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Early brain potentials link repetition blindness, priming and novelty detection

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To study mechanisms of visual object identification in humans, event-related potentials (ERPs) were recorded during successful or unsuccessful identification of rapid, serially presented words (unrepeated or repeated). We observed 'repetition blindness' (RB): more repeated than unrepeated words were incorrectly reported. ERPs from repetition-blinded words exhibited little or none of the enhanced positivity found for correctly reported repeated words, resembling instead ERPs from any unrepeated sequence initially, but only incorrectly reported unrepeated sequences later. Thus it appears that in RB an early (220 ms) neural operation that normally initiates facilitated processing from immediate repetition priming erroneously processes a repeated item as novel. This operation (possibly in basotemporal neocortex) appears to induce differential subsequent processing of novel *vs* repeated information.

Key words: ERP; Novelty detection; P300; Perceptual categorization; Repetition blindness; Repetition priming; Temporal lobe; Visual attention; Visual perception; Word identification

Introduction

Visual images are analyzed within many brain areas. Although the extraction of visual features and object identities has been well studied, few have explored the perceptual operations involved in organizing categorical information into episodically structured representations of discrete objects and events. One way to study the construction of episodic representations of perceptual events is to explore a case where this individuation process fails: 'repetition blindness' (RB).[1] At very high presentation rates people report two items less accurately if they are the same than if they are different. In this study we measured event-related potentials (ERPs) in an RB task to explore the time course of recognition, individuation, and RB for words.

Materials and Methods

A red fixation square preceded each sequence (white-on-black) of three 4–7 letter words and four 7-symbol strings (Fig. 1). Two words were critical (C1 in lower case, C2 in upper case) and a third word (in upper case) either preceded C1 ('preceding word' condition) or intervened between C1 and C2 ('intervening word' condition). In each condition half of the 96 sequences contained all unique words ('unrepeated'); in the other half C1 and C2 were the same ('repeated'). Each participant was randomly assigned to one of four lists of counterbalanced (randomly intermixed) sequences. Participants maintained fixation until 2 s after each sequence, when they reported every word seen.

Electroencephalographic activity was recorded (250 Hz, bandpass 0.01–100 Hz) from 26 tin scalp electrodes in a geodesic arrangement on a plastic cap and from lateral and below eye electrodes referenced to the left mastoid and re-referenced to the average of left and right mastoids for analysis. Trials containing artifacts were eliminated. ERPs (62.5 Hz, bandpass 0.01–50 Hz) were time-locked to C2 onset (1771 ms before, 1288 ms after). As the locus of RB within sequences is uncertain (though C2 is likely),[1] ERPs were analyzed using three baselines: –1771 to –1651 ms (pre-fixation), –851 to –651 ms (end of fixation), and –651 to 0 ms (during sequences before C2). This report focuses on effects significant irrespective of baseline ($p < 0.05$). For brevity, statistics are reported for only the –1771 to –1651 baseline.

'Correct' trials were defined as those where all three words were correctly reported; the traditional criterion of only C1 and C2 correct (herein used primarily to confirm behavioral RB) is inappropriate for ERPs as it confounds diverse errors. Incorrect trials were those where only C2 was incorrectly reported. ERPs were analyzed over six time windows; in each, one ANOVA included midline (Fpz, Cz, 23, Oz) and another lateral (all other) electrodes with within-subject factors of electrode (E), hemisphere (H), trial type (T: unrepeated correct or incorrect, repeated correct or incorrect) and word order (W: preceding or intervening word). To include a between-subjects factor of list (L), 16 participants

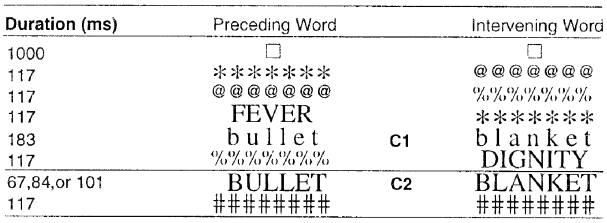

FIG. 1. Examples of rapid serial visual presentation of preceding or intervening word order sequences (no interstimulus interval). C2 was repeated (shown) or unrepeated. Participant's C2 duration (usually 84 ms) determined during practice.

