



Object-based attention and visual area LO

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ABSTRACT

We investigated the neural basis of so-called “object-based attention” by examining patient D.F., who has visual form agnosia caused by bilateral damage to the lateral occipital (LO) area of the ventral visual stream. We tested D.F.’s object-based attention in two ways. In the first experiment, we used a spatial cueing procedure to compare the costs associated with shifting attention within versus between two separate outline figures. D.F. did not show the normal advantage of within-object over between-object attention shifts. In the second experiment, we used a complementary paradigm in which two separate stimuli, presented either on the same or on different objects, have to be identified as the same or different. We found no evidence for the normal pattern of superior performance for within versus between figure comparisons. In a third experiment, we checked that D.F. showed normal shift costs for invalid as opposed to valid cueing in a standard Posner spatial attention task. In a final experiment, we compared horizontal versus vertical attention shifting in group of healthy controls without the presence of outline rectangles, and found that their pattern of shift costs was indistinguishable from that seen in D.F. when the rectangles were present (Experiment 1). We conclude that whilst D.F. has a normal spatial orienting system this is completely uninfluenced by object structure. We suggest that area LO may mediate form processing precisely at the stage where visual representations normally influence the spread of attention.

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1. Introduction

Ungerleider and Mishkin (1982) first proposed that the cortical processing of visual information was divided into two functionally and anatomically distinct streams. Within their interpretive framework the extraction and representation of objects was viewed as the preserve of the ventral stream. It is now clear from both primate and human research, however, that shape selectivity is a feature of both the dorsal and ventral streams (Milner & Goodale, 1995, 2006). These two forms of shape encoding are not mere replicas of each other but show distinct patterns of selectivity and generalization (James, Humphrey, Gati, Menon, & Goodale, 2002; Lehky & Sereno, 2007). Furthermore Milner and Goodale (1995) have argued that the shape representations in each stream differ not only in their nature, but more importantly in their function. Shape representations in the ventral stream are used to inform perception, while shape representations in the dorsal stream are used to guide actions.

Visual form, however, not only drives recognition and action but also influences the allocation of attention: it is easier to shift attention within a single object form than between two separate

forms (Duncan, 1984; Egly, Driver, & Rafal, 1994). This influence is thought to play a role in fine tuning the construction of perceptual representations, by focusing visual processing on those elements of a scene that group together (Driver, Davis, Russell, Turatto, & Freeman, 2001). It is unclear whether the same or similar influences of visual structure might also operate on attentional selection within the shape representations that guide manual actions to those objects. In terms of Milner and Goodale’s (1995, 2008) two visual-systems framework, we would predict that the classical perceptual “object-based” attention effects would be mediated within the ventral stream, and therefore not play a direct role in guiding manual actions. The well studied patient D.F. has a bilateral brain lesion that is centred on ventral-stream area LO, which is known through neuroimaging research to play a crucial role in shape perception (James, Culham, Humphrey, Milner, & Goodale, 2003; Kourtzi & Kanwisher, 2001). D.F. therefore provides a strong test of the potential role of area LO not just in perception, but also in object-based attention. D.F. is, however, clearly able to segregate candidate objects for manual action, and to use that visual information to calibrate her movements towards such objects. Thus if object-based attention operates not only within the perceptual domain, but also during the processing of candidate objects for action, it should be intact in D.F., at least within the dorsal stream. An absence of classical perceptual object-based attention effects in D.F. would suggest that this influence of visual structure upon attention is either not important for guiding manual actions towards

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visual objects, or that it is organized quite separately within the two visual streams.

D.F.'s impairment in shape perception may also be informative in terms of the debate within the object-based attention literature regarding the level in the ventral stream at which visual structure influences attention. At present, although the ability of visual structure to influence attention is uncontroversial (Scholl, 2001), it is still unclear at exactly what level of representation object shape exerts its influence on attention. Indeed Driver et al. (2001) have persuasively argued that referring to the influence of visual structure upon attention as "object-based" is strictly inappropriate (though we will continue to use this questionable nomenclature within the present paper). They argue that it is not objects, in the sense of the visual units that provide the mental furniture for visual recognition and visual cognition, that influence our allocation of attention. Rather, they argue, attention interacts with earlier visual information at the stage of scene segmentation, thereby serving to structure the visual input to enable genuine object representations to be extracted later in the system.

Early segmentation mechanisms and later object representations certainly appear to have quite different neural bases: there is evidence that edge extraction and figure-ground assignment take place in the primary visual cortex (Lamme, 1995), whereas shape as a property of objects is associated with activity in the lateral occipital (LO) cortex (Kourtzi & Kanwisher, 2001; Malach et al., 1995). The neural basis of object-based attention, however, still remains unclear. For example whilst Müller and Kleinschmidt (2003) have provided neuroimaging evidence that the enhanced activation of locations within objects manifests itself within the primary visual cortex, they accept that this could well reflect feedback from higher ventral- or dorsal-stream areas. Evidence supporting the putative role of the lateral occipital area comes from a recent study by Martinez et al. (2006), who investigated object-based attention using a combination of EEG and fMRI. They found that object-based attention was clearly associated with the enhancement of the N1 component of the ERP waveform. They go on to argue that this component principally reflects activation in the lateral occipital complex, while noting that other areas too can contribute to the N1 component (Di Russo, Martinez, & Hillyard, 2003).

