

Sequential resolution of fragmented visual percepts: Experimental investigation of a subject's perceptual experience after a right medial temporal stroke

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Abstract

This report concerns the fragmented visual percepts in a woman, TR, following a right entorhinal–perirhinal infarct. In a previous report, Weddell [Weddell, R. A. (2005). A visual disorder producing highly selective deletion of recurring letters. *Cortex*, 41, 471–485] linked TR's highly selective tendency to delete recurrent letters with her fragmented percepts. The conflation of same-identity form elements was attributed to anterior extrastriate damage, which reduced the amount of information sustainable in fully resolved visual percepts, and the present experimental investigation of her subjective account of segment formation and resolution completes the story. She said that complex objects and long words first appeared as blurred regions, which sometimes included form elements. It is argued that figure-centred attentional mechanisms subdivided this blurred region into up to 3–4 parts. String length, lexical status (word vs. nonword), and background colour and/or luminance determined fragment length. Two rules described the fragment resolution sequence: largest segments usually resolved first, left-to-right resolution accounting for a few sequences. This resolution sequence occurred when stimuli were exposed too briefly for saccadic exploration, implicating endogenous attentional shifts. Experiment 4 confirmed TR's assertion that spatial, orthographic, and phonological information were stored during the fragment resolution process. Moreover, TR exerted considerable voluntarily control over the fragment resolution sequence and some influence over fragment length. Finally, these findings were interpreted in terms of an extended version of a neural network model of vision largely derived from nonhuman primate studies.

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1. Introduction

Studies of loss of phenomenal vision after destruction of primary visual cortex (e.g., Weiskrantz, 1986) and of visual neglect (e.g., Driver & Vuilleumier, 2001) strikingly demonstrate our lack of awareness of some visual processes. Whilst verbal report of visual experiences is unnecessary for some experimental paradigms used

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with brain damaged human and nonhuman primates (Stoerig & Cowey, 1997), the robust denials of subjective vision by correctly performing brain injured humans perhaps provides the most compelling evidence for blindsight. Similarly, functional magnetic imagery (fMRI) investigations of the neural substrate of visual consciousness usually depend on subjects' verbal or manual report of their subjective experiences (e.g., Portas, Strange, Friston, Dolan, & Frith, 2000).

Anecdotal accounts of subjects' visual experiences are often found in individual case studies (e.g., Humphreys & Riddoch, 1987), but researchers rarely attempt systematic analyses of subjective experience, preferring to rely on "objective" measures such as accuracy and/or latency of naming or matching responses. This reluctance no doubt reflects concerns about the reliability of subjective accounts of potentially evanescent experiences, especially when reasoning ability and/or communication skills are often compromised. Nevertheless, the intriguing perceptual experiences of brain injured subjects can surely provide unique scientific data on the neural basis of consciousness when, for example, the percepts are sufficiently repeatable and the subject retains adequate cognitive capacity to represent them. Consequently, the present report describes TR, a woman who consistently described her percepts of words and objects as a series of resolving parts.

A tendency to attend to parts rather than the whole is common to many visual perceptual disorders. Thus, in Balint's syndrome, a dorsal stream visual dysfunction, visual attention is sometimes so restricted that only parts of objects or words are seen (Rizzo & Vecera, 2002). Undue focus on object parts also occurs in cases of ventral stream pathology. For example, one subject's difficulty in simultaneously apprehending all object parts was attributed to impaired figure-ground formation (Kartsounis & Warrington, 1991), while Thaiss and De Bleser (1992) argue that subjects with integrative agnosia focus on parts, missing critical object features because they cannot integrate global forms with local features. Reports of object recognition deficits rarely clarify whether the object appears as (a) whole and connected but the subject unduly focuses on particular parts or (b) a series of separate parts.

The present report explores TR's assertion that words and objects often appeared as an initial blur, which split into segments that resolved sequentially. Her fragmented percepts did not appear to reflect disordered dorsal stream processes, since the present Experiment 6 indicated significant capacity to direct visual attention in space and neuroradiological evidence of right anteromedial temporal damage indicated ventral stream pathology.

The present experiments show that fragment number increased with letter string length, suggesting a limit to the number of form elements supportable in a fully resolved fragment. This is consistent with previous evidence that TR selectively deleted recurring letters (e.g., *loop* → *lop*), deletion rate increasing with string length (compare Experiments 3 and 4 of Weddell (2005)). Previously reported experiments with Navon-style letters (1977) indicated limits to the variety of forms supportable in a fully resolved percept. Thus, TR perceived same-element global forms as whole (Fig. 1, top) and undivided and different-element forms as a resolving sequence of same-symbol fragments (Fig. 1, bottom; leftmost loop of d, line, then rightmost loop). It was argued that damage in anterior extrastriate visual circuits had reduced the amount of visual information supportable in a fully resolved fragment. Moreover, the deficit was essentially visual since she deleted recurring letters and symbols (such as Σ and $*$) in words, meaningful forms, and nonsense forms.

Experiments 1–3 document visual and lexical influences on fragment length and resolution order. Experiments 4–6 show that processing time increases with fragment number and demonstrate top-down or goal directed influences on segment formation and resolution sequence.

2. Case report

TR, a predominantly right-handed woman aged 29, developed left-sided weakness and sensory impairment on 10.1.93. CT, on 11.1.93, found a small infarct in the right parahippocampal region, involving the entorhinal and perirhinal cortices (Fig. 2) and, on 20.9.93, demonstrated slight prominence of the right temporal horn. On 16.6.93, she exhibited topographical disorientation, marked prosopagnosia, visual object agnosia, semantic memory loss, impaired colour naming (1/5) but not colour matching (5/5), and surface dyslexia. There was no visual neglect or dysphasia. Bedside tests revealed full visual fields (acuity, J1 in both eyes). Testing several years later found impaired ability to detect left-sided flicker at eccentricities greater than 1°, and random dot stereograms demonstrated generally reduced stereoacuity, which was particularly marked on the left (Randot

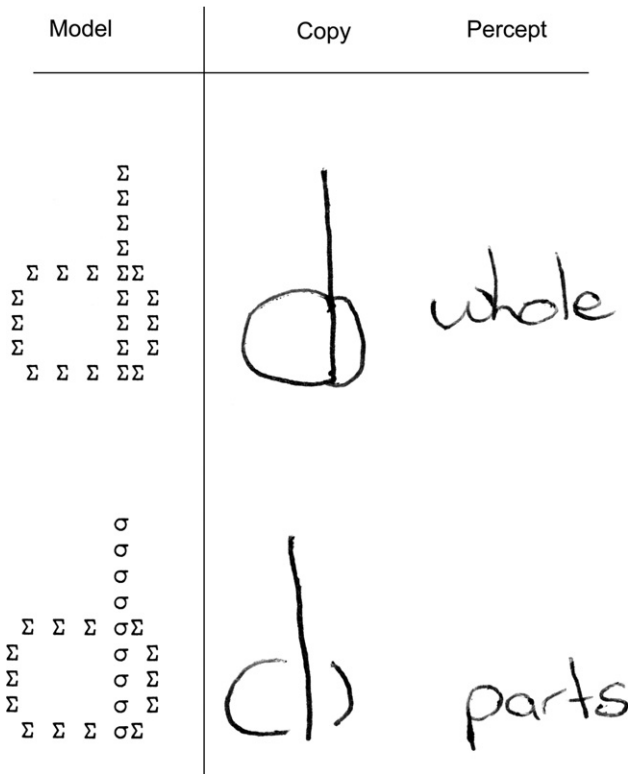


Fig. 1. Same (i) or different (ii) symbol groupings of local elements yielded global forms that were unfragmented or fragmented, respectively.

Stereotests, 1995). The latter deficits cannot explain her higher order perceptual difficulties, since she perceived different letter digrams and trigrams exposed for 17–168 ms at 2°–4.6° on either side of fixation only slightly less accurately than controls, and she usually deleted (69.2% deletions) one letter from same-letter digrams on either side of fixation (Weddell, 2005).

Her initial marked story and design recall deficits were relatively mild by January 1994. WAIS-R Verbal IQ was 61 and 81, while Performance IQ was 68 and 87 in June 1993 and January 1994, respectively. Slow reading in June 1993 was replaced by rapid (not letter-by-letter) reading in January 1994, corresponding National Adult Reading Test (Nelson & Willison, 1991) scores increased from 4/50 to 32/50, the later score yielding a premorbid Full Scale IQ-estimate of 108, which fitted education and occupation. Psychometric scores were very similar in August 1997, but semantic memory and object recognition difficulties resolved significantly between 1995 and 1997. Thus, in a test of TR’s knowledge of 73 objects, she chose from 4 options for each of 8 characteristics: 4 visual and structural characteristics (shape, colour, size, and name of part) and 4 semantic features (animate vs. inanimate, superordinate category, function, and most common location). TR earned 1 point when at least 8 of 10 university porter controls selected the same option and 0 otherwise (controls earned 1 if 7+ other controls chose that option). In April 1995, TR’s performance was significantly inferior to controls on 1 visual feature, colour (Kruskal–Wallis, $p < .04$), her scores being within the control range for the 7 remaining characteristics. One year later, TR’s performance did not differ significantly from control levels on any of the 8 characteristics. The Birmingham object recognition battery (BORB; Riddoch & Humphreys, 1993) also found object recognition recovered between 1995 and 1997. Thus, Association Matching (measuring semantic memory) scores increased from 20/30 to 28/30, while object decision scores increased from 70/128 to 109/128 (both initial, but not final, scores indicating impairment). Despite these gains, her unduly slow naming of overlapping figures in both administrations of the BORB revealed persistently



Fig. 2. CT image of right perirhinal–entorhinal infarct. Reprinted, with permission, from Weddell (2005).

impaired figure-ground formation, while topographical disorientation and prosopagnosia persisted throughout the period of experimental study (1998–2002).

In 1996, TR made 56 errors on the Farnsworth–Munsell 100-hue test, placing her between the 40th and 50th percentile of the normative sample (Farnsworth, 1957). Her score of 17/25 on the Ishihara Test for Colour Blindness (1994) was within normal limits, but low probably due to previously reported perceptual grouping difficulties.

Fig. 3i shows TR's drawing of her perceptual response to the word *slips*, which resolved in two parts: *sl* first and *ps* second. She first saw a blurred region. Misaligned letterforms sometimes appeared within the blur but, in the present example, the diffusely blurred region roughly conformed to the word shape with “bumps” representing ascending (i.e., *l*) and descending (i.e., *p*) features of letters. (The term “ascender” will subsequently denote both ascender and descender letters.) This blurred region then divided into two segments, which she said were separated by a 1–2 mm “... void” (subsequently, the term “segment” refers to a blurred section) TR then attended to the largest and darkest segment, while the other blurred section faded somewhat. She said she attempted to construct the longest fragment possible by left-to-right matching of the emerging letterforms with potentially corresponding sound sequences. Thus, Fig. 3i indicates that resolution of the first fragment entailed the initial emergence of *sl* followed by the appearance of the *i* (subsequently, the term “fragment” will refer to segments fully resolved into letters). Having resolved one fragment, it returned to a blurred state (the clear space still separating it from adjacent blurred segments or the next resolving fragment), and she usually resolved the next largest of the remaining blurred segments. She finally placed each stored phonological representation in its correct left-right location by mapping it onto its corresponding visual segment. The word was recognised at this point. TR's copy of a cigar drawing (Fig. 3ii) shows that objects were also perceived as a resolving fragment sequence: the tip resolved first, the body second, and a space separated fragments.

