Unconscious Familiarity-based Color-Form Binding:

Rappaport, Sarah J.; Riddoch, M Jane; Chechacz, Magdalena; Humphreys, Glyn W

DOI:

[10.1162/jocn_a_00904](https://doi.org/10.1162/jocn_a_00904)

License:

None: All rights reserved

Document Version

Publisher's PDF, also known as Version of record

Citation for published version (Harvard):

Rappaport, SJ, Riddoch, MJ, Chechacz, M & Humphreys, GW 2016, 'Unconscious Familiarity-based Color-Form Binding: Evidence from Visual Extinction', *Journal of Cognitive Neuroscience*, vol. 28, no. 3, pp. 501-516. https://doi.org/10.1162/jocn_a_00904

[Link to publication on Research at Birmingham portal](#)

Publisher Rights Statement:

Unconscious Familiarity-based Color-Form Binding: Evidence from Visual Extinction. Sarah J. Rappaport, M. Jane Riddoch, Magda Chechacz, and Glyn W. Humphreys. *Journal of Cognitive Neuroscience* 2016 28:3, 501-516

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

Unconscious Familiarity-based Color–Form Binding: Evidence from Visual Extinction

Sarah J. Rappaport¹, M. Jane Riddoch², Magda Chechlac², and Glyn W. Humphreys²

Abstract

■ There is good evidence that early visual processing involves the coding of different features in independent brain regions. A major question, then, is how we see the world in an integrated manner, in which the different features are “bound” together. A standard account of this has been that feature binding depends on attention to the stimulus, which enables only the relevant features to be linked together [Treisman, A., & Gelade, G. A feature-integration theory of attention. *Cognitive Psychology*, 12, 97–136, 1980]. Here we test this influential idea by examining whether, in patients showing visual extinction, the processing of otherwise unconscious (extinguished) stimuli is modulated by presenting objects in their correct (familiar) color. Correctly colored objects showed reduced extinction when they had a learned color, and this

color matched across the ipsi- and contralesional items (red strawberry + red tomato). In contrast, there was no reduction in extinction under the same conditions when the stimuli were colored incorrectly (blue strawberry + blue tomato; Experiment 1). The result was not due to the speeded identification of a correctly colored ipsilesional item, as there was no benefit from having correctly colored objects in different colors (red strawberry + yellow lemon; Experiment 2). There was also no benefit to extinction from presenting the correct colors in the background of each item (Experiment 3). The data suggest that learned color–form binding can reduce extinction even when color is irrelevant for the task. The result is consistent with preattentive binding of color and shape for familiar stimuli. ■

INTRODUCTION

Visual extinction is a relatively common neurological problem following unilateral brain damage, classically associated with but by no means confined to damage to posterior parietal cortex (Chechlac et al., 2013; Karnath, Himmelbach, & Küker, 2003). It is revealed behaviorally by successful detection of a single contralesional item but failure to detect the same stimulus when it is accompanied by a more ipsilesional stimulus. As the difficulty with contralesional stimuli manifests only in the presence of a competing ipsilesional item, extinction can be considered as a pathological bias in the normal competition for selection (Duncan, Humphreys, & Ward, 1997). Within this framework, the contralesional item has a reduced capacity to capture attention, and consequently, the ipsilesional stimulus is assigned the greater selection “weight,” winning the competition for selection and awareness. Despite the poor awareness shown to contralesional items under bilateral presentation conditions, there is evidence that extinction can be mediated by stored knowledge of the stimuli. For example, Kumada and Humphreys (2001) found less extinction when the contra- and ipsilesional items formed a word (g o) than when they formed a nonword (o g). Ward, Goodrich, and Driver (1994) reported that extinction was

reduced when participants were presented with a horizontal line (—) and arrow head stimulus (<) that made up an arrow, compared with when the line was vertical so that the familiar shape was not formed. Previous work has shown that extinction can reduce when items in the contra- and ipsilesional fields group on the basis of a Gestalt property such as symmetry, common color, surface polarity, brightness, and enclosure (Mattingley, Davis, & Driver, 1997; Gilchrist, Humphreys, & Riddoch, 1996; see Humphreys, 1998, for an overview);¹ however, in cases such as Kumada and Humphreys (2001) and Ward et al. (1994), low-level grouping is equated between the familiar and unfamiliar items. The data suggest instead that items are grouped on the basis of activating a common stored representation. These results suggest that items undergoing extinction can be processed sufficiently to enter into grouping with an ipsilesional stimulus. According to Attentional Engagement Theory (Duncan & Humphreys, 1989), items that group may share a single “attentional weight” and be selected together rather than acting as competitors for attention (Duncan et al., 1997; Mattingley et al., 1997; Ward et al., 1994). This sharing of an attentional weight can be based on both shared physical properties of the stimuli and on whether the stimuli form a familiar whole.

One account of extinction is that it reflects poor binding of the features of contralesional items, exacerbated by the presence of the ipsilesional stimulus (Baylis, Gore,

¹University of Birmingham, ²University of Oxford

Rodriguez, & Shisler, 2001; Baylis, Driver, & Rafal, 1993). In particular, poor binding of the features to their location can lead to poor perceptual report. Patients showing extinction can also be impaired at reporting conjunctions of color and form, consistent with general problems in binding visual features (Humphreys, Hodsell, & Riddoch, 2009). This fits with theories that assume that binding is contingent on visual attention—a key tenet of Feature Integration Theory (Treisman & Gelade, 1980).

There is recent evidence, however, that the attentional constraints on binding may be much less when the stimuli have learned color–form relations. Classic evidence for attentional constraints on binding comes from studies off visual search, where there is typically inefficient (attention-dependent) search for targets defined by a conjunction of features relative to distractors (Treisman & Gelade, 1980)—even if the features making up the target can be detected efficiently. Such results suggest that participants must attend to each item to bind the features so that the conjunction target can be selected. However, Walsh and colleagues (Ellison & Walsh, 1998; Loble & Walsh, 1998; see also Su et al., 2014) have shown that search for target conjunctions can become efficient after practice. Furthermore, TMS to attentional regions of the brain disrupts search initially but no longer does so after practice (Walsh, Ashbridge, & Cowey, 1998). Such results are consistent with attention not being required for binding once feature relations are learned.

Additional results come from studies where participants have long-term knowledge of color–form relations. Rappaport, Humphreys, and Riddoch (2013) had participants search for objects (e.g., find the corn) that appeared among distractors with similar shapes (aubergine, carrot, lemon). The objects could be in their correct colors (e.g., yellow corn) or in an incorrect color (purple corn). In each case, one set of distractors (the lemon) shared its color with the target. When the stimuli were in incorrect colors, search was inefficient; this is consistent with previous studies of attentional involvement in conjunction search. In contrast, targets in their correct colors “popped out.” This result was not due to top–down prediction when participants were told the identity of the target. In their Experiment 3, Rappaport et al. presented targets in their incorrect color on the majority of trials and in their correct color on a minority of trials. When the target was absent, participants directed eye movements to distractors carrying the expected, incorrect color (e.g., purple)—consistent with the top–down expectation being for the incorrect color. However, despite this, search remained most efficient for targets in their correct color. The result suggests that there can be preattentive binding of familiar shape and color and that this conjunctive information can then guide search to a target. Wildegger, Riddoch, and Humphreys (2015) recently extended this result and showed that there was increased perceptual sensi-

tivity to correctly colored objects; this occurred even when correctly colored objects had a low probability of occurring, and it held across different display sizes. Wildegger et al. argued that stored color–form knowledge was activated in a bottom–up manner to influence perceptual processing. Interestingly in both Wildegger et al. (2015) and Rappaport et al. (2013), the results held only when the correct colors were presented on the surface of the objects and not when colors fell in the local background.

