Rapid Attentional Selection of Non-native Stimuli despite Perceptual Narrowing

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Abstract

Visual experiences increase our ability to discriminate environmentally relevant stimuli (native stimuli, e.g., human faces) at the cost of a reduced sensitivity to irrelevant or infrequent stimuli (non-native stimuli, e.g., monkey/ape faces)—a developmental progression known as perceptual narrowing. One possible source of the reduced sensitivity in distinguishing non-native stimuli (e.g., one ape face vs. another ape face) could be underspecified attentional search templates (i.e., working memory representations). To determine whether perceptual narrowing stems from underspecified attentional templates for non-native exemplars, this study used ERP (the N2pc component) and behavioral measures in a visual search task, where the target was either an exemplar (e.g., a specific ape face) or a category (e.g., any ape face). The N2pc component, an ERP marker of early attentional selection emerging at 200 msec poststimulus, is typically modulated by the specificity of the target and, therefore, by the attentional template—the N2pc is larger for specific items versus categories. In two experiments using both human and ape faces (i.e., native and non-native stimuli), we found that perceptual narrowing affects later response selection (i.e., manual RT and accuracy), but not early attentional selection relying on attentional templates (i.e., the N2pc component). Our ERP results show that adults deploy exemplar level attentional templates for non-native stimuli (as well as native stimuli), despite poor downstream behavioral performance. Our findings suggest that long-term previous experience with reduced exemplar level judgments (i.e., perceptual narrowing) does not appear to eliminate early attentional selection of non-native exemplars.

INTRODUCTION

Long-term visual exposure increases our ability to discriminate environmentally relevant stimuli (native stimuli) compared with irrelevant or infrequent stimuli (non-native stimuli; e.g., Scott, Pascalis, & Nelson, 2007). In other words, the trade-off for more efficient discrimination of native stimuli is a reduced sensitivity to non-native stimuli. This developmental progression, known as perceptual narrowing, occurs from 6 to 9 months of age. Two classic examples of perceptual narrowing come from studies of speech perception and face perception. Werker and Tees (1984) showed that infants from an English-speaking environment could easily discriminate two non-native (Salish) speech contrasts at 6 months of age, but not at 12 months of age unless consistently exposed to those contrasts (see also Kuhl, Tsao, & Liu, 2003; Cheour et al., 1998). Similarly, Pascalis, de Haan, and Nelson (2002) showed that infants at 6 months of age could discriminate between two human faces or between two monkey faces, but infants at 9 months of age could only discriminate between two human faces. Perceptual narrowing itself is experience dependent, rather than dependent on maturation: Indeed, Scott and Monesson (2009) showed that if infants at 6 months of age received training to individuate monkey faces for the 3-month period until tested at 9 months of age, they retained the ability to discriminate between monkey faces (see also Pascalis et al., 2005). This effect also has been documented extensively with own-race vs. other-race faces (for a review, see Anzures et al., 2013).

Perceptual narrowing impacts one’s ability to discriminate non-native exemplars (i.e., one face from another face) from infancy through adulthood (e.g., Mondloch, Maurer, & Ahola, 2006; Pascalis et al., 2002), and therefore, it also affects target selection in visual search tasks (Simpson, Buchin, Werner, Worrell, & Jakobsen, 2014). Results from visual search tasks can provide evidence for the mechanism underlying the reduced sensitivity with non-native stimuli. By presenting targets and distractors simultaneously, visual search tasks require active guidance via attentional templates that utilize top-down target-defining features to enable target selection (see Ölivers, Peters, Houtkamp, & Roelfsema, 2011). Attentional templates can be a single feature (e.g., red), a specific exemplar/item (e.g., red truck), or even a category (e.g., any vehicle) and are stored in working memory to confirm the presence or absence of a target in a visual search array. Target selection in visual search tasks affords a new perspective on perceptual narrowing: the
potential to study the earliest evidence of attentional template deployment at the neural level prior to behavioral responses for specific non-native exemplars (e.g., a specific ape face) relative to specific native exemplars (e.g., a specific human face). This study investigated whether perceptual narrowing (observed at the behavioral level) affects early target selection (at the neural level) because of differential attentional template deployment in a visual search task.

