

Glyn Humphreys: Attention, Binding, Motion-Induced Blindness

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Abstract: Glyn Humphreys' research on attention and binding began from feature-integration theory, which claims that binding together visual features, such as colour and orientation, requires spatially selective attention. Humphreys employed a more inclusive notion of binding and argued, on neuropsychological grounds, for a multi-stage account of the overall binding process, in which binding together of form elements was followed by two stages of feature binding. Only the second stage of feature binding, a re-entrant (top-down) process beginning in posterior parietal cortex and returning to early visual areas, required attention. In line with his commitment to converging evidence, Humphreys considered that investigating the role of attention in motion-induced blindness could be a route to better understanding of the cognitive role of the attention-dependent second stage of feature binding. He suggested that this role might be to resolve ambiguity and to generate a single consistent interpretation of the perceptual input.

1. Introduction

Glyn Humphreys' work ranged widely over cognition and its disorders, including spatial attention, feature binding, visual search, visual object and word recognition, action and its effects on attention and perception, bilingualism, theory of mind, and self-bias. Much of his work was in neuropsychology and, as Humphreys said, 'one sees such a variety of disorders in the neuropsychology clinic that it is difficult to focus on just one subject if you have the bug of curiosity' (Humphreys, 2016a, p. ix).

In work with Jane Riddoch, Humphreys reported many neuropsychological cases, sometimes returning to the same case in a succession of papers spanning many years. For example, Riddoch and Humphreys (1987) provided the first detailed description of patient HJA, who suffered from integrative visual agnosia, and he subsequently figured in more than thirty papers. Some aspects of patient HJA's visual processing were intact and his conceptual knowledge about objects was impressively detailed. But his visual object recognition was severely impaired because his visual processing did not group together information about the parts of an object, to yield a structural

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description of the whole object.¹ Humphreys and Riddoch's work in neuropsychology extended to the development of fuller and briefer assessments for patients following stroke, the Birmingham Cognitive Screen (BCoS; Humphreys, Bickerton, Samson and Riddoch, 2012) and the Oxford Cognitive Screen (OCS; Demeyere, Riddoch, Slavkova, Bickerton and Humphreys, 2015). These are used widely in the UK National Health Service and the OCS is also used internationally.

Humphreys was also an enthusiast for methods and techniques – not only the behavioural methods of cognitive psychology and cognitive neuropsychology, but also implemented computational models of cognitive processes, eye tracking, structural and functional brain imaging (MRI, EEG), lesion-symptom mapping, and more. He attached a high value to converging evidence from different sources: 'any single approach has its own limitations [and so] it is important to use different techniques in order to try and converge on a robust account' (Humphreys, 2016a, p. x).

This article is an attempt – inevitably partial and selective – to convey something of the theoretical depth and broad interest of Glyn Humphreys' research on attention and binding. We begin from feature-integration theory, which claims that binding together visual features, such as colour and orientation, requires spatially selective attention (Section 2). Humphreys employed a more inclusive notion of binding that encompassed, not only feature binding, but also grouping of local parts into a more global shape, for example. We use the term 'form binding' for this binding or grouping together of components or elements of a form, contour, or shape (e.g. the three line segments that make up a triangle). Humphreys showed that there was a division to be made empirically, and not just terminologically, between stages of the overall binding process. Specifically, form binding could be spared in patients whose feature binding was severely impaired following damage to parietal cortex (Section 3).

Humphreys assembled a considerable body of evidence showing that the attentional requirements of form binding were low (Section 4). He went on to show that even the attentional requirements of feature binding could sometimes be reduced if combinations of colour and shape, for example, were familiar and learned. There was also evidence of unconscious or implicit binding of unlearned and arbitrary feature combinations in parietal patients, whose explicit feature binding was severely impaired (Section 5). This led to a further division between two stages – early and late – of feature binding, with only the second stage requiring spatially selective attention. Thus, the multi-stage process of binding in vision (Humphreys, 2001) would comprise form binding and then two stages of feature binding. There was evidence that the attention-dependent second stage of feature binding involved re-entrant (top-down) processes, beginning in posterior parietal cortex and returning to early visual areas. But, with so much binding apparently not making heavy

¹ Humphreys and Riddoch's case study of patient HJA continued for more than twenty-six years (beginning in 1981, when they first met him). Patient HJA figured in two books (Humphreys and Riddoch, 1987, 2014) and nineteen of the papers about him are now collected in *A Reader in Visual Agnosia* (Humphreys and Riddoch, 2016).

demands on attention, it was important to understand the cognitive role of this second stage of feature binding (Section 6).

The final section of the article turns to the interesting phenomenon of motion-induced blindness, in which stationary visual targets, presented in the midst of a moving array, seem to disappear. Crucially, and perhaps paradoxically, a target is more likely to disappear if attention is directed to it. In line with his commitment to converging evidence, Humphreys considered that investigating the role of attention in motion-induced blindness could be a route to better understanding of the cognitive role of the second stage of feature binding. He suggested that the role of this re-entrant process might be to resolve ambiguity and to generate a single consistent interpretation of the perceptual input.

2. Attention and Binding: Feature-Integration Theory

Several strands of Glyn Humphreys' research begin from Anne Treisman's *feature-integration theory* of attention (Treisman and Gelade, 1980). Visual information processing in the brain shows considerable specialisation, with different neural regions processing information about different 'dimensions' of the visual world, such as colour, orientation, size, motion, and so on. Visual 'features' are particular values along these dimensions (e.g. red and green on the colour dimension). As they figure in feature-integration theory, visual features are properties that are instantiated by objects, rather than parts of objects (Treisman and Gormican, 1988, p. 16).

In our normal visual perceptual experience of objects, features belonging to different dimensions are integrated; they are seen to be properties of the same object. We see a vertical red bar and a horizontal green bar. How does it come about that the information about colour (red, green) and the information about orientation (vertical, horizontal), which are processed somewhat separately in the brain, are nevertheless combined correctly in visual experience? This, in massively simplified form, is (one version of) the *binding problem* (Treisman, 1996).

According to Treisman's feature-integration theory (FIT), in a first stage of visual processing, the distribution of features in space is registered using map-like representations – one map for each feature on the colour dimension (perhaps red, green, blue, yellow), one map for each feature on the orientation dimension (perhaps vertical, horizontal, 45° clockwise, 45° anticlockwise), and so on. This early processing does not require spatially selective attention. It is automatic and in parallel, across features, dimensions, and locations. Treisman (2006) suggested that, even without feature binding, this automatic processing could give the gist of a scene (e.g. whether it is a mountain landscape or a kitchen) and compute mean values on visual dimensions (e.g. the average size of presented objects).

Binding together of features as belonging to a single object depends, according to FIT, on a second stage of visual processing, in which spatially selective attention is focused on spatial locations serially. When attention is focused on a location, the features that are represented (in their separate feature maps) as being instantiated at that

location (e.g. colour feature red and orientation feature vertical) are highlighted and integrated. Thus, 'focal attention provides the "glue" which integrates the initially separable features into unitary objects' (Treisman and Gelade, 1980, p. 98).

