Mutual interplay between perceptual organization and attention: a neuropsychological perspective

Céline R. Gillebert and Glyn W. Humphreys
Department of Experimental Psychology, University of Oxford, United Kingdom

To appear in:
Oxford Handbook of Perceptual Organization
Oxford University Press
Edited by Johan Wagemans

Acknowledgements

We would like to thank Lee de-Wit and one anonymous reviewer for their valuable feedback on this chapter. Preparation of this work was supported by an ERC Advanced Investigator Award to GWH and a Sir Henry Welcome Fellowship to CRG.

1. Introduction

The visual system possesses the remarkable ability to rapidly group elements in a complex visual environment based on a range of factors first elucidated by the Gestalt psychologists, including proximity, similarity and common fate (Wertheimer, 1923). However, there is also a competition for neural representation, given constraints on neuronal tuning and the presence of large receptive fields at higher levels of visual association cortex (Desimone & Duncan, 1995). To deal with the complexity that exists in the environment, there need to be processes which prioritize the information that is most relevant to on-going behaviour. Representing the world efficiently requires both the selection of a fraction of the information that reaches our senses and the organization of this information into coherent and meaningful elements.

In this chapter, we discuss the dynamic interplay between (on the one hand) visual, selective attention and (on the other) perceptual organization, two important processes that allow us to perceive a seamless, integrated world. In describing this interplay, we will draw on evidence from neuropsychology, which provides striking examples where (i) perceptual organization appears to operate despite a patient having a very poor ability to select visual information, and (ii) spatial attention appears to operate even when perceptual organization is impaired. At least at first sight, such evidence provides one of the strongest examples of perceptual organization being independent of visual attention. Whether this is a robust conclusion will be something we will review. In this chapter, we will predominantly focus on perceptual grouping.

1.1. A neuropsychological example of the interplay of attention and perceptual organization

As we shall review, neuropsychology provides many striking examples of the interplay between attention and perceptual organization. A case described by Alexander Luria in 1959 provides a good illustration. Luria reported a patient with simultanagnosia after bilateral occipitoparietal brain injury – a major impairment in 'seeing' more than one object at a time.

The patient was shown two versions of the Star of David, formed by two overlapping triangles. When the triangles differed in colour, the patient only reported a single triangle. However, when triangles were the same colour, the patient immediately perceived the complete star. Similarly, when two separate shapes were briefly exposed, only one was seen at a time. Nevertheless, when the shapes were identical, or combined into a single structure through a connecting line, their perception was facilitated (Luria, 1959). This case study demonstrates how perceptual organization (notably grouping by similarity or connectedness) can determine where attention is allocated and which objects are accessible for explicit report.

The mutual interplay between perceptual grouping and attention can be assessed through different lenses, answering at least three distinct but related questions:

- Can perceptual grouping constrain visual attention, determining which objects will be selected and be candidates for explicit report?
- Can perceptual grouping occur even without (focused) attention, or does perceptual grouping fully depend on the availability of attentive resources?
- Can visual attention modulate perceptual grouping, determining how elements are grouped to form meaningful wholes?

Note that evidence that perceptual grouping constrains attention, and that grouping can operate without focused attention, can be taken to indicate that attention has no influence on grouping. However this would be an incorrect inference, since evidence for grouping without attention does not necessarily indicate that attention does not modulate grouping under appropriate conditions. This is the conclusion we will come to.

In the next paragraphs, we will first define the concept of “visual attention”, distinguish it from the concept of “awareness”, and describe the most common attentional neuropsychological deficits after stroke. We will then tackle each of our questions, drawing on evidence from neuropsychological studies in patients with attention deficits, along with evidence from behavioural and neuroimaging studies in healthy volunteers. We will then outline a framework for the dynamic modulation of perceptual grouping by attention. In particular, we will argue that perceptual grouping is weakly constrained by visual attention, but that attention nevertheless can play a role in dynamically altering the ‘weighting’ of elements in any organized structure, especially under conditions in which stored knowledge and learning cannot play a major role.

2. Visual attention

2.1. Assigning attentional priorities

Visual attention can be defined as the set of cognitive functions that prioritize visual information according to our current task goals and expectations. Many models of selective attention posit that processing resources are allocated to perceptual units on the basis of the dynamically evolving peak of activity in an “attentional priority map” (e.g., Bays, Singh-Curry, Gorgoraptis, Driver, & Husain, 2010; Bisley & Goldberg, 2010; Bundesen, 1990; Gillebert et al., 2012; Ipata, Gee, Bisley, & Goldberg, 2009; Mavritsaki, Heinke, Allen, Deco, & Humphreys, 2011; Ptak, 2012; Vandenberghe & Gillebert, 2009; Vandenberghe, Molenberghs, & Gillebert, 2012). The attentional priority map provides an abstract, topographical representation of the environment in which each object (or location) is ‘weighted’ by its sensory characteristics and its current behavioural relevance. At any given moment in time, attention is directed towards the object (or location) with the highest priority (e.g., Koch & Ullman, 1985; Treisman, 1998). These models are strongly based on the concept of a salience map. The concept of a saliency map was proposed by Itti and Koch (Itti & Koch, 2000; Koch & Ullman, 1985) to refer to a map which encodes the local conspicuity (physical ‘saliency’) in the visual scene. The term priority map however goes beyond this to posit the joint influence of bottom-up and top-down factors, such as behavioural goals and expectations (Bisley & Goldberg, 2010; Ptak, 2012; Vandenberghe & Gillebert, 2009). The attentional priority map is a key concept in the Theory of Visual Attention (TVA) (Bundesen, 1990; Bundesen, Habekost, & Kyllingsbæk, 2005, 2011), a mathematical framework related to the biased competition account (Desimone & Duncan, 1995), which we will return to discuss in detail. Evidence from single-unit studies, functional neuroimaging, and lesion-symptom mapping in patients with brain damage suggests that attentional priorities are encoded in a network of frontoparietal areas – the so-called dorsal attention network – which includes the intraparietal sulcus and the frontal eye fields (Bisley & Goldberg, 2010; Corbetta & Shulman, 2002; Gillebert et al., 2012; Gillebert et al., 2011; Ptak, 2012; Vandenberghe & Gillebert, 2009).