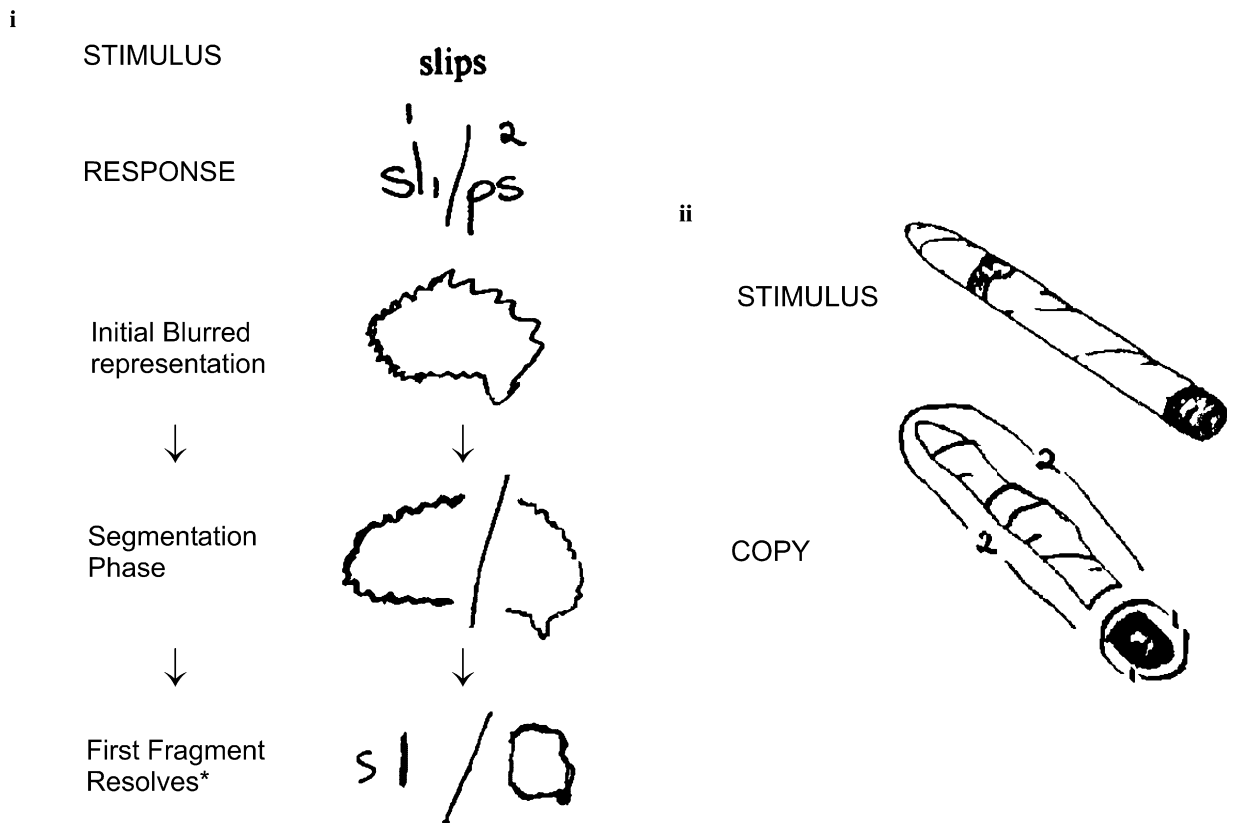


Fig. 3. (i) TR's illustration of initial stages of the word fragment resolution sequence (*resolution of *i* follows the appearance of *sl*). (ii) TR's illustration of her fragmented percept of a cigar drawing.

3. Experimental investigation of fragment resolution

3.1. Experiment 1: Effects of lexical status, length, and size on fragmentation

This experiment evaluates the effects of lexical status (real words vs. legal nonwords vs. illegal nonwords), string length and font size on two measures of fragmentation: the number of fragments and largest fragment size. It also asks if fragment boundaries are consistently located between the same letters in different test sessions.

3.1.1. Methods

Stimulus Set 1 comprised 40 words. Swapping syllables across Set 1 words produced 40 Set 2 orthographically legal and phonologically plausible non-words. Re-ordering letters within Set 1 words yielded 40 Set 3 orthographically and phonologically illegal nonwords. Each Set comprised ten 7-, 8-, 9-, and 10-letter items.

In block 1, these randomly ordered 120 stimuli were exposed continuously, individually, and in 36-point Times New Roman font (up to 5.9° long). All stimuli were presented twice in a second test session: 12-point stimuli (up to 2.5° long) in block 2, a 1-h break, and then the 36-point version in block 3. TR transcribed her percept of each stimulus, locating fragment boundaries with a slash (e.g., *morning* → *morn/ing*). Comparison of blocks 1 and 3 vs. 2 evaluates the effect of print size on fragmentation. Comparison of blocks 1 vs. 3 measures response consistency across sessions.

In this and subsequent experiments, ANOVA with Newman–Keuls tests post hoc tests were used in parametric statistical analyses. Otherwise, Mann–Whitney *U* or χ^2 analyses followed Kruskal–Wallis one-way ANOVA or backward elimination Loglinear modelling (in the latter case, at least 80% of cells contained 5

or more cases). All significant ($p < .05$) effects and trends ($p < .1$) will be reported, while non-significant effects are occasionally documented.

3.1.2. Results

There were few (5.8%) errors: 1.7% single letter deletions, 1.4% single letter substitutions, 1.1% single letter additions, 0.6% letter transpositions, or some combination of the first four error categories (1.1%). Small print (10.8%) elicited significantly ($\chi^2_{df=1} = 8.19, p < .004$) more errors than large print (3.3%). Moreover, errors varied with lexical status: words, none; legal nonwords, 3; illegal nonwords yielded the remainder (mostly legalisation errors, e.g., *vrseiec* → *vrseic*). Subsequent analyses included errors because their exclusion did not alter results.

Stimuli were mostly broken into 2–3 fragments, 1 illegal nonword generating 4. A loglinear model evaluated the effects of Length (7 and 8 vs. 9 and 10 Letters), Set, and Print Size on fragment number (2 vs. 3 and 4). Fragment number increased significantly ($\chi^2_1 = 107.91, p < .001$) with stimulus length (Fig. 4i). Words were significantly less fragmented than legal nonwords, which were less fragmented than illegal nonwords ($\chi^2_2 = 36.12, p < .001$). The significant ($\chi^2_2 = 8.29, p < .02$) Set × Length interaction arose because short words and legal nonwords often yielded two parts, most other stimulus groups fragmenting into 3 (Fig. 4i). No term including Print Size approached significance.

A further loglinear model determined the influence of Set, Length, and Print Size on Largest Fragment size (2 and 3 vs. 4 vs. 5 and 6 letters). Largest Fragment size (LF) increased significantly ($\chi^2_2 = 43.91, p < .001$) with string length (Fig. 4ii). Lexical status × LF was significant ($\chi^2_4 = 32.28, p < .001$): word LF's were larger ($M = 4.1$ letters, $SD = 0.5$) than legal nonword LF's ($M = 3.9, SD = 0.6$), which were larger than illegal nonword LF's ($M = 3.7, SD = 0.6$). The Set × Length term approached significance ($\chi^2_2 = 5.45, p < .07$) since between-Set LF differences mostly affected shorter letter strings (Fig. 4ii). Again, no term including Print Size approached significance.

Consistency of fragmentation was assessed by comparing large font blocks (1 vs. 3). A large majority of words (85.7%) and legal nonwords (86.8%) were fragmented identically or with a single letter shift in fragment location (e.g., *tire\tain* and *tire\tain*). Fragment location was identical or shifted by 1 letter in rather ($\chi^2_2 = 5.88, p < .06$) fewer illegal nonwords (67.5%).

3.1.3. Discussion

Fragment number and LFs both increased with string length. If LF's were inflexibly limited to a fixed number of letters, then fragment number would increase with string length and 10-letter nonwords might typically generate 5 fragments, since many 4-letter items in Experiment 3 (see below) generated two 2-letter fragments.

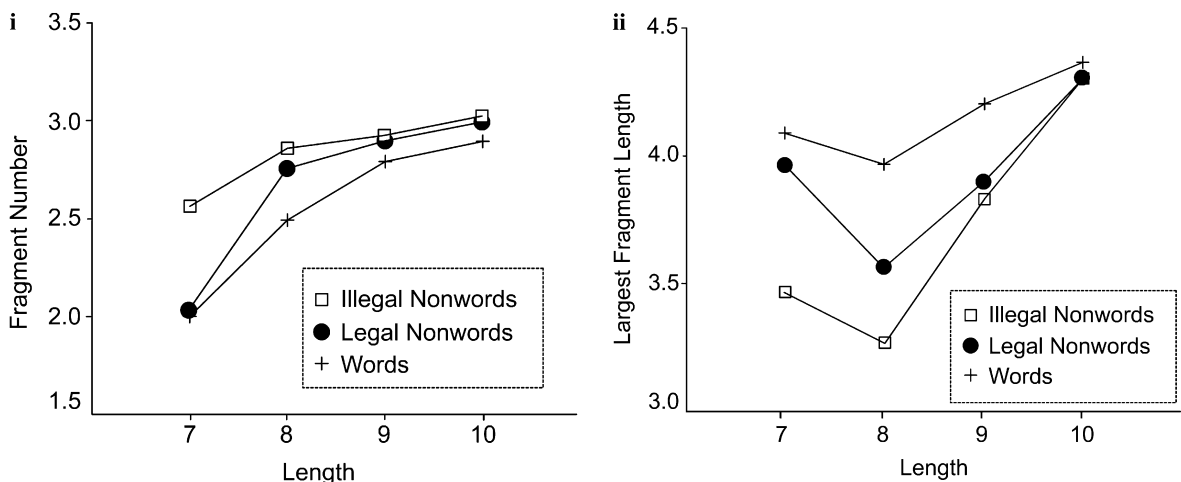


Fig. 4. (i) Variation of fragment number with string length and lexical status. (ii) Variation of LF with string length and lexical status.

However, stimuli were rarely segmented into 4 and never into 5 parts. This combined increase in fragment number and LF with string length suggests figure-centred segmentation. Thus, if figure-centred segmentation processes typically subdivided blurred figures into up to 3 (but never more than 4) parts, then segment length would increase with string length. Indeed, since some 8-letter words and all 10-letter words were segmented into 3 in this experiment, average segment length was inevitably greater for 10-letter words. Similarly, if the absolute retinotopic extent of LF's was inflexibly defined, then LF would have halved and fragment number would have doubled for the large print stimuli used in this experiment. Thus, figure-centred segmentation also fits the constant relationship between fragment number and LF after doubling print size.

The modest inconsistency in fragment length across sessions suggests that segment boundaries were approximately rather than precisely located, though words generally produced fewer fragments and longer LF's than illegal nonwords, legal nonword fragment number and LF's being intermediate. Interestingly, TR often said that segment number remained constant throughout the resolution process. If true, legal strings would generate fewer segments from the outset. This might be achieved by top-down attentional constraints on segment boundary locations based on automatic or covert perceptual gleaning of sufficient letter-sequence information to bias the number of segments produced or even the locations of their boundaries. For example, information indicating a probably illegal string might tend to shorten average segment length, automatic pre-perceptual processes extracting slightly different partial information on each occasion, which might have produced a degree of inconsistency in segmentation.

However, without strong independent evidence that partial analysis of lexical information influences segmentation top-down, it is perhaps more parsimonious to suppose that bottom-up processes initially constrained segmentation. Thus, segmentation may have been based on early-stage information (e.g., from a low spatial frequency filter (Olshausen, Anderson, & Van Essen, 1993)), segment length being initially identical for words and illegal nonwords. TR said that she actively tried to construct the longest fragment possible by matching it to stored phonological sequences. On this view, interactions between stored subword representations and segments would resolve a greater proportion of "legal" relative to "illegal" segments (since illegal strings consist of a series of single letters and/or short often low probability legal sequences). The remaining segments would assimilate any unresolved portions, and TR would not detect the consequent shifting of segment boundaries since unresolved/partially processed portions were inevitably indefinite. Moreover, TR said that she sometimes generated an extra segment when she could not resolve a string, and illegal strings would be particularly liable to trigger this process because they contain fewer and shorter consecutive letter sequences corresponding to familiar/stored orthographic and/or phonological representations.

Finally, whether or not top-down attentional constraints influence initial segmentation, TR's trial and error experimental fitting of stored representations to segments would tend to produce more consistent fragment boundaries when strings consisted of highly probable letter sequences rather than several equally low probability and illegal sequences.

3.2. Experiment 2: Largest fragments resolve first

TR consistently asserted that the largest or darkest blurred segment resolved first and informal questioning revealed that the darkest segments usually included ascender letters. Consequently, the present study predicted that she would first resolve the leftmost or rightmost letters when strings began or ended with ascenders, respectively.

Experiment 2 also explored her introspections about segment stability. When asked, TR usually replied that segment number remained constant throughout the resolution process, but she occasionally said that she had to create an extra segment when she found she could not resolve a particular segment, suggesting (a) that her reduced processing capacity could only resolve the stimulus if it was further segmented and (b) a degree of voluntary control over segmentation. Moreover, she said that individual letters sometimes appeared during fragment resolution. Letters emerged in the segment as it resolved (see Fig. 3i—TR illustrated resolution of the first fragment just before the letter *i* appeared). Letters also emerged in segments adjacent to the resolving fragment. The latter letters were separated from the resolving fragment by the inter-segment gap; in TR's words, they appeared "... on the other side of the void." Consequently, the present experiment asks if the resolving fragment has a tendency to "rob" one or two letters from adjacent segments: more specifically,

how often did the fragment boundary or inter-segment “void” disappear or shift as the currently resolving fragment assimilated emergent letters from adjacent segments?

3.2.1. Methods

Set 1 stimuli were the ten 7-, 8-, 9-, and 10-letter words of Experiment 1. Letters in each Set 1 word were reordered to produce a corresponding orthographically and phonologically illegal Set 2 nonword with all ascender letters at the beginning (e.g., *production* → *ptdoiucrn*). Reversing letter order yielded Set 3 stimuli (e.g., *ptdoiucrn* → *nrcouiodtp*), which ended in ascenders. There was a 12-point and 36-point version of each item. Each of the individually presented 120 words and nonwords appeared in random order in a first session: half of these items were in large print. The remaining 60 large and 60 small items appeared in the second session. TR was encouraged to view the stimuli briefly. She transcribed each one, indicating fragment boundaries with a slash, numbering resolution order, and underlining letters emerging in adjacent segments. For example,

$$\text{neuiecnlf} \rightarrow \overset{2}{\text{neu}} \backslash \overset{3}{\text{iec}} \backslash \overset{1}{\text{nlf}}$$

indicated that (a) the rightmost fragment (*nlf*) resolved first with the middle fragment resolving last and (b) the first letter of the middle fragment appeared as the second fragment (*neu*) was resolving.