Here we tested extinction patients with correctly or incorrectly colored images of objects, and objects on a trial could match in their shape or color. In Experiment 1, participants were required either to verbally report the identity of the stimulus at each location or to point to an image of the item (if the patient had a naming deficit), reporting “nothing” when no item was detected. Color was irrelevant to the report task. On single-item trials, targets were presented in isolation in the contra- or ipsilesional visual field, and they carried either their familiar (correct) color or an incorrect color. In Experiment 1, the conditions for two-item trials were determined by the identity and color of the ipsilesional stimulus in relation to the contralesional item; they are illustrated in Figure 1. The examples listed here assume that the contralesional item is correctly colored and green (e.g., green lettuce). The conditions were (i) *Same Shape, Same Color, Both Correct* (identical correctly colored items were presented bilaterally [ipsilesional item: green lettuce, Figure 1A(a)]); (ii) *Same Shape, Different Color, Contralesional Correct* (items differed in color only such that one item was presented in the original hue and the other in the inverted version [ipsilesional item: purple lettuce, Figure 1A(b)]); (iii) *Different Shape, Same Color, Both Correct* (the items had different identities; both were in the correct, matching colors [ipsilesional item: green pea-pod, Figure 1A(c)]); and (iv) *Different Shape, Different Color, Contralesional Correct* (the items differed both in color and identity and only the contralesional item was in its correct color [ipsilesional item: purple pea-pod, Figure 1A(d)]). These four conditions were replicated when the contralesional item had an incorrect color (Figure 1A(a–d)).

We observed that there was reduced extinction when the contralesional and ipsilesional items had matching familiar colors. In Experiment 2, we tested whether this effect was driven just by the ipsilesional item having a familiar color or whether both items had to be colored correctly. We included new conditions in which the stimuli had the same physical color, but the color was correct only for the ipsilesional item. Was coloring this item correctly sufficient to reduce extinction, or did both items have to be colored correctly? We found that both items must be correctly colored to benefit.

In Experiment 3, we used a subset of the conditions from Experiment 1 (conditions (iii) and (iv)) and either presented the colors on the surface of the object or

Figure 1. Example stimulus pairings on two-item trials in Experiment 1. For example, in A, the contralesional (left) item is a correctly colored green lettuce depicted in each of the following conditions: (a) *Same Shape, Same Color (SS-SC), Both Correct*; (b) *Same Shape, Different Color (SS-DC), Contralesional Correct*; (c) *Different Shape, Same Color (DS-SC), Both Correct*; and (d) *Different Shape, Different Color (DS-DC), Contralesional Correct*. The examples in B cover when the contralesional (left) item was an incorrectly colored purple lettuce: (a) *Same Shape, Same Color, Both Incorrect*; (b) *Same Shape, Different Color, Contralesional Incorrect*; (c) *Different Shape, Same Color, Both Incorrect*; and (d) *Different Shape, Different Color, Contralesional Incorrect*.

in the background. It is possible that the effects depend on the conceptual knowledge of the colors accessed from the object shapes, which is then verified against the color present. In that case, benefits to objects with the same learned colors should be found with gray level images of the objects on colored backgrounds, because access is based on object shape and then verification of a spatially proximal color. Hence, the same result is predicted if the mere presence of the color and shape is critical, rather than the color and shape features being integrated (the color on the object's surface). A further possibility is that there is grouping based on items having the same learned color, even if the color is not present on the object's surface (Lloyd-Jones, Roberts, Leek, & Fouquet, 2012). Again, it should not matter if the color is on the object's surface or in the background. In contrast to these proposals, the colors had to be present on the surfaces of the objects for contralesional items to benefit from having its learned color present and matching that of the ipsilesional object. It is not the mere presence of the correct color but its spatial positioning and grouping on the object surface that is critical.

The data suggest that grouping based on a common surface color across the items countered the effects of extinction, but this took place only when the colors were correct for the items. Furthermore, this arose even though color was irrelevant for report. We propose that there is unconscious binding of learned colors and forms in patients showing extinction, and these bound relations can modulate grouping and selection. Potential

mechanisms for these effects are elaborated in the General Discussion.

EXPERIMENT 1

Materials and Methods

Case Histories

Seven patients who had suffered a stroke and exhibited visual extinction took part in Experiment 1. Extinction in these patients was independently confirmed in a study requiring the patients to report two different letters (A–D, each $1^\circ \times 0.5^\circ$ high and wide) presented for 200 msec either alone, 3° to the left or right of fixation, or bilaterally in the same locations. Twenty age-matched control participants made minimal errors under these conditions and no more than a difference of one item on reporting items on the left and right sides of space. In contrast to this, the current patients all showed significantly worse report of the contralesional item under bilateral relative to unilateral presentation conditions (and in all cases, this difference was well outside the control range). Three of the patients had damage including inferior posterior parietal cortex on MRI scan (JB, PM, and RH), and one had clinical symptoms in word finding and verbal STM consistent with damage to the same area (patient DB for whom no MRI scan was available). The other three patients (AS, DT, and JW) had damage outside the posterior parietal cortex but nevertheless showed visual extinction. The scans are presented in Figure 2. In four patients

Figure 2. MRI scans for the patients in Experiments 1 and 2. Left side of scan = left hemisphere.

(AS, JB, JW, and PM), there was evidence of bilateral damage (Figure 2), but extinction was still clearly manifest on one side of space. This side, derived from the independent letter report task, was designated the contralesional side for the subsequent analyses. MRI scans are shown in Figure 2. The patients were aged 68–75, were all male apart from JB, and had had their stroke at least 2 years previously and were in a chronic state of recovery when tested. All patients consented to participate in the experiments, and the protocol was approved by the departmental ethics review board in the School of Psychology, University of Birmingham. Details of their clinical impairments are presented in Table 1.

Table 1. Clinical Impairments of Patients in Experiments 1 and 2

Patient	Age (years)	Aetiology	Clinical Impairment
AS	70	Stroke	Left extinction
DT	68	Stroke	Right extinction
JB	68	Stroke	Left extinction
JW	72	Stroke	Left extinction
PM	70	Stroke	Left extinction, word finding, mild simultanagnosia
RH	72	Stroke	Right extinction, right neglect dyslexia

Six of the patients (AS, DB, DT, JW, PM, and RH) took part in Experiment 1. Of these, AS, DB, PM, RH, and an additional patient, JB, took part in Experiment 2 (DT and JW being unavailable).

Apparatus

Observers viewed stimuli on an LG (UK) monitor (~26° × 33°) seated centrally approximately 65 cm from the display. Stimulus presentation was controlled using MatLab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and run on a Dell personal computer.