2.1 Two Predictions: Illusory Conjunctions and Visual Search

Treisman and Gelade (1980) pointed to five predictions of FIT; here we discuss just two. The first is this: 'If focused attention to particular objects is prevented ... the features of the unattended objects are "free floating" with respect to one another' (1980, p. 100). Without attention, features may be incorrectly combined in perceptual experience so that *illusory conjunctions* occur. For example, if a red horizontal bar and a green vertical bar are presented while a subject's attention is otherwise occupied, then the subject might recombine the colour and orientation features and report having seen a red vertical bar. Treisman and Schmidt (1982) presented the results of experiments testing this prediction and concluded that, when neurologically healthy subjects' attention is loaded, they make illusory conjunction errors (ICEs). Furthermore, at least some of these errors are 'consciously and confidently experienced as perceived physical objects' (1982, p. 138).

The existence of ICEs under conditions of attentional load provides support for Treisman and Gelade's (1980) claim that 'attention is necessary for the *correct* perception of conjunctions' (p. 98). Further support can be gathered by looking at a display such as one presented by Jeremy Wolfe (2012, Figure 1). There are thirty-six plus signs and six Xs, each made up of a green bar and a purple bar. If you direct your attention to the top left plus sign, you can see that the vertical bar is purple and the horizontal is green. As you maintain your attention at that location, you can see that, outside the focus of your attention, there are more green and purple plus signs, and also some Xs. But, for any given plus sign, it is impossible to tell whether it is the vertical bar or the horizontal bar that is green, unless you redirect your attention.

Examples like this are important because they show that there is a binding problem – solved by focal attention, according to FIT – quite independently of whether the first-stage (preattentive) processing of information about colour, orientation, size, motion, and so on is carried out in wholly separate neural regions.

The second prediction of FIT that we shall discuss concerns visual search tasks, in which a target stimulus is to be detected amongst non-target stimuli (distractors). A target may be distinguished from distractors by a single feature (e.g. by a colour feature – a *red* horizontal bar amongst green vertical and horizontal bars) or it may be distinguished by a conjunction of features (e.g. by a conjunction of colour and orientation features – a *red vertical* bar amongst green vertical and red horizontal bars).

According to FIT, detection of a target that is defined by a conjunction of features requires focal attention; so attention would need to be directed to the locations of stimuli in succession until the target was found. In contrast, detection of a target that is defined by a single feature is automatic and in parallel across locations.

It does not require serial checking of locations of stimuli; rather, the target ‘pops out’ from the distractors. Thus, time to a positive response (‘target present’) should increase approximately linearly with the number of distractors for *conjunction search*, but should be approximately independent of the number of distractors for *feature search*. Treisman and Gelade (1980) presented the results of experiments in which the slopes of the graphs of reaction time against display size (RT/display size slopes) were more than 20 msec/item for conjunction search, but less than 10 msec/item for feature search.

2.2 Efficiency in Visual Search

The results of Treisman and Gelade’s (1980) visual search experiments supported a distinction between *inefficient conjunction search* (with RT/display size slopes of greater than 20 msec/item) and *efficient feature search* (with slopes of less than 10 msec/item). However, subsequent research has painted a more complex picture. Wolfe, Cave and Franzel (1989) conducted a series of conjunction search experiments, beginning with a colour-shape search very similar to Treisman and Gelade’s (1980) Experiment 1. Wolfe and colleagues found an average slope of 7.5 msec/item – much closer to the slope of Treisman and Gelade’s feature search (3.1 msec/item) than to the slope of their conjunction search (28.7 msec/item).

One factor that influences the efficiency of visual search is the discriminability of targets from distractors. In Wolfe and colleagues’ (1989) experiment (using saturated colours on a black computer screen), the target (a red O) was easily distinguished from green Os and red Xs. In Treisman and Gelade’s experiment (using coloured inks on white cards), the target (a green T) was less easily distinguished from brown Ts and green Xs. Treisman and Gelade (1980, Experiment 2) and Wolfe and colleagues (1989, Experiment 7) both confirmed that reducing target-distractor discriminability increased the slope of conjunction search.

A second factor that influences the efficiency of visual search is heterogeneity of the distractors. Using a conjunction search with distractors varying across three colours and three orientations, Wolfe and colleagues (Experiment 8) found an RT/display size slope of 25.9 msec/item. In fact, with sufficiently heterogeneous distractors, even a feature search may produce an RT/display size slope of 16 msec/item (Treisman, 1988, p. 210). It is important for what follows that some conjunction searches have been shown to be more efficient than some feature searches.

These two factors (reduced target-distractor discriminability and increased distractor heterogeneity) result in less efficient searches (with steeper RT/display size slopes). But how exactly do more homogeneous distractors with high target-distractor discriminability explain the very shallow slopes in Wolfe and colleagues’ conjunction searches? Wolfe proposed, as a modification of FIT, a *guided search theory* (Wolfe *et al.*, 1989; for a recent review, see Wolfe, 2014): a parallel search for a feature can guide the more serial search for a conjunction of features. For example, in a conjunction search for a red O amongst green Os and red Xs, none of the green items could be a red O. So a parallel search for the feature

green could provide information about (the approximate locations of) items that could be excluded from the search for the target. With the green items set aside, a serial search through the red items – or, better still, another parallel search (for shape) – could differentiate a red O from red Xs. Thus, even in a conjunction search, attention can sometimes be guided efficiently to the target (for a similar proposal, see Treisman, 1988, p. 226; Treisman and Sato, 1990).

2.3 Feature Binding in Patients with Parietal Damage

Posterior parietal cortex is implicated in directing spatially selective attention (Corbetta and Shulman, 2002; Posner, 2016). Consequently, FIT predicts that patients with posterior parietal damage would have problems with feature binding and would experience illusory conjunctions.

Cohen and Rafal (1991) investigated illusory conjunctions in a patient, EA, with a left-side parietal lesion, and found that she made a large number of ICEs when stimuli were presented on the right side (the side opposite to the lesion; the *contralesional* side). Humphreys and colleagues (Humphreys, Cinel, Wolfe, Olson and Klempen, 2000, Experiment 1) investigated illusory conjunctions in a patient, GK, with bilateral parietal lesions. If one coloured letter was presented, patient GK was generally able to report the letter and its colour. But if three coloured letters were presented (one at fixation and one on each side) then patient GK was less successful in reporting the central letter and its colour, and made many ICEs.

Illusory conjunctions may also give rise to difficulties with conjunction search, so that patients with unilateral parietal lesions and impaired binding on the *contralesional* side have problems on both target-present and target-absent trials. On target-present trials, they might sometimes fail to detect a conjunction target (e.g. a red X) on the *contralesional* side. On target-absent trials, they might, because of an ICE, report a target on the *contralesional* side although no target was actually present (e.g. report a red X when only green Xs and red Os were present).

Humphreys, Hodsoll and Riddoch (2009, Experiments 1 and 2) investigated visual search in patients with unilateral posterior parietal damage. Crucially, they used an *easy* colour-shape conjunction search (for coloured letters), which allowed efficient search by neurologically healthy subjects, and a *difficult* orientation feature search (for tilted lines), resulting in inefficient search.