3.2.2. Results

Nonwords elicited all errors: single-letter deletions ($N = 6$, e.g., *tdreiemne* → *tdreimne*) and/or substitutions ($N = 3$).

Print size did not influence fragment number ($\chi^2_1 = 0.43$, NS) or LF ($\chi^2_1 = 0.28$, NS): consequently, subsequent analyses pooled data across size. Most (98.8%) nonwords yielded 3 fragments. Significantly ($\chi^2_1 = 45.90$, $p < .001$) more words (27.5%) resolved in two parts, the remainder fragmenting into 3. Length significantly ($\chi^2_3 = 42.56$, $p < .001$) influenced fragmentation: 3 fragments were produced by a few (10%) 7-letter, most (80%) 8-letter, and all 9- and 10-letter words. LF's were 3 (46.3%) to 5 (4.3%) letters long. A loglinear model evaluated the effects of Set (1 vs. 2 vs. 3) and Length (7 and 8 vs. 9 and 10 Letter) on LF (3 vs. 4 and 5 Letter). Longer strings elicited longer LF's ($\chi^2_1 = 59.60$, $p < .001$). Words produced longer LF's than nonwords ($\chi^2_2 = 58.26$, $p < .001$). The Length \times Set interaction was significant ($\chi^2_2 = 12.76$, $p < .002$) because LF's increased steadily with length for nonwords, while LF's were larger for short 7-letter words than for 8- and 9- but not 10-letter words. Presumably, the latter effect reflects TR's ability to “squeeze” 7-letter words into 2 fragments.

Set markedly ($\chi^2_4 = 123.82$, $p < .001$) influenced segment resolution order largely because the first fragment to resolve usually contained an ascender (Table 1). Thus, leftmost Set 2 segments with ascenders usually resolved first (e.g., *fdncneioec* → *fdnc* \ . . . \ . . . → . . . \ *nei* \ . . . → . . . \ . . . \ *oec*). Rightmost Set 3 segments usually resolved first (e.g., *eaunscsbt* → . . . \ . . . \ *bt*). The distribution of Set 1 first fragments also reflected ascender location. Indeed, ascenders were confined to the rightmost or leftmost segment of 15 words, and that segment resolved first in 14 of these (e.g., *sec* \ *re* \ *tary* → . . . \ . . . \ *tary*). All possible resolution orders occurred. Left-to-right fragment resolutions (i.e., 123 or 12) were most common (37.71%), but right-to-left (321 or 21) resolutions were frequent (21.8%).

For 2-fragment responses, the first fragment contained significantly (Wilcoxon $z = 2.84$; $p < .005$) more letters ($M = 3.9$; $SD = 0.4$) than the second ($M = 3.3$; $SD = 0.6$). Decreasing length with order of appearance also affected 3-fragment responses (Friedman $\chi^2_2 = 76.54$, $p < .001$): first ($M = 3.2$; $SD = 0.7$), second

Table 1
Set influences location of initially resolving segment

	Leftmost	Middle	Rightmost
Set 1 ^a (e.g., <i>principal</i>)	12	31	36
Set 2 (e.g., <i>plprciain</i>)	70	10	0
Set 3 (e.g., <i>niaicrplp</i>)	12	23	45

^a Resolution order was not recorded for 1 word.

($M = 2.9$; $SD = 0.6$), and third ($M = 2.5$; $SD = 0.7$) fragments. This progression appeared in separate analyses of words and nonwords.

The foregoing 3 factors can describe all initial fragment appearances. Thus, most (89.5%) initial fragments contained an ascender. In a further 5.9% of cases, the initially resolving fragment contained more letters than the fragment(s) containing ascenders. Otherwise (4.6%), the initially resolving fragment was to the left of the ascender fragment.

A single letter sometimes appeared in a segment adjacent to the currently resolving fragment. It was always immediately right of the resolving fragment (e.g., *fdncneioec* → ... \nei\o...; never *fdncneioec* → ... f\nei\... or *fdncneioec* → ... \nei\...c). TR said that the resolving fragment attracted this letter, which “tried to” move across the illusory inter-fragment void. She said she always resisted this regrouping because the resolving fragment had already been phonologically encoded. The letter never appeared in 2-fragment responses. On 2/79 occasions, it emerged from the first segment after it had returned to a blurred state, as the second fragment resolved. Otherwise, it emerged from still unresolved segments: mostly (59/79) the third segment, as the first ($N = 1$) and second ($N = 58$) resolved. It sometimes (18/79) popped out of the second segment as the first resolved. The latter difference was highly significant ($\chi^2 = 65.73$, $p < .001$). Single-letter appearances were more common ($\chi^2 = 47.70$, $p < .001$) in nonwords (43.8%) than in words (11.3%), but they were not affected by length ($\chi^2 = 4.28$, NS).

3.2.3. Discussion

As in Experiment 1, words generated fewer and longer fragments than illegal nonwords. Moreover, fragment number and LF both increased with string length and to the same degree for both print sizes. The latter effects have already been attributed to figure-centred segmentation, foreground strings being subdivided into up to 4 segments. Experiment 2 also clarified TR’s observation that she first resolved the “darkest” segments, which usually contained (a) ascenders, and/or (b) most letters: i.e., darkest segments were those representing the highest proportion of stimulus contour. Moreover, she reported a tendency to resolve fragments left-to-right, and a weak rightward resolution bias was confirmed.

Three rules constrained the emergence of single letters from segments adjacent to the currently resolving one. First, though single letters sometimes emerged from the second segment, as the first fragment resolved, they more commonly emerged from the third as the second resolved. Since later fragments were shorter than first fragments, under-utilisation of the processing capacity of extrastriate circuits during resolution of second and third fragments may have left sufficient residual capacity for the resolution of an additional letter. Second, if only the foregoing rule were operating, then single letters would (a) most often re-appear in the first or second segment as the shortest (third) fragment resolved, and (b) single letters would appear equally often in the first and third segments during resolution of the second fragment. In fact, single letters rarely (2/79) emerged from a segment that had already been resolved. This suggests that attentional inhibition of previously resolved segments (bottom-up (Olshausen et al., 1993) and/or top-down (Watson & Humphreys, 1997)), biased visual processing in favour of not-yet-resolved segment(s). Third, single letters always emerged to the immediate right of the resolving fragment (e.g., *fdncneioec* → ... \nei\o...): non-adjacent or left-sided letters never emerged; and it usually (96.2%) emerged from the segment that resolved next. It is hypothesised that emergence reflected left-to-right spreading attentional enhancement. Indeed, TR frequently said that she tried to construct the longest fragment by left-to-right matching of visual elements with potential phonemes.

Interestingly, letters emerged in segments adjacent to the resolving fragment most commonly of illegal nonwords, and emerging letters never jumped across the inter-segment gap. This is consistent with her assertion that segment boundaries were usually stable throughout resolution, but it is equally possible that the segment boundaries were less fixed or precise than she realised. Thus, TR’s introspections indicated that letters emerged when her visual circuits could identify more graphemes than she could encode into phonological sequences (especially illegal sequences), consequently, failure to encode all of a segment may have resulted in the **expulsion** of the unencoded grapheme from the fragment. In short, the latter expulsion process may have been inaccessible to conscious awareness, and her interpretation that segment boundaries were stable and the resolving fragment attracted but could not absorb the emergent letter may have been post hoc.

3.3. Experiment 3: Effects of background, size, and exposure duration on fragmentation

Experiments 1 and 2 used continuously exposed stimuli, which did not control the influence of saccadic exploration on fragmentation. Therefore, Experiment 3 also presented stimuli for 101 ms (i.e., before saccades are normally initiated) to see if endogenous attentional shifts were sufficient for segmentation and fragment resolution. Furthermore, TR observed that colour facilitated word and object recognition; consequently, Experiment 3 examined the effects of background colour on fragmentation. The effect of font size on fragmentation was also re-considered. Computer-presented stimuli were large in 4 conditions and, to facilitate comparison with the results of Experiments 1 and 2, stimuli of the same size as were used previously were also continuously presented on a computer monitor (VDU) and on paper.

3.3.1. Methods

Black letter stimuli were 72 high frequency ($M = 385.9$ per million; Kucera & Francis, 1967), low frequency ($M = 1.7$ per million), and orthographically legal and phonologically plausible nonwords. Each set of 72 included twelve 4-, 5-, 6-, 7-, 8-, and 9-letter items. All ascenders occupied the beginning ($N = 6$) or end ($N = 6$) of 4- and 5-letter items, or the beginning ($N = 4$), middle ($N = 4$), or end of 6- to 9-letter stimuli (e.g., *dinosaur*, *conspinus*, or *variety*).

All 216 stimuli, 2.1° – 4.6° long, appeared in black letters (Luminance, 0.01 cd/m^2) at the centre of a 34 cm computer VDU against a 4.77 cd/m^2 red background for 101 ms in the R_{101} condition, and continuously in the R_c condition. Stimuli set against a white 15.76 cd/m^2 background produced the W_{101} and W_c conditions. The 216 items, 0.8° – 1.9° long, also appeared against white on the VDU and on paper in continuous conditions $W_{\text{vdu-small}}$ and $W_{\text{paper-small}}$, respectively. Items printed on A4 paper (luminance approximately 0.33 cd/m^2 for black contours and 1.46 cd/m^2 for white background) were individually presented through a moving $1.9^\circ \times 5.7^\circ$ window in a black sheet of card. All 216 items, allocated to 4 blocks (matched for length, frequency, and ascender location), were presented in each session. Each block was allocated to different experimental conditions, which were administered across 6 sessions in counterbalanced order. As in Experiment 2, TR represented fragment boundaries with a backslash, numbering resolution order.

3.3.2. Results

There were 1.1% additions (e.g., *credilons* → *cre\dil\ions*), 3.3% deletions (e.g., *trauma* → *tra\ma*), and 1.3% deletions and additions (e.g., *wasp* → *ga\p*): 5 errors involved more than 2 letters. Error rate varied with condition ($\chi^2_5 = 115.51$, $p < .001$). It was comparably low in continuously exposed conditions: R_c (0.5%), W_c (0.9%), $W_{\text{paper-small}}$ (2.3%), and $W_{\text{vdu-small}}$ (1.9%). Briefly exposed conditions elicited substantially more errors, a white background (W_{101} , 19.9%) yielding significantly more than a red background (R_{101} , 8.8%). Errors increased ($\chi^2_5 = 41.91$, $p < .001$) with length (4-letter, 1.4%; 9-letter, 12%) and varied ($\chi^2_2 = 20.15$, $p < .001$) with frequency (high, 3%; low, 4.4%; nonword, 9.7%). These length and frequency effects appeared comparable across the 6 conditions. Analyses using all responses are reported, unless exclusion of errors yielded different results (nonwords, 8- and 9-letter words, and the 10 remaining errors also being excluded to match stimuli across conditions).

Stimuli ranged from being unfragmented (12.7%) to generating 4 fragments (3.2%). LF, which included all letters of unfragmented stimuli, ranged from 2 (12.3%) to 9 (0.1%) letters. Table 2 shows that stimulus condition markedly influenced number of parts ($\chi^2_{15} = 452.07$, $p < .001$) and LF (Kruskal–Wallis $p < .001$). Data distributions precluded statistical evaluation of most interaction effects. Contrasting the pooled red (R_{101} and R_c) vs. white (W_{101} and W_c) conditions assessed Background, red eliciting fewer ($\chi^2_3 = 260.21$, $p < .001$) and longer (Mann–Whitney $z = 18.86$, $p < .001$) fragments. W_c vs. $W_{\text{vdu-small}}$ supposedly assessed Size, large stimuli yielding fewer ($\chi^2_2 = 9.63$, $p < .008$) and longer (Mann–Whitney $z = 2.73$, $p < .006$) fragments. The display Medium comparison ($W_{\text{vdu-small}}$ vs. $W_{\text{paper-small}}$) showed paper stimuli elicited fewer (Mann–Whitney $z = 4.97$, $p < .001$) and longer (Mann–Whitney $z = 4.59$, $p < .001$) fragments than VDU stimuli. Unlimited exposures (W_c and R_c) produced longer (Mann–Whitney $z = 3.00$, $p < .003$) and rather fewer ($\chi^2_3 = 7.47$, $p < .06$) fragments than brief exposures (W_{101} and

Table 2
Stimulus display conditions influence fragment number and length

	Fragment number, $M(SD)$	Letters in LF, $M(SD)$
VDU presentation		
Red continuous (R_c)	1.6(0.6)	4.6(1.2)
Red 101 ms (R_{101})	1.9(0.7)	4.2(1.1)
White continuous (W_{101})	2.5(0.6)	3.1(0.6)
White 101 ms (W_c)	2.6(0.6)	3.0(0.6)
White small ($W_{\text{vdu-small}}$)	2.7(0.6)	2.9(0.6)
Paper presentation		
White small ($W_{\text{paper-small}}$)	2.4(0.6)	3.2(0.7)

R_{101}), but the latter differences became nonsignificant when errors, nonwords, and 8–9 letter stimuli were excluded.