Stimuli

Twelve stimuli were selected from the Viggiano stimulus set (Viggiano, Vannucci, & Righi, 2004) as they were “color diagnostic” (i.e., the objects were each associated with a specific color). To modify the chromaticity of these stimuli, the color of each pixel was rotated by 180° in DKL color space (Derrington, Krauskopf, & Lennie, 1984) using custom-written MatLab routines in conjunction with the CRS “Color Toolbox.” This allowed for systematic manipulation of the color while maintaining luminance and contrast. All stimuli were rendered on a white background and subtended 2.2° × 2.2° when viewed at the specified distance. These were then presented 8.7° from

Table 2. Number of Sessions Completed and the Stimulus Duration Used for Each Patient in Experiment 1

	<i>Patient</i>					
	<i>AS</i>	<i>DB</i>	<i>DT</i>	<i>JW</i>	<i>PM</i>	<i>RH</i>
No. of sessions	5	4	3	4	3	3
Stimulus duration (msec)	650–750	300–500	375–425	400–450	100–500	550–600

the left and/or right from a central fixation cross. On the different shape trials, individual items were randomly paired together, but this pairing was then maintained for each of the different shape conditions (the 2×2 combination for the contra- and ipsilesional items having the correct or incorrect color).

Design

Four participants made verbal reports on the identity of the stimulus at each location, reporting “nothing” when no item was detected. Three patients who expressed some difficulties with verbal responding (DB, PM, RH) were given an answer sheet that had each item (12 items) depicted in grayscale, and the patients were allowed to point to their selection. All participants were also asked to point to where the stimulus appeared. There were no time limits on responses. On trials where they thought there were two items but could not identify the second item, participants were asked to guess. Each stimulus appeared on the contralesional and ipsilesional side in each of six conditions both in the original (correct) and inverted (incorrect) color versions. On single-item trials, targets were presented in isolation in the contra- or ipsilesional visual field. The conditions for two-item trials were determined by the identity and color of the ipsilesional stimulus in relation to the contralesional item (see Figure 1).

Procedure

Prior to testing, the experimenter explained the task, and each patient was familiarized with the stimuli and the

displays. Practice sessions allowed the stimulus duration to be roughly titrated to prevent floor or ceiling effects with approximately 60% accuracy on single-item trials. This was done at the start of each testing session, resulting in different stimulus durations across but not within experimental blocks. The stimulus conditions were randomly presented within each block. The average number of sessions per patient is detailed in Table 2, which also presents the average exposure duration for each participant.

All trials started with a black fixation cross ($0.9^\circ \times 0.9^\circ$) that was presented centrally on a white background. Participants were reminded to maintain fixation on this cross. A verbal “ready” warning initiated the start of trial; the fixation cross was removed and was replaced by the stimulus display. Each session consisted of 144 trials (48 one-item and 96 two-item trials). There were 12 trials per condition per block (the 8 two-item conditions listed in Figure 1 plus 4 single-item trials for correct and incorrect colored stimuli in the contra- and ipsilesional fields). Within each session, the trials were fully randomized.

Results and Discussion

None of the patients showed any sign of neglect when making their response. On two-item trials, all of the patients tended to report (and point to) the ipsilesional stimulus prior to the contralesional one. The proportion correct data in Experiment 1 were converted to arcsin values to avoid floor effects in some conditions ($y = 2 * \arcsin(\sqrt{p})$), where p is the proportion correct). Because the response type (pointing vs. verbal response)

Table 3. Proportion Correct Responses for Individual Patients in Experiment 1

<i>Patient</i>	<i>SS-SC</i>		<i>SS-DC</i>		<i>DS-SC</i>		<i>DS-DC</i>	
	<i>Contra Correct</i>	<i>Contra Incorrect</i>	<i>Contra Correct</i>	<i>Contra Incorrect</i>	<i>Contra Correct</i>	<i>Contra Incorrect</i>	<i>Contra Correct</i>	<i>Contra Incorrect</i>
AS	0.236	0.327	0.291	0.273	0.345	0.182	0.200	0.310
DB	0.522	0.520	0.409	0.431	0.409	0.318	0.250	0.25
DT	0.576	0.478	0.333	0.454	0.515	0.424	0.273	0.242
JW	0.300	0.341	0.182	0.250	0.318	0.182	0.159	0.182
PM	0.606	0.515	0.606	0.394	0.652	0.333	0.394	0.273
RH	0.424	0.333	0.364	0.394	0.242	0.182	0.202	0.02

Figure 3. Experiment 1 mean proportion of correct reports on one- and two-item trials according to whether the contralesional stimulus was correctly colored or not.

varied across the patient group, as did the number of sessions, an initial analysis was performed with Condition as the within-subject factor and Response type and Session as the between-subject factors. There was a main effect of Condition ($F(7, 98) = 5.191, p < .001$), but there were no interactions between Condition, Type, and Session (all $ps > .05$). Thus, the Condition effect was not differentially affected by the type of response or the session. The mean data across sessions for individual participants are presented in Table 3. Subsequently, the different conditions were analyzed with each session included as a separate data point (treated as participants²) and Patient as a between-subject factor to generalize the results over patients.

The mean proportions of contralesional stimuli correctly identified on one- and two-item trials are displayed in Figure 3, according to whether the contralesional stimulus was in the correct or incorrect color (averaging across conditions of shape similarity on two-item trials). The patients were more accurate at identifying a contralesional

Figure 4. Mean proportion correct in each of the two-item trial conditions. These are: Same Shape–Same Color (SS-SC), Same Shape–Different Color (SS-DC), Different Shape–Same Color (DS-SC), and Different Shape–Different Color (DS-DC). The bar colors depict whether the contralesional item was in its correct color (dark gray) or its incorrect color (light gray). Error bars indicate SEM.

item presented in isolation than when it was presented simultaneously with an ipsilesional stimulus (Figure 3; $F(1, 17) = 35.866, p < .001$), a pattern of performance indicative of visual extinction. There was a slight benefit for correctly rather than incorrectly colored items ($F(1, 17) = 2.174, p = .159 ns$). There was no interaction ($F < 1.0$).

The data on two item trials were analyzed using a repeated-measures ANOVA including Learned color of the contralesional item (correct or incorrect), Shape (same or different), and Perceptual color (same or different) as within-subject factors and Patient as a between-subject factor. There were main effects of the Learned color of the contralesional item ($F(1, 17) = 7.33, p = .015$), shape ($F(1, 17) = 11.31, p = .004$), and perceptual color ($F(1, 17) = 25.65, p < .001$). Whether the contralesional item was in its correct color interacted with shape similarity between the stimuli ($F(1, 17) = 10.25, p = .005$). There were no other effects (three-way interaction, $F(4, 17) = 2.10, p > .05$). The results are shown in Figure 4.

Decomposition of the color–shape Congruency $\times$ Shape similarity interaction was done using Bonferroni-corrected t tests. When the items had the same shape, there was no effect of whether the contralesional item was in its correct color ($t < 1.0$). When the items had different shapes, there was better report when the contralesional item was in its correct color than when it was in its incorrect color ($t(22) = 3.76, p < .01$). When the contralesional item had an incorrect color, there was also better report of two items that had the same shape than two items with different shapes ($t(22) = 4.17, p < .01$). When the contralesional items had a correct color, there was only a trend for performance to be better when they had the same shape ($t(22) = 2.21, p > .05$).

It is important to rule out the possibility that participants were biased to make guesses from the ipsilesional item and therefore artificially inflated accuracy when the identity of the items was repeated. Our findings, however, are not consistent with this explanation, as the vast majority of errors were because of omissions (91.65% of error trials) rather than incorrect responses. Furthermore, incorrect identification responses did not differ across conditions (see Table 4).