On target-present trials, parietal patients' detection of targets presented on the *contralesional* side was worse on the conjunction search than on the feature search. In contrast, when targets were presented on the *ipsilesional* side of the display (the same side as the lesion) parietal patients detected targets better on the (*easy*) conjunction search than on the (*difficult*) feature search. Control patients, with fronto-temporal but not parietal damage, and neurologically healthy control subjects, showed this latter pattern of performance for targets on both sides of the display.

On target-absent trials, there was a crucial finding for parietal patients on the conjunction search. When parietal patients incorrectly reported that a conjunction

target was present on a target-absent trial, they were more likely to say that the supposed target was on the contralesional side of the display than that it was on the ipsilesional side. No such bias toward localising supposed targets on the contralesional side was shown by parietal patients on the feature search, nor by control patients or healthy control subjects on either search.

The results of Humphreys and colleagues' (2009) Experiments 1 and 2 showed that patients with posterior parietal lesions have a specific difficulty in binding features presented on the contralesional side. The conjunction search was easier than the feature search – allowing more efficient search in healthy subjects – but parietal damage reversed those search efficiencies. In the next section, we turn from feature binding to form binding and consider, once again, questions about efficiency (for neurologically healthy subjects) and impairment (in parietal patients).

3. Form Binding Without Attention: Evidence from Visual Search

One way to understand the facts about visual search efficiency and item similarity (target-distractor discriminability and distractor heterogeneity) would be as peripheral aspects of a theory of visual search in which the core was still the distinction between conjunction search and feature search. As against this, Duncan and Humphreys (1989) not only rejected the simple binary distinction between inefficient conjunction search and efficient feature search, but also argued that item similarity (between target and distractors, or between distractors) was more crucial for a theory of visual search than the distinction between conjunction search and feature search (see also Desimone and Duncan, 1995).

3.1 Efficiency in Form-conjunction Search

In two experiments (Duncan and Humphreys, 1989, Experiments 1 and 4), neurologically healthy subjects searched for an upright letter L target amongst distractors, which were variously oriented letter Ts. The target and the distractors each involved the same two components – one vertical stroke and one horizontal stroke (of the same length) – but the vertical and horizontal strokes were combined differently in the two letters, L and T. Duncan and Humphreys regarded this as a conjunction search because the vertical and horizontal strokes were conjoined in the target and also figured in the distractors. Perhaps it was not, strictly speaking, a feature-conjunction search in Treisman's sense; the component strokes were not properties, but parts, of the letter L. We shall refer to it as a *form-conjunction search* because the strokes were components or elements of a form, contour, or shape. One of Duncan and Humphreys' main points in their paper was that the same principles govern efficiency, whether a search is a feature search, a feature-conjunction search, or a form-conjunction search.

In their experiments, target-distractor discriminability and distractor heterogeneity were varied independently. The four experimental conditions and corresponding

	Homogeneous distractors	Heterogeneous distractors
High target-distractor discriminability (Experiment 1)	Either all upright Ts or all 90° rotated Ts Slope = 3 msec/item	Mixed upright Ts and 90° rotated Ts Slope = 3 msec/item
Low target-distractor discriminability (Experiment 4)	Either all 180° rotated Ts or all 270° rotated Ts Slope = 8 msec/item	Mixed 180° rotated Ts and 270° rotated Ts Slope = 16 msec/item

Table 1 Reaction time/display size slopes for four experimental conditions from Duncan and Humphreys (1989, Experiments 1 and 4).

RT/display size slopes are set out in Table 1. The efficiency of visual search was influenced by both kinds of item similarity and the two item-similarity factors interacted. When the target was highly discriminable from the distractors, increasing distractor heterogeneity had relatively little effect (top row); and when the distractors were homogeneous, reducing the discriminability of the target had relatively little effect (left column). But reduced target-distractor discriminability and increased distractor heterogeneity together had substantial effects on search efficiency (bottom right cell).

Duncan and Humphreys interpreted these results in terms of ‘spreading suppression’ (1989, p. 446). Distractor Ts could be perceived as a group and rejected together – *but only if* the target L was substantially less similar to the Ts than the Ts were to each other. When the distractor Ts were heterogeneous and also similar to the target L (Table 1, bottom right cell), suppression that spread to encompass both kinds of T would have been liable to engulf the target L as well. In that condition, some more stepwise process of selection was required and visual search became less efficient.

3.2 Form-conjunction Search in Patients with Parietal Damage

According to FIT, binding together the features of a single object (e.g. colour and orientation) requires spatially selective attention. Does binding or grouping together the lines or curves that make up a two-dimensional shape (e.g. the vertical and horizontal strokes of a letter L) require attention in the same way that binding colours to orientations does?

Humphreys, Hodsoll and Riddoch (2009, Experiments 4 and 5) investigated form-conjunction search in parietal patients, control patients, and healthy control subjects. The target was an upright letter L or (in a separate experiment) a less familiar rotated letter L, and distractors were heterogeneously oriented Ts. Search for an L amongst heterogeneously oriented Ts (or *vice versa*) is relatively inefficient for neurologically healthy subjects (Duncan and Humphreys, 1989; Wolfe *et al.*, 1989, Experiment 4). But the difficult form-conjunction search task was still easier than

the difficult orientation feature search that Humphreys and colleagues used in their Experiments 1 and 2 (see above, Section 2.3). The crucial question was whether the parietal patients would have a specific difficulty binding form elements (vertical and horizontal strokes) on the contralesional side.

On target-present trials, detection of the target was better on the form-conjunction search than on the feature search for the parietal patients, just as it was for the control patients and the healthy control subjects. When subjects gave a false-positive response on a target-absent trial, there was no evidence – for any group on either task – that subjects' answers to the question whether the supposed target was on the left or the right side of the display were biased toward the contralesional side.

In summary, the patients with unilateral parietal lesions, who had a specific difficulty in binding features presented on the contralesional side, did *not* have a similar difficulty in binding form elements on the contralesional side. Thus, there was an empirical divide between form binding and feature binding and the vulnerability of different visual searches to parietal damage was not predicted by the degree of inefficiency of the searches for neurologically healthy subjects.

4. Form Binding Without Attention: Evidence from Extinction

Humphreys presented further neuropsychological evidence supporting the claim that the attentional requirements of form binding are low, and much of this evidence came from studies of visuospatial extinction. In this neuropsychological condition, patients with unilateral lesions are able to notice and report a single stimulus, even when it is presented on the contralesional side, but they fail to detect the same stimulus when a second stimulus is presented, at the same time, on the ipsilesional side. Thus, extinction involves competition for visual attentional selection; and the competition favours stimuli on, or further toward, the ipsilesional side. The stimulus that loses the competition for selection is extinguished.

Visuospatial extinction may be reduced when ipsilesional and contralesional stimuli that would otherwise compete for visual attentional selection form a group in accordance with Gestalt, or more recent, principles of proximity, similarity, continuity, closure, collinearity, connectedness and so on (Wertheimer, 1923; Palmer and Rock, 1994). Stimuli that group together, and are processed as parts of a single unit, are more likely to be selected together (Ward, Goodrich and Driver, 1994). The fact that extinction can be reduced in this way demonstrates that, despite the patients' lesions, and consequent impairment of attention, 'stimuli in the contralesional field [are] processed to at least a level at which they can enter into grouping relationships with ipsilesional items' (Humphreys, 2001, p. 385).