Lexical status did not influence the number of parts (Kruskal–Wallis, NS). However, it did influence LF (Kruskal–Wallis, $p < .02$), LF being similar in high ($M = 3.57$ letters; $SD = 1$) and low ($M = 3.52$; $SD = 1$) frequency words, but shorter in nonwords ($M = 3.38$; $SD = 1$). Fragment number and LF increased with string length (both Kruskal–Wallis, $p < .001$), this combined increase occurring in all 6 conditions.

An evaluation of the effects of Ascender Location (Left vs. Middle vs. Right) and Exposure Duration (W_{101} and R_{101} vs. W_c and R_c) on First Fragment (Ascender Absent vs. Present) yielded a significant Ascender Location x Exposure Duration x First Fragment interaction ($\chi^2_2 = 9.25$, $p < .01$). Ascenders in any location usually resolved first, but different exposure duration and/or involvement of saccades may underlie the slight increase in initial resolution of centrally-located ascenders of continuously-exposed stimuli (W_c and R_c : left, 77.5%; middle, 95.8%; right, 59.3%) than of briefly exposed stimuli (W_{101} and R_{101} : left, 83.3%; middle, 84.1%; right, 68.8%). Moreover, separate analyses of 2, 3, and 4 fragment responses consistently showed that letter number decreased with fragment order (first > second > third > fourth; all Wilcoxon $p < .001$): this decrease occurred in continuous and brief exposure conditions. Further, fragmented stimuli more commonly resolved left-to-right (brief = 42.1%; continuous = 37.5%) than right-to-left (brief = 30.6%; continuous = 26.5%). As in Experiment 2, these 3 factors strongly constrained the first fragment to resolve. Thus, the initially resolving fragment usually (75.2%) contained an ascender, contained most letters in a further 16% of responses, or was to the left of the fragment containing the ascender or most letters in 6.9% of responses.

Finally, pooling across sessions, the first and final 108 trials were contrasted to assess possible effects of fatigue from this lengthy task: within-session error rate ($\chi^2_1 = 0.79$, NS), number of parts ($\chi^2_3 = 0.38$, NS), and LF ($t = 0.18$, NS) did not differ significantly. However, comparing the initial (1–3) and final (4–6) test sessions, error rate ($\chi^2_1 = 22.93$, $p < .001$) fell from 8.8% to 2.6%. This between-session practice effect may simply reflect greater familiarity with the experimental situation. Alternatively, TR's improved accuracy may stem from greater resolution power following a strategic “decision” to increase fragment number ($\chi^2_3 = 31.95$, $p < .001$) from ($M = 2.2$, $SD = 0.8$) to ($M = 2.3$; $SD = 0.7$) and to correspondingly decrease LF ($t = 4.85$, $p < .001$) from ($M = 3.6$; $SD = 1.2$) to ($M = 3.3$; $SD = 0.9$). It would be implausible to argue that increased fragment number and decreased LF in later sessions are mere mathematical consequences of the reduced error rate and, in any case, both effects remained highly significant when errors were excluded.

3.3.3. Discussion

Several features of fragmentation were similar for continuously- and briefly-exposed stimuli: therefore, endogenous attentional shifts were sufficient to produce them, saccades being unnecessary. Specifically, for continuously (Experiments 1–3) and briefly (Experiment 3) exposed stimuli, fragment number and LF always increased with string length. The latter effect has already been attributed to figure-centred segmentation, which subdivides the unresolved visual signal into a maximum of 4 sectors. Moreover, first fragments usually contained ascenders, and/or most letters, and/or were leftmost whether exposure was brief or continuous.

The second main result is that background influenced stimulus resolution. Thus, a red background generated fewer errors, and fewer and longer fragments. Two possible explanations are discussed. First, luminance contrast (LC) and colour contrast define black on red contours, while only LC defines black on white letter

contour boundaries. LC was virtually identical for large black letters against white (LC = 0.492) and against red (LC = 0.497); consequently, colour contrast increased contour information in the red background condition. The resulting increased signal to noise ratio might have facilitated form resolution, thereby encouraging generation of longer segments. Second, VDU background colour and luminance are confounded in this study, white being considerably brighter than red. Unpublished results suggest that background colour and luminance separately influence fragmentation, but the luminance effect (controlling for figure and background colour, fragmentation increased with luminance) was stronger than the colour effect (green elicited more fragments than red when figure and ground were isoluminant). Moreover, TR frequently said that the background strongly attracted her attention, once adding that she might miss stimuli appearing on the VDU if she did not expect to see them. If neural activity representing the background competitively suppressed the signal in the smaller and darker area representing the figure, then background suppression might grow as background luminance increased. In effect, increasing background luminance might reduce the signal to noise ratio: consequently, black on white stimuli may have evoked shorter segments to successfully resolve their noisier signals. Indeed, the increase in fragment number in later sessions corresponded with improved accuracy.

Though large and small stimuli were similarly fragmented in Experiments 1 and 2, large VDU stimuli elicited longer and fewer fragments than small stimuli in Experiment 3. It is suggested that large VDU stimuli attract attention more strongly than small VDU stimuli. Thus, light diffuses from white background pixels adjacent to black letter contour pixels, which become a lighter shade of grey. Large letters had wider contours than small letters: therefore, this lightening extended across the entire width of the narrow contours of small letters, while it was relatively confined to the edges of the broader contours of large stimuli, which would retain a black central region. Presumably, this artifactual lowering of mean LC of small letters yielded a noisier signal: indeed, TR said that small print VDU letters tended to “. . . run into each other. . .”, and she may have shortened segments to ensure resolution. Similarly, luminance diffusion is not significant on paper; consequently, same-sized small stimuli may have been less fragmented on paper (with its sharp step down in luminance at contour edges) than on the VDU (which provides noisier contour information through its more gradual downward luminance gradients).

3.4. Experiment 4: Fragment resolution involves temporary storage of orthographic, spatial, and phonological information

TR said that she sequentially resolved each segment by matching it to its corresponding phonological codes, which were each temporarily stored until all segments had been resolved, and the word could be assembled. Therefore, Experiment 4 tested the prediction that lexical decision latencies would increase with fragment number. Moreover, a coloured background elicited fewer fragments and errors in Experiment 3. If, as was suggested, TR's difficulty with a white background was entirely visual, then the relationship between fragment number and lexical decision latencies would be similar for TR's most preferred (yellow on red) and least preferred (black on white) figure-ground combinations. Consequently, it was predicted that colour and fragment number would not interact.

Experiment 4 also examined the type of information stored in working memory during the resolution process. Thus, Experiments 1, 2, and 3 show that a minority of segments resolved in a strictly left-to-right sequence. Therefore, TR would usually miscategorise words as nonwords if she merely replayed the stored phonological representations in their resolution order and based lexical decisions solely on this phonological information. Clearly, a high rate of correct decisions would require access to some visual information during the replay phase. For example, recall of the relative spatial locations of originating segments might be sufficient for most lexical decisions—replaying stored phonological representations in the spatially correct left-to-right order would tend to increase the accuracy of lexical decisions. However, if she only relied on visual spatial information, lexical decisions about pseudohomophones (e.g., *sistem*) should be especially error prone. Moreover, TR might incorrectly copy *sistem* as *system* if she saw it as 2 fragments (*sis* and *tem*), especially when the “incorrect” segment resolved first (e.g., *sistem* → *sis*/. . . → . . ./*tem*). In contrast, when the “incorrect” segment resolved last (e.g., *sistem* → . . ./ *tem* → *sis*/. . .), the surviving visual representation of the “incorrect” grapheme sequence might be sufficient to transcribe pseudohomophone correctly. Consequently, TR (a) made lexical decisions about and (b) copied pseudohomophones.

Finally, TR said that unfragmented stimuli were read automatically – they did not engage the considerable working memory processes (phonological encoding, storing, and replay) she believed necessary for reading fragmented stimuli. Consequently, Experiment 4 used subvocal counting in an attempt to interfere with the working memory processes engaged during sequential fragment resolution. It was predicted that counting would selectively interfere with lexical decisions about fragmented stimuli.

3.4.1. Methods

Stimuli included sixteen 3-, 4-, 6-, and 7-letter frequency-matched words. Two sets of nonwords were also presented. All 64 words were converted into orthographically legal and phonologically plausible nonwords by changing one of the last 3 letters (e.g., *country* → *countoy*). A further sixteen 6- and 7-letter pseudohomophones were derived from high frequency words by converting at least one of the initial 3 letters (e.g., *became* → *beacame*). This set of pseudohomophones was not matched with a corresponding group of words, as no prediction could be made about the frequency of incorrect decisions about pseudohomophones (i.e., categorisation as words could have ranged from 0–100%).

Stimuli, subtending 1.8°–4.4° of visual angle, were exposed after a 1 s delay for 168 ms at the centre of a VDU in two randomly ordered 80-item blocks matched for word length and stimulus type (word, nonword, and pseudohomophone). Block 1 stimuli were yellow (15.16 cd/m²) on red (4.77 cd/m²) and were followed by block 2 black (0.01 cd/m²) on white (15.76 cd/m²) stimuli in the first session. The remaining items were presented in counterbalanced order in a subsequent session. With her right forefinger, TR pressed right- or left-sided keys of a response box for words or nonwords, respectively, the computer storing decision latencies for subsequent analysis. She then indicated the number of fragments seen. Finally, she was asked if the initial or end part of pseudohomophones appeared first.

All 320 stimuli were presented in counterbalanced order in a third session with 2 procedural changes: TR began counting upwards in ones from a random 3-digit number before stimulus presentation, ending counting after making the decision; she was not asked about pseudohomophone fragment resolution order.

In a fourth session, the 32 black on white pseudohomophones used in this experiment plus the 32 parent words were exposed for 168 ms. TR transcribed each item, representing fragment boundaries with a slash and indicating order of fragment appearance.

3.4.2. Results

Table 3 gives the number of fragments evoked by each experimental condition, and loglinear modelling assessed the effects of Lexical Status (Word vs. Legal Nonword vs. Pseudohomophone), Colour (Black on White vs. Yellow on Red), and Count (Absent vs. Present) on Fragment (1 vs. 2 and 3). The significant ($\chi^2_1 = 15.01$, $p < .001$) Colour x Fragment term reflects the greater fragmentation of black on white stimuli, as in Experiment 3. TR saw fewer fragments in the counting condition (Count x Fragment; $\chi^2_1 = 5.54$, $p < .02$). Interestingly, counting reduced fragment number for black on white ($\chi^2_2 = 16.77$, $p < .001$) but not for coloured ($\chi^2_1 = 0.33$, NS) stimuli. Finally, the significant ($\chi^2_2 = 102.35$, $p < .001$) Lexical Status x Fragment

Table 3
Number of fragments by lexical status, counting condition, and colour (Number of wrong lexical decisions in brackets)

	Black on White			Yellow on Red		
	Word	Nonword	Pseudohomophone	Word	Nonword	Pseudohomophone
–Counting						
1 Part	18(0)	12(0)	0(–)	34(0)	27(0)	1(1)
2 Part	44(0)	46(1)	25(1)	30(0)	37(2)	31(1)
3 Part	2(0)	6(0)	7(0)	0(–)	0(–)	0(–)
+Counting						
1 Part	27(0)	26(2)	0(–)	36(0)	30(0)	1(0)
2 Part	35(0)	38(12)	32(20)	28(0)	33(2)	31(3)
3 Part	2(0)	0(–)	0(–)	0(–)	1(0)	0(–)

term largely arises because 6 and 7 letter pseudohomophones were on average longer (and therefore more fragmented, see Experiments 1–3) than 3–7 letter words and legal nonwords. Thus, when the analysis was repeated after excluding pseudohomophones, the significance of one term changed – Lexical Status \times Fragment approached significance ($\chi^2_1 = 3.23, p < .08$).