The results here indicate positive effects of stimulus similarity on extinction. Thus, extinction reduced when the stimuli had the same shape relative to when they had different shapes, contrary to at least some prior findings where extinction has been reported to increase between similar stimuli (e.g., Baylis et al., 2001). In addition, color

Table 4. Percentage of Incorrect Trials Where Patients Made an Erroneous Response (rather than an Omission) in Experiment 1

	SS-SC	SC-DC	DS-SC	DS-DC
Correct color	8.35	8.26	8.53	8.97
Incorrect color	9.07	9.32	10.26	13.23

similarity benefitted performance even though color was irrelevant to the report task, which also goes against some prior reports which have argued that similarity along the response dimension is critical (Baylis et al., 1993). Rather than indicating increased competition between similar items, our data indicate that shape similarity was beneficial, consistent with the similar items grouping and being selected together. Note also that we failed to find differences between patients who had contrasting (verbal and pointing) responses, consistent with the present results not being strongly response-related (see Table 3). We return in the General Discussion to consider the relations between findings where similarity reduces extinction and cases where similarity increases extinction.

In addition to the similarity effects, there were effects of whether the contralesional object carried its familiar color. In particular, when the stimuli differed in shape, report of the contralesional stimulus benefitted when it was in its correct color. This result is consistent with color–shape binding taking place for contralesional items and with this then cueing attention more strongly than when the stimuli are in the incorrect color (see Rappaport et al., 2013). This result is consistent with learned color–shape relations being coded preattentively prior to the contralesional item entering awareness.

Experiment 2 provided a further test of whether there was coding of the color–shape relationship for contralesional stimuli. It also tested again whether grouping by color could modulate performance even though color was irrelevant to the report task. In Experiment 2, the items were never the same shape, but they could be

the same color. In this case, there was never a grouping along the report-relevant dimension. Are there effects of color grouping under this circumstance? Also, are any effects of color grouping modulated by whether the objects are in their familiar (correct) colors? In Experiment 1, the benefit for different shape, correctly colored stimuli tended to be strongest when the stimuli had the same physical color (Figure 3), although the three-way interaction was not reliable. Any enhancement of the correct color effect in this condition could have come about because participants quickly identified the ipsilesional item in its correct color and then attended to the contralesional item because it had the same color. According to this “ipsilesional identification account,” report of a contralesional item should be good as long as the ipsilesional item is in the correct color (e.g., when a yellow [incorrect] contralesional strawberry is paired with yellow [correct] ipsilesional lemon). This was evaluated here. Example stimuli are depicted in Figure 5.

EXPERIMENT 2

Method

The method matched that in Experiment 1, except that only five patients participated (AS, PM, DB, and RH from Experiment 1 plus new patient JB). There were eight conditions (see Figure 5). In the examples in Figure 5A, the contralesional stimulus had its correct color (e.g., green lettuce on the left). There were four conditions: (a) *Same Color, Ipsilesional Correct Color*; (b) *Same*

Figure 5. Example stimulus pairings on two-item trials in Experiment 2. (A) Conditions where the contralesional item (shown here on the left) is in its correct color: (a) *Same color items, Ipsilesional item, Correct*; (b) *Same Color, Ipsilesional item, Incorrect*; (c) *Different Color, Ipsilesional item, Correct*; (d) *Different Color, Ipsilesional item, Incorrect*. (B) Conditions where the contralesional item (left) is in an incorrect color: (a) *Same Color, Ipsilesional item, Correct*; (b) *Same Color, Ipsilesional item, Incorrect*; (c) *Different Color, Ipsilesional item, Correct*; (d) *Different Color, Ipsilesional item, Incorrect*.

Color, Ipsilesional Incorrect Color; (c) Different Color, Ipsilesional Correct Color; and (d) Different Color, Ipsilesional Incorrect Color. In the examples in Figure 5B, the contralesional (left) stimulus had an incorrect color (red lettuce). There were then four conditions: (e) Same Color, Ipsilesional Correct Color; (f) Same Color, Ipsilesional Incorrect Color; (g) Different Color, Ipsilesional Correct Color; and (h) Different Color, Ipsilesional Incorrect Color. The number of blocks each patient took part in is given in Table 5, along with the exposure durations for each participant. JB and AS made verbal identification responses; the other patients made pointing responses.

Results and Discussion

As for Experiment 1, the proportion correct data were converted to arcsin values. An initial analysis was performed with Condition as the within-subject factor and Response type and Session as the between-subject factors. Again there was a main effect of Condition ($F(7, 56) = 3.070, p < .008$), but none of the interactions between Condition, Type, and Session proved reliable (all $ps > .05$).

To test for the general effect of extinction, a comparison was made of reports of correctly and incorrectly colored contralesional items on one- and two-item displays, averaging across the similarity conditions (see Figure 6). Each patient was included as a between-subject factor and the sessions entered as separate participants. Patients were significantly more accurate at identifying a contralesional item when it was presented in isolation than when it appeared simultaneously with an ipsilesional stimulus ($F(1, 9) = 59.53, p < .001$), confirming visual extinction. There was a borderline benefit for contralesional items presented in their correct color relative to an incorrect color ($F(1, 11) = 4.84, p = .06\ ns$). There was no interaction ($F < 1.0$).

Performance in each of the two-item trial types for each patient is illustrated in Table 6. These data were analyzed using a repeated-measures ANOVA including Contralesional color–shape (correct/incorrect), Ipsilesional color–shape (correct/incorrect), and Color repetition (same/different) as factors. There was a reliable main effect of Color repetition ($F(1, 9) = 44.67, p < .001$) and Contralesional item color–shape ($F(1, 9) = 8.78, p < .025$). There was no effect of the Ipsilesional stimulus color–shape

Table 5. Number of Sessions Completed and the Stimulus Duration Used for Each Patient in Experiment 2

	Patient				
	AS	DB	PM	RH	JB
No. of sessions	3	3	3	4	2
Stimulus duration (msec)	600	325–400	200	500–575	275

Figure 6. Mean proportion correct accuracy data for one- and two-item trials in Experiment 2.

($F(1, 9) = 1.875, p = .214\ ns$). However, all factors interacted ($F(1, 10) = 7.78, p < .025$, for the three-way interaction). This interaction is depicted in Figure 7. The three-way interaction was generalized across patients (there was no interaction with the Patient factor).

To decompose the three-way interaction, we considered first the trials where the contralesional item was in the correct color. Here there was an effect of Color repetition ($F(1, 9) = 14.63, p < .01$) and an interaction between Color repetition and whether the ipsilesional color was correct ($F(1, 9) = 13.03, p < .01$). The interaction was broken down using pairwise comparisons between the conditions with Bonferroni correction. When both items had the same correct colors, performance was better than in the conditions where (i) the items had the same colors and the ipsilesional color was incorrect ($t(13) = 3.87$), (ii) the items were of different colors but both were correct ($t(13) = 5.07$), and (iii) the items had different colors and the ipsilesional one was incorrect ($t(13) = 4.28$; all $ps < .01$). There were no other effects (all $ps > .05$).

When the contralesional item was colored incorrectly, there was again an effect of Color similarity ($F(1, 9) = 20.00, p < .01$), but no other effect (smallest $p = .124$).

Again, the majority of errors were due to omissions (90%) rather than incorrect responses, and the incorrect responses did not differ across the conditions (see Table 6). This suggests that the effects were not inflated by participants guessing the contratarget from the ipsilesional item.