2.2. Attention and awareness

If not identical, attention and awareness are often considered to be two sides of the same coin (e.g., Posner, 1994). The implicit assumption behind this posits that attending an object is necessary and sufficient for awareness of the object. However, ample evidence has been provided that attention and conscious awareness can be dissociated, both at a cognitive level and a neural level (Kentridge, 2011; Koch & Tsuchiya, 2007; Wyart & Tallon-Baudry, 2008). In particular, attention is not sufficient to give rise to awareness (see also Chapter 50 by Schwarzkopf and Rees). For example, spatial attention can facilitate the processing of stimuli which do not reach awareness in patients with blindsight (Kentridge, Heywood, & Weiskrantz, 1999). It remains debated, however, whether or not conscious awareness can occur in the absence of attention (Prinz, 2011).

2.3. Neuropsychological deficits of visual attention

Impairments in visual attention are a frequent consequence of brain lesion, with the incidence of problems being particularly high after right hemisphere brain damage (Stone, Halligan, & Greenwood, 1993). Patients with attention deficits may fail to be aware of items in the side of space opposite the lesion (*hemispatial neglect*), show impaired report of an item on the contralesional side of space only when simultaneously presented with an ipsilesional item (*visual extinction*), or they may be poor at detecting multiple visual items, regardless of where the stimuli appear in space (*simultanagnosia*).

Patients with *hemispatial neglect* are typically unaware of stimuli presented on the side of space contralateral to the brain damage, even in the absence of sensory or motor loss. In its most extreme form, these patients may act as if the contralesional side of the world does not exist. A spontaneous and sustained deviation of the eyes and head towards the ipsilesional side of space may form the core deficit underlying the neglect syndrome, although patients with neglect often exhibit a variety of other attentional and spatial deficits (Karnath & Rorden, 2012). Neglect should therefore be considered a heterogeneous disorder which affects attentional, intentional and representational processes to different degree, depending the extent of the damage onto parietal (Golay, Schnider, & Ptak, 2008), temporal (Hillis et al., 2005; Ptak & Schnider, 2005) or prefrontal cortex (Husain & Kennard, 1997; Verdon, Schwartz, Lovblad, Hauert, & Vuilleumier, 2010). However, the core deficit of the neglect syndrome, i.e. biased orienting of attention, has been suggested to be specifically induced by structural or functional damage to a set of regions surrounding the sylvian fissure, including the inferior parietal lobule, the superior/middle temporal cortex and underlying insula, and the ventrolateral prefrontal cortex (Karnath & Rorden, 2012). Hemispatial neglect differs from sensory syndromes, such as hemianopia, in being modulated by contextual variables, such as motivation (Malhotra, Soto, Li, & Russell, 2013), experience (Rossetti et al., 1998), expectancy (Geng & Behrmann, 2006; Riddoch & Humphreys, 1983), task demands (Vuilleumier & Rafal, 2000), novelty (Karnath, 1994), and the organization of the visual input itself (Driver & Halligan, 1991). The syndrome is diagnosed on the basis of a set of conventional neuropsychological tests (Heilman, Watson, & Valenstein, 1993; Humphreys, Bickerton, Samson, & Riddoch, 2012; Mesulam, 2000; Vallar & Perani, 1986), such as cancellation, line bisection, and copying.

Visual extinction differs from hemispatial neglect as it is usually only detected with brief presentations of at least two competing stimuli (Heilman et al., 1993). Patients with visual extinction fail to detect a contralesional stimulus only when it is presented together with a competing ipsilesional stimulus. In the conventional clinical task for extinction in the visual domain, the patient is presented with either a visibly wiggling finger on the left or the right side, or with two wiggling fingers concurrently on both sides (Bender, 1952; Humphreys et al., 2012). Patients with visual extinction can detect a single stimulus on either side, but are impaired at detecting the contralesional stimulus when two stimuli are presented simultaneously on opposite sides. Visual extinction, primarily associated with damage to the right temporoparietal junction (e.g., Chechlacz et al., 2013; Ticini, de Haan, Klose, Nagele, & Karnath, 2010; Vossel et al., 2011), has typically been attributed to the brain lesion biasing attentional selection, so that less attentional weight is allocated to the contra- relative to the ipsilesional side of space. The weight assigned to the contralesional side can be sufficient for a single contralesional item to be detected, but this item then loses any competition for selection when a competing stimulus appears simultaneously on the ipsilesional side (Duncan, Humphreys, & Ward, 1997).

Patients with simultanagnosia, typically induced by bilateral lesions of the occipito-parietal cortex and underlying white matter (Chechlacz et al., 2012), show impaired report of two stimuli relative to one, are poor at integrating multiple objects in a scene, and at integrating local elements into a coherent object (Bálint, 1909; Rizzo & Vecera, 2002). In other words, simultagnosic patients are biased towards selecting the local shape representations (unless counteracted by grouping between local elements) rather than more global stimuli (Shalev, Humphreys, & Mevorach, 2004).

These deficits of visual attention may be a consequence of damage to or dysfunction of the attentional priority map (Ptak & Fellrath, 2013). For example, patients with hemispatial neglect may fail to assign attentional priorities to events in the contralesional side of space – resulting in a competitive advantage for ipsilesional events to be candidates for attentional orienting. In particular, visual attention deficits in patients with hemispatial neglect may be driven by impairment in integrating bottom-up and top-down factors to compute attentional priorities (Dombrowe, Donk, Wright, Olivers, & Humphreys, 2012; Ptak & Fellrath, 2013).

3. Perceptual grouping influences the assignment of attentional priorities

In this section, we will argue that perceptual grouping can influence attentional priorities and can therefore determine which elements in the visual field are selected. In particular, we will demonstrate that items that belong together are selected together, even if one of the items is irrelevant for the current task goal or if it has a competitive disadvantage in patients with visual attention deficits.

3.1. Evidence from patients with attention deficits

Perceptual grouping based on both low-level and high-level factors can result in recovery from extinction, attenuation of neglect and the ability to see more than one item in simultanagnosia.