Table 3 shows that TR only made false positive errors, suggesting that she categorised a stimulus as a word when in doubt. This response bias yielded perfect lexical decisions for words but not for nonwords. Importantly, she rarely categorised unfragmented strings wrongly, making most errors when identifying fragmented stimuli. The difference between unfragmented and fragmented error rates was significant for black on white stimuli ($\chi^2_2 = 8.77, p < .003$) and near-significant for coloured stimuli ($\chi^2_2 = 3.28, p < .07$), while counting increased the error rate for black on white stimuli ($\chi^2_2 = 32.05, p < .001$) but not for coloured stimuli ($\chi^2_2 = 0.11, NS$). In short, subvocal interference and colour interactively influenced lexical decision error rates (Table 3). Moreover, comparing pseudohomophones with other nonwords, significantly more pseudohomophones were incorrectly categorised ($\chi^2_1 = 8.83, p < .003$). Though this effect was confined to the black on white counting condition (Table 3), it strongly suggests storage of phonological information in working memory. Finally, 3 observations indicate that decisions about pseudohomophones and nonwords were also constrained by stored visual orthographic information. First, in the absence of subvocal interference, the “incorrect” fragment of the pseudohomophone resolved first on 32 occasions, but TR categorised all but 2 of these as nonwords: consequently, these 30 correct lexical decisions were not based solely on the phonological representation activated by that first fragment. Second, TR transcribed the briefly-exposed 32 black on white pseudohomophones of the main experiment in the final session. The “incorrect” fragment resolved before the final fragment in 16 of these (e.g., *sumwhat* \rightarrow *sum*\... \... \rightarrow ... \wh\... \rightarrow ... \... \at), but she made only one error. The remaining 16 pseudohomophones and 32 words were all correctly transcribed. Third, during subvocal counting, accuracy of decisions about fragmented stimuli was at ceiling levels or significantly (Binomial, $p < .04$) above chance in all sub-conditions except for black on white pseudohomophones (Binomial, NS).

Table 4 gives lexical decision latencies for differently fragmented stimuli in each experimental condition. The reciprocals (excluding an outlier and 3-fragment response latencies) became the dependent variable in a $2 \times 2 \times 2 \times 2$ ANOVA with Fragment number (1 vs. 2), Count (Absent vs. Present), Colour, and Response (Word vs. Nonword) as factors. The response main effect was highly significant ($F_{1,605} = 62.50, p < .001$) because, as expected, word categorisations were more rapid than nonword categorisations.

Most importantly, the Fragment main effect was highly significant ($F_{1,605} = 71.79, p < .001$), and this factor did not interact significantly with any other term. Fig. 5 includes the data for 3-fragment stimuli, as there were a sufficient number of cases for this. Fig. 5 confirms the stepwise increase in lexical decisions with each increase in fragment number. It also demonstrates that the stepwise increase is not due to string length per se. For example, it shows that response times for 6-letter stimuli increased stepwise with each increase in fragment

Table 4
Mean (SD) lexical decision latencies by colour, counting condition, response, and fragment number

		Unfragmented, <i>M</i> (<i>SD</i>)	2 Parts, <i>M</i> (<i>SD</i>)	3 Parts, <i>M</i> (<i>SD</i>)
–Counting				
Black/White	No	1048.2 (227.3)	1546.3 (692.7)	2000.9 (770.7)
	Yes	891.1 (309.6)	1217.5 (626.1)	–(–)
Red/Yellow	No	987.3 (244.1)	1475.1 (961.3)	–(–)
	Yes	825.1 (134.7)	1064.6 (431.5)	–(–)
+Counting				
Black/White	No	1541.8 (691.5)	1861.2 (693.6)	–(–)
	Yes	1208.7 (415.4)	1448.3 (649.7)	–(–)
Red/Yellow	No	975.3 (434.7)	1394.3 (703.7)	–(–)
	Yes	839.8 (170.4)	1072.6 (554.5)	–(–)

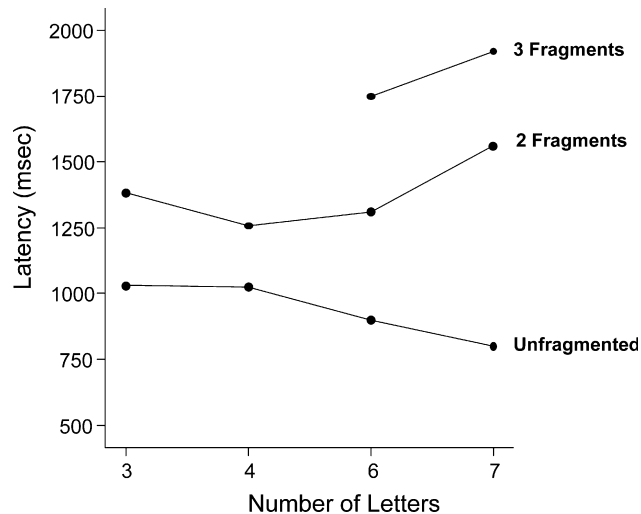


Fig. 5. Lexical decision latencies increase stepwise with fragment number.

number. Indeed, only 1 correlation coefficient between string length and decision times (computed within the 17 cells of Table 4 containing sufficient data points) achieved significance.

The effect of colour was highly significant ($F_{1,605} = 54.12, p < .001$), decision latencies being shorter for coloured than for black and white stimuli. Count ($F_{1,605} = 16.32, p < .001$) and Count \times Colour ($F_{1,605} = 23.06, p < .001$) were significant because decisions about black on white stimuli were selectively longer in the counting condition. In contrast, counting did not influence decision latencies for yellow on red stimuli.

The number of fragments, error rates, and decision latencies for the first 80 and final 80 trials were contrasted within each of the 4 Colour \times Count cells. In the second part of the sessions, TR tended ($\chi^2 = 5.96, p < .06$) to perceive fewer fragments in the black on white no count condition, she tended (Fisher Exact $p < .06$) to produce slightly fewer errors in the red on yellow count condition, and lexical decisions were faster in all 4 sub-conditions (all $p < .01$). Thus, there was no clear change in speed-accuracy trade-off and her performance did not fatigue in these somewhat demanding conditions (including the particularly demanding black on white count condition). On the contrary, there was some improvement with practice, since decision latencies decreased generally, though fragment numbers and error rates remained broadly comparable.

3.4.3. Discussion

The following results supported TR's introspections. First, lexical decision latencies increased stepwise with fragment number in each condition of this experiment, as might be expected if fragments resolved sequentially. Second, TR said she stored phonological codes during fragment resolution and, as predicted, subvocal interference of phonological working memory selectively impaired lexical decisions about fragmented but not unfragmented stimuli. Third, TR said that coloured stimuli were easier to read than black and white stimuli and, indeed, 3 findings fit the hypothesis that the signal to noise ratio is higher for coloured than for black on white stimuli. Thus, lexical decisions were substantially faster for coloured stimuli. Moreover, coloured stimuli were less fragmented than black on white stimuli in Experiment 4, replicating the results of Experiment 3. Similarly, coloured stimuli generated fewer errors than black on white stimuli in Experiments 3 and 4.

Experiment 4 also explored the type of information stored in working memory. It assumes that the relative spatial locations of segments must have been encoded in some way because reconstruction of the stimulus would have been quite unreliable if TR could only use resolution order plus the orthographic and/or phonological information contained within separate segments. Experiment 4 specifically asked if TR simply mapped the within-figure locations of each fragment onto the temporal resolution sequence (e.g., the middle, rightmost, and leftmost segments went into phonological memory first, second, and last, respectively). If so, she might have merely replayed/attended to phonological representations in the spatially correct left-to-right

sequence, and categorised familiar phonological sequences as words. However, that spatial information would have been insufficient because TR correctly categorised and transcribed pseudohomophones when the “incorrect” segment resolved first. Consequently, stored orthographic information must have influenced her copying responses. It is suggested that TR identified pseudohomophones as nonwords because, though the phonological component of the representation sequence was familiar, her representation of the orthographic sequence did not match any stored real word representation. That is, when TR read the resolved pseudohomophone fragments left-to-right, the stored orthographic representation tuned to the corresponding word was not activated as would have been the case if the corresponding word had been visually exposed. On the other hand, stored spatial and orthographic information were also insufficient. Thus, if her lexical decisions were solely based on orthographic codes then lexical decisions about pseudohomophones and legal nonwords would have been equally accurate. That is, the particular interference by counting on pseudohomophone decisions implies that at least some lexical decisions depended at least partly on stored phonological information.

TR said that she quickly and automatically read unfragmented stimuli. If correct, unfragmented strings would directly activate orthographic and phonological representations, which may or may not match/activate a stored real word representation, obviating the need for working memory. Indeed, subvocal interference of working memory processes did not reduce lexical decision accuracy for unfragmented strings in this experiment. In contrast, counting interfered with lexical decisions about fragmented strings, which required phonological working memory support. However, it is necessary to explain why counting selectively impaired lexical decisions about fragmented black on white stimuli, leaving coloured stimuli unaffected. It is hypothesised that counting used some but not all working memory capacity and the spare capacity was sufficient for correct categorisation of coloured 2-fragment stimuli. In contrast, counting left insufficient capacity for reliable categorisation of 3-fragment stimuli. Therefore, TR reduced black on white fragment number in the counting condition of this experiment, so that all nonwords generated unfragmented or 2-fragment percepts. However, this compensatory strategy increased in black on white LF, and it is argued that this reduced fragment resolution accuracy. In sum, counting increased noise in phonological working memory when identifying 2-fragment coloured and black on white strings, but counting additionally overloaded visual processing capacity, and the latter extra demand produced the highest error rate and decision latencies in the black on white counting sub-condition. Additionally, TR said that coloured stimuli were generally “clearer” (i.e., in the non-counting condition), and so may have created a stronger orthographic memory trace than black on white stimuli: counting would interfere less, if reconstruction of coloured stimuli depended less on phonological working memory.

3.5. *Experiment 5: TR voluntarily influenced segment number*

Several observations indicated that TR could voluntarily increase segment number, and that this increased visual resolution accuracy. She said that she sometimes subdivided a segment if she had difficulty resolving it. Moreover, increasing fragment number in the course of Experiment 3 may have correspondingly reduced error rate. Conversely, reducing fragment number in the black on white counting sub-condition of Experiment 4 may explain its particularly high error rate. TR’s hypothesised capacity to voluntarily increase or decrease the spatial extent of segments was tested in a preliminary single case experiment with the following instructional phases: No Instruction Baseline → Increase Fragment Number → Decrease Number → Increase Number. She initially asserted that she would be unable to follow these instructions. However, in the event, she increased, then decreased, and finally increased fragment number relative to baseline. However, continuously exposed stimuli were used, so the contribution of voluntary eye movements was uncontrolled. Consequently, Experiment 5 essentially repeated the latter study, and included briefly exposed stimuli. It also tested the hypothesis that voluntary decreases and increases in segment length would reduce and increase error rates, respectively.

3.5.1. *Methods*

Stimuli were 48 high frequency ($M = 255.02$ per million, range = 1789–50), low frequency ($M = 1.87$ per million, range = 1–3), and orthographically legal and phonologically plausible nonwords. Each of these groups comprised eight 4-, 5-, 6-, 7-, 8-, and 9-letter items. Each black letter stimulus subtending an angle

of 2.1°–4.6° was exposed against white in the centre of a VDU, 72 were continuously exposed and 72 were exposed for 101 ms.

The 144 stimuli were randomly allocated to 8 sets matched for frequency and length. There were 2 sets of randomly ordered stimuli per block, exposures being unlimited for one set and 101 ms for the other. For the first block of the first session, TR was strongly encouraged to fragment each stimulus into 4, if possible. For the final block of that session, she was encouraged to resolve the entire string without fragmenting it. Instruction order was reversed when blocks 3 and 4 were presented in the next session. Accurate perception of the entire string was an important but secondary goal during these 4 blocks. Block 1 was presented again in the third session, but TR was strongly encouraged to refrain from fragmenting any stimulus, even if that meant that it remained unresolved.

TR read each stimulus aloud and reported the fragment number. If she made an error, she transcribed what she had seen, representing fragment boundaries with a slash. Segment length was not measured directly in this study (a) to minimise the effect of task responses on visual perception, and (b) because LF had sharply decreased (or increased) when she complied with the instructions to increase (or to decrease) fragment number in the above-mentioned single case pilot experiment.

3.5.2. Results

TR only made deletion errors. Deletion rate varied significantly with task instructions (Kruskal–Wallis $\chi^2_2 = 49.33$, $p < .001$). She deleted fewest when she increased fragment number and minimised errors ($M = .07$ letters; $SD = 0.4$ letters). She deleted rather more ($M = 0.25$ letters; $SD = 1.0$ letters) when she attempted to minimise both fragment number and errors. Considerably more letters were deleted when she minimised fragment number and disregarded accuracy ($M = 1.19$ letters; $SD = 1.3$ letters). TR said that letters tended to run into each other when she minimised fragment number. Error rate increased marginally with string length (Kruskal–Wallis $\chi^2_5 = 8.56$, $p < .13$), but did not vary significantly (Kruskal–Wallis $\chi^2_2 = 2.33$, NS) with lexical category or exposure duration (Mann–Whitney U, $z = 1.08$, NS).

Task instructions significantly (Kruskal–Wallis $\chi^2_2 = 71.48$, $p < .001$) altered fragment number (Fig. 6). Attempts to increase fragment number produced most ($M = 2.79$ parts, $SD = 0.7$); minimising fragment number and errors produced fewer ($M = 1.90$, $SD = 0.6$), while minimising fragments and disregarding accuracy elicited fewest ($M = 1.47$, $SD = 0.6$). As in previous experiments, fragment number increased significantly (Kruskal–Wallis $\chi^2_5 = 53.76$, $p < .001$) with string length (Fig. 6): this effect being apparent within each instruction condition (all Kruskal–Wallis $p < .04$). Fragment number was unrelated to lexical status (Kruskal–Wallis, NS) and exposure duration (Mann–Whitney $z = 0.70$, NS).