4.1 Preattentive Binding in the Form Domain

Patient GK, with bilateral parietal lesions, showed symptoms of Balint's syndrome, including difficulty in describing complex scenes containing multiple objects

(simultanagnosia). He also displayed visuospatial extinction, with visual selection biased toward the right side (Gilchrist, Humphreys and Riddoch, 1996).

Gilchrist and colleagues investigated the effect of grouping on extinction in patient GK, using black and white circles and squares. According to grouping principles of similarity (in colour) and collinearity, two circles of different colours (one black and one white) would be least likely to group together (neither grouping cue); two circles of the same colour could group because of similarity (one grouping cue); two aligned squares of different colours could group because of collinearity (one grouping cue); and two aligned squares of the same colour would be most likely to group together (both grouping cues).

Patient GK's extinction was reduced when grouping was more likely (ranging from only 8% detection of two different-coloured circles to 46% detection of two same-coloured squares). In accordance with the grouping principle of proximity, the improvement in detection when two squares of the same colour were presented was diminished when the squares were further apart. Humphreys, Cinel and colleagues (2000, Experiment 4) further extended these findings to encompass grouping effects of connectedness.

Boutsen and Humphreys (2000) found a similar reduction of extinction when two equilateral triangles were presented with their bases aligned or with their axes of symmetry aligned, by comparison with no alignment (one triangle rotated 90° relative to the other). In this case, three line elements were preattentively bound into a triangular contour and then preattentive grouping of the two triangles was based on the contour itself (base-alignment) or on axis information that was derived from, although not present in, the contour itself (axis-alignment).

4.2 Preattentive Recognition of Possibilities for Action

Reduction of visuospatial extinction does not always depend on grouping in accordance with low-level principles. Riddoch and colleagues (Riddoch, Humphreys, Edwards, Baker and Willson, 2003) found that action relations could also modulate extinction. Five patients with parietal damage were shown pictures of objects that could be used together in action (e.g. corkscrew and wine bottle, watering can and flowers). The objects were positioned either correctly or incorrectly for action and the patients' task was to identify the objects. The key finding was that patients were significantly more likely to identify both objects when they were positioned correctly for action than when they were positioned incorrectly. The correctly positioned action-related objects were coded as a unit, overcoming the competition for selection.

Interestingly, even when only one object was identified, correct positioning of the two objects for action still influenced the patients' performance. If the two objects were positioned incorrectly for action then the object that was identified was likely to be the ipsilesional object (as would be expected in visuospatial extinction). But if the objects were positioned correctly for action then the object that was identified was likely to be the 'active' partner in the action-related pair (the

object that is typically moved in the action; e.g. corkscrew, watering can), whether it was presented on the ipsilesional or the contralesional side of space. Thus, correct positioning of two objects for action, not only reduced extinction overall, but also modulated the pattern of residual extinction, with attention being directed first to the ‘active’ partner.

Subsequent experiments showed that there was an effect of the possibility of action (even if the two objects are not frequently used together; e.g. wine bottle and bucket) and an additional effect of the objects being frequently used together (e.g. wine bottle and glass); that is, there were effects of both affordance and familiarity (Riddoch, Humphreys, Hickman, Clift, Daly and Colin, 2006). Also, the effect of correct positioning of objects for action could not be explained in terms of low-level grouping principles (Riddoch, Pippard, Booth, Rickell, Summers, Brownson and Humphreys, 2011).²

4.3 Extinction Reduced by Stored Knowledge about Words

Boutsen and Humphreys observed (2000, p. 897): ‘Grouping may operate on the basis of both low-level visual (“bottom-up”) cues and top-down (stored) knowledge.’ Stored knowledge that two objects (a wine bottle and a glass) are frequently used together in a pouring action provides one example of this latter (stored knowledge) kind of case.

A second example is provided by stored knowledge about words. Kumada and Humphreys (2001) reported that, when patient GK was presented with two letters, one on the left and one on the right of fixation, he was better able to identify both letters correctly – his left-side extinction was reduced – when the letters formed a word (e.g. ‘if’, ‘my’), rather than a nonword (e.g. ‘iy’, ‘mf’).

When patient GK was not asked to identify the letters but simply to report the number of letters presented (none, one, or two), his performance was not significantly better for words than for nonwords. However, when grouping by similarity was reduced (by presenting the two letters in different colours), there was, once again, an effect of grouping by familiarity (stored knowledge about words). Patient GK’s detection of two differently coloured letters was significantly worse when they did not form a word.

5. Feature Binding Without Attention?

We have seen that attentional selection can be modulated, and extinction reduced, by bottom-up grouping, by recognition of possibilities for action, by stored knowledge

² The effects of information about possibilities for action on visual attention and perception are the focus of many of Humphreys’ papers, both neuropsychological studies and experiments with neurologically healthy subjects. For reviews, see Humphreys and Riddoch, 2007 and Humphreys, Kumar, Yoon, Wulff, Roberts and Riddoch, 2013.

that two objects are frequently used together in an action, or by stored knowledge that two letters form a word. Thus, despite parietal damage and impaired attention, stimuli presented on the contralesional, as well as those on the ipsilesional, side are processed up to a level that allows forms or shapes to be bound or grouped together.

In this section, we turn back to feature binding. Is there evidence that patients with impaired attention can sometimes achieve correct feature binding?

5.1 Extinction Reduced by Learned Feature Conjunctions

Rappaport and colleagues (Rappaport, Riddoch, Chechlacz and Humphreys, 2016) investigated whether extinction could be reduced by stored knowledge of feature conjunctions (specifically, colour-shape conjunctions).

They presented coloured pictures of objects, one on each side of fixation, to patients with visuospatial extinction. The patients' task was to identify both objects. Each object had a single 'correct' (familiar, learned) colour (e.g. red strawberry, yellow banana) and objects were shown sometimes in the correct colour and sometimes in an incorrect colour. We should expect that extinction would be reduced by similarity (e.g. when the two objects were shown in the same colour). The new and critical question was whether extinction would be reduced further when the objects – particularly the object on the contralesional side, in danger of extinction – were the correct colour (e.g. when the strawberry on the contralesional side was red).

The results showed an effect of colour similarity, as expected, and an effect of learned colour-shape conjunctions. (Here, we focus on the results of Experiment 2.) The two objects were always different in shape, and they were sometimes shown in the *same* colour although only one was the *correct* colour. The key finding was that extinction was reduced most when the two objects were shown in the same colour and that colour was correct for both objects (e.g. contralesional red strawberry and ipsilesional red tomato). It was not sufficient that the ipsilesional object should be the correct colour (e.g. red tomato) and that the contralesional object should be the same colour, if that colour was incorrect (e.g. red lemon).