3.1.1. Low-level grouping

Recovery of extinction can be obtained when the contralesional item groups with the ipsilesional item on the basis of the Gestalt principles of similarity (Berti et al., 1992; Ptak, Valenza, & Schnider, 2002; Ward, Goodrich, & Driver, 1994) (but see Baylis, Driver, & Rafal, 1993; Vuilleumier & Rafal, 1999, 2000), proximity (Pavlovskaya, Soroker, & Bonneh, 2007), symmetry (Ward et al., 1994), connectedness (Driver, Mattingley, Rorden, & Davis, 1997; Humphreys, 1998), brightness (Gilchrist, Humphreys, & Riddoch, 1996), collinearity (Boutsen & Humphreys, 2000; Gilchrist et al., 1996; Mattingley, Davis, & Driver, 1997; Pavlovskaya et al., 2007), common shape (Gilchrist et al., 1996; Humphreys, 1998; Ptak & Schnider, 2005) and common contrast polarity (Gilchrist et al., 1996; Humphreys, 1998).

Mattingley, Davis and Driver (1997), for example, presented a patient with left-sided extinction with a sequence of displays, consisting of four circles arranged to form a square (Figure 1A). On each trial, quarter-segments were briefly removed from the circles either from the left, from the right, from both sides, or not at all. The patient's task was to detect the side of the offsets. When the segments were configured such that no grouping emerged, bilateral removal of quarter-segments induced extinction: the patient made more errors for offset detections on the left side which were presented together with right-sided offsets, when compared with unilateral left presentations. Extinction, however, was less severe when the stimulus configuration could be grouped to form a Kanizsa square (see also Conci et al., 2009).

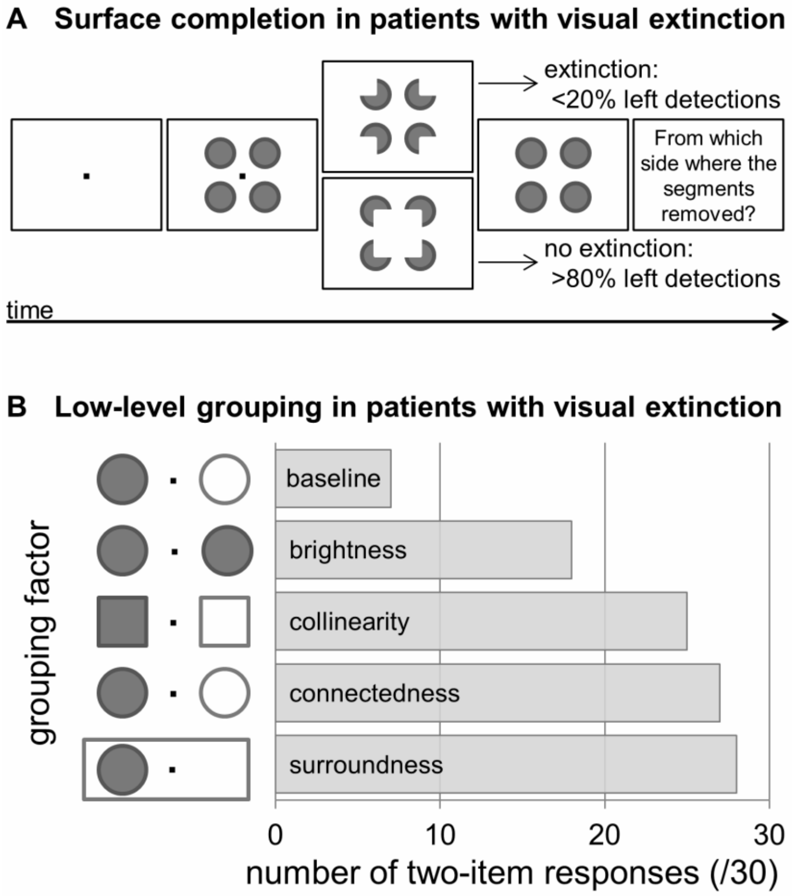

Figure 1. Perceptual grouping and recovery from extinction. (A) Example of a task requiring discrimination between displays where segments were briefly removed from circles on the left, right, both sides or on neither side. On bilateral trials, when segments were removed on the outer side of the circle, extinction occurred. When segments were removed on the inner side of the circle, inducing a Kanizsa figure, no extinction was observed. Adapted from Mattingley et al. (1997). (B) Results on a detection task from two-item displays as a function of the grouping among the contra- and ipsilesional item. The task required the discrimination between displays with no, one, or two items. Adapted from Humphreys (1998).

Several of these factors were investigated in GK, a patient who suffered bilateral lesions of the occipito-parietal and parieto-temporal region, resulting in Bálint's syndrome and in extinction of left-sided targets. Humphreys and colleagues (Gilchrist et al., 1996; Humphreys, 1998) presented GK either with a single stimulus in the left or right visual field, or with two stimuli, one in the left and one in the right visual field. GK showed recovery from extinction if the elements had: the same brightness (two white or two black circles), collinear edges (with aligned squares), a connecting line (joining circles with opposite contrast polarities), and inside-outside relations (e.g., a left-field circle appearing within a surrounding rectangle) (Figure 1B). Grouping not only operated between items presented in the impaired and his 'better' visual field, but also when both items were presented within the impaired visual field.

These data suggest that patients with visual attention deficits can explicitly report the contralesional stimulus if perceptual grouping allows it to be processed together with the ipsilesional stimulus. The benefit of perceptual grouping may result from attentional priorities being assigned to the perceptual group as a whole, rather than to the items constituting the group, therefore facilitating the selection of individual items within the group. In other words, the ability to compute attentional priority for one item in the display (e.g., the ipsilesional item in extinction) may spread this attentional priority to the item with which it is grouped.

3.1.2. High-level grouping

As well as there being evidence for low-level grouping in neglect and extinction, there is also evidence for grouping based on higher-level perceptual properties of stimuli, where access to stored knowledge is required.