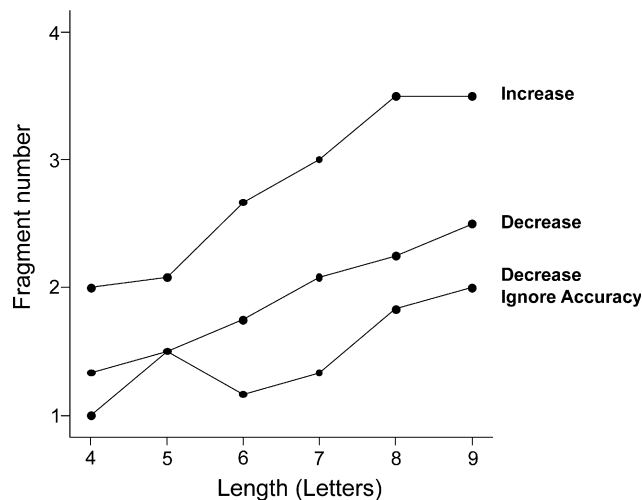


Fig. 6. TR voluntarily controlled fragment number.

3.5.3. Discussion

This experiment confirms that TR could voluntarily influence fragment number. This effect was apparent at both exposure durations, suggesting that she could voluntarily influence covert attentional processes engaged during segmentation.

Moreover, as in Experiments 3 and 4, black on white letter deletions increased with lengthening LF, this increase rising sharply when she minimised segment number and ignored accuracy. This raises the possibility that TR normally used her quite considerable control over segmentation to optimise her fragment resolution capacity. Apparently, she normally constructed segments of a length that her compromised visual circuits could probably resolve. Hence, TR varied segment number within limits that preserved accuracy when that was prioritised, but she clearly could generate segments of a length outside that optimal resolution range when accuracy could be ignored.

Even in the third session, TR could not fully comply with the instruction to desist from fragmenting the stimulus. This suggests an automatic component to segmentation processes. Similarly, TR never generated more than 4 fragments: she sometimes produced 1-letter fragments so, if fragmentation were entirely under voluntary control, she would be able to produce as many fragments as there were letters. Moreover, string length likely constrained this automatic process since length influenced fragment number, even when TR ignored accuracy.

3.6. Experiment 6: Evidence of voluntary control over the segment resolution sequence

Experiments 2 and 3 supported TR's claim that 2 rules governed the sequential resolution of fragmented percepts. First, she said that "darkest" segments resolved first, and first segments usually included a greater proportion of letterform contour than other segments (i.e., they contained ascender letters and/or more letters). Second, as she reported, fragments tended to resolve left-to-right.

Experiment 6 asked if TR could voluntarily override these 2 rules. She initially believed that her capacity to do that was quite limited. However, 3 possibilities were considered. First, if fragment resolution were entirely automatic, then she could not obey instructions (a) to resolve segments without ascenders first and/or (b) to resolve segments right-to-left. Second, if she had considerable voluntary control, then she would always obey these instructions. Third, if the fragment resolution sequence were only partly automatic then she might sometimes follow one or both of these instructions in specific conditions. Therefore, TR was instructed to focus over various delay periods (0–2000 ms) on leftmost or rightmost segments of words with ascenders at the attended end or the unattended end.

This design also assessed TR's capacity to resolve the initially non-attended segments after delays of up to 2 s. The only specific hypothesis for this essentially exploratory aspect of the study was that ability to resolve unattended segments would decline after longer delays.

3.6.1. Methods

Fifty-six 6- and 7-letter words in black characters (0.01 cd/m^2) appeared on a white background (15.76 cd/m^2). Each word contained ascender letters occupying either the first ($N = 56$) or final ($N = 56$) letter positions (e.g., *grocers* or *convoy*). Words subtended 3.8° – 4.4° of visual angle. The third or fifth letter of 7-letter words overlapped the fixation point. In 50% of 6 and 7 letter words, 4 letters fell within the left visual field (e.g., xxxx + xx, x represents 1 letter and + represents fixation point), while 4 letters fell entirely within the right field (e.g., xx + xxxx) in the remainder.

Trials began with a written instruction to focus on the leftmost or rightmost segment for 0, 100, 200, 500, 1000, 1500, or 2000 ms. A small red fixation cross next appeared for 1000 ms, and then the stimulus, exposed for 70 ms to preclude saccades. Finally, screen dimming (3.66 cd/m^2) after delays of 0, 100, 200, 500, 1000, 1500, or 2000 ms cued TR to resolve the remaining letters. Randomly ordered stimuli were presented in 4 blocks of 28 trials matched for length, location of ascender letters, asymmetric position relative to fixation, and delay. In the initial session, she attended to leftmost fragments in the first and fourth block, and rightmost fragments in the second and third blocks. Blocks 1–4 were presented in a subsequent session, except that she attended to the opposite end of each stimulus. Her stimulus transcriptions indicated fragment boundaries with a slash, the unresolved letter(s) with a hyphen, and fragment resolution order: e.g.,

preview \rightarrow pre¹/v²-w

shows the first fragment consisted of 3 letters while the second included central unresolved letters.

Blocks 1–4 were presented once to 2 control subjects (C1 aged 50 and vision corrected, and C2 aged 26), who automatically read entire words. To make their task more similar to TR's, they attended to the letters on the left or right of fixation. When the screen dimmed, they first transcribed the attended (left- or right-sided) letters and then the unattended letters, inserting a space between groups.

3.6.2. Results

TR demonstrated considerable voluntary control over the fragment resolution sequence, obeying the instruction to attend to the leftmost or rightmost segment in all 224 trials. TR's first fragment transcriptions rarely (4/224) included letter omissions and/or substitutions (e.g., *honours* \rightarrow hum/-/urs, first fragment underlined); 1 and 3 were incorrectly transcribed at delays of 100 and 500 ms, respectively. First fragments generally (Wilcoxon $z = 6.63$, $p < .001$) included most letters ($M = 3.5$; $SD = 0.6$), leaving an average of 3.0 ($SD = 0.7$) remaining letters. First fragment length remained around 3.61 letters ($SD = 0.6$) over the 0–1000 s delay intervals but declined a little to 3.28 letters ($SD = 0.5$) with longer delays (Kruskal–Wallis, $p < .03$).

Lengths of the second and/or third fragments to resolve could not be reliably measured because 78.6% of stimuli included omissions and/or substitutions. However, the ratio *letters correct*/[*letters correct* + *omissions* + *substitutions*] represents individual letter identification probability for first fragments and for the remaining letters. Individual identification probabilities for remaining letters varied with delay (Fig. 7). At each delay interval, identification probabilities were significantly (all Wilcoxon $z > 2.95$, $p < .003$) lower for remaining than for first fragment letters, which stayed close to unity. Moreover, remaining letter identification probability declined stepwise with increasing delay (Kruskal–Wallis, $p < .001$). Thus, fewest errors were made when the screen dimmed immediately after stimulus presentation, the first significant downward step (Mann–Whitney $z = 2.69$, $p < .007$) occurring between 0 and 100 ms. Identification probability was constant over the 100–500 ms range (Kruskal–Wallis, NS) before stepping down again, this step achieving significance

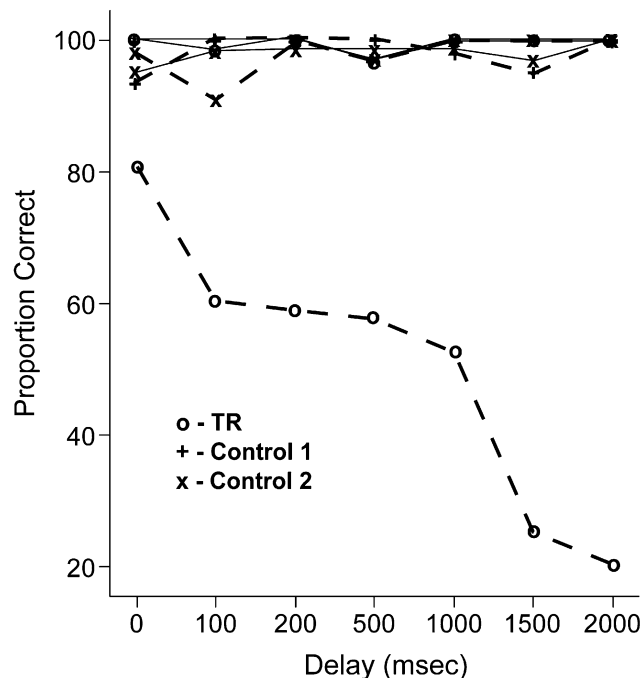


Fig. 7. Effects of delay on attended (solid lines) and unattended segments (broken lines) in TR and controls.

between 1000 and 1500 ms (Mann–Whitney $z = 3.23$, $p < .001$). Comparison of the first vs. the final trials of test sessions revealed a constant error rate ($t = 0.55$, NS).

Most (72.8%) stimuli elicited 2 segments, the remainder yielding 3 segments. A loglinear model assessed the effects of Word Length (6 vs 7 letters) and Delay (0–500 vs. 1000–2000 ms) on Fragment Number (2 vs. 3). Length \times Delay \times Fragment Number was significant ($\chi^2_1 = 4.72$, $p < .03$). As in previous Experiments, longer words elicited more fragments. Fragment number also increased with delay, this increase being slightly steeper for 6- than for 7-letter words. Importantly, this increased fragmentation did not reflect the slight shortening of first fragments at 1500–2000 ms delays, since fragmentation increased over the 0–1000 ms delay interval when first fragment size remained constant ($\chi^2_4 = 9.46$, $p < .05$).

Several findings indicated reduced functioning in the left visual field. Thus, first attended fragments were longer ($\chi^2_3 = 26.03$, $p < .001$) on the right ($M = 3.7$; $SD = 0.6$) than on the left ($M = 3.3$; $SD = 0.6$). Identification probability was higher for remaining letters on the right than on the left ($t = 3.58$, $p < .001$). There were rather more remaining-letter fragments on the right than on the left ($\chi^2_1 = 5.07$, $p < .03$), but this was because TR saw rather more remaining letters (correct + substituted) on the right ($M = 1.8$; $SD = 1.1$) than on the left ($M = 1.2$; $SD = 0.9$). Nevertheless, all of the foregoing effects of delay were evident on both sides: thus, as delay lengthened, first fragment lengths decreased (both Mann–Whitney $z = 1.96$, $p < .05$), remaining letter errors increased (both Kruskal–Wallis, $p < .001$) as did fragment number (both $\chi^2_2 < 3.85$, $p < .05$).

Control subjects correctly transcribed most stimuli (C1, 94.6%; C2, 90.2%). Letter identification probabilities in initially attended and non-attended word sectors were comparable for C1 and C2 (Wilcoxon, NS). The near-ceiling accuracy of transcriptions for attended and non-attended sectors did not decrease with delay (Fig. 7). Thus, contrasting identification probabilities in the 0–500 vs. 1000–2000 ms conditions, delay did not differentiate transcription accuracy for C1's attended (Mann–Whitney $z = 1.29$, NS) or unattended (Mann–Whitney $z = 1.23$, NS) sectors. C2's identification rate for attended sectors did not change with delay (Mann–Whitney $z = 0.35$, NS), but non-attended sectors elicited marginally more errors in the shorter delay conditions (Mann–Whitney $z = 1.75$, $p < .08$). More importantly, TR's first fragment transcriptions were within the control range. Her first fragment identification rate was comparable to that achieved by C1 at each delay (all Mann–Whitney $z < 0.71$, NS) and a little higher than the identification rate achieved by C2 in the 0 ms (Mann–Whitney $z = 2.02$, $p < .05$) and 1500 ms (Mann–Whitney $z = 2.02$, $p < .05$) delay conditions. Moreover, first fragment length did not differ from the control attended sector length (Kruskal–Wallis, NS). In contrast, Fig. 7 shows that TR's remaining letter transcriptions were significantly more error prone than the non-attended sector transcriptions of C1 or C2 at all delays (all Mann–Whitney $z < 2.08$, $p < .04$). Finally, considering first-attended sectors, these were significantly longer (Mann–Whitney $z = 5.74$, $p < .001$) and more error prone (Mann–Whitney $z = 2.20$, $p < .03$) on the right than on the left for C2 but not C1 (both Mann–Whitney $z < 1.28$, NS). Considering non-attended sectors, these were non-significantly longer (Mann–Whitney $z = 1.19$, NS) and more error prone (Mann–Whitney $z = 2.03$, $p < .05$) than left-sided non-attended sectors for C1, while they were significantly shorter for C2 (Mann–Whitney $z = 5.73$, $p < .001$) but no more error prone C2 (Mann–Whitney $z = 1.08$, NS). In short, control data suggest that the longest sector produced more errors independently of laterality or order attended/reported.