The distinction drawn by Driver et al. between early scene-parsing mechanisms and later object-based processing can also be examined at a behavioural level. Again, however, the picture remains as yet unclear. On the one hand object-based attention can be demonstrated when attention simply has to move across some horizontal lines (Avrahami, 1999), suggesting that such simple segmentation cues are able to modulate attention. On the other hand, several researchers have demonstrated that the influence of visual structure upon attention is modulated by high-level factors such as the perceptual interpretation of the nature of the shape (Chen, 1998) and previous perceptual experience of that shape (Zemel, Behrmann, Mozer, & Bavelier, 2002).

The present study seeks to shed light on this issue by examining object-based attention in patient D.F. Her pattern of impairment, both in terms of its neural locus and its manifestation as visual form agnosia, provides a strong test for the level at which visual structure influences attention. D.F.'s lesion has resulted in a complete bilateral disruption of processing in area LO whilst leaving functionally intact processing in the primary visual cortex, which plays a pivotal role in feeding information to her largely-intact dorsal stream to guide manual actions (James et al., 2003). Despite her severe impairment in visual form perception (Milner et al., 1991) D.F. is still able to perform basic scene segmentation tasks. For example, if asked to count the number of disks in a display D.F. is able to segment these from their background and report with near-perfect accuracy (Carey, Dijkerman, Murphy, Goodale, & Milner, 2006). By

examining the nature of object-based attention effects in D.F. we can therefore test the level at which visual structure in the ventral stream influences attention. We have done this by using two complementary experimental paradigms. In Experiment 1, we used the paradigm of Egly et al. (1994), in which a Posner-style spatial cueing procedure is used to compare attention shifting made either within or between two separate outline figures. Despite the similar distance over which attention has to shift from an invalid cue in either case, healthy subjects show a reliable reaction-time advantage of within-object over between-object attention shifts. In the second experiment, we used the complementary paradigm of Marino and Scholl (2005), in which two stimulus elements have to be compared either within the same outline figure or between two separate figures. Healthy subjects are facilitated in making same/different judgements for targets that fall within the same figure.

2. Participants

D.F. was aged 53 at the time of testing. Her clinical background has been described in detail elsewhere (Goodale & Milner, 2004; Milner et al., 1991) and MRI scans of her lesions have been presented by James et al. (2003). Experiments 1–3 additionally used eight age-matched control subjects (mean age = 51; S.D. = 4, for Experiments 1 and 2, mean age = 52; S.D. = 4 for Experiment 3). Experiment 4 used six healthy control subjects (mean age = 30; S.D. = 8). All control subjects had normal or corrected to normal vision and were students or staff at Durham University.

3. Experiment 1

3.1. Methods

Experiment 1 used an adaptation of the cueing paradigm devised by Egly et al. (1994). Participants were presented with two white outline rectangles subtending 17° by 3.6° of visual angle oriented vertically 6.5° either side of the centre of the screen. The rectangles had a white outline, 8 pixels thick, presented on a black background. This outline display was present throughout each experimental session. At the start of a trial one of four possible target locations at the end of one of the rectangles would be cued with a bright grey square that would appear for 200 ms (see Fig. 1, top right). The participant was then presented with a red or green target of similar size, which they were asked to discriminate by pressing one of two buttons as quickly and accurately as possible, using the left index finger for one button and the right index finger for the other. The target could appear in one of three locations relative to the cue: either in the identical location (valid cue trial), at the other location on the same object (invalid within-object trial), or at the homologous location on the other rectangle (invalid between-object trial). These three trial types are illustrated in Fig. 1 (bottom three panels). There was a 1500 ms inter-trial interval during which only the two rectangles remained present on the screen. Participants were tested in 6 blocks of 96 trials. Fifty percent of the trials were validly cued, 25% were invalidly-cued within-object and 25% invalidly cued between-objects. The order of trial types was randomly counterbalanced within each block. Trials with inaccurate responses and those with reaction times likely to be anticipations (less than 150 ms) or mis-keyings (more than 1500 ms) were removed prior to analysis. Any remaining outliers (responses that were two standard deviations above or below the mean for each subject in each condition) were also removed. This procedure removed 6% of trials as outliers.

The stimuli in Experiments 1, 2 and 4 were displayed on an Eizo F55 17-in. (600×800 pixels) colour monitor, driven by a Cambridge Research Systems VSG 2/5 graphics system at 100 Hz. Responses in all experiments were recorded using a Cambridge Research Systems CT3 button-box.