The N2pc is the ideal neural measure for this study because it is the established ERP marker for early target selection (e.g., Eimer, 1996; Luck & Hillyard, 1994). It is an enhanced negativity emerging at around 200 msec poststimulus at occipitotemporal electrodes contralateral to the hemifield of a visual target and reflects the spatial selection of a visual target among distractors. Critically, the N2pc is dependent on the top-down attentional set of the observer (e.g., Eimer, Kiss, Press, & Sauter, 2009; Eimer & Kiss, 2008). For example, Eimer and Kiss demonstrated that a reliable N2pc is obtained in response to singleton stimuli that share a dimension with an upcoming target (e.g., the color red), but not when these highly salient stimuli do not share dimensions with targets.

In general, the N2pc is modulated by target–distractor relations (e.g., smaller vs. larger target array size, crowding, physical similarity, semantic relatedness) and template specificity (e.g., one vs. multiple different targets, specific item vs. categories). If target–distractor relations are held constant, the N2pc becomes a marker of the specificity of the attentional template deployed by observers during attentional selection. Searching for multiple different targets (e.g., any numeral or a red or green numeral) reveals a smaller N2pc (i.e., a less precise attentional template) compared with searching for specific exemplars (e.g., a specific red numeral; Grubert & Eimer, 2013). Although attentional templates have been thought to be capacity limited (e.g., Olivers et al., 2011), more abstract “features” such as category targets (e.g., any numeral, Nako, Wu, & Eimer, 2014; Wu et al., 2013; or any clothing item, Nako, Wu, Smith, & Eimer, 2014) also can efficiently guide attention at very early stages of processing. However, the N2pc tends to be attenuated for categories (e.g., any numeral) compared with specific items (e.g., the numeral 3) presumably because specific items utilize more precise templates. Categories of items typically reduce the specificity of the search template because of a larger range of possible targets compared to exemplar search (indexed by the N2pc; Nako, Wu, & Eimer, 2014; Nako, Wu, Smith, et al., 2014; Wu et al., 2013), thereby resulting in category search being more difficult than exemplar search (as evidenced at behavioral levels; Nako, Wu, & Eimer, 2014; Nako, Wu, Smith, et al., 2014; Wu et al., 2013; Yang & Zelinsky, 2009).

One possible source of the perceptual narrowing effect (i.e., reduced sensitivity in distinguishing non-native exemplars) could be underspecified search templates. Typical perceptual narrowing studies have shown that non-native stimuli (e.g., monkey/ape faces) become difficult to distinguish compared to native stimuli (e.g., human faces; Mondloch et al., 2006). Given this behavioral effect, it follows that finding any ape face in a visual search task would be easier than finding a specific ape face, because the latter requires discrimination among exemplars. Once a category becomes easier to identify behaviorally compared with specific items within the category, is this effect due to more precise category level than exemplar level attentional templates?

If reduced sensitivity to non-native exemplars results from a template deficit (e.g., an incorrect or underspecified template), then attentional selection of a specific ape face should be impaired at both early (N2pc) and late (behavioral) stages of processing compared with search for any ape face (the category; Experiment 1). By comparison, search for a specific human face (Experiment 2) should be robust. To minimize effects of low-level visual differences (e.g., ape faces tend to be darker than human faces), the ape faces and human faces were split into two experiments with two separate groups of participants. To isolate the modulation of the N2pc because of target precision, we controlled for target–distractor similarity by using the same stimulus set within an experiment to compare specific item vs. category search.

**EXPERIMENT 1: APE FACES**

**Methods**

**Participants**

Twenty volunteers (M = 26.55 years, SE = 1.30, 11 women) provided data, with six additional participants excluded either because of excessive eye movements (<50% trials kept, n = 5) or incorrect behavioral responses (<75% accuracy, n = 1).

**Stimuli, Design, and Procedure**

The stimuli consisted of eight black-and-white ape faces (adapted from Mollison, 2004) and eight other animal faces (Figure 1, top) on a black background. The images subtended 2.67° × 1.91° and were equated by their number of black pixels (F(1, 14) < .30). In a single session, each participant completed two tasks: (1) Exemplar Search and (2) Category Search. We counterbalanced the task order across participants. The Exemplar Search task required participants to search for a specific ape face, which was indicated at the beginning of the task. The Category Search task required participants to search for any ape face. Before the start of both tasks, we showed participants the entire inventory of ape and distractor animal faces. Each task consisted of 11 consecutive blocks.