3.6.3. Discussion

Experiments 2 and 3 demonstrate an especially robust tendency to resolve leftmost fragments containing ascender letters first, but these influences must have been weakly automatic or entirely voluntary since she could voluntarily override them: she always obeyed instructions to first resolve segments that (a) lacked ascenders, and/or (b) were rightmost. Moreover, she could voluntarily arrest the resolution sequence: i.e., she could focus her attention on the first fragment without resolving the remainder until so instructed. TR said that, when she sustained attention on the first fragment, she subvocally rehearsed its corresponding phonological sequence. This use of articulatory-phonological rehearsal may have been a mere epiphenomenal consequence of her attentional selection of one particular segment or it may have facilitated her attentional “lock” on that segment by, for example, occupying the articulatory loop and so precluding phonological read-out of the remaining letters.

The second main observation is that first and remaining fragments pursue differing perceptual careers. Thus, at all delays, her remaining letter transcriptions elicited more errors than first fragment transcriptions,

which were relatively error-free. The 0 ms delay remaining letter transcriptions probably correspond to the second and third fragment transcriptions in Experiments 2 and 3, and these were also rather more error prone than first fragment transcriptions. This increase in second and third fragment error rate in Experiments 2, 3, and 6 may at least partly reflect degradation of information stored in short-term visual memory. Experiment 6 extends findings from Experiments 2 and 3 by showing that the information degraded further after an extra 100 ms delay, while additional delays of up to 500 ms caused no more degradation, and further accelerating decline developed subsequently (1000–2000 ms). Moreover, TR said that she subdivided a segment if she could not resolve it and, indeed, she responded to the progressive degradation of visual information by increasing fragment number as delay lengthened.

The percepts of TR and controls differed qualitatively. Controls could meaningfully attend to the left- or right-most sector of the stimulus. However, in contrast to TR, controls made few errors in their transcriptions of non-attended sectors because, it is argued, control subjects could not prevent the automatic visual categorisation and phonological encoding of the entire word; consequently, they retrieved the entire unfragmented word after the delay rather than separately retrieving the attended and unattended sectors.

4. General discussion

Investigators typically rely on blindsight subjects' essentially negative subjective account (i.e., of absence of visual experience). The positive visual experiences of subjects with deficient visual object perception are rarely subjected to formal investigation, but the present report attempted (a) to quantify TR's fragmented visual experiences, and (b) to test her subjective impressions of the fragment resolution process. Clearly, it is necessary to identify consistency parameters for her subjective experiences. Thus, fragment number increased with string length in Experiments 1–3, and in unreported analyses of data from Experiments 4–6. LF also consistently increased with string length in Experiments 1–3, and these effects were relatively independent of font size (Experiments 1 and 3). It was argued that figure-centred attentional mechanisms segmented partially processed stimulus representation into 2, 3, and sometimes 4, but never 5+ sectors.

Experiments 2 and 3 supported and clarified TR observations that the darkest segment resolved first and that segments tended to resolve left-to-right. They showed that 2 rules described selection of the first segment for resolution: first fragments represented the largest contour length (containing ascenders and/or most letters) and/or were to the left of the longest segment. Experiment 3 further showed that endogenous spatial attentional processes were sufficient to generate the foregoing effects, as these were apparent in responses to stimuli exposed too briefly for saccadic exploration (Experiment 3).

TR said that certain colours facilitated visual perception, and Experiments 3 and 4 and several unpublished experiments consistently found that background strongly influenced fragmentation: though Experiment 3 confounded background colour and luminance effects, it was argued that the undue attentional pull of the high luminance background was probably the predominant influence. TR said that letter strings often appeared as a resolving fragment sequence, and Experiment 4 demonstrated the predicted stepwise increase in lexical decision latencies with fragment number. Experiment 4 also confirmed the prediction that fragmented strings would yield more reading errors. She indicated that she stored phonological representations of resolved fragments in working memory, and used them to reconstruct the stimulus at the end of the resolution phase. Indeed, this is consistent with her particularly high pseudohomophone error rate during the subvocal interference condition of Experiment 4. Moreover, she said that during the reconstruction phase, she mapped phonological representations onto her residual visual impression of the string, and that introspection was supported by indications that her reconstructions also required stored spatial and orthographic information. For example, her ability to correctly transcribe pseudohomophones when the incorrect fragment resolved first must have relied on stored orthographic information, and Experiment 6 further showed that this stored orthographic information degrades rapidly after 1000 ms, since her ability to read unattended fragments deteriorated sharply after longer delays.

TR said that she sometimes subdivided segments that were difficult to resolve and several observations indicated a relationship between fragment number and error rate. For example, her error rate increased with decreasing fragment number in Experiments 3 and 5, while the number fragments constructed for the unattended sector of Experiment 6 words increased as visual information deteriorated with increasing delay. These

various observations support a central thesis of this study: fragmentation is due to a reduction in the amount of information supportable in a visual percept.

Finally, TR's subjective reports of fragment resolution often implied a degree of voluntary control, and Experiment 5 showed a limited measure of control over fragment length, while Experiment 6 demonstrated considerable ability to focus attention on particular segments.

4.1. Neuroanatomical considerations

Neuroradiological studies indicated that the damage involved anterior temporal circuits, which represent both visual fields and are not retinotopically organised (Rolls & Deco, 2002). Thus, the initial CT scan demonstrated a small right perirhinal-entorhinal infarct, and subsequent MRI found dilation of the anterior horn of the right lateral ventricle. Primate neurophysiological studies of ventral visual pathways (Desimone, Schein, Moran, & Ungerlieder, 1985; Hasselmo, Rolls, & Baylis, 1989; Tanaka, Fujita, Kobatake, Cheng, & Ito, 1993) show that neurons respond to increasingly complex forms as visual information feeds forward from V1 (e.g., edges) through to anterior inferotemporal cortex (e.g., faces). Early primate lesion studies confirm that anterior inferotemporal lesions impair monkeys' ability to discriminate complex forms (Fuster, 1995), and recent research suggests that performance on some visual perceptual tasks depends on integration of complex visual information in the perirhinal cortex of non-human primates and man (Lee, Barense, & Graham, 2005). Intriguingly, Bohbot et al. (1998) reported "signs of perceptual fragmentation" during copying. Unfortunately, this term was not precisely defined, but Rey-Osterieth figure copying was selectively impaired in subgroups with damage in the region of the right hippocampus and overlying cortex so, presumably, some subjects with damage in this region exhibited perceptual fragmentation.

On the one hand, TR was prosopagnosic and unilateral right hemisphere lesions can produce prosopagnosia (Landis, Regard, Bliedle, & Kleihues, 1988). On the other hand, subjects with unilateral anteromedial temporal damage often perform well on tests of visual perception (Lee et al., 2005). Moreover, neuroradiological studies only demonstrated a small area of structural damage. Consequently, it is suggested that dysfunction extended beyond the region suggested by CT and MRI. Indeed, SPECT and PET scanning has demonstrated temporal hypofunction extending beyond a MRI-defined medial temporal region of structural brain damage (Holdstock, 2005). Furthermore, TR had an ischaemic stroke and (Mumby et al., 1996) found that ischaemic lesions of the rat hippocampus caused more severe deficits than excision lesions. Specifically, performance was impaired on a delayed non match to sample task, which is associated with perirhinal cortical damage. However, subsequent histological investigations found no differences in cell counts in rodent homologues of human parahippocampal cortices. Moreover, the present data confirm that the area of dysfunction extended beyond the neuroradiologically anomalous right anteromedial temporal region, which represent **both** visual fields **non-retinotopically**. Thus, there was evidence of lateralised visual deficits implicating dysfunction in more posteriorly located circuits that **retinotopically** represent **unilateral** visual fields. The Case Report documents impaired flicker detection beyond 1° in the left visual field and particularly reduced stereoacuity on the left. Moreover, circumscribed lesions of the retinotopic TEO in monkeys impaired visual form processing in the corresponding part of the visual field (De Weerd, Peralta, Desimone, & Ungerleider, 1999), and Experiment 6 indicated relatively poorer visual form processing in the left field. For example, right-sided first-attended fragments were longer: though there were correspondingly fewer remaining letters on the left, her identification of left-sided remaining letters was more error prone. In contrast, the longest sector yielded most control subject errors independently of laterality or order attended. Whilst damage to right hemispheric retinotopic visual cortices producing visual perceptual deficits in the left visual field deficit (i.e., areas V1 through to TEO (Rolls & Deco, 2002)) may contribute to TR's perceptual difficulties, it cannot fully explain their bilaterality. For example, she usually correctly identified different-letter pairs, and selectively deleted one member of same-letter pairs presented to the right or left of fixation at exposure durations too brief for saccade initiation (see Case Report). Moreover, damage to right hemisphere retinotopic structures cannot explain TR's deteriorating identification of right-sided remaining letters with lengthening delay. Right-sided letters extended more than 2.2° to the right of fixation in Experiment 6 and so they must have been identified via intact left hemisphere visual pathways – they could not have been identified via the right hemisphere V1 sector receiving midline information from the narrow nasotemporal overlap region of the retina (Fendrich, Wessinger, & Gazzaniga, 1996).

4.2. Neural model

The foregoing considerations link TR’s fragmented percepts with right anterior extrastriate (i.e., PR, TE, and TEO/V4) dysfunction. The latter conclusions largely exploit our understanding of visual electrophysiology and wiring in infrahuman primates, which is considerably more detailed than our understanding of human visual pathways. Furthermore, since TR’s selective recurring letter and other form deletions and fragmented percepts were predominantly visual (i.e., they were not specifically lexical or semantic, equally affecting words, nonwords, real objects, and nonsense objects), [Weddell \(2005\)](#) was able to interpret TR’s selective form deletions in terms of the [Rolls and Deco \(2002\)](#) neural model of primate visual neuroanatomy and electrophysiology. Thus, [Fig. 8](#) represents the successive passage of the visual signal through the human homologues of the macaque V1 → V2 → V4 → TEO (posterior inferotemporal) → TE (anterior inferotemporal) → PR (perirhinal) cortices (V1/V2, V4/TEO, and TE/PR combined to simplify). [Fig. 8](#) shows that convergent outputs of V1/V2 neurons, selectively tuned to contour elements, create V4/TEO neuron groups selectively tuned to more complex visual forms (including letters). Further convergence tunes TE/PR neurons to respond to more complex patterns (including letter groups). This successive convergence coarsens retinotopic organisation, macaque neurons V1 and TE having average receptive field (RF) diameters of 0.5° and 40°, respectively ([Rolls & Deco, 2002](#)). Extending the model to fit humans, it was argued that TE/PR activity tuned to orthographic representations of words and subword units in both visual fields feeds forward to left posterolateral temporal cortex ([Small et al., 1996](#)) where the signal activates the corresponding phonological representations

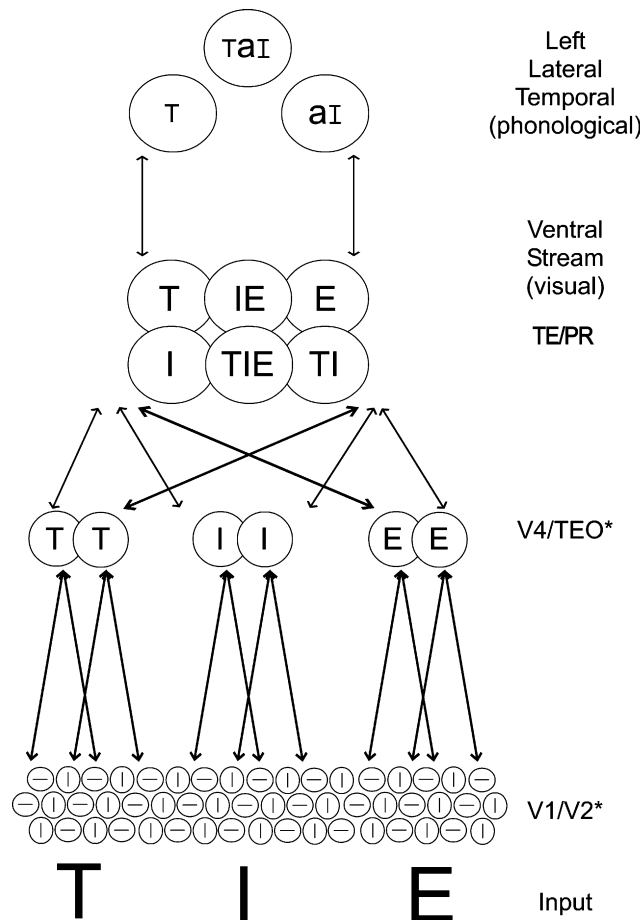


Fig. 8. Model of V1 to lateral temporal circuitry supporting visual-phonological representations of letter strings (asterisk marks retinotopically organised components possibly modulated by dorsal stream spatial attentional processes).