Hemispatial neglect is attenuated for familiar words or compound word pairs compared to meaningless strings or unrelated word pairs (Behrmann, Moscovitch, Black, & Mozer, 1990; Braet & Humphreys, 2006; Brunn & Farah, 1991; Riddoch, Humphreys, Cleton, & Fery, 1990; Sieroff, Pollatsek, & Posner, 1988), or when two visual elements form a meaningful whole (Seron, Coyette, & Bruyer, 1989). Also extinction is reduced if elements are both part of a known shape or a familiar configuration (Kumada & Humphreys, 2001; Vuilleumier, 2000; Vuilleumier & Sagiv, 2001; Vuilleumier, Sagiv, et al., 2001; Ward et al., 1994), or if there are associative relations between separate words (Coslett & Saffran, 1991). For example, Ward et al. (1994) found recovery from extinction when two symbolic stimuli formed a familiar configuration (e.g., an arrow <-) relative to an unfamiliar configuration (e.g., V-). Similarly, patients with extinction are better at identifying left-sided letters in words than in non-words (Kumada & Humphreys, 2001). Interestingly, Kumada and Humphreys reported by word-level grouping between letters over-rode effects of whether the letters failed to group using low-level similarity relations. These authors reported that having two letters with opposite contrast polarities (one white, one black, against a grey background) disrupted report when the letters formed a nonword, but there was recovery of the contralesional letter irrespective of the contrast polarity when the letters formed a word.

Hence, when participants are presented with pairs of objects that do not group on the basis of low-level Gestalt factors, extinction can still be modulated by the relationship between the stimuli. This argument is also supported by evidence that visual extinction is reduced when there is an action relation between the contra- and ipsilesional objects. When stimuli are positioned where they appear to be engaged in a common action (e.g., a bottle pouring into a glass), patients show less extinction than when the objects are depicted in locations where they could not be used together (e.g., bottle pouring underneath a glass; Riddoch, Bodley Scott, & Humphreys, 2010; Riddoch et al., 2006; Riddoch, Humphreys, Edwards, Baker, & Willson, 2002). Several factors appear to contribute to this result. The effect is stronger when objects are used frequently together, and are correctly positioned for the action (Riddoch et al., 2006), but it is also eliminated if the objects are inverted (Riddoch et al., 2011). Such results suggest that the familiarity of the action as it is standardly seen (with objects in their usual orientation for the interaction) is important for grouping the objects for selection. Riddoch et al. (2010) additionally suggest that it is the implied motion from one object to another which links the objects together so they are encoded as a single perceptual unit.

3.1.3. When perceptual grouping is disruptive for patients with attention deficits

Whereas grouping has a beneficial effect on the report of contralesional items in patients when there is a meaningful relationship between the contra- and ipsilesional items, it may negatively affect the ability to name the left-side item in some cases. For example, within the syndrome of neglect it is possible to distinguish between patients who show a deficit to stimuli on one side of space in relation to the body, and patients whose deficits reflect the position of parts within an object (so-called egocentric versus allocentric neglect; see Chechlacz et al., 2010; Humphreys & Riddoch, 1994; Verdon et al., 2010). Positive effects of grouping on the perceptual report of neglected stimuli may be evident in egocentric neglect, where the coding of elements within a group reduces the egocentric attentional bias. However, grouping may be disruptive for patients with allocentric neglect (Buxbaum & Coslett, 1994; Humphreys & Heinke, 1998; Tian et al., 2011; Young, Hellawell, & Welch, 1992). For example, Young et al. (1992) reported the case of a patient able to report two images of the left half of different faces but who showed a lack of awareness for the left half of a chimeric face formed by linking the left and right sides of two faces. In this case, grouping the left and right sides of a face induced neglect, presumably because there was biased allocation of attention to an object-based representation of the stimulus. In some models (e.g., Heinke & Humphreys, 2003), the setting of attentional weights within an object-centred representation can be separated from setting attentional weights within a spatial priority map for separate objects. The reference frame is indeed important when making predictions about the effect of grouping in patients with spatial attention disorders (Behrmann & Tipper, 1994; Tipper & Behrmann, 1996). Behrmann and Tipper presented neglect patients with two circles to the left and the right of the midline, one coloured red and the other blue. When grouping the circles by a connected line induced an object-centred reference frame, and the object rotated such by 180 degrees, patients ignored the ipsilesional item (contralesional side of the object) and reported the contralesional item (ipsilesional side of the object).

The distinction between egocentric and allocentric neglect also links onto the presence of respectively more anterior and posterior brain lesions, and more dorsal versus ventral lesions within posterior parietal cortex (Chechlacz et al., 2010; Verdon et al., 2010). Beneficial effects of grouping may reflect spared ventral coding within patients with egocentric neglect in patients with more dorsal lesions, while more ventral lesions may impact on spatial coding within allocentric representations.

3.1.4. Neural basis

At which level of representation does perceptual organisation influence the distribution of attentional weights? The evidence cited above clearly demonstrated that perceptual grouping can influence the distribution of attentional weights, despite structural or functional damage to the dorsal attention network. In contrast, lesions of the ventral visual stream, such as the lateral occipital complex, are associated with agnosia, an impaired object recognition that cannot be attributed to visual loss (see Chapter 28 by Behrmann and colleagues for a discussion of prosopagnosia, an impairment of face recognition). In the case of apperceptive agnosia, the percept of the object is not fully constructed – hence these patients may have deficits in perceptual grouping. Double dissociations can indeed be found. In contrast to neglect (Schindler et al., 2009), patients with agnosia can normally orient their attention to the contralesional visual field, but their allocation of attention is not influenced by objects (de-Wit, Kentridge, & Milner, 2009; Vecera & Behrmann, 1997). We conclude that perceptual organization can influence the distribution of attentional weights through representation in the ventral visual stream rather than in the parietal cortex. Nevertheless, the setting of spatial attentional weights can be dissociated from such ventral input, in cases of agnosia (de-Wit et al., 2009; Vecera & Behrmann, 1997)

3.2. Evidence from healthy volunteers

Reminiscent of the beneficial effects of grouping in neuropsychological cases, responses from normal participants to multiple targets are facilitated when the targets groups on the basis of Gestalt cues (Behrmann, Zemel, & Mozer, 1998; Duncan, 1984; Lavie & Driver, 1996; Vecera & Farah, 1994), or when the objects are positioned for action (Roberts & Humphreys, 2011). In selective attention tasks, however, the grouping of targets and distractors can disrupt performance. For example, target-distracter grouping by low-level factors such as colour similarity, connectedness, common motion, continuation (Baylis & Driver, 1992; Driver & Baylis, 1989; Harms & Bundesen, 1983; Kahneman & Henik, 1981; Kramer & Jacobson, 1991), or high-level factors such as familiarity (Green & Hummel, 2006), increases the level of interference by the distracter. Similarly, the ability to keep track of independently moving targets in multiple-object tracking tasks (Pylyshyn & Storm, 1988) is impaired when the targets are merged to form objects with distracters, for example by connectedness (Howe, Incledon, & Little, 2012; Scholl, Pylyshyn, & Feldman, 2001).