In Experiment 2, the stimuli on two-item trials always differed in shape, and items again had to be reported by their shape. As in Experiment 1, although color was irrelevant to report, we again found that color affected performance. Report of the contralesional item was better when it was in its correct color (the main effect of Contralesional color–shape). This is consistent with correctly colored items not only being easier to identify (Price & Humphreys, 1989) but also attracting attention (to avoid extinction; Rappaport et al., 2013). In addition, extinction was reduced most when the ipsi- and contra-stimuli were both in their familiar correct colors, and the

Table 6. Proportion Correct Responses for Individual Patients in Experiment 2

Patient	<i>Contralesional Correct Color</i>				<i>Contralesional Incorrect Color</i>			
	<i>Same Color</i>		<i>Different Color</i>		<i>Same Color</i>		<i>Different Color</i>	
	<i>Ipsi Correct Color</i>	<i>Ipsi Incorrect Color</i>	<i>Ipsi Correct Color</i>	<i>Ipsi Incorrect Color</i>	<i>Ipsi Correct Color</i>	<i>Ipsi Incorrect Color</i>	<i>Ipsi Correct Color</i>	<i>Ipsi Incorrect Color</i>
AS	0.417	0.194	0.222	0.167	0.138	0.222	0.167	0.111
DB	0.083	0.028	0.083	0.111	0.111	0.111	0.083	0.083
PM	0.444	0.306	0.306	0.278	0.194	0.111	0.056	0.167
RH	0.208	0.104	0.104	0.104	0.125	0.083	0.063	0.083
JB	0.438	0.225	0.268	0.333	0.280	0.518	0.208	0.125

color was the same in the two stimuli. Notably, it was not sufficient for the ipsilesional item to carry its correct color and share its physical color with the contralesional stimulus (same color, contralesional item incorrect). These data go against the “pure ipsilesional identification” account of performance, which proposes that fast identification of a correctly colored ipsilesional item enables participants to attend to a contralesional stimulus, particularly when it carries the same physical color as the ipsilesional stimulus. Here both items needed to be in their correct (familiar) color, and this color needed to match across the objects for extinction to reduce. The data again point to the contralesional stimuli having pre-attentively bound representations of color and shape, when the items have familiar colors. The effect of having a common color across the ipsi- and contralesional stimuli further indicates that having matching, familiar correct colors facilitated grouping between the ipsi- and contralesional items. Grouping between the stimuli reduced extinction and enabled both items to be selected together (Humphreys, 1998).

In addition to this finding, there was some benefit when the items carried the same physical color, even when the color of the contralesional item was incorrect

(Figure 5B(a) and (b)). This indicates some color-based grouping based on shared perceptual properties of the stimuli, in addition to effect of learned color (as in Figure 5A(a) and (b)), although any benefit was weaker than when the colors were also learned for those items.

EXPERIMENT 3

We have taken the data so far to indicate that extinction patients can show implicit binding of stored color–shape relations because (i) extinction is reduced for objects presented in their familiar colors and (ii) this is modulated by color-based grouping between ipsi- and contralesional stimuli. However, other accounts of the data are feasible. One possibility is that the mere presence of the stored color and shape in the contralesional field is sufficient to facilitate the processing of these items so that they can sometimes be reported and enter into grouping relations; however, the color and shape may be processed independently and are not necessarily integrated together. For instance, there may be access to stored knowledge based on familiar object shape and then verification of a spatially proximal color; in this case, the presence of the color on the surface of the object should

Figure 7. Mean proportion of correct responses on two-item trials in Experiment 2. Left: Contralesional item in its correct color. Right: Contralesional item in its incorrect color. The bar color indicates the color of the ipsilesional item (dark gray = correct color; light gray = incorrect color).

Figure 8. MRI scans for patients PH and RR (Experiment 3).

not be critical. In contrast with this prediction, in studies of visual search, we have noted that colors need to be presented on the surface of the object to generate “pop out” and facilitated perception (Wildegger et al., 2015; Rappaport et al., 2013), but this is not necessarily the case for extinction patients. We assessed this in Experiment 3, where we tested two patients showing visual extinction on images where color was presented on the surface of the objects or in the background. If the integration of color on the surface of the shape is not critical, then objects presented on the correct background color should be facilitated, just as when the correct colors are presented on the surface of the object. A further possibility is that there is access to stored knowledge about color from the shape of the object and that this then combines with the presence of the correct color to facilitate identification and grouping. Lloyd-Jones et al. (2012) conducted an ERP study of repetition priming with correctly and incorrectly colored pictures of objects and found evidence for effects of shape change on the early N1 component occurring earlier than the effects of shape + color change (on P2). They argued that there is fast access to shape-based representations of objects prior to access to representations that unite color and shape; moreover, access to shape representations may cue the retrieval of color knowledge, and this may be sufficient to generate the color-based grouping we observed. According to this argument, there should be grouping and reduced extinction from presenting two gray level representations of objects that have a common color in real life because of shape-mediated retrieval of object color. In that case, there should be improved per-

formance for items having the same real-life color irrespective of whether the color falls on their surface or the background.

Method

We recruited two new patients, both of whom showed visual extinction (a failure to notice the contralesional item under bilateral presentation conditions) when pictures of objects were presented for relatively brief durations and masked. PH and RR were respectively 34 and 42 years old, respectively. Both had suffered left hemisphere strokes resulting in damage to the left temporal and parietal cortices extended anteriorly into the left frontal cortex (Figure 8). Both patients were in a chronic state and had had their strokes over 2 years before testing. Both had expressive aphasia and impaired verbal working memory. Because of their aphasia, the patients made pointing responses to a set of line drawings depicting the objects used in the experiment. Pilot work established that, when photographic images of objects were presented for 100 msec and immediately followed by a mask of random colored line segments (for 200 msec), the patients were able to identify about 80% of the contralesional objects presented alone, but this fell to around 40% on bilateral presentation trials. Age- and education-matched controls were able to identify all the items under the same conditions.

The images of the objects were matched in size to those in Experiments 1 and 2, and each was presented within a square of $2.2^\circ \times 2.2^\circ$. The images were shown either with the full color rendered on the surface of the

Figure 9. Example stimuli from Experiment 3. (A) The images were shown in full color that was either correct (red strawberry, green pea) or incorrect for the object (green strawberry, red pea). (B) The objects were shown as gray level images on a local colored background that was either correct or incorrect for the object.

object (see Figure 9A) or with the color filling the background of the local square surrounding the object image (Figure 9B). We presented a subset of the conditions used previously. The objects always differed in shape, and the contralesional item was always presented with its correct color. Pairs of items either had the color on their surfaces or the objects were depicted in gray level and had their colors in the background. There were four conditions both when the colors were on the surface and when they were on the background: (i) *Ipsilesional item in its correct color and same as the contralesional object* (e.g., red strawberry + red radish); (ii) *Ipsilesional item in an incorrect color and same as the contralesional item* (red strawberry + red pea); (iii) *Ipsilesional item in its correct color but different to the contralesional item* (red strawberry + green pea); and (iv) *Ipsilesional item in an incorrect color and different to the contralesional object* (red strawberry + green radish). There were eight objects, each of which was paired with another object that had the same color in real life (strawberry–radish, apple–pea, lemon–corn, orange–carrot) and with one of the other colored items (for different color trials: strawberry–pea, apple–corn, lemon–carrot, orange–radish). In the bilateral presentation conditions, each object appeared four times on the contralesional side and four times on the ipsilesional side in each of the color conditions, making 32 trials in each color condition and 256 bilateral trials in the experiment (128 color on surface, 128 color in the background). Each object was also presented four times in the correct color and four in the incorrect color on the contralesional and on the ipsilesional sides of space, in both the surface color and background color conditions, leading to 128 unilateral trials. The stimuli were presented in a random order in three trial blocks.