3.2. Results

Here and throughout the paper, all statistics are reported as two-tailed. The control group clearly demonstrated the object-based attention effect reported by Egly et al. (1994), in that invalidly cued targets appearing on a different object took longer to recognize than invalidly cued targets appearing on the same object [$t(7) = 2.35$, $p = 0.051$, within-object mean RT 468 ms, between-object mean RT

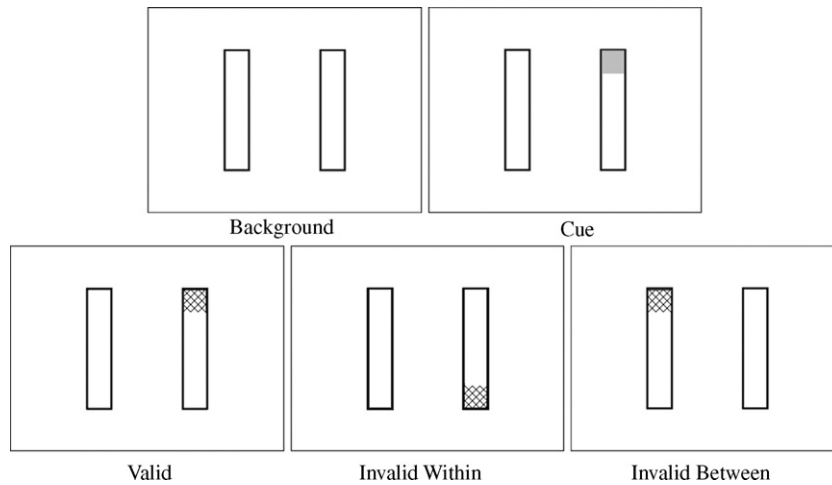


Fig. 1. Experiment 1. Illustrative stimuli for the object-based cueing paradigm. The targets (cross-hatched) were green or red, the outline rectangles were white on a black background.

483 ms]. D.F., however, showed a quite different pattern of performance. While she was faster to respond to validly cued than to invalidly cued targets ($t(498) = 7.993$, $p < 0.001$), she did not show the normal advantage for within-object invalid trials over between-object invalid trials [valid mean RT 726 ms, invalid within-object mean RT 882 ms, invalid between-object RT 839 ms] (Fig. 2).

It is quite apparent that D.F.'s performance is in general slower than that of controls. However, what is most critical in interpreting our studies is determining whether the difference in D.F.'s reaction times across within- and between-objects conditions is what one might expect of a normal observer or whether her behaviour differs significantly from that of our control sample. It is common to treat the means and variances of data obtained from control *samples* as if they were *population* parameters rather than sample statistics. Doing so when comparing difference scores with relatively small

control sample sizes of the order we use here can lead to highly inflated Type-I error rates (see, e.g. Crawford & Garthwaite, 2005). We have therefore adopted an approach suggested by Crawford and Garthwaite (2002, 2007) in which the mean and variance of the scores obtained from the control sample are treated correctly as statistics in the course of assessing the likelihood that the patient's scores were drawn from the same population as control sample's. We have used Crawford and Garthwaite (2007) Bayesian calculation for within subject control scores as this allows us to preserve raw, unstandardised, reaction-time measures in our calculations.

Comparing D.F.'s difference score (between-object invalid vs. within-object invalid RTs) with those of the sample indicates that D.F.'s RT difference lies at the extreme of normal observers' performance. The Bayesian estimate of the percentage of the control population estimated to show a more extreme RT difference is 2% (i.e. $p = 0.02$). Accuracy was near ceiling for the control subjects in both between- and within-object trials and these did not differ statistically [$t(7) = 1.37$, $p = 0.21$]. D.F. has good colour discrimination (Milner & Heywood, 1989) and indeed responded correctly on every trial. Her accuracy did not differ from that of the controls on Crawford and Garthwaite's test [$p = 0.66$].

3.3. Interim discussion

According to our use of a variation of Egly et al.'s (1994) paradigm it is clear that D.F. did not show the normal influence of objects upon attention. If anything, she showed an apparent reversal of the normal trend. It is possible, however, that this trend merely reflects the differential difficulty of making a vertical as opposed to a horizontal shift within this task, since we did not balance our experimental design to rule out this possibility. We examined this interpretation in Experiment 4. But first we sought in Experiment 2 to establish whether the absence of an object-based attention effect in D.F. could be replicated using a quite different experimental paradigm.

4. Experiment 2

4.1. Methods

Experiment 2 employed a modified version of the two-item comparison paradigm employed by Marino and Scholl (2005), in which participants are asked to report whether two items, either located on the same object or on two different objects, are the same or different. The display in this experiment contained the same pair of rectangles as used in Experiment 1, which again formed the background that was present throughout each experimental session. On each trial the participant was presented with two square patches of colour (equi-frequently red or green), which