Egly, Driver and Rafal (1994) provided further evidence suggesting that attention is allocated to perceptual groups. In their study, participants were presented with two rectangles. Attention was briefly cued to one end of one of the rectangles, and participants were asked to detect a target presented either on a validly or on an invalidly cued location. On invalid trials, reaction times were faster when the target appeared within the same rectangle that was cued than when it appeared at an equal distance from the cue but in a different rectangle. Here a spread of attention within an object can facilitate selection. The results also apply to objects that require perceptual completion due to occlusion and objects formed from subjective contours (Moore, Yantis, & Vaughan, 1998) or contour alignment (Norman, Heywood, & Kentridge, 2013). Interestingly, relevant to our understanding the relations between attention and awareness, the same-object advantage occurs even when participants are unaware of these objects (Norman et al., 2013). In the study by Norman and colleagues (2013), the objects were rendered invisible to the participants: Texture elements in the objects had an orientation contrast of 90 degrees to the elements in the background. When the texture elements both inside and outside of the object boundaries are continually reversed at a high frequency, participants are unaware of the objects. Despite being unaware of the objects, participants were faster in discriminating the target's colour when the cue and the target appeared within the same object relative to when they appeared in different objects. Hence, similarly to the neuropsychological evidence, the data suggest that perceptual grouping can operate without attention and awareness.

Converging evidence for an enhanced processing of unattended stimuli which group with attended stimuli comes from fMRI and event-related brain potentials (ERPs) studies: relevant and irrelevant elements which group through an illusory contour elicit a very similar response pattern in visual cortex (Martinez, Teder-Salejarvi, & Hillyard, 2007; Martinez et al., 2006) and there is neural activation of unattended items if they share a featural property with an attended item (Saenz, Buracas, & Boynton, 2002).

These studies suggested that attention has a tendency to spread throughout perceptual group (Richard, Lee, & Vecera, 2008). In other words, attending to one element of a perceptual group can cause attention to spread to other elements of the same perceptual group, and therefore enhancing the sensory representation of these elements. Inversely, grouping between distracter elements can facilitate visual search because distracters can be rejected together - a process termed spreading suppression (e.g., Dent, Humphreys, & Braithwaite, 2011; Donnelly, Humphreys, & Riddoch, 1991; Duncan & Humphreys, 1989; Gilchrist, Humphreys, Riddoch, & Neumann, 1997; Humphreys, Quinlan, & Riddoch, 1989). Hence, the outcome of perceptual grouping constrains visual attention.

Not only can attention spread throughout a perceptual group, a good perceptual group can in itself capture attention (Humphreys & Riddoch, 2003; Humphreys, Romani, Olson, Riddoch, & Duncan, 1994; Kimchi, Yeshurun, & Cohen-Savransky, 2007; Yeshurun, Kimchi, Sha'shoua, & Carmel, 2009). Kimchi and colleagues (2007) presented participants with displays containing eight distracters and a target defined from its location relative to a cue. On some trials, a subset of the elements grouped to form a diamond based on the Gestalt principle of collinearity. Compared to the condition when no perceptual group was present in the display, reaction times to the target were shorter when the cue appeared within the perceptual group and longer when the cue occurred outside the perceptual group (Kimchi et al., 2007). Similarly, given two stimuli, simultagnosic patients tend to perceive the stimulus whose parts grouped more strongly (Humphreys et al., 1994), even when the strong group is less complex than the competing weak group (Humphreys & Riddoch, 2003). Furthermore, Humphreys and Riddoch (2003) showed attention is drawn to the location of the strong group, facilitating the identification of a subsequently presented letter in that location.

4. Perceptual grouping can operate without selection by attention

According to many theories of attention, fundamental visual processes, such as figure-ground segmentation and perceptual grouping, are fully pre-attentive: they occur automatically, without attention, effort or “scrutiny” (Julesz, 1981; Marr, 1982; Neisser, 1967; Treisman, 1982). This view has drawn support from behavioural experiments in normal participants, such as visual search, showing that reaction times increase as a function of the number of distracter groups rather than individual distracter elements (Treisman, 1982). An opposing account suggests that little, if any, perceptual organization can occur in the absence of attention: perceptual organization cannot proceed without attention being allocated to the location where organization is computed (Ben-Av, Sagi, & Braun, 1992), or, in other words, without the attentional priority of that location being high.

Support for the latter view can be derived from dual-task experiments, where observers are unable to explicitly report perceptual groups whilst attention is concurrently engaged in a demanding task not involving the groups (Ben-Av et al., 1992). Mack, Rock, and their colleagues (Mack, Tang, Tuma, Kahn, & Rock, 1992; Rock, Linnett, Grant, & Mack, 1992) developed the “inattention paradigm” to determine whether perceptual grouping can occur not only in the absence of attention to the constituent elements, but also when there is not even the intention to perceive the elements. Participants were presented with a task-relevant cross in the centre of the screen, along with a task-irrelevant Gestalt grouping display in the background (Figure 2A). The task was to determine whether the vertical or horizontal line of the cross was longer. The basic finding, replicated in several studies (Mack & Rock, 1998), was that the observers were unable to report anything about how the elements in the background grouped, when surprise questions were given retrospectively.