(four in each of four list groups, right handed, half women) who exhibited RB were selected from the 21 recorded (UCSD community members, native English speakers, 18–27 years, normal/corrected vision). Of these 16, only subsets had enough repeated correct (11 people) or unrepeated incorrect (14 people) trials to form reliable averages; comparisons involving them had correspondingly fewer participants. Statistics were also calculated with all participants' data to evaluate whether such exclusion caused selection bias; since it did not, these additional statistics are not reported beyond the basic RB performance effect. Performance ANOVAs were the same (minus electrode factors). Where appropriate, *post hoc* ANOVAs were performed on preceding or intervening word conditions or electrode pairs (indicated as: left, right). Greenhouse-Geisser adjustments to degrees of freedom were applied to ERP analyses to correct for violation of the sphericity assumption.

Results

Performance: RB was observed irrespective of correctness criterion (Table 1, columns 1,2), although using the traditional criterion people were overall less accurate in the preceding (42%, $n = 16$; 43%, $n = 21$), than intervening (52%, $n = 16$, 55%, $n = 21$), word condition. Moreover, on incorrect repeated (RB) *vs* unrepeated (UI) trials people tended to report no word whatsoever for C2 (column 3) and, even when they did, these incorrectly reported repeated C2 words contained fewer letters from the actual C2 words, generally (column 4), and in their proper position relative to each other (column 5).

ERPs: The comparison between ERPs to RB and unrepeated correct (UC) trials is strongest since all 16 participants were available (Table 2; Fig. 2). However, since it confounds repetition and accuracy, further comparisons will resolve the contributions of each to these effects. RB and UC ERPs did not differ reliably until 400–600 ms after C2, when UC began to show greater posterior positivity. Between 400 and 500 ms, midline differences were reliable only in the preceding word condition ($F(1,12) > 14$, $p < 0.01$); between 500 and 600 ms, lateral posterior differences were reliable in both word order conditions. Stimulus order (and/or timing) thus may affect when (and/or which) neural systems are engaged. Moreover, changes in the scalp distribution of effects suggest that these neural systems are engaged differentially over time. Between 500 and 600 ms differences occurred bilaterally over occipitoparietal sites (df(1,3)14,17: $F = 7.42$, $p < 0.05$, 15,16: $F = 10.92$, $p < 0.01$; Ol, Or: $F = 18.39$, $p < 0.01$). In contrast, between 800 and 1000 ms differences were larger over the left hemisphere. An apparent frontal difference was not significant (700–1288 ms, preceding word, ANOVA five anterolateral pairs: $F < 3$, $p > 0.12$).

Comparing unrepeated incorrect (UI) with UC ERPs reflect identification and report accuracy unconfounded with repetition (Table 2; Fig. 2; $UI_{n=14}$). Overall these late differences (after 400 ms) strongly resembled those for the RB *vs* UC comparison. Thus the greater late posterior positivity for UC trials was

Table 1. Performance on stimulus sequences with unrepeated *vs* repeated words

	Repetition blindness		Incorrect C2 reports		
	Traditional criterion[a]	ERP criterion[b]	Word for C2 reported (albeit wrong; %)	For wrong reported C2 words: % correct letters	
				in any position	in correct position
Unrepeated	63 (61)	50 (48)	89	57	41
Repeated	31 (37)**,[c]	28 (32)**	57**	36*	22*

The repetition blindness effect: fewer repeated trials correct (columns 1, 2). For repeated (RB) relative to unrepeated incorrect trials, no word tends to be reported for C2 (column 3) and reported C2 words are less correct (column 4: letters the reported and the shown C2 words share: column 5: letters the reported and the shown C2 words share that are also properly positioned [phone and cone share three such letters]). 16 ERP (or 21) participants' performance, $**p < 0.001$, $*p < 0.01$. [a]Per cent C1 and C2 correct. [b]Per cent C1 and C2 and word correct. [c]Trial type × word order interaction, $p < 0.01$.

Table 2. ANOVA results for ERP comparisons over six time epochs

	0–400 ms	400–500 ms	500–600 ms	600–700 ms	700–1288 ms	800–1000 ms
UC *vs* RB						
Midline	–	TxW**	T*,TxW*	–	T**	T**
Lateral	–	–	TxE^{+}	–	T*	T**,TxE*,TxH^{+}
UC *vs* UI						
Midline	–	TxW**	TxW**	T^{+}	T**,TxW^{+}	T**
Lateral	–	TxW**	TxW**	–	T*,TxW^{+}	T**
UC *vs* RC						
Midline	T*	–	–	–	T**	TxE**
Lateral	T^{+}	–	TxE*,TxH*	TxH***	T***	TxE***,TxH*
RB *vs* UI						
Midline	–	T^{+}	–	–	–	–
Lateral	–	–	–	–	–	TxH*
RB *vs* RC						
Midline	T^{+}	T*	T*	T*	T^{+}	T^{+}
Lateral	–	T^{+}	T*	T^{+}	T^{+}	–