Across the two search tasks (Exemplar and Category), there were four trial types: Exemplar Match, Category Match, Foil, and No Target trials (Figure 1, bottom). In the Exemplar Search task, each block consisted of
28 Exemplar Match trials (specific target ape face appeared in search array), 28 Foil trials (nontarget ape face appeared), and 6 No Target trials (no ape faces appeared). The Category Search task did not include Foil trials because all foils became targets in that task. Therefore, in the Category Search task, each block contained 28 Category Match trials (any ape face in search array) and 28 No Target trials (no ape faces). There were 1298 trials throughout the experimental session. Each trial consisted of a search array displayed for 200 msec that had two stimuli, one on each side of the fixation point to elicit the N2pc from ipsilateral and contralateral electrode sites (Figure 2). The search array was followed by a response period of 1600 msec where only a small white fixation dot was displayed. Participants indicated target presence or absence with left and right arrow keys with the right hand.

**EEG Recording and Data Analysis**

EEG was DC-recorded from 32 scalp electrodes at standard positions of the extended 10/20 system (500 Hz sampling rate; 40 Hz low-pass filter) and referenced to averaged earlobes. A 100-msec prestimulus baseline was used on epochs from −100 msec to 500 msec relative to the search array onset. The following criteria for artifact rejection were applied: horizontal EOG exceeding ±25 μV, vertical EOG exceeding ±60 μV, and all other channels exceeding ±80 μV. After artifact rejection and including only correct trials based on the behavioral measure, the average percentage of trials retained per participant was 73%. Mean N2pc amplitudes were obtained between 220 and 320 msec after search array onset at lateral posterior electrodes PO7 and PO8 (Wu et al., 2013).
Results

Behavioral Results

A repeated-measures ANOVA revealed a difference in RT, $F(3, 57) = 4.14, p = .01, \eta = .18$, and Accuracy, $F(3, 57) = 10.33, p < .001, \eta = .35$, among the four trial types (Exemplar Match, Category Match, Foil, and No Target; Figure 3). Behavioral performance was evaluated by comparing the target present trials (Exemplar and Category Match trials) and the target absent trials (Foil and No Target trials; Figure 3). For target present trials, there were faster RTs, $t(19) = 2.42, p = .026$, and higher accuracy, $t(19) = -2.81, p = .011$, when selecting any ape face versus a specific ape face. Thus, in line with other perceptual narrowing experiments showing reduced ability to discriminate among non-native exemplars, here we showed that accuracy was higher and RTs were faster when search was at the category level than at the exemplar level (which required discrimination among non-native exemplars). For target absent trials, accuracy was higher when no ape face appeared versus when a foil appeared, $t(19) = -6.74, p < .001$, but there was no difference in RT, $t(19) = .42$.

ERP Results

The N2pc component was evaluated for Exemplar Match, Category Match, and Foil trials (Figure 4; No Target trials were not included because there was no preidentified target or foil). An ANOVA confirmed a significant main effect of Laterality, $F(1, 19) = 153.98, p < .001, \eta = .88$, and a significant interaction between Trial type and Laterality, $F(2, 38) = 5.45, p = .008, \eta = .22$. $t$ tests comparing contralateral and ipsilateral ERP mean amplitudes confirmed the presence of target N2pc components in all three trial types ($ps < .001$). Paired $t$ tests revealed that the N2pc amplitude for Exemplar Match trials was larger than that for Category Match trials, $t(19) = -2.79, p = .012$. The N2pc amplitude for Foil trials was smaller than that for Exemplar Match trials, $t(19) = -2.61, p = .017$, and not different from Category Match trials, $t(19) = 1.44$. During Foil trials, an attention shift was seen to “other ape faces” (i.e., foil N2pc) that were correctly identified as nontargets (i.e., target absent behavioral response). We found that early exemplar selection was superior to early category selection, based on more specific exemplar level attentional templates, because specific targets elicited larger N2pc components than category targets.