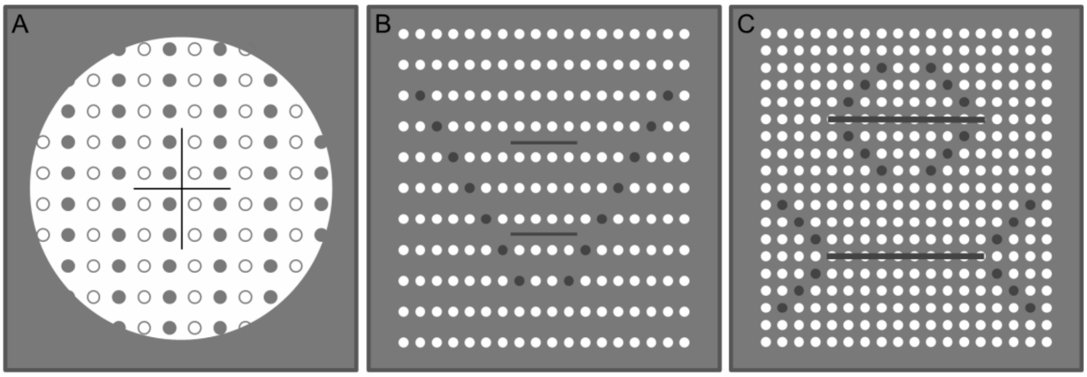

Figure 2. Perceptual grouping without awareness or attention. (A) Example of a display used in the “inattention paradigm” developed by Mack, Rock and colleagues (1992). Participants were to judge which of the two arms of the cross was longer. The elements in the background could be grouped by color similarity. Participants were asked surprise questions about the background grouping. (B-C) Example of a type of display used by Moore and Egeth (1997). Participants were to judge which of two horizontal lines was longer, while dots in the background formed displays such as in the Ponzo (B) or Müller-Lyer illusion (C). Line judgments were influenced by the illusions.

However, the inability to explicitly report grouping, i.e. not being aware of it, when attention is engaged in a concurrent demanding task does not necessarily imply that perceptual grouping in itself requires attention. In studies of patients with blindsight, and also in normal observers with stimuli presented under masking conditions, there can be enhanced perceptual processing of stimuli that the observer is unaware of, indicating that attention to the location of an object does not necessarily imply awareness of that object (Kentridge et al., 1999); awareness can be dissociated from attention. In addition, limited explicit report/awareness of a stimulus may, for example, also reflect poor encoding of the item into memory. To counteract this criticism, Moore and Egeth (1997) used an *implicit* measure to measure perceptual grouping: observers were to judge the length of line segments, presented along with background elements that were entirely task-irrelevant. The background elements were arranged so that, if perceptually grouped, they could induce optical illusions, such as the Ponzo illusion (Figure 2B) the Müller-Lyer illusion (Figure 2C). Although observers appeared unaware of the background elements when retrospectively questioned, arrangement of the elements clearly modulated line length judgments. For example, when the background pattern could induce the Ponzo illusion (Figure 2B), the line that was closer to the converging end of the background pattern was judged to be longer than the line that was further away from the converging end. This suggests that perceptual grouping can occur without attention. Several other studies in healthy volunteers and patients with hemispatial neglect support these findings (Chan & Chua, 2003; Kimchi & Razpurker-Apfeld, 2004; Lamy, Segal, & Ruderman, 2006; Russell & Driver, 2005; Shomstein, Kimchi, Hammer, & Behrmann, 2010). For example, Shomstein and colleagues (2010) investigated whether perceptual grouping in the poorly attended (contralesional) visual field of neglect patients affected performance on stimuli presented in the intact (ipsilesional) visual field. To assess this, they adapted a paradigm developed by Russell and Driver (2005): they asked patients with hemispatial neglect to perform a change detection task on complex target stimuli, successively presented to the ipsilesional hemifield (Figure 3A). At the same time, irrelevant distracter elements appeared in the contralesional hemifield, either changing or retaining their perceptual grouping on successive displays. Changes in perceptual grouping of the contralesional distracters produced congruency effects on the attended (ipsilesional) target-change judgment – for example, the time take to decide that two ipsilesional stimuli differed was speeded if the grouping relations in the contralesional field changed. This effect was the same magnitude in neglect patients and control participants. Again it appears that perceptual grouping can take place in the absence of attention allocated to the elements forming the perceptual grouping.