The stimuli were presented on a Dell PC with a 21-in. monitor (1024 × 768 pixels, 100 Hz) using E-Prime software (Version 2.0) (Psychology Software Tools, Inc.; www.pstnet.com).

Results

Pooling the data across patients on two-item trials, 94% (250/266 errors) involved errors on the contralesional item and correct report of the ipsilesional stimulus, and 92% of these errors (230) involved omissions. There were correct reports of two items on 55% (142/256) of the trials with a surface color and on 41% (104/256) of the trials with a background color. On unilateral trials, a correctly colored contralesional single item was correctly identified on 88% (28/32) and 84% (27/32) of the trials respectively when the color was on the surface and when it was in the background. Given that only two patients were tested here, we used log-linear analyses rather than parametric statistics. Report of the contralesional item on one-item trials was better than reports of two-item correct trials, both for surface colored objects ($\chi^2(1) =$

12.07, $p < .001$) and for objects with a colored background ($\chi^2(1) = 21.96$, $p < .001$). There was evidence for extinction.

The two-item trials were analyzed using a log-linear model for trials where the color was on the object surface and trials where the color was in the background. The factors were whether the ipsilesional color was correct for the item, whether it was the same physical color as the contralesional stimulus, and whether the response was correct or wrong. When the color was on the object surface, the best fitting model was for the three-way interaction ($\chi^2 = 0$ for the model fit; $\chi^2(1) = 7.27$, $p < .01$, for the interaction). There was better report of two items when the ipsi- as well as the contralesional items had its correct color and when they were both of the same physical color (see Figure 10). There was no effect of having the same physical color when the ipsilesional stimulus had an incorrect color (31/64 for both the same and the different color conditions). When the color was in the background, there was only an effect of whether trials were correct or not ($\chi^2(6) = .913$, $p = .989$, for the best fitting model; $\chi^2(1) = 9.05$, for the effect of correct vs. error trials, $p < .01$). There were more incorrect than correct trials, but this was not modulated by the different conditions.

When the color was on the surface of the objects, the data resembled those in Experiment 2: There was a better report of two items when both the contra- and ipsilesional objects had the correct color and the color was the same for both stimuli. However, in this case, there was no effect of the items having the same physical color. Any advantage for the “correct and same color” condition was lost, however, when the color fell in the background. Thus, there was no evidence for two item reports benefitting from having the same learned color or from the presence of the same color in the background of both the contra- and ipsilesional displays (even when this color was correct for both stimuli). This result is difficult to explain if the benefit was due to independent processing of color and shape and also if the benefit was due to grouping based on color information retrieved from the shape of the objects (which should have occurred with colored and gray level objects alike). The correct colors needed to be on the surface of the objects to generate the effects.

GENERAL DISCUSSION

Our findings are consistent with the idea that, despite the presence of visual extinction, not only are the basic principles of low-level perceptual organization spared (Humphreys, 1998; Mattingley et al., 1997; Gilchrist et al., 1996) but there can also be high-level coding of stimulus attributes (e.g., the binding of learned form–color conjunctions). Here we demonstrate that presenting stimuli with familiar color–shape combinations in the contralesional field reduces extinction (Experiment 1)

Figure 10. Proportion correct accuracy data for two-item trials for each patient in Experiment 3. Left: The color was depicted on the surface of the object. Right: The color was presented in the local background for the object. Top figures, patient PH. Bottom figures, patient RR.

and also supports stronger color-based grouping between contra- and ipsilesional stimuli (Experiments 2 and 3). The effects did not arise, however, if the colors were presented surrounding but not on the surface of the objects (Experiment 3). This last result supports the idea that the color and shape need to be spatially integrated to generate the benefits to report, and there are no effects based on the independent processing of color and shape or on conceptual color knowledge accessed from object shape (cf. Lloyd-Jones et al., 2012). The results do fit with the proposal that learned color and shape are bound together preattentively to influence grouping and modulate whether contralesional items enter awareness. It should also be noted that the beneficial effects of items having their correct color occurred here, although color was irrelevant to the main report task, consistent with the effects of color and shape binding arising at early processing stages prior to task relevance affecting performance.

The important new result is that learned color-form relations modulated performance. Notably, when the stimuli had different shapes, there was recovery from extinction for items carrying their learned colors (red strawberry and red tomato) relative to stimuli with matching physical colors only (blue strawberry and blue tomato). This result did not simply reflect the presentation of an ipsilesional item in the correct color—there was no recovery of extinction when the ipsilesional item

was correct and the contralesional item had an incorrect but matching color (e.g., red lemon–red tomato, for a patient with left extinction; Experiment 2). Having the contralesional item in its correct color reduced omissions, indicating that the contralesional item was then brought into conscious awareness. Also this effect was particularly striking when the contra- and ipsilesional items shared color (Experiment 2). We conclude that there was stronger grouping when both the ipsi- and contralesional stimuli had the same learned color, and this enabled the contralesional item to be selected.

Previous neuropsychological studies have also pointed to there being preattentive binding of color and form. For example, Wojciulik and Kanwisher (1998; see also Cinel & Humphreys, 2006; Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997) reported data on Stroop interference in a simultanagnosic patient who was unable to explicitly report whether a color was assigned to a color or a neutral word, consistent with preattentive binding of color and form. In this and other similar studies (Cinel & Humphreys, 2006; Robertson et al., 1997), the stimuli could not be reported, and so binding appears to have occurred implicitly. In addition, the relations between the stimulus features were essentially arbitrary and not determined by prior knowledge. Here, in contrast, the binding between color and form determined whether stimuli entered awareness and so modulated explicit report. Also, the critical factor was whether the color

and shape of an object had a learned relationship. This is the first time that effects of a learned relationship have been documented in such patients.

One explanation for these findings is that stored object-based representations are accessed preattentively and that these representations are sensitive to both learned shape and color. Strong activation of these learned conjunctive representations, by correctly colored objects, enables the representations to group, facilitating report of the contralesional stimuli. There is prior evidence that processing in the contralesional field can be sufficiently elaborate to extract the identity and semantic details of stimuli even if the items are never consciously perceived (McGlinchey-Berroth, Milberg, Verfaellie, Alexander, & Kilduff, 1993). Here we propose that the representations do not only reflect learned shape but also the conjunctive relations of shape and color. This does not mean that shape representations are not accessed earlier than color–shape knowledge, but it does mean that color–shape knowledge is recruited sufficiently rapidly for items to only subsequently enter awareness.

There is emerging neurophysiological evidence for the existence of conjunctive representations from early cortical regions through to inferotemporal cortex (Rust & DiCarlo, 2010; Seymour, Clifford, Logothetis, & Bartels, 2009, 2010). In addition, there is electrophysiological evidence from humans for a rapid neural response to objects appearing in the correct color (Lu et al., 2010), consistent with early perceptual coding of learned color–shape relations. Also, as we have noted, studies of visual search (Wildegger et al., 2015; Rappaport et al., 2013) have shown uniquely efficient responses to targets with learned color–shape relations, even when participants are set to search for targets in a nonstandard color (the set is to search for a purple corn but a yellow corn target “pops out”; Rappaport et al., 2013, Experiment 3). This last result fits with the efficient coding of learned conjunctions of color and shape being a bottom–up process based on the activation of stored color–shape representations. We suggest that these stored representations are activated bottom–up from the image allowing objects to be linked to their familiar color automatically, and these representations then enter into grouping based on their common color. In this way correct color–shapes are unitized preattentively at early stages of visual processing. Grouping may be better supported when stimuli have learned representations for a variety of reasons. One is that color was not relevant to the report task and so may receive little top–down attentional support. Without such task-based attention, color-based grouping may be weak especially if the color is not bound a priori to the object; note that we found some evidence for physical color grouping when items were in their incorrect colors in Experiment 2, but the effects were relatively small and not replicated in Experiment 3. Possibly, the activation of stored conjunctive representations for stimuli could feedback to support perceptual representations of the colors, facilitating

grouping and the linkage of attentional weights through shared perceptual representations (e.g., as proposed by Duncan & Humphreys’s [1989] Attentional Engagement Theory). In this way, activation from stored representations may substitute for the attentional feedback that would occur when the task is to report the colors of the stimuli.

