive to a marker effect of orthographic processing—the transposed-letter effect—but not to the effects of visual similarity. This finding clearly suggests that monkeys use a truly orthographic code rather than a visual code. Monkeys had a hard time with nonwords that differed by only one letter from the learned real word (i.e., the false-positive error rate was not much different from the hit rate for real words), which could be taken to challenge our previous finding (Grainger, et al., 2012) that monkeys were able to discriminate words from nonwords. However, these nonwords of one-letter difference were much more similar to the real words than the nonwords we previously used. Thus, the high error rate for these nonwords actually provides strong evidence that baboons are capable of orthographic processing. The strong correlation between word accuracy and the size of the transposed-letter effect suggests that monkeys have acquired orthographic representations, the strength of which determines how readily a transposed-letter nonword will be mistaken for a known word. Given that models without flexible orthographic codes fail to capture transposed-letter effects in humans, we believe that such simplistic models will also fail to capture transposed-letter effects in monkeys.

Reading and writing are recent cultural inventions in humans. Although baboons do not have human-like language, they are sensitive to a classic marker of orthographic processing. These findings suggest that the front end of reading (Grainger & Dufau, 2012) is

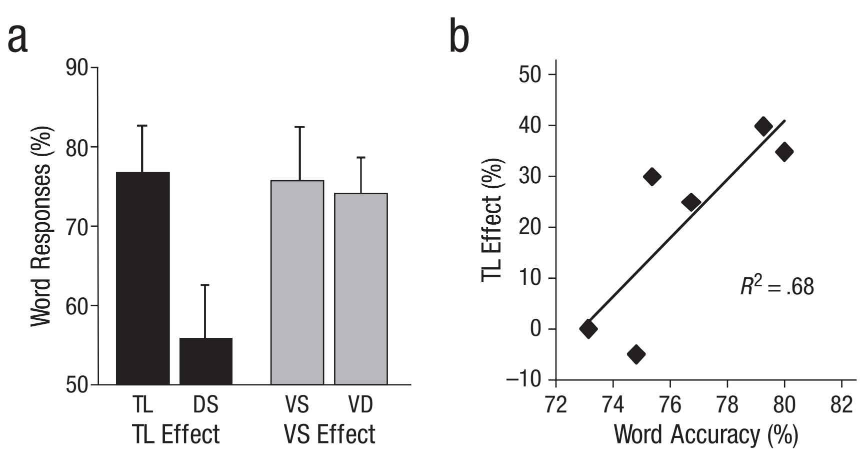

Fig. 1. Results. The graph in (a) shows the average percentage of nonwords classified as words (false positives) as a function of nonword type. Nonword types consisted of transposed-letter (TL) and double-substitution (DS) nonwords (used to index the TL effect) and visually similar (VS) and visually dissimilar (VD) nonwords (used to index the visual-similarity effect). Error bars indicate standard errors of the mean. The scatter plot (with best-fitting regression line) in (b) shows the TL effect as a function of word-classification accuracy. The TL effect was calculated by subtracting the false-positive error rate for TL nonwords from the false-positive error rate for DS nonwords.

supported by neural mechanisms that are much older than the behavior itself and are not linguistic in nature (Platt & Adams, 2012).

Author Contributions

J. C. Ziegler, J. Fagot, and J. Grainger conceived the study and designed the experiment. S. Dufau selected the stimuli; J. Fagot, M. Montant, and S. Dufau implemented the experiment; J. Fagot conducted the experiment; and T. Hannagan and S. Dufau analyzed the data. J. C. Ziegler wrote the first draft of the manuscript, and all authors contributed equally to revisions.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

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