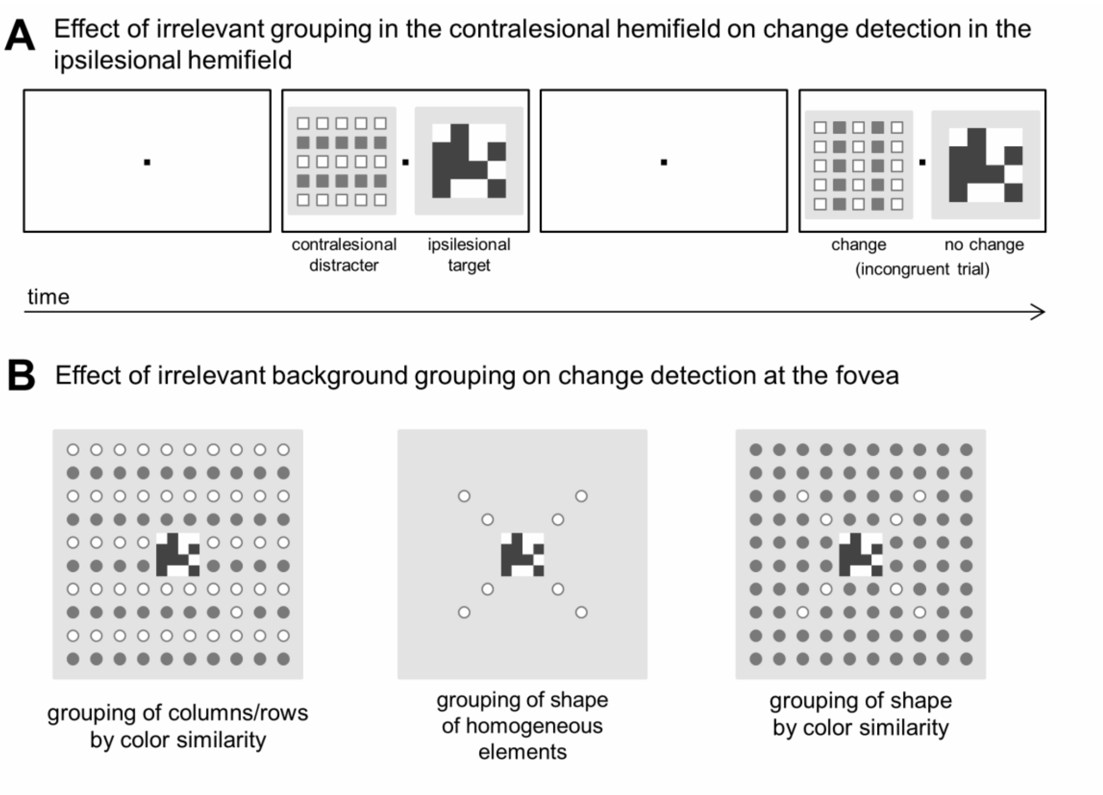

Figure 3. Perceptual grouping without attention in neglect and healthy volunteers. (A) Example of the change detection paradigm used by Shomstein et al. (2010). Participants were asked to judge whether successively presented checkerboards in the ipsilesional hemifield were the same or different, while the grouping in the contralesional hemifield was manipulated independently. (B) Example of displays used in similar change detection task by Kimchi and Razpurker Apfeld (2004). The elements in the background were grouped into columns/rows by similarity, into a shape, or into a shape by colour similarity.

There is converging evidence too from patients with simultanagnosia. Even though normal participants can show a bias to global hierarchical shapes, rather than to their local constituents (Navon, 1977) (see Figure 4A) (see Chapter 17 by Kimchi, for a detailed analysis of the processing of hierarchical figures), simultagnosic patients tend to show a local bias – they may recognize the local elements whilst being poor at explicitly reporting the global shape (Huberle & Karnath, 2006; Karnath, Ferber, Rorden, & Driver, 2000). However, the same patients can be faster at naming the local letters when their identity is congruent with the global letter compared to when it is incongruent. These congruency effects again suggest that, even if the global shape is not available for explicit report, grouping based on proximity of local elements can still occur in simultagnosic patients.

In line bisection tasks, patients with hemispatial neglect have to indicate the midpoint of a horizontal line presented on a piece of paper in front of them. Deviation of the estimated midpoint towards the side of brain damage is typically regarded as being indicative of hemispatial neglect. Vuilleumier and colleagues (Vuilleumier & Landis, 1998; Vuilleumier, Valenza, & Landis, 2001) used Kanizsa-type illusory figures to examine whether patients with neglect would also deviate from the midpoint when marking the midpoint of illusory contours rather than real contours (Figure 4B). Bisection judgments in neglect patients were similar on Kanizsa stimuli with illusory contours and connected stimuli with real contours, even though the patients could not detect the contralateral inducers explicitly. These results suggest that neglect patients can implicitly group inducing elements prior to the stage where the attentional bias towards the ipsilesional side of space arises. Interestingly, patients with lesions extending posteriorly to the lateral occipital complex did not show this systematic bisection pattern, suggesting that implicit grouping may depend on the integrity of lateral occipital areas (Vuilleumier, Valenza, et al., 2001).

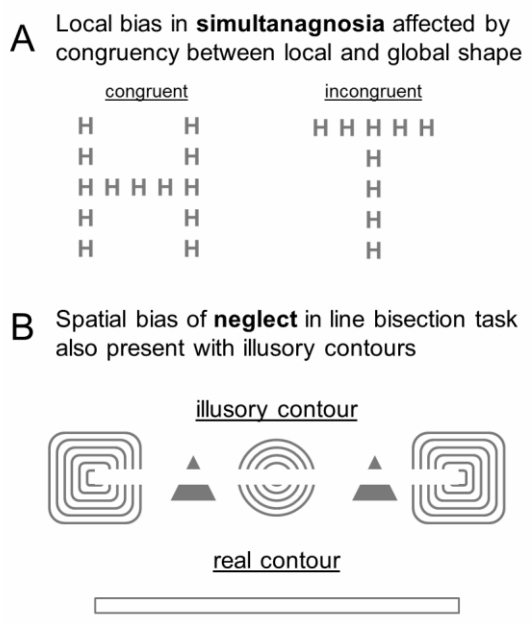

Figure 4. Implicit perceptual grouping in simultanagnosia and neglect. (A) Patients with simultanagnosia are typically poor at explicitly reporting the global shape in hierarchical letter, but are faster at identifying the local shapes when congruent with the global shape. (B) In line bisection tasks, the midpoint indicated by patients with neglect typically deviate towards the side of brain damage, even when bisecting an illusory contour. Adapted from Vuilleumier et al. (2001).

Other evidence that perceptual grouping can occur without observers paying attention to the constituent elements comes from functional magnetic resonance imaging (fMRI) studies in healthy volunteers. One line of work has exploited the visual suppression that occurs between simultaneously presented, proximal visual elements. These competitive interactions appear to occur automatically, without attention, in early visual cortex (Kastner, De Weerd, Desimone, & Ungerleider, 1998; Reynolds, Chelazzi, & Desimone, 1999). McMains and Kastner (2010) assessed whether the level of competitive interaction induced by task-irrelevant elements varied as a function of the strength of perceptual grouping between the elements. They found that competitive interactions in early visual cortex and V4 were reduced when the elements could be grouped on the basis of the Gestalt principles of collinearity, proximity or illusory contour formation compared when the same stimuli could not be grouped, even if these elements were task-irrelevant and observers performed a concurrent demanding task (McMains & Kastner, 2010).