Discussion

In comparing both accuracy and RT for Category Match trials (any ape face) and Exemplar Match trials (a specific ape face), we obtained the behavioral response typical of perceptual narrowing studies with non-native stimuli (e.g., Mondloch et al., 2006). Although all participants were able to perform the task in general (high accuracy, relatively quick RT), participants displayed superior behavioral performance when searching for any ape face compared to a specific ape face, as predicted. Importantly, we also found the characteristic neural response (compared to previous category search studies; Nako, Wu, Smith, et al., 2014; Wu et al., 2013) of enhanced exemplar level selection compared with category level selection (i.e., larger N2pc for Exemplar than Category Match trials) because of the specificity of the template. These contrasting results indicate that lack of exposure to non-native stimuli does not affect exemplar level attentional templates. Although the adult participants exhibited a delay in RTs when searching for a specific ape face, they nonetheless could deploy a precise attentional template for that exemplar. The N2pc component obtained during Foil trials indicates that nontarget ape faces did initially attract attention prior to pressing a “target absent” response. That the amplitudes of the Foil and Category N2pc components were very similar suggests that participants initially engaged in category search regardless of the task (Exemplar or Category search). However, a large proportion of correct responses during Exemplar search trials indicate that participants did complete the task correctly. Importantly, a larger N2pc component in
the Exemplar Match trials compared to the N2pc in the Foil trials demonstrates early exemplar level discrimination based on precise search templates. To confirm that the behavioral effects in Experiment 1 are reflective of perceptual narrowing and that the N2pc is also intact for native stimuli, we conducted Experiment 2 using the same procedure, but with human faces.

EXPERIMENT 2: MALE AND FEMALE HUMAN FACES

Methods

Participants

Twenty-one volunteers ($M = 21.67$ years, $SE = .59$, 12 women), who had not participated in Experiment 1, completed this study. Eleven additional participants were excluded either because of excessive eye movements (<50% trials kept, $n = 9$) or incorrect behavioral responses (<75% accuracy, $n = 2$).

Stimuli, Design, and Procedure

Instead of ape faces, Experiment 2 displayed male and female human faces (Figure 5) in full color on a white background. These isolated faces were a subset of the stimuli used in Rossion and Caharel (2011). Half of the participants searched for male targets, whereas the other half searched for female targets. In other words, if a participant searched for female faces, the distractors were male faces, and vice versa. In all other aspects, Experiment 2 followed the design and procedure of Experiment 1. After artifact rejection and including only correct trials based on the behavioral measure, the average percentage

Figure 4. ERP results from Experiment 1. Grand-averaged ERPs elicited in response to search arrays on target (Exemplar and Category Match) and Foil trials at posterior electrodes PO7/8 contralateral and ipsilateral to a target item for Experiment 1. N2pc difference waveforms were obtained by subtracting ipsilateral from contralateral ERP waveforms at PO7/8 for each task condition. Shaded area indicates the time window during which the N2pc was assessed.

Figure 5. Stimuli from Experiment 2. Male and female human faces (in full color) were used as search stimuli. Half of the participants received male faces as distractors and female faces as targets, whereas the other half received the opposite.
of trials retained per participant was 73%. As in Experiment 1, mean N2pc amplitudes were obtained between 220 and 320 msec after search array onset at lateral posterior electrodes PO7 and PO8.

Results

Behavioral Results

A repeated-measures ANOVA revealed a difference in RT, $F(3, 60) = 8.70, p < .001, \eta = .30$, and Accuracy, $F(3, 60) = 3.32, p = .026, \eta = .14$, among the four trial types (Figure 6). For target present trials, there were slower RTs, $t(20) = 2.14, p = .045$, when selecting any male or female face versus a specific human face, whereas accuracy did not differ, $t(20) = .87$. For target absent trials, RTs were slower when no male or female face appeared versus when a foil appeared, $t(20) = 2.83, p = .010$, but there was no difference in Accuracy, $t(20) = .20$. The overall difference in accuracy revealed from the ANOVA was driven by a difference between target present and target absent trials, $t(20) = 2.73, p = .013$.