Theoretical Implications

Our findings have important theoretical implications. First, dominant theories of visual processing (e.g., Feature Integration Theory) distinguish between an early preattentive processing stage, which codes perceptual features in a spatially parallel manner, and a later focal attentional stage, which is required to bind visual features (Treisman & Gelade, 1980). However, visual extinction patients show (by definition) poor attention to contralesional stimuli, yet here we show evidence for color–form binding. Our findings indicate that features can be bound together preattentively provided that the relations between the features are learned. This contradicts a basic tenet of Feature Integration Theory (Treisman & Gelade, 1980).

A somewhat different account of binding has been proposed by Humphreys (2001, in press), suggesting that attention plays a confirmatory rather than a necessary role in binding. According to this account, feature relations can be coded preattentively, but this coding may often be noisy when there are multiple items with shared features in the visual field (as is typical in conjunction search tasks, for instance). Under these circumstances, top–down attentional feedback acts to stabilize the conjunctive codes that are formed, enabling the combined information to feed forward for object recognition. The degree to which attention is demanded for integration will then depend on several factors—featural overlap between stimuli in the field, whether the features have an already learned relationship and so forth. Here (see also Rappaport et al., 2013) we show that, when stimuli have long-term learned relations, the requirement for attentional involvement in binding is small.

A second issue raised by our findings concerns the role of color and shape in object processing. Here our findings provide evidence for preattentive unitization of combined shape and surface color information. It is difficult to reconcile these findings within a purely “edge-based” account of object processing, which allocate a role for surface information only at a late stage of object identification, presumably after awareness (Biederman & Ju, 1988). Our findings fit better with a “surface-plus-edge” account where diagnostic colors could form part of an object’s perceptual representation and are therefore influential at the earliest stage of processing (Davidoff, 2001; Tanaka, Weiskopf, & Williams, 2001). Our data indicate that this early mediation of perceptual processing by learned color–form bindings takes place outside awareness and modulates grouping. An argument for

rapid access to learned color–shape representations could still be consistent with “pure shape” representations being accessed earlier (Lloyd-Jones et al., 2012), but it does mean that color–shape knowledge is recruited preattentively to then facilitate entry into awareness.

Relations to Prior Work

A final point to note here is that we report positive effects of stimulus similarity on visual extinction. In several other reports (Rafal, Danziger, Grossi, Machado, & Ward, 2002; Baylis et al., 1993, 2001; Vuilleumier & Rafal, 2000), investigators have noted the opposite—namely that extinction is increased for similar stimuli. In addition, in the studies reporting negative effects of stimulus similarity, performance has only been affected by response-relevant dimensions of stimuli, not when the dimensions are irrelevant for report (e.g., Baylis et al., 1993). Also participants have typically had to localize the items. However, here the effect of color arose despite it being irrelevant for report, and participants had to localize and identify the items. One reason why color may have been beneficial here is that we used pictures of real stimuli with familiar colors. We suggest that this enables color and shape to be integrated early in visual processing, with the result that color modulates subsequent processing. The learned linkage of color and shape with familiar objects may also make it more difficult to attend selectively to shape and ignore color, even when only shape is relevant for report. Evidence for a failure to ignore shape when attending to the color of familiar objects comes from Naor-Raz, Tarr, and Kersten (2003). These authors presented pictures of familiar objects in correct or incorrect colors. The time to name the color of the objects was speeded when the color was correct for the object relative to when it was incorrect (see also Menard-Buteau & Cavanagh, 1984). With arbitrary color–shape relations, however, it may be possible to attend more selectively to one dimension, minimizing the effect of color when shape is the only dimension relevant to report.

The role of the task seems less critical, given that we used identification and localization, which has previously been associated with negative effects of stimulus similarity (see Vuilleumier & Rafal, 2000). In contrast, in many investigations showing positive effects of similarity, simple enumeration responses have been required (how many items are present?). Nevertheless, other investigators have also demonstrated positive effects of grouping based on stored knowledge when stimuli have to be identified (Kumada & Humphreys, 2001). At least with familiar stimuli, any contrast between identification and localization, on the one hand, and enumeration, on the other, seems not to be vital. Perhaps once items become highly familiar, their identity can be accessed as rapidly as the items can be enumerated, and so both report tasks are sensitive to early grouping. With less well-learned stimuli, the slow emergence of identity information

may make processing vulnerable to other factors, such as problems in establishing individuated tokens of each item for sequential report.

Alongside these effects of familiarity with the stimuli and task, the grouping cues often vary across experiments. For instance, in the studies of Baylis et al. (1993, 2001), stimuli were presented at wide eccentricities (e.g., 12° and 15° from fixation, respectively) and were separated by a central fixation cross. Grouping is negatively affected by interitem distance (Pavlovskaya, Sagi, Soroker, & Ring, 1997; Gilchrist et al., 1996). Rafal et al. (2002) reported negative effects of similarity with words presented closer to fixation (3°), but grouping may not be particularly strong between words in any case. It is feasible that further disruption to grouping may be caused by a central fixation cross, which may interfere with grouping across the left and right visual fields. It is noteworthy that, in studies reporting positive effects of perceptual grouping, the fixation cross is typically offset on trial onset (Gilchrist et al., 1996; Ward et al., 1994). We suggest that our conditions enabled the stimuli to be grouped when they shared shape and learned color. In contrast, if items are encoded sequentially, then report of repeated items might prove difficult if previous token representations have been formed. In this last case, similarity may be detrimental to performance.

In summary, in three experiments here we find novel evidence for preattentive binding of learned color–shape associations, which modulate grouping and recovery from extinction. The data indicate that learned color–shape relations exert an influence at an early stage of processing, guiding selective attention. Because of this early binding of learned color and shape, effects of color then emerge on the shape report. These findings have important implications both for theories of visual attention and object processing.

Acknowledgments

The authors thank Dirk Ostwald for his assistance with stimulus inversion. This work was supported by grants from the Stroke Association and the NIHR Oxford cognitive health clinical research facility. It was completed as partial fulfilment of a PhD at the University of Birmingham by the first author.

Reprint requests should be sent to Glyn W. Humphreys, Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford, United Kingdom, OX1 3UD, or via e-mail: glyn.humphreys@psy.ox.ac.uk.

Notes

1. Some studies have shown negative rather than positive effects of stimulus similarity on extinction (Rafal et al., 2002; Baylis et al., 2001; Vuilleumier & Rafal, 2000; Baylis et al., 1993). In the General Discussion, we return to review possible reasons for this discrepancy.
2. This obviated the potential “weighting” problem given that not all patients contributed the same amount of data.