It is not likely that Rappaport and colleagues' finding depended on a top-down prediction or expectation that objects would be presented in their correct colours. In related work, using a visual search task with neurologically healthy subjects, Rappaport, Humphreys and Riddoch (2013) showed that visual search was efficient for correctly coloured targets even when, in the context, subjects expected incorrectly coloured targets.³

Using signal detection theory, Wildegger, Riddoch and Humphreys (2015) demonstrated enhanced perceptual sensitivity for learned colour-shape conjunctions (again, even when subjects expected incorrectly coloured targets). They

³ For further discussion of learned conjunctions, see Treisman, 1988, pp. 215–6 and Humphreys, 2016b, pp. 1913–4, 1925–7.

argued that stored colour-shape knowledge has a bottom-up influence on perceptual processing (quite unlike a top-down prediction or expectation). Humphreys suggested (2016a, p. xx; 2016b, p. 1926) that there are neural representations of learned feature conjunctions at a relatively early stage of visual processing; and there is evidence from event-related potentials (ERP; Lu, Xu, Jin, Mo, Zhang and Zhang, 2010) and from fMRI (Seymour, Clifford, Logothetis and Bartels, 2010) that would support such a proposal.

In summary, there is some evidence that the attentional requirements for correct binding of visual features may be reduced when feature combinations are familiar and learned. Might there also be evidence of correct binding of even unlearned and arbitrary combinations of features in patients with severely impaired spatially selective attention?

5.2 Implicit Feature Binding

Implicit feature binding in patients with parietal damage would provide evidence of correct binding of features despite impaired attention. The requirements for attribution of implicit functioning (e.g. implicit knowledge, or memory, or face recognition) are well understood (Davies, 2015). For implicit feature binding, the requirement would be that some aspect of a patient's performance is best explained as drawing on internalised information about feature binding, although this information is not available for explicit report.

Cinél and Humphreys (2006) used a Stroop-like paradigm to demonstrate implicit feature binding in patient GK. The basic Stroop effect (Stroop, 1935) is that, when asked to name the colour in which a word is printed, subjects are slower to respond when the word is a colour word that is inconsistent with the colour in which it is printed (e.g. a green coloured word PURPLE) than when the word is consistent with the colour (e.g. green GREEN). Patient GK showed a Stroop-like interference effect when he was presented with pairs of colour words, one printed in a chromatic colour and the other in white, and was asked to name the non-white colour. His pattern of performance was most plausibly explained as drawing on information in his visual system, about which word was coloured rather than white. But under the same conditions, patient GK performed no better than chance when asked to report explicitly which of two non-colour words (e.g. green CASUAL and white HAPPY) was coloured rather than white.⁴

Evidence of implicit functioning always raises the question whether it results from reduced levels of activation in the system responsible for explicit functioning or from a separate and independent system whose activity is not accessible to consciousness. Humphreys rejected the idea that implicit and explicit feature binding might be the products of independent systems and favoured the view that implicit binding

⁴ For related findings with patient RM, see Robertson, Treisman, Friedman-Hill and Grabowecky, 1997 and Wojciulik and Kanwisher, 1998.

effects draw on an early stage of the normal feature binding process. He also allowed that this early feature binding was not, by its nature, inaccessible to consciousness (Gillebert and Humphreys, 2010, p. 975).

6. Stages of Feature Binding

Along with the primary division between form binding and feature binding, Humphreys proposed a secondary division between early and late stages of feature binding. The early stage was understood as a process of rapid, but unstable and transient, binding of visual features. The late stage was understood as a slower process of *consolidation*, yielding more stable and lasting representations of feature conjunctions (Gillebert and Humphreys, 2010). On this two-stage account of feature binding, only the second stage would require spatially selective attention. The first stage would, in principle, allow correct – albeit unstable and transient – binding of unlearned and arbitrary combinations of features, without making heavy demands on attention. When feature combinations were familiar and learned, binding could be stable, even though its attentional requirements were modest.

In this section, we address two questions about the two-stage (early *versus* late) account of feature binding. The first takes us back to illusory conjunction errors: At what stage, early or late, do they arise? The second is more fundamental: What is the nature of the second or late stage of feature binding?

6.1 The Time Course of Illusory Conjunction Errors

Patients with parietal damage make large numbers of illusory conjunction errors (ICEs) and Gillebert and Humphreys (2010) investigated the time course of ICEs in a series of experiments with patient GK. Their aim was to assess ICEs that arose at earlier or later stages of visual processing. In the first experiment, they examined ICEs as a function of patient GK's reaction times, on the assumption that slower responses were more likely to be influenced by later stages of processing.

A coloured letter (target) was presented at fixation and a second coloured letter (distractor) was presented on either the left or the right of fixation. Patient GK's task was to report the target letter and its colour (e.g. red A). To analyse the time course of ICEs, patient GK's responses were divided equally into five reaction-time bins, from the fastest responses to the slowest. (Patient GK's responses were all slow compared with responses by neurologically healthy subjects.)

Overall, patient GK (who suffered from visuospatial extinction, with a rightward attentional bias), made more ICEs with a right-side, than with a left-side, distractor. The key finding was that, with a right-side distractor, while patient GK made ICEs across the range of reaction times, there was a sharp increase in ICEs in responses with the longest reaction times, compared with the other four bins. A second finding, with left-side or right-side distractors, was that there were more ICEs in responses with the shortest reaction times, compared with the three intermediate reaction-time bins. These findings suggested that, in patient GK, the

later consolidation process was impaired and noisy, resulting in a large number of ICEs amongst his slowest responses; and that the early binding process was also somewhat impaired, resulting in some ICEs amongst his fastest responses.

In a subsequent experiment, Gillebert and Humphreys manipulated the exposure duration, on the assumption that longer exposure would allow the later consolidation process to influence performance. They also asked patient GK, following each response to a presented target, to report whether he was certain or uncertain/guessing. There were two interesting findings. First, patient GK made more ICEs with the longer exposure duration. Second, there was a difference between the two exposure durations in patient GK's certainty or uncertainty about his ICE responses. With the shorter exposure, he was mostly certain about his ICE responses – that is, certain that they were correct (as if the phenomenology was that of perceptual immediacy). With the longer exposure, in contrast, he was predominantly uncertain about his ICE responses (as if the phenomenology was more confusing).

Gillebert and Humphreys proposed that, according to the two-stage account of feature binding, patient GK was impaired in both early and late binding processes. When he responded faster or the exposure duration was shorter, the information that was drawn on came predominantly from the early binding process. When more time was available (slower responses or longer exposure duration), the later consolidation process – which was assumed to be impaired and noisy in patient GK – came into operation. There were more ICEs and patient GK was less certain about his responses. Braet and Humphreys (2009, Experiment 1) reported that another patient with bilateral parietal lesions, PF, also made more ICEs with longer exposure durations.

6.2 Re-entrant Processes in Feature Binding

In a re-entrant neural process, top-down signals are sent from a higher-level neural area to the lower-level areas from which it receives input. In visual processing, re-entrant processes can be conceptualised as comparing high-level perceptual hypotheses with the fine-grained information available in lower visual areas. Re-entrant processes have played an important role in the science and philosophy of consciousness. For example, Block (2005) proposed that conscious experience of motion required, not only activation of visual area V5, but also a fast (< 50 msec) re-entrant (top-down) process from V5 to visual area V1 (Pascual-Leone and Walsh, 2001).