Whether or not perceptual grouping requires attentive resources may, however, also depend on the type of perceptual grouping involved (Han, Humphreys, & Chen, 1999; Han, Song, Ding, Yund, & Woods, 2001; Han, Ding, & Song, 2002; Kimchi & Razpurker-Apfeld, 2004). Kimchi and Razpurker-Apfeld (2004) used Russell & Driver's paradigm (2005) to study different forms of grouping under inattention. On each trial, participants were presented with two successive displays; each containing a central target matrix surrounded by task-irrelevant grouped background elements, and individuals performed a demanding change detection task on the target matrix. Grouping between the background elements stayed the same or changed across successive displays, independent of any change in the target matrix. Grouping of columns/rows by colour similarity and grouping of shape by homogeneous elements affected performance on the central change detection task (Figure 3B). Grouping of shape by colour similarity, however, did not result in congruency effects, suggesting that the latter form of grouping is contingent upon the availability of (sufficient) attentional resources. Whether or not attention is necessary for grouping to occur, may not be an all-or-none phenomenon. Kimchi and colleagues (Kimchi & Peterson, 2008; Kimchi & Razpurker-Apfeld, 2004) proposed that a continuum of attentional requirements exists as a function of the processes involved in different types of grouping. According to this view, grouping of shape by colour similarity may be a weaker form of grouping requiring more attentional resources.

Other evidence for attention playing a necessary role in grouping is suggested by both brain imaging and neuropsychological evidence. These studies indicate that damage to posterior parietal cortex, a brain region implicated in attentional control, disrupts grouping (e.g., Zaretskaya, Anstis, & Bartels, 2013). Global pattern coding, for which local integration processes are not sufficient, also seem to depend on the integrity of brain areas controlling attention, such as the intraparietal cortex. Lestou et al. (under review) observed reduced activity to global radial and concentric Glass patterns in structurally preserved intermediate regions such as the lateral occipital complex, after lesions of the intraparietal cortex . This suggests that the intraparietal cortex plays a critical role in modulating grouping in regions such as the lateral occipital cortex, which are typically thought to respond to perceptual groups. Furthermore, perceptual grouping in neglect patients may not be as efficient in patients compared to healthy volunteers. Han and Humphreys (2007) examined the role of the fronto-parietal cortex in top-down modulation of perceptual grouping by recording ERPs from 2 patients with fronto-parietal lesions and 8 controls. In controls grouping by proximity and collinearity was indexed by short-latency activity over the medial occipital cortex and long-latency activity over the occipito-parietal areas. For the patients, however, both the short- and long-latency activities were eliminated or weakened.

We can conclude from the above studies that some types of perceptual grouping can occur without focused attention, although attentive resources appear to be necessary for the outputs of these grouping processes to be accessible for explicit report. In contrast, other forms of grouping cannot be accomplished optimally without focused attention (see also Kimchi, 2009). Additional research is needed to investigate in more detail which forms of grouping require attentional resources.

5. Attention constrains perceptual grouping

Several studies indicate that attention can modulate neural activity associated with grouping in early visual cortex (e.g., Casco, Grieco, Campana, Corvino, & Caputo, 2005; Freeman, Driver, Sagi, & Zhaoping, 2003; Freeman, Sagi, & Driver, 2001; Khoe, Freeman, Woldorff, & Mangun, 2006; Wu, Chen, & Han, 2005). Freeman et al. (2001) showed that contrast thresholds for a central Gabor stimulus are lower when it is flanked by collinear, oriented grating stimuli, but only when the flankers are attended. In a subsequent study, Freeman and colleagues (2003) showed that the attentional modulation persists even for high flanker contrasts, suggesting that attention acts by integration of the local elements into a global form, rather than by changing the local sensitivity to the flankers themselves. Goldsmith and Yeari (2003) demonstrated that effects of grouping are found under conditions of divided attention – allowing attention to spread across the visual field - but that grouping effects are reduced under conditions of focused attention. Effects of attention have also been observed for higher-level types of grouping. For example, Roberts & Humphreys (2011) showed that the benefit of positioning pairs of objects for action is reduced by cueing attention towards one of the objects. Converging evidence has been obtained using fMRI (Han, Jiang, Mao, Humphreys, & Gu, 2005) and ERP techniques (Han, Jiang, Mao, Humphreys, & Qin, 2005) by Han and colleagues showing that proximity grouping is modulated by whether stimuli fall within an attended region. Furthermore, De Haan and Rorden (2010) showed that similarity grouping can be modulated by whether or not the grouping mechanism is relevant for the task.

Other studies (McMains & Kastner, 2011) hypothesized that attentional modulation of cortical activity may vary as a function of the degree of perceptual grouping in the display. Participants were presented either with a strong perceptual group (i.e. an illusory shape), a weak perceptual group (i.e. an illusory shape with ill-defined borders), or no perceptual group. McMains and Kastner observed that the amount of attentional modulation on competitive interactions in early visual cortex depended on the degree of competition left unresolved by bottom-up processes: attentional modulation was greatest for displays without perceptual groups - when neural competition was little influenced by bottom-up mechanisms - and smallest, although still significantly present, for displays containing a strong perceptual group. However, when observers paid attention to the elements forming the perceptual group, competitive interactions were similar for all levels of perceptual grouping, suggesting that bottom-up and top-down processes interact dynamically to maximally resolve neural competition.

6. Discussion and framework.

The results we have reviewed, drawn from behavioural and neuroimaging studies with both normal observers and neuropsychological patients are consistent with the view that, whilst not being *necessary* for at least some forms of perceptual grouping, visual attention can nevertheless modulate grouping. The modulation effects are stronger on some forms of grouping than others, and attention seems necessary in order for explicit report and awareness of the perceptual groups to take place.

One framework to account for the array of data is that offered by TVA (Bundesen, 1990). TVA suggests that selection is directed by an attentional priority map that can be affected both by bottom-up cues (e.g., the strength of local Gestalt grouping between proximal elements, the 'goodness' of the perceptual object) and top-down factors (e.g., stored knowledge about how objects interact, or stored knowledge about words). Strong bottom-up grouping could pull attentional priority to stimuli, enabling selection to be captured by the group. In addition, strong top-down knowledge could push attentional prioritisation to matching stimulus elements (see also Humphreys & Riddoch, 1993). Importantly, these 'push and pull' operations may still operate even if the attentional priority map is damaged or operating under conditions of noise due to brain lesion. Our conclusion is that attentional selection is dynamically set by bottom-up stimulus factors, top-down knowledge and the allocation of attention to space and within grouped regions of objects.

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