ERP Results

The N2pc component was evaluated for Exemplar Match, Category Match, and Foil trials (Figure 7). An ANOVA confirmed a significant main effect of Laterality, $F(1, 20) = 54.75, p < .001, \eta = .73$, and a significant interaction between Trial type and Laterality, $F(2, 40) = 9.43, p < .001, \eta = .32$. $t$ tests comparing contralateral and ipsilateral ERP mean amplitudes confirmed the presence of target N2pc components in all trial types ($ps < .001$). Paired
Comparing Experiments 1 and 2

A mixed-design ANOVA comparing the RTs from Experiments 1 and 2 revealed an interaction between Experiments and Trial type, $F(3, 57) = 9.15, p < .001$, driven by faster Category and No Match RTs for Experiment 1 compared with Experiment 2. The significant interaction between Experiments and Trial types, $F(3, 57) = 12.38, p < .001$, driven by higher accuracy in Exemplar and Foil trials and lower accuracy in No Target trials in Experiment 2 compared with Experiment 1. Similar to RT, the significant interaction between accuracy in experiments remained when considering only Exemplar and Category trials, $F(1, 19) = 10.26, p = .005, \eta^2 = .35$. Critically, an ANOVA comparing the N2pc amplitudes from Experiments 1 and 2 revealed only a main effect of the three trial types (Exemplar, Category, Foil), $F(2, 38) = 13.90, p < .001, \eta = .42$, and no interaction between Experiments (ape vs. human faces), $F(2, 38) < .03$ (Figure 8), unlike the behavioral effects.

Discussion

In contrast to Experiment 1, RT was slower for category search compared to exemplar search, although accuracy did not differ between the two. The RT results are typical of perceptual narrowing effects with native stimuli, especially with faces isolated from other gender cues such as hairstyle. Interestingly, the same neural responses were obtained in this experiment compared to Experiment 1: better exemplar level selection compared to category level selection (i.e., larger N2pc for Exemplar than Category Match trials) because of the specificity of the exemplar level template. The neural and behavioral results obtained in Experiment 2 are typical of previous N2pc studies where behavior and N2pc components are positively associated (e.g., better RT and accuracy correlated with a larger N2pc; Wu et al., 2013). As in Experiment 1, the Foil N2pc in Experiment 2 also indicates that non-target male or female faces did initially attract attention prior to a “target absent” response. Besides showing exemplar level discrimination (comparing N2pc components in Exemplar Match and Foil trials in Experiment 2), our ERP results revealed that adults used similarly precise attentional templates for both native and non-native stimuli: There were no N2pc amplitude differences between experiments.

GENERAL DISCUSSION

This study investigated whether perceptual narrowing (i.e., better discrimination for native exemplars compared to non-native exemplars) impacts target selection in a visual search task. We used an early neural marker of selection (N2pc component) and late behavioral responses (RT and accuracy) to measure the efficiency of target selection based on attentional search templates (i.e., working memory representations). We found behavioral responses typical of perceptual narrowing effects: worse performance for specific non-native targets (i.e., specific ape faces) compared with category targets (i.e., any ape face) and the reverse for native stimuli (i.e., male and female human faces). By contrast, the neural effects revealed larger N2pc components for specific targets compared with category targets for both native and non-native stimuli. The neural effects are entirely consistent with previous work showing that the N2pc is dependent on target specificity (e.g., Nako, Wu, Smith, et al., 2014; Grubert & Eimer, 2013). Although both behavioral and neural results logically follow from previous research, what is novel is their dissociation and inclusion in the same study. Both measures tend to be correlated because typically they are both influenced by attentional templates (Nako, Wu, & Eimer, 2014; Nako, Wu, Smith, et al., 2014; see also Anderson, Vogel, & Awh, 2013). Because the N2pc is highly dependent on the top-down attentional set of the observer (Eimer & Kiss, 2008), our ERP results therefore demonstrate that adult observers (who seem to have reduced sensitivity to non-native exemplars) do, in fact, deploy precise early exemplar level attentional templates for non-native exemplars. However, the early deployment of these specific non-native templates does not seem to be maintained at later response stages, given poor performance for specific non-native targets (i.e., ape faces).