Humphreys proposed that the second stage of feature binding, which required spatially selective attention, involved a re-entrant process beginning in posterior parietal cortex and returning to early visual areas (Humphreys and Riddoch, 2006; Gillebert and Humphreys, 2010; Humphreys, 2016b).⁵ Converging evidence for

⁵ On the role of re-entrant processes in feature binding, see also Di Lollo, Enns and Rensink, 2000; Hochstein and Ahissar, 2002; Treisman, 1996, 2006; Wolfe, 2012.

this proposal came from experiments using transcranial magnetic stimulation and object substitution masking.

6.2.1 Disrupting Re-entrant Processes with TMS. Braet and Humphreys (2009, Experiment 3) used transcranial magnetic stimulation (TMS) with neurologically healthy subjects to investigate the role of re-entrant processes in feature binding. On each trial, while attention was focused at fixation, two coloured letters (e.g. red X and green O) were presented close together at one of four locations (top, bottom, left, right). One letter (the target) was always F or X; the other letter (the distractor) was always O. The task was to identify the target letter and its colour (e.g. red X). Two TMS pulses (separated by 50 msec) were administered over the right posterior parietal cortex at one of six time points, from 0–50 msec to 250–300 msec after onset of the two-letter display.

Braet and Humphreys reported that ICEs occurred at a rate significantly greater than chance when TMS was administered at any of the last four time points (100–150 msec to 250–300 msec after display onset) and the number of ICEs was greatest when TMS was administered at the 150–200 msec time point. Thus, feature binding was disrupted by TMS administered over the right posterior parietal cortex in neurologically healthy subjects, just as it is impaired by posterior parietal cortex lesions in neuropsychological patients. The time course of the disruption suggested that the feature binding that depends on spatially selective attention is a relatively late process, beginning in posterior parietal cortex about 100 msec after display onset – consistent with Humphreys' two-stage account.

6.2.2 Disrupting Re-entrant Processes with OSM. In another experiment with neurologically healthy subjects, Bouvier and Treisman (2010) provided further evidence about the role of re-entrant processes in feature binding. They used object substitution masking (OSM), which can be understood as selectively disrupting re-entrant processing (Di Lollo *et al.*, 2000; Enns and Di Lollo, 2000; Di Lollo, 2010).

In a typical OSM paradigm, there is a display of several items, of which one (the target) is surrounded by four small dots. After a brief exposure duration (10–45 msec), the display items disappear, but the four dots remain for a period of up to a few hundred milliseconds. Now consider a re-entrant signal as a high-level perceptual hypothesis about the target item surrounded by the four dots. If this signal reaches lower visual areas during the period after the display items disappear, but while the four dots remain, then there will be a mismatch between the hypothesis and the lower-level information, and perception of the target will be impaired (Di Lollo *et al.*, 2000). Thus, the four dots not only indicate which item is the target, but also function as a mask, restricting perception of the item that they surround.

In Bouvier and Treisman's study, the display included (with one exception, see below) six plus signs, each with one white bar and one coloured bar, and the target item was indicated by four small dots surrounding it. The exposure duration for the six display items was 75 msec and the four-dots mask remained for 300 msec after

the display items disappeared. Thus, processing of re-entrant signals arriving at lower visual areas during the 300 msec after the display items disappeared would be liable to disruption.

The task was to report the colour and orientation of the (chromatically) coloured bar in the target item. Importantly (the exception mentioned above), on half of the trials, the target item was not a complete plus sign, but only a single coloured bar (vertical or horizontal). When the target item was a complete plus sign, the orientation judgement required binding the chromatic colour feature to the correct orientation feature (vertical or horizontal); but the colour judgement did not require binding, as only one (chromatic) colour was present. No binding was required when the target was a single bar, as only one colour and one orientation were present.

Feature binding was selectively disrupted in this OSM paradigm. When the target was a plus sign, orientation judgements (which required feature binding) were seriously impaired by the four-dots mask (compared with a no-mask condition, which was equivalent to a four-dots mask duration of 0 msec rather than 300 msec). In contrast, when no binding was required, performance was not affected by the four-dots mask.

Braet and Humphreys (2009) showed that feature binding was disrupted when TMS was applied to the right posterior parietal cortex 100 msec or more (and particularly 150–200 msec) after display onset. Bouvier and Treisman (2010) showed that feature binding was disrupted in an OSM paradigm with an exposure duration for display items of 75 msec. In their paradigm, re-entrant signals sent from posterior parietal cortex between 100 msec and 200 msec or more after display onset would have reached lower visual areas in the crucial period – after the display items disappeared but while the four-dots mask remained.

Thus, different experimental methods provide converging evidence that the attention-dependent stage of feature binding requires re-entrant processes that begin in posterior parietal cortex, perhaps about 100 msec after display onset. This provides an answer to our question about the nature of the second or late stage of feature binding. But what is its cognitive role? What does it add to all the form binding and feature binding processes that do not make heavy demands on attention?

7. Motion-induced Blindness

Glyn Humphreys investigated motion-induced blindness (MIB) in research with Orna Rosenthal, Anne Aimola Davies, and Martin Davies. The MIB phenomenon is clearly of interest in its own right but Humphreys also regarded the role of attention in MIB as potentially contributing to our understanding of the attention-dependent second stage of feature binding. The key idea (to which we return below, Section 7.4) was that both involve a perceptual ‘drive to consistency’.

In a typical MIB paradigm, the subject fixates a central point while stationary visual targets are presented in the midst of a moving array. Often, the targets are one or more yellow dots and the moving array is a rotating grid of blue crosses or a

dynamic pattern of blue dots. The remarkable finding is that the targets repeatedly seem to disappear – ‘as if erased in front of the observer’s eyes’ (Bonneh, Cooperman and Sagi, 2001, p. 798) – and then reappear a few seconds later, and they continue through illusory disappearance-reappearance cycles. (For a review, including dynamic MIB displays, see Bonneh and Donner, 2011.) In contrast to inattentional blindness, which is the subject’s failure to notice an unexpected object or event, right in front of their eyes, when attention is otherwise engaged (Mack and Rock, 1998; Simons and Chabris, 1999), an MIB target is *more* likely to seem to disappear if it is the focus of attention, and less likely if attention is otherwise engaged.

7.1 Attention, Binocular Rivalry and Competition

Schölvinck and Rees (2009) used an MIB paradigm with a grid of blue crosses rotating around fixation and two yellow target dots, one on the left and one on the right of fixation. On each trial, subjects were instructed to maintain fixation, direct attention to one dot (e.g. to the left dot), and report when either or both of the dots seemed to disappear. The first illusory disappearance of either dot brought the trial to an end. The key finding was that the probability that the attended target (left or right) would disappear first was significantly higher than the probability that the unattended target would disappear first.

In a second experiment, a single target dot was presented and subjects indicated when the target disappeared and when it reappeared. At the same time, subjects performed a no-load, low-load, or high-load detection task at fixation. The key finding was that, as the attentional load of the detection task increased, the average number of disappearance-reappearance cycles in a two-minute trial decreased.

In summary, while directing attention to an MIB target increases the probability that it will seem to disappear, withdrawing attention from the whole display (target and moving array) reduces the number of disappearances and reappearances.