REFERENCES

- Baylis, G. C., Driver, J., & Rafal, R. D. (1993). Visual extinction and stimulus repetition. *Journal of Cognitive Neuroscience*, 5, 453–466.
- Baylis, G. C., Gore, C. L., Rodriguez, P. D., & Shisler, R. J. (2001). Visual extinction and awareness: The importance of binding dorsal and ventral visual pathways. *Visual Cognition*, 8, 359–379.
- Biederman, I., & Ju, G. (1988). Surface versus edge-based determinants of visual recognition. *Cognitive Psychology*, 20, 38–64.
- Brainard, D. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 3.
- Chechacz, M., Rotshtein, P., Hansen, P. C., Deb, S., Riddoch, M. J., & Humphreys, G. W. (2013). The central role of the temporo-parietal junction and the superior longitudinal fasciculus in supporting multi-item competition: Evidence from lesion symptom mapping of extinction. *Cortex*, 49, 487–506.
- Cinell, C., & Humphreys, G. W. (2006). On the relations between implicit and explicit spatial binding: Evidence from Balint's syndrome. *Cognitive, Affective and Behavioral Neuroscience*, 6, 127–140.
- Davidoff, J. (2001). *Cognition through colour*. Cambridge, MA: MIT Press.
- Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology*, 357, 241–265.
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, 96, 433–458.
- Duncan, J., Humphreys, G. W., & Ward, R. (1997). Competitive brain activity in visual attention. *Current Opinion in Neurobiology*, 7, 255–261.
- Ellison, A., & Walsh, V. (1998). Perceptual learning in visual search: Some evidence of specificities. *Vision Research*, 38, 333–345.
- Gilchrist, D., Humphreys, G. W., & Riddoch, M. J. (1996). Grouping and extinction: Evidence for low-level modulation of visual selection. *Cognitive Neuropsychology*, 13, 1223–1249.
- Humphreys, G. W. (1998). Neural representation of objects in space: A dual coding account. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 353, 1341–1351.
- Humphreys, G. W. (2001). A multi-stage account of binding in vision: Neuropsychological evidence. *Visual Cognition*, 8, 381–440.
- Humphreys, G. W. (in press). Feature confirmation in object perception: Feature integration theory 26 years on from the Treisman Bartlett lecture. *Quarterly Journal of Experimental Psychology*.
- Humphreys, G. W., Hodsell, J., & Riddoch, M. J. (2009). Fractionating the binding process: Neuropsychological evidence from reversed search asymmetries. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 627–647.
- Karnath, H.-O., Himmelbach, M., & Küker, W. (2003). The cortical substrate of visual extinction. *NeuroReport*, 14, 437–442.
- Kumada, T., & Humphreys, G. W. (2001). Lexical recovery from extinction: Interactions between visual form and stored knowledge modulate visual selection. *Cognitive Neuropsychology*, 18, 465–478.
- Lloyd-Jones, T. J., Roberts, M. V., Leek, E. C., & Fouquet, N. C. (2012). The time course of activation of object shape and shape + colour representations during memory retrieval. *PLOS One*, 7, e48550.
- Lobley, K., & Walsh, V. (1998). Perceptual learning in visual conjunction search. *Perception*, 27, 1245–1255.
- Lu, A., Xu, G., Jin, H., Mo, L., Zhang, J., & Zhang, J. X. (2010). Electrophysiological evidence for effects of color knowledge in object recognition. *Neuroscience Letters*, 469, 405–410.
- Mattingley, J. B., Davis, G., & Driver, J. (1997). Pre-attentive filling in of visual surfaces in parietal extinction. *Science*, 275, 671–674.
- McGlinchey-Berroth, R., Milberg, W. P., Verfaellie, M., Alexander, M., & Kilduff, P. (1993). Semantic processing in the neglected visual field: Evidence from a lexical decision task. *Clinical Neuropsychology*, 10, 79–108.
- Menard-Buteau, C., & Cavanagh, P. (1984). Localisation de l'interférence forme/couleur au niveau perceptuel dans une tâche de type Stroop avec des stimuli-dessins [Localization of form/color interference at the perceptual level in a Stroop task with drawings]. *Canadian Journal of Psychology/Revue canadienne de psychologie*, 38, 421–439.
- Naor-Raz, G., Tarr, M. J., & Kersten, D. (2003). Is color an intrinsic property of object representation? *Perception*, 32, 667–680.
- Pavlovskaya, M., Sagi, D., Soroker, N., & Ring, H. (1997). Visual extinction and cortical connectivity in human vision. *Cognitive Brain Research*, 6, 159–162.
- Pelli, D. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 5.
- Price, C. J., & Humphreys, G. W. (1989). The effects of surface detail on object categorisation and naming. *Quarterly Journal of Experimental Psychology*, 41A, 797–828.
- Rafal, R., Danziger, S., Grossi, G., Machado, L., & Ward, R. (2002). Visual detection is gated by attending for action: Evidence from hemispatial neglect. *Proceedings of the National Academy of Sciences, U.S.A.*, 99, 16371–16375.
- Rappaport, S. J., Humphreys, G. W., & Riddoch, M. J. (2013). The attraction of yellow corn: Reduced attentional constraints on coding learned conjunctive relations. *Journal of Experimental Psychology: Human Perception and Performance*, 39, 1016–1031.
- Robertson, L., Treisman, A., Friedman-Hill, S. R., & Grabowecy, M. (1997). The interaction of spatial and object pathways: Evidence from Balint's syndrome. *Journal of Cognitive Neuroscience*, 9, 295–317.
- Rust, N. C., & DiCarlo, J. J. (2010). Selectivity and tolerance (“invariance”) both increase as visual information propagates from cortical area V4 to IT. *Journal of Neuroscience*, 30, 12978–12995.
- Seymour, K., Clifford, C. W. G., Logothetis, N. K., & Bartels, A. (2009). The coding of color, motion, and their conjunction in the human visual cortex. *Current Biology*, 19, 177–183.
- Seymour, K., Clifford, C. W. G., Logothetis, N. K., & Bartels, A. (2010). Coding and binding of color and form in visual cortex. *Cerebral Cortex*, 20, 1946–1954.
- Su, Y., Lai, Y., Huang, W., Tan, W., Qu, Z., & Ding, Y. (2014). Short-term perceptual learning in visual conjunction search. *Journal of Experimental Psychology: Human Perception and Performance*, 40, 1415–1424.
- Tanaka, J., Weiskopf, D., & Williams, P. (2001). The role of color in high-level vision. *Trends in Cognitive Sciences*, 5, 211–215.
- Treisman, A., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12, 97–136.
- Viggiano, M. P., Vannucci, M., & Righi, S. (2004). A new standardized set of ecological pictures for experimental and clinical research on visual object processing. *Cortex*, 40, 491–509.

- Vuilleumier, P., & Rafal, R. (2000). A systematic study of visual extinction between- and within-field deficits of attention in hemispatial neglect. *Brain*, 123, 16.
- Walsh, V., Ashbridge, E., & Cowey, A. (1998). Cortical plasticity in perceptual learning demonstrated by transcranial magnetic stimulation. *Neuropsychologia*, 36, 45–49.
- Ward, R., Goodrich, S. J., & Driver, J. (1994). Grouping reduces visual extinction: Neuropsychological evidence for weight linkage in visual selection. *Visual Cognition*, 1, 101–129.
- Wildegger, T., Riddoch, M. J., & Humphreys, G. W. (2015). Stored color–form knowledge modulates perceptual sensitivity in search. *Attention, Perception & Psychophysics*, 77, 1223–1238.
- Wojciulik, E., & Kanwisher, N. (1998). Implicit but not explicit feature binding in a Balint's patient. *Visual Cognition*, 5, 157–181.