An early (0–400 ms) ERP effect is exhibited by repeated correct (RC) trials compared with either unrepeated correct (UC) or repeated incorrect (RB) trials. This early effect is absent in either comparisons: UC and unrepeated incorrect (UI) trials diverge from each other and from RB trials after 400 ms. Midline or lateral site ANOVAs: trial type (T), word order (W), electrode (E), hemisphere (H). ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, – $p > 0.05$ with three tested baselines, $^{+}p < 0.05$ with two out of three baselines and $p < 0.16$ with other baseline.

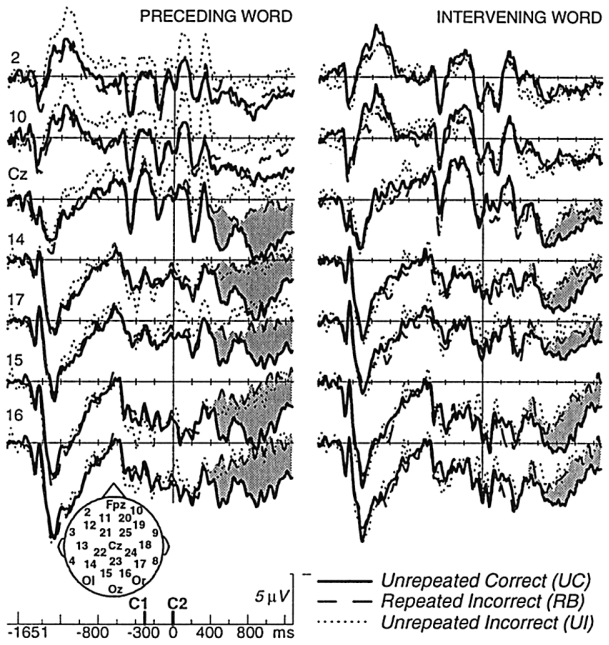

FIG. 2. Repetition blindness and incorrectness: grand averaged ERPs to unrepeated correct and incorrect trials *vs* repeated incorrect (RB) trials. First sign of incorrectness occurs 400 ms after C2, where correct trials are more positive than incorrect ones, regardless of repetition. Schematic head shows electrode locations.

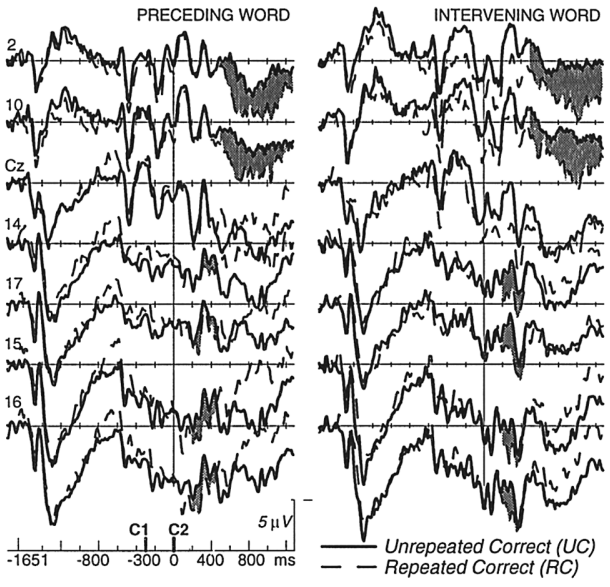

FIG. 3. Immediate repetition priming: grand average ERPs to unrepeated *vs* repeated correct trials. Repetition with correct report yielded more positivity between 220 and 340 ms posteriorly and between 500 and 1288 ms anteriorly. Both repetition priming effects were absent in RB.

primarily an index of accurate identification and report processes.