Schölvinck and Rees compared MIB with binocular rivalry (Blake and Logothetis, 2002), noting that, like the rate of target disappearance and reappearance in MIB, the rate of perceptual alternation in binocular rivalry is slowed when attention is withdrawn (Paffen, Alais and Verstraten, 2006). They also linked attention with competition and proposed that directing attention to an MIB target enhances competition between the target and the moving array, while withdrawing attention reduces competition.

However, it is not straightforward to provide an explanation of the role of attention in MIB by drawing on the analogy with binocular rivalry. We can say that there is competition between the target dot(s) and the moving array. But MIB does not involve perceptual alternation between the target(s) and the moving array; rather, the moving array always remains visible.

7.2 Depth Ordering

Bonneh and colleagues (2001) found the most MIB when the moving array of dots appeared as a rotating 3-D sphere. But many studies use an MIB display with a

2-D grid of blue crosses rotating around fixation and this is effective in producing target disappearances.

Graf, Adams and Lages (2002) presented such a display stereoscopically and varied binocular disparity to investigate the role in MIB of the depth ordering between the 2-D rotating grid and three yellow target dots. The clear finding was that there was more MIB when the rotating grid appeared in front of the target dots than when the grid and the targets appeared in the same depth plane; and there was more MIB in this second condition than when the grid appeared behind the targets. Graf and colleagues suggested that, although the moving blue crosses never physically occluded the yellow target dots, the grid of crosses may have been processed by the visual system as a completed surface which, if in front of the target dots, and if opaque, would have occluded the dots. In short, 'dot disappearance was modulated according to simple occlusion principles' (Graf *et al.*, 2002, p. 2733).

Thus, it is plausible that the depth ordering of the moving array (perceived as a dynamic moving surface) and the targets is a factor in MIB. It is also important to note, however, that substantial levels of MIB are still experienced when targets and moving array are in the same depth plane (as in the vast majority of MIB studies).

7.3 Cue-invariance and Convexity

There are many different visual depth cues and the question arises whether the depth effect for MIB is cue-dependent or cue-invariant. Is the effect specific to depth-from-disparity cues or does it extend to monocular depth cues, for example?

The aims of Rosenthal and colleagues' study (Rosenthal, Davies, Aimola Davies and Humphreys, 2013) were (i) to use monocular structure-from-motion cues (Andersen and Bradley, 1998), rather than binocular disparity; (ii) to use an undulating surface, convex or protruding in some regions and concave or receding in others, rather than a planar surface; and (iii) to match the local features of the moving array across the convex and concave regions. To achieve their aims, Rosenthal and colleagues used an array of moving blue dots (see Figure 1) that appeared (because of structure-from-motion cues) as a rotating tilted hourglass (with open ends; like two goblet bowls joined at the base). The viewer could see only the outside of one bowl (convex region; bottom right in Figure 1) but could see into the other bowl (concave region; top left in Figure 1). The convex region could be in the left or in the right visual field. Two stationary yellow target dots were presented, one in the convex region and the other in the concave region. Target dots were never actually occluded by the blue dots in the moving array and the local features of the moving array around the targets were equated between the convex and concave regions.

On each trial, subjects were instructed to maintain fixation on a small central red square, while attending to the two target dots, and to report the disappearance of one or both of the targets. The measure of MIB was the average number of single-target disappearances reported in each 90-second trial.

The key finding was that there were significantly more disappearances for the target in the convex (protruding) region than for the target in the concave (receding)

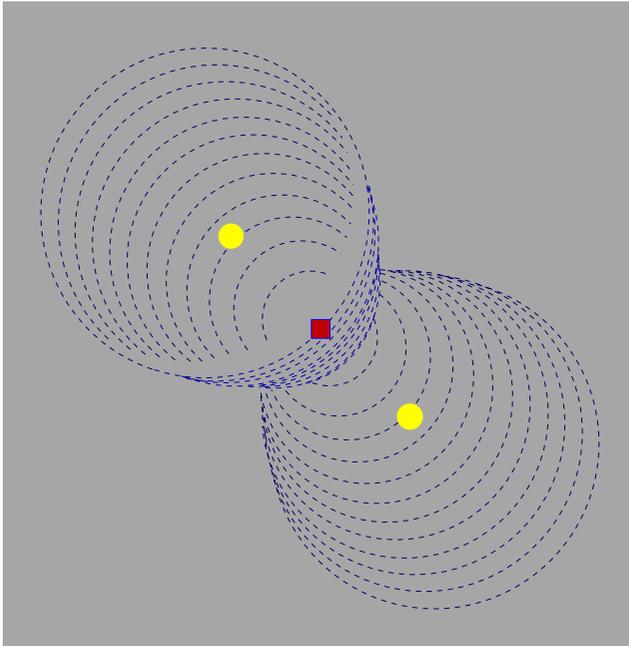


Figure 1 Snapshot of the MIB display used by Rosenthal *et al.* (2013). In the actual display, the background was black, the central fixation square was red, the moving array of dots was blue, and the stationary target dots were yellow. [Colour figure can be viewed at wileyonlinelibrary.com].

region. This clear effect of convexity *versus* concavity on MIB in a study using structure-from-motion cues, rather than binocular disparity, suggests that the depth effect for MIB may be cue-invariant. That is, MIB may be modulated by whether the surface implied by the moving array appears to protrude in front of the target, independently of the cues that determine this appearance of protrusion.

In addition to the convexity effect, there was an effect of visual field, with more target disappearances in the left visual field than in the right, and the convexity effect was significant in the left visual field but not in the right visual field (Rosenthal *et al.*, 2013, p. 1356, Figure 1). Other studies have found similar visual-field differences in MIB (Bonneh *et al.*, 2001). The finding of more MIB in the left visual field might be explained by a leftward bias of attention – because attention makes target disappearance more likely. The leftward bias of attention might be explained, in turn, by the task requirement for global processing of the moving array in the MIB display and consequent right-hemisphere activation – because hemispheric activation biases attention toward the opposite side, and global, rather than local, processing is associated with the right hemisphere (Yovel, Yovel and Levy, 2001).

Finally, Rosenthal and colleagues (2013, p. 1358) proposed that the distribution of attention might play a larger role in the explanation of their results. If protruding surfaces are more salient than receding surfaces (Hoffman and Singh, 1997) then the

distribution of attention – and, consequently, of MIB disappearances – should be biased in favour of the convex region, at the expense of the concave region. Thus, the convexity effect might be mediated by the direction of attention to the convex region (or the withdrawal of attention from the concave region). In its boldest form, the proposal would be that the convexity effect is explained by attention to the protruding surface, independently of the depth ordering between the surface and the target dot.

7.4 The Drive to Consistency

Humphreys approached MIB with the idea that there was a perceptual ‘drive to consistency’ that led to the selection of one interpretation from two or more mutually inconsistent interpretations of perceptual input – or equivalently, confirmation of one from a range of competing perceptual hypotheses.⁶ In some cases, such as ambiguous figures (e.g. the Necker cube), no interpretation would be uniquely adequate to the perceptual input, and vision would alternate – with one interpretation being selected while the other was suppressed. This idea of a perceptual drive to consistency, leading to alternating resolutions of ambiguity, applied naturally to binocular rivalry. The aim was to apply it to MIB as well. There are three issues to consider.