(cf., Plaut, McClelland, Seidenberg, & Patterson, 1996). Weddell (2005) suggested that compromised anterior extrastriate circuits were capable of identifying short letter strings in the first forward pass of the visual signal from V1. However, longer strings generally failed to activate one stored TE/PR representation, giving rise to TR's phenomenal experience of a visual figure that defined global shape but that lacked awareness of every constituent letter identity, so she characterised these figures as "blurred" (see Fig. 3i). Weddell (2005) further proposed that segmentation of the information converted long unresolvable strings into a series of shorter and resolvable strings and, indeed, longer strings were more fragmented (Experiments 1–6), and errors increased as fragments lengthened (Experiments 3–5).

Moreover, the present Experiments 3, 5, and 6 indicate that segmentation entailed covert attentional processes, since TR segmented stimuli exposed too briefly for saccade initiation. Clearly, segmentation involved spatial subdivision of the visual signal, so it must have subdivided the part of the dynamic visual representation that is spatially distributed. That is, primate neuroanatomy and neurophysiology suggests that the occipito-temporal component of the visual percept consists of re-entrant activity across ventral extrastriate cortices, with spatial extent represented more posteriorly and anterior cortices representing whole object information. On this view, the spatial subdivision occurred in the retinotopic component of the dynamic representation: i.e., in TEO/V4 and/or V1/V2.

Thus, whereas the first report focused on recurrent form deletion, the present report considers the evolution of TR's visual percepts. Further exploiting our more detailed understanding of primate vision, the Rolls and Deco (2002) model is modified to explain the covert direction of attention to the first segment. The latter authors argued that covert shifts in spatial attention involves direct parietal enhancement of retinotopic zones in V1 (and perhaps V4/TEO). Essentially, projections from dorsal stream retinotopic parietal salience maps onto ventral stream retinotopic cortices (via parietal back-projections to V1 and projections to V4). These projections enable the parietal neural ensemble representing the most salient zone to enhance activity in the corresponding V1/V2 ↔ V4/TEO segment. Enhancement of activity in the most salient segment would effectively feed forward data from that unresolved segment to compromised TE/PR networks, which would largely allocate their reduced processing resources to that segment. On resolution of the first fragment, activity in these ensembles would self-inhibit (Olshausen et al., 1993), leaving parietal projections to highlight the next most salient segment.

Importantly, segmentation and the fragment resolution sequence were not entirely automatic. Experiments 5 and 6 demonstrate TR's considerable voluntary control over segment length and resolution order, suggesting some frontal cortical-subcortical control over these processes. The Rolls and Deco (2002) model implements prefrontal cortical (PFC, putatively area 46) projections to TE neural ensembles representing different objects. However, though PFC cortical neurons represent spatial and object information (Rao, Rainer, & Miller, 1997), the TE is not retinotopically organised. Consequently, the PFC → TE link probably cannot mediate voluntary shifts of spatial attention onto particular retinotopically distributed segments, but PFC could direct spatial attention through its reciprocal connections with the frontal eye field (FEF; Goldman-Rakic, 1987). FEF is also reciprocally connected with V4 and TEO, as well as TE (Bullier, Schall, & Morel, 1996). Moreover, activation at a point in the retinotopically organised FEF enhanced neural activity in the corresponding retinotopic region of V4 (Moore & Armstrong, 2003), and FEF activation increased conscious awareness of backwardly masked visual stimuli (Grosbras & Paus, 2003).

Finally, Fuster (2001) argued that re-entrant excitatory loops between ventral stream structures and the PFC regions with which they are reciprocally connected sustain the visual percept in working memory. Similarly, fMRI evidence has linked transient responses in occipito-temporal areas to perceptual processing while the more sustained activity in the prefrontal cortex (PFC) has been linked with sustaining the percept and visual information over memory delays (Portas et al., 2000; Courtney, Ungerleider, Keil, & Haxby, 1997). Indeed, Experiment 4 showed that fragment resolution involved temporary storage of spatial, orthographic, and phonological information, and primate neurophysiological studies indicate that the properties of different PFC neural populations might contribute to these processes. For example, Fuster, Bodner, and Kroger (2000) described a group of frontal cortical neurons that (a) integrated visual and auditory cues and (b) sustained their selective visual-auditory activity across time. Thus, Experiment 4 indicated that TR temporarily stored orthographic and phonological information about the first fragment, before next encoding the second fragment into orthographic and phonological forms (also storing that result if there was a third segment).

In neural terms, it is suggested that, as the visual information from the first fragment progressively fed forward in the ventral stream it was encoded into orthographic forms in TE and PR, which interacted with language structures to generate the fragment's phonological component. These representations plus the V4/TEO sensory representation of the first segment's within-figure spatial location also fed forward into PFC and FEF circuits (Webster, Bachevalier, & Ungerleider, 1994). These frontal memory circuits continued to represent this orthographic, phonological, and spatial activity after attention switched to the second fragment. When each fragment was represented by its own frontal ensemble (including cells tuned to their orthographic and/or phonological and/or spatial features), then a top-down enhancement of activity in all frontal ensembles might have enhanced the sensory and perceptual activity surviving in posterior structures (Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999), and this would enable identification of the entire stimulus. On this view, in Experiment 6, when attentional selection prevented information from proceeding to TE, then that segment's uncategorised signal continued to recycle within $V1/V2 \leftrightarrow V4/TEO \leftrightarrow$ frontal eye field retinotopic circuits (Bullier et al., 1996), but it degraded stepwise over time.

4.3. Final comments

The present study demonstrates that when brain injured subjects' phenomenal reports are consistent, they can be experimentally supported or falsified and so can fruitfully guide experimental investigation of dysfunctional perceptual experiences that have received comparatively limited attention hitherto. Indeed, studies of lack of phenomenal experience in studies of covert awareness after brain damage provide a unique and continuing stream of information about the nature consciousness, and it is argued that studies of the positive phenomenal experiences of the brain injured are also likely to provide unique information about consciousness. Finally, it is suggested that, until fMRI and other functional studies clarify the regional connectivity and the temporal evolution of activation in the human brain, greater use of the infrahuman primate model of vision might facilitate understanding dysfunctional perceptual experiences in at least some cases.

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References

- Bohbot, V. D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia*, *36*, 1217–1238.
- Bullier, J., Schall, J. D., & Morel, A. (1996). Functional streams in occipito-frontal connections in the monkey. *Behavioural Brain Research*, *76*, 89–97.
- Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1997). Transient and sustained activity in a distributed neural system for human working memory. *Nature*, *386*, 608–611.
- Desimone, R., Schein, S. J., Moran, J., & Ungerleider, L. G. (1985). Contour, color and shape analysis beyond the striate cortex. *Vision Research*, *25*, 441–452.
- De Weerd, P., Peralta, M. R., Desimone, R., & Ungerleider, L. G. (1999). Loss of attentional stimulus selection after extrastriate cortical lesions in macaques. *Nature Neuroscience*, *2*, 753–758.
- Driver, J., & Vuilleumier, P. (2001). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*, *79*, 39–88.
- Farnsworth, D. (1957). *Farnsworth–Munsell 100-hue test for colour vision*. Baltimore MD: Munsell Color.
- Fendrich, R., Wessinger, C. M., & Gazzaniga, M. S. (1996). Nasotemporal overlap at the retinal vertical meridian: investigations with a callosotomy patient. *Neuropsychologia*, *34*, 637–646.
- Fuster, J. M. (2001). The prefrontal cortex – an update: time is of the essence. *Neuron*, *30*, 319–333.
- Fuster, J. M. (1995). *Memory in the cerebral cortex: an empirical approach to neural networks in the human and nonhuman primate*. Cambridge: MIT.
- Fuster, J. M., Bodner, M., & Kroger, J. K. (2000). Cross-modal and cross-temporal association in neurons of frontal cortex. *Nature*, *405*, 347–351.
- Goldman-Rakic, P. S. (1987). Circuitry of primate prefrontal cortex and regulation of behaviour by representational memory. In F. Plum (Ed.), *Handbook of physiology, the nervous system, higher functions of the brain, section 1* (Vol. V, pp. 373–417). Bethesda, MD: American Physiological Society.

- Grosbras, M.-H., & Paus, T. (2003). Transcranial magnetic stimulation of the human frontal eye field facilitates visual awareness. *European Journal of Neuroscience*, *18*, 3121–3126.
- Hasselmo, M. E., Rolls, E. T., & Baylis, G. C. (1989). The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behavioural Brain Research*, *32*, 203–218.
- Holdstock, J. S. (2005). The role of the human medial temporal lobe in object recognition and object discrimination. *Quarterly Journal of Experimental Psychology B*, *58*, 326–339.
- Humphreys, G. W., & Riddoch, M. J. (1987). *To see but not to see: Case study of visual agnosia*. Hove: Psychology Press.
- Ishihara, S. (1994). *Ishihara's tests for colour-blindness*. Tokyo: Kanehara Shuppan.
- Kartsounis, L. D., & Warrington, E. K. (1991). Failure of object recognition due to a breakdown of figure-ground discrimination in a patient with normal acuity. *Neuropsychologia*, *29*, 969–980.
- Kucera, H., & Francis, W. N. (1967). *Computational analysis of present-day American english*. Providence: Brown University Press.
- Landis, T., Regard, M., Bliestle, A., & Kleihues, P. (1988). Prosopagnosia and agnosia for noncanonical views. An autopsied case. *Brain*, *111*, 1287–1297.
- Lee, A. C. H., Barense, M. D., & Graham, K. S. (2005). contribution of the human medial temporal lobe to perception: bridging the gap between animal and human studies. *Quarterly Journal of Experimental Psychology B*, *58*, 246–268.
- Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, *421*, 370–373.
- Mumby, D. G., Wood, E. R., Duva, C. A., Kornecook, T. J., Pinel, J. P., & Phillips, A. G. (1996). Ischemia-induced object-recognition deficits in rats are attenuated by hippocampal ablation before or soon after ischemia. *Behavioral Neuroscience*, *110*, 266–281.
- Navon, D. (1977). Forest before trees: the precedence of global features in visual perception. *Cognitive Psychology*, *9*, 353–383.
- Nelson, H. E., & Willison, J. R. (1991). *National adult reading test* (Second ed.). Windsor: NFER-NELSON.
- Olshausen, B. A., Anderson, C. H., & Van Essen, D. C. (1993). A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. *Journal of Neuroscience*, *13*, 4700–4719.
- Plaut, D. C., McClelland, J. L., Seidenberg, M. S., & Patterson, K. (1996). Understanding normal and impaired word reading: computational principles in quasi-regular domains. *Psychological Review*, *103*, 56–115.
- Portas, C. M., Strange, B. A., Friston, K. J., Dolan, R. J., & Frith, C. D. (2000). How does the brain sustain a visual percept? *Proceedings of the Royal Society of London B*, *267*, 845–850.
- Randot Stereotests. (1995). Chicago: Stereo Optical Co.
- Rao, S. C., Rainer, G., & Miller, E. K. (1997). Integration of what and where in primate prefrontal cortex. *Science*, *276*, 821–824.
- Riddoch, M. J., & Humphreys, G. W. (1993). *Birmingham object recognition battery*. Hove: Lawrence Erlbaum.
- Rizzo, M., & Vecera, S. P. (2002). Psychoanatomical substrates of Balint's syndrome. *Journal of Neurology, Neurosurgery, and Psychiatry*, *72*, 162–178.
- Rolls, E. T., & Deco, G. (2002). *Computational neuroscience of vision*. New York: Oxford University Press.
- Small, S. L., Noll, D. C., Perfetti, C. A., Hlustik, P., Wellington, R., & Schneider, W. (1996). Localizing the lexicon for reading aloud: replication of a pet study using fMRI. *Neuroreport*, *7*, 961–965.
- Stoerig, P., & Cowey, A. (1997). Blindsight in man and monkey. *Brain*, *120*, 535–559.
- Tanaka, K., Fujita, I., Kobatake, E., Cheng, K., & Ito, M. (1993). Serial processing of visual object-features in the posterior and anterior parts of the inferotemporal cortex. In T. Ono, L. R. Squire, M. E. Raichle, D. I. Perrett, & M. Fukuda (Eds.), *Brain mechanisms of perception and memory: from neuron to behaviour*. New York: Oxford University Press.
- Thaiss, L., & De Bleser, R. (1992). Visual agnosia: a case of reduced attentional spotlight? *Cortex*, *28*, 601–621.
- Tomita, H., Ohbayashi, M., Nakahara, K., Hasegawa, I., & Miyashita, Y. (1999). Top-down signal from prefrontal cortex in executive control of working memory. *Nature*, *401*, 699–703.
- Watson, D. G., & Humphreys, G. W. (1997). Visual marking: prioritizing selection for new objects by top-down attentional inhibition of old objects. *Psychological Review*, *104*, 90–122.
- Webster, M. J., Bachevalier, J., & Ungerleider, L. G. (1994). Connections of inferior temporal areas TEO and TE with parietal and frontal cortex in macaque monkeys. *Cerebral Cortex*, *4*, 470–483.
- Weddell, R. A. (2005). A visual disorder producing highly selective deletion of recurring letters. *Cortex*, *41*, 471–485.
- Weiskrantz, L. (1986). *Blindsight: a case study and implications*. New York: Clarendon Press.