Comparing repeated correct (RC) with UC sequences explores whether RB *vs* UC differences reflect general repetition effects: indeed they do not (Table 2, Fig. 3). Here there was greater posterior positivity for repeated than unrepeated trials from well before 400 ms; ANOVAs over 20 ms time windows (0–400 ms) revealed significant main effects of trial type at lateral and midline sites between 220 and 339 ms. Between 500 and 1288 ms, RC was also more positive than UC anteriorly while UC

Table 3. Scalp locations of late ERP effects for repeated *vs* unrepeated correct

RC *vs* UC effect	Location	500–600 ms	700–1288 ms	800–1000 ms
Trial type	Anterior lateral	2.10*	2.10*	2.10*
Trial type × electrode	Anterior midline			Fpz, Cz**,[a]
Trial type	Posterior lateral	Ol,Or**	15, 16* Ol, Or**	15, 16* Ol, Or**
Trial type × hemisphere	Posterior lateral	14, 17*4, 8*	Ol, Or*, 22, 24*	Ol, Or**

Anterior and posterior differences are significant but index somewhat distinct effects since hemispheric asymmetry occurs only posteriorly. Left, right or [a]anterior, posterior electrode pair ANOVAs, $**p < 0.01$, $*p < 0.05$.

was more positive (as in previous comparisons) than RC posteriorly, especially over the left hemisphere (Table 3).

Comparing RB with UI trials with accuracy better equated (Table 2; Fig. 2) further evaluates whether RB trials merely reflect unsuccessful identification and report processes, although many factors (e.g., variable attention, forgetting) may induce an incorrect report. While RB trials exhibited slightly more early positivity, this was restricted to the intervening word condition (200–400 ms, 2/3 baselines). Thus RB trials did not generally show more early positivity than unrepeated trials, although they may under some circumstances. Rather, differences between RB and UI trials occured more consistently late after C2 (800–1000 ms).

In contrast, RC trials differed from RB trials early on (Table 2); RC trials were continuously more positive starting from 200–400 ms (midline: $p < 0.05$; lateral: two baselines $p < 0.01$, other baseline $p < 0.12$).

Discussion

When input is rapid, the number and severity of identification errors are exacerbated by repetition, raising the question of whether mechanisms supporting identification for repeated and unrepeated items differ. For unrepeated words, correct report was associated with posterior positivity, the P3b (typically peaking around 600 ms), presumably reflecting the explicit identification categorization, and decision processes enabling report.[2–4] Incorrect trials showed little of this positivity regardless of item repetition. Specifically, before 400 ms unrepeated but correct (UC) trials differed little if at all from incorrect trials (RB or UI), whereas later (400–800 ms) UC trials exhibited greater posterior positivity. This would appear to suggest that RB results from problems with late processes and that the main mechanisms leading to RB do not differ from those underlying incorrect report in general.

However, this cannot be the case. RB trials lacked not only late ERP characteristics associated with correctness (P3b) but also earlier facilitation effects on repetition. Correct repeated (RC) trials exhibited more posterior positivity than other trials early in processing (by 220 ms after C2). This early repetition effect probably indexes a subcomponent of the ERP immediate repetition priming effect,[2,3,5] which typically onsets between 220 and 300 ms and features decreased P3b peak latency (around 400 ms) and attenuated amplitude of the N400 (reflecting conceptual analyses), besides greater P3b amplitude (also observed at longer lags).[2,3] Later, RC trials exhibit the largest frontal positivity. This effect peaked too late (700–1000 ms) to be a typical P3a peak (300–400 ms), which is also enhanced by immediate repetition and related to working memory (WM) activation.[3] Nonetheless, it may reflect some reorganization of items within WM for report, since participants tended to report repetitions as 'word twice' rather than saying the 'word' twice.

Both these ERP repetition effects were absent or markedly diminished on RB trials. The ERP pattern indicates that repetition facilitates explicit identification processes if and only if it is detected before 220 ms after the repeated item. By 220 ms after C2 onset, C1 (processed for 520 ms) is probably undergoing analyses associated with explicit categorization, identification and report preparation (P3b). These analyses have not yet begun for C2. RB thus seems to be initially a consequence of the failure by an earlier neural mechanism(s) to detect repeated information.

We therefore maintain that any RB account must entail some difference in the early perceptual processing of repetition blinded items compared with correctly reported, repeated items. In particular, we suggest that RB occurs at or immediately after C2 has been perceptually categorized at some early level. By perceptual categorization (also called 'type recognition'[1]) we mean the match of incoming perceptual information to the stored representation of a word or object in memory, a process which according to prior scalp ERP evidence from normal subjects can occur by 150 ms after stimulus presentation.[6] Similarly, intracranial ERP recordings from posterior basotemporal neocortex in patients shows selective responses between 150 and 200 ms to letterstrings but not faces, while in adjacent neocortex these ERPs are elicited by faces but not letterstrings. These basotem-

poral ERPs, reflecting prelexical analysis of letter-strings or face detection,[7–9] precede ERP effects of immediate repetition[2,3] and those indexing explicit identification accuracy (400 ms,[10] UC *vs* UI). Thus an early neural process subserving perceptual categorization may trigger repetition facilitation effects, and the failure of the latter effect may be implicated in RB. Specifically, we speculate that the early perceptual system initially implicated in RB (and immediate repetition priming) is responsible for discriminating between new and redundant input. Moreover, the outcome of this discrimination subsequently induces differential processing of novel and repeated items, consistent with late differences between RC and other trials.

This proposal is consistent with findings that neurons in monkey inferotemporal (IT) cortices (with neurons selective for particular objects) are sensitive to repetition. Units in posterior IT discriminate novel from repeated items if no more than one item intervenes,[11] and neurons in anterior IT can perform the discrimination when any number of items intervene.[12,13] Neural systems initiating RB thus may differ depending upon the number of intervening items; indeed our RB ERP effects differed for no *vs* one intervening item.

In the monkey, the IT interacts with systems (pulvinar, parietal cortex) controlling attention and orienting.[14] In humans, interactions between these systems may also orchestrate selective attention to a particular object, thereby gating access of novel *vs* repeated objects to a stable representation in WM.[14–16] A prefrontal–posterior cortical WM system, implicated in facilitated processing after immediate repetition,[3] may participate in the network directed by IT. Failure by IT to detect a repetition may consequently induce attentional and orienting structures to process the repeated item as novel, thereby inducing further difficulties processing the repeated item and ultimately RB. Perhaps the participation of different areas within these systems underlies orthographic *vs* phonological RB.[17,18]

Rival accounts of RB have placed the locus of the effect at different stages of processing of the critical item, including (i) its initial recognition or perceptual categorization,[19] (ii) its encoding as a discrete object/event distinct from C1,[20] (iii) the stabilization of its representation in WM,[21] (iv) the loss of this representation from WM,[22] or (v) a variety of report biases.[23] Our finding of less positivity for RB than RC trials is consistent with the suggestion that in RB C2 activation fails to reach threshold (stage i).[24] The similarity of ERPs before 400 ms between RB and any unrepeated trials, wherein both C1 and C2 are two distinct, novel items and processed as such, suggests that any loss of the distinction between C1 and C2 happens after 400 ms (consistent with a hybrid of stages ii and iii). Finally, although we found relatively late differences between RB and RC trials (starting late enough for stage iv though probably not v), the presence of early differences in this comparison shows that these later effects cannot be the sole cause of RB. A more parsimonious account is that the later effects are a consequence of the earlier effects rather than a primary cause of RB.

Conclusions

Using ERPs to explore general identification processes and the phenomenon of RB, we found evidence that RB and immediate repetition priming may share an early perceptual operation (before 220 ms) for discrimination of novel from redundant (i.e. repeated) visual information (a short-term novelty detector). This perceptual neural operation seems to be activated before explicit identification (around 400 ms) and occurs early enough to constrain the direction of subsequent processing. At rapid presentation rates, this operation erroneously classifies some repeated items as novel thereby inducing problems with their later processing and ultimately yielding RB. Despite this tendency, ERPs reveal facilitated processing for accurately reported repeated items, the 'immediate repetition priming' effect. Our results extend understanding of ERP immediate repetition priming effects by demonstrating they are less likely to occur at high presentation rates (RB) and by placing a lower time limit on the operation of the prefrontal-posterior cortical WM system implicated in this immediate repetition facilitation. We suggest that the perceptual operation that initially mediates RB and priming may involve ventral temporal cortices for discriminating novel and repeated items, perhaps interacting with attention and orienting systems (pulvinar nucleus, parietal cortex) to control processes supporting later explicit object identification.

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General Summary
Recordings of activity from the human brain across time (event-related potentials, ERPs) suggest that about 400 ms elapse before written words can be identified sufficiently to be reported, at least when words are presented at rapid rates (about 6/s). Using such presentation rates, we observed 'repetition blindness' (RB), where people less accurately report repeated words than unrepeated words. Our ERP results suggest that RB is a consequence of processing errors in early brain areas (within 220 ms after a word) that discriminate novel from repeated information. At slower presentation rates, we suggest that these same brain areas (probably posterior basal temporal regions) trigger the improved identification and decision processes that are typically observed with immediate repetition (observed herein for correctly reported, repeated items). Such neural processing appears to constrain the direction of subsequent processing of novel *vs* repetitious information perhaps by interacting with systems that control attention.