First, if the perceptual drive to consistency is to result in perceptual alternation then there should be some locus of perceptual ambiguity in MIB. This may seem unpromising because, in a typical MIB display with a rotating 2-D grid of crosses, there is no obvious ambiguity in the presentation of the moving array and the target dots. Nevertheless, Humphreys suggested that, at the level of information processing in the visual system, there is ambiguity as to the depth of the yellow target dots relative to the surface constituted by the moving blue crosses or dots – perhaps resulting from inconsistency between different depth cues. Depth-cue manipulations (Graf *et al.*, 2002; Rosenthal *et al.*, 2013) would then shift the balance between competing interpretations of, or hypotheses about, the depth ordering. If that were correct then the first role of an attention-dependent process of interpretation selection would be to resolve those ambiguities – perhaps alternating between mutually inconsistent resolutions. There may be additional ambiguity as to whether the surface is completed and, if so, whether it is opaque. We shall assume, for simplicity, that the surface is processed as completed and opaque.

Second, it is not straightforward to apply the analogy with binocular rivalry because the perceptual alternation in MIB is not between the moving array and the target dots. If there is competition, it is uneven. Here, to simplify further, we leave aside the possibility that the blue opaque surface and the yellow dots are at exactly

⁶ In this section, I draw on a grant application written in August 2010 and on a presentation that Humphreys gave at a *Mind & Language* workshop on Neuroscience, Psychology and Philosophy, held at Birkbeck College on 10 October 2011. The account of MIB disappearance briefly sketched here departs from the boldest form of Rosenthal and colleagues’ (2013) proposal.

the same visual depth, and consider the other two depth-ordering interpretations. If the yellow dots are in front of the blue opaque surface then both can be part of the visual scene, but if the opaque surface is in front of the yellow dots then the dots are occluded. Thus, given the assumption of opacity, resolution of the ambiguity of depth ordering determines the outcome of the uneven competition between the moving array and the target dots.

The third issue concerns the content of the visual system's competing hypotheses. When the surface and dots are both visible, the visual system's hypothesis about the distal scene can be, simply, that there are yellow dots in front of an opaque blue surface. When the dots are occluded, it is not so plausible that the visual system's hypothesis can be along the lines that there is an opaque blue surface occluding yellow dots. There is nothing internally inconsistent about the hypothesis that objects are wholly occluded, but it is not obvious that it is an admissible hypothesis for a visual system (although the visual system does represent partially occluded objects). The visual system's hypothesis about the distal scene would, instead, be that there is an opaque blue surface – and that is all.

It may be that the visual system also constructs hypotheses that are not exclusively about the distal scene. Perhaps it constructs hypotheses about aspects of the incoming signal that cannot be coherently explained in terms of the distal scene (e.g. a signal apparently originating from a location that is wholly occluded), attributing them instead to damage to the visual system itself. New and Scholl (2008) suggested that 'the visual system may discount that stimulus as akin to a scotoma, and may thus expunge it from awareness' (2008, p. 655). This interpretation, too, would reflect the visual system's drive to consistency – as would the system's abandoning the hypothesis when an eye movement revealed that the supposed scotoma did not move with the retina.

In Humphreys' approach, the drive to consistency (and interpretation selection, ambiguity resolution, or hypothesis confirmation) was linked, not only with MIB, but also with the attention-dependent consolidation process in his two-stage account of feature binding (Braet and Humphreys, 2009; Gillebert and Humphreys, 2010). If this putative connection between MIB and feature binding could be substantiated then it would provide a potential route for converging evidence. The role of attention in MIB might cast some light on the cognitive role of the attention-dependent late stage of feature binding (or *vice versa*).

For example, if the role of attention in MIB is to resolve ambiguity in depth ordering (perhaps alternating between interpretations) then the cognitive role of the second-stage re-entrant process in feature binding might also be something like that – resolving ambiguity or inconsistency by selecting between competing interpretations or perceptual hypotheses.⁷ Unbound visual features or unstable

⁷ In later work, Humphreys (2016b, p. 1924) described the second stage of feature binding as a process of 'attentional confirmation' in which 'hypotheses suggested by the initial stage are confirmed through top-down feedback'.

bindings do present the visual system with a kind of ambiguity and sometimes the ambiguity is evident in perceptual experience – as when seeing, but not attending to, a crowded array of coloured plus signs (Wolfe, 2012; see above, Section 2.1). Attention is required if the correct selection is to be made between possible resolutions of the ambiguity.

Perhaps, Humphreys suggested, the cognitive role of the attention-dependent, re-entrant stage of feature binding is to resolve ambiguity or inconsistency. Equivalently, perhaps the re-entrant process is constrained to generate a single consistent interpretation of the perceptual input. When no single interpretation is adequate to the input, such a process may result in perceptual alternation, as in MIB.

8. Conclusion

Neuropsychological case studies played a major role in Glyn Humphreys' research and this was certainly evident in the work that we have reviewed here. Beginning from Treisman's FIT, Humphreys employed a more inclusive notion of binding and then argued, on empirical grounds, for a primary division between form binding and feature binding. Patients with posterior parietal lesions had a specific difficulty in binding visual features presented on the contralesional side but did not have a similar difficulty in binding form elements – thus, binding fractionated. Importantly, the vulnerability of the different visual searches to parietal damage was not predicted by the degree of inefficiency of the searches for neurologically healthy subjects. Patient studies in which visuospatial extinction was reduced provided further evidence that the attentional demands of form binding were low.

Humphreys showed that even the attentional requirements of feature binding could sometimes be reduced and he argued for a secondary division between early and late stages of feature binding. He also argued for a secondary division within form binding, between binding oriented elements into contours and binding contours into shapes of whole objects (Humphreys, 2001). Patient HJA was severely impaired in the second kind of form binding and suffered from integrative visual agnosia (Riddoch and Humphreys, 1987) but the first kind of form binding remained intact (Giersch, Humphreys, Boucart and Kovács, 2000). Once again, binding fractionated.

Form binding, and even the early stage of feature binding, make only modest demands on attention, but the second or late stage of feature binding is attention-dependent. It was important to know the neurocomputational nature, and the cognitive role, of this second-stage feature binding process. Humphreys provided evidence that the process was re-entrant – and there was converging evidence from Bouvier and Treisman (2010). As for the cognitive role of this attention-dependent, re-entrant stage of feature binding, Humphreys suggested that it was to resolve ambiguity or inconsistency. This attention-dependent feature binding is not a prerequisite for consciousness; rather, conscious experience extends to unattended and unresolved ambiguity and even inconsistency. But it does seem

plausible that re-entrant feature binding – constrained by a perceptual drive to consistency – is a function of consciousness, to the extent that it normally involves the conscious direction of spatially selective attention.

Humphreys' research on attention and binding, selectively reviewed here, is substantial, theoretically deep, illuminating, and of evident interdisciplinary interest. It is also just part of a much larger and more widely ranging body of work – as is perhaps indicated by the fact that the articles by Humphreys referenced here amount to less than five per cent of his publications. His achievements are truly monumental.

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