Figure 8. Mean N2pc amplitudes for Exemplar and Category Match trials, as well as Foil trials, for both experiments from 220 to 320 msec after stimulus onset. Error bars represent standard error.
What then could be the source of the perceptual narrowing effect? Would other ERP components representing later response stages reflect the perceptual narrowing effect (i.e., larger for category vs. specific items for non-native stimuli)? Our current findings leave open the question of whether perceptual narrowing might instead be indexed by other ERP components, namely, the SPCN (working memory maintenance for target identification, 400–600 msec; see Eimer, 2014) and the P3 (stimulus evaluation and working memory updating for discrimination; Polich, 2012), which both typically correlate with RT and accuracy or the lateralized readiness potential—a later measure of stimulus–response activity (Luck et al., 2009; Eimer, 1998). Interestingly, post hoc analyses on the SPCN and P3 revealed that these later components, like the N2pc, did not follow the perceptual narrowing behavioral effect. However, this study was not optimized to measure these components because of the temporal contamination of the SPCN by the N2pc and because of the simultaneous presentation of targets and distractors minimizing the P3. We are hesitant to draw strong conclusions from these later component effects and would require optimal experimental designs to replicate these effects. Pinpointing the exact neural stage at which perceptual narrowing operates is important, and this study provides the foundation for future work in this area. From the current study, we can rule out the possibility that early selection (i.e., attentional template formation and deployment) is the source of this inferior exemplar level performance.

The current study supports a growing literature on dissociations between early neural processing and later behavioral responses. These other studies often have tested sequential discrimination abilities in populations with cognitive disabilities. Studies on developmental prosopagnosia (famous vs. nonfamous faces; Eimer, Gosling, & Duchaine, 2012), schizophrenia (Luck et al., 2006, 2009), congenital amusia (pitch processing; Moreau, Jolicouer, & Peretz, 2009), and auditory perceptual narrowing (Hindi phonemes; Rivera-Gaxiola, Csibra, Johnson, & Karmiloff-Smith, 2000) have all found early discrimination abilities for targets that are difficult to distinguish behaviorally. For example, Rivera-Gaxiola et al. (2000) found a robust MMN, an ERP indicating preattentive discrimination of a deviant (i.e., oddball) within a sound sequence, for non-native Hindi sounds with non-Hindi-speaking participants. Our study moves beyond sequential discrimination tasks (e.g., oddball tasks) by implementing a visual search task to induce task-dependent attentional template deployment. Our ERP results revealed that, in addition to intact early exemplar level discrimination for non-native stimuli (the N2pc component from exemplar trials was larger than those from foil trials for ape faces), adults deploy similarly precise attentional templates for both native and non-native stimuli (no differences in N2pc amplitude between experiments using native and non-native stimuli).

Our study addresses a fundamental question in cognition: How does long-term previous experience impact distinct processing stages? Our results suggest that long-term previous experience with reduced exemplar level judgments (i.e., perceptual narrowing) does not appear to eliminate better early attentional selection of non-native exemplars compared to non-native categories in cognitively healthy adults. The ERP patterns follow the likely “default mode” in early selection processes—better search for exemplars because of more precise attentional templates compared to categories. In previous work, we have found similar N2pc patterns for familiar, novel, and newly trained simple categories versus specific items (e.g., Wu et al., 2013). It seems that, in these cases, the specificity of the attentional template is the main factor modulating the N2pc (assuming target–distractor similarity is controlled). This high-fidelity representation of a target is relevant to studies of perceptual learning of non-native stimuli. If the loss of perceptual discrimination were the primary effect of perceptual narrowing, there would be no substrate available from which recovery could be based.

The N2pc is, however, strongly modulated by learning under other circumstances. Given that the N2pc is a marker of top–down attentional selection, previously acquired knowledge of a target is a requirement to complete the task and determines the presence or absence of the N2pc. It is likely that expertise training with monkey faces (e.g., monkey zookeepers) could enhance the N2pc. In the present study, however, the N2pc components were identical between Experiments 1 and 2, the latter using native human face stimuli. Future work could use different types of training (implicit, explicit, feedback) to identify the key factors underlying how learning (both short term and long term) modulates the N2pc and other neural markers of top–down selection (see Wu et al., 2013).

By understanding how attention and learning interact, we can gain insight into visual and auditory plasticity from expertise training (e.g., Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Williams, Tarr, & Tanaka, 1998; Pisoni, Aslin, Perry, & Hennessy, 1982), especially in adulthood after the typical “critical periods” in infancy. Perceptual narrowing seems to affect only later stages of processing, which then allows the potential to acquire proficiency with non-native stimuli through expertise training. Investigating attention and learning interactions will reveal insights into flexible cognitive strategies that enable the development of proficiency beyond critical periods in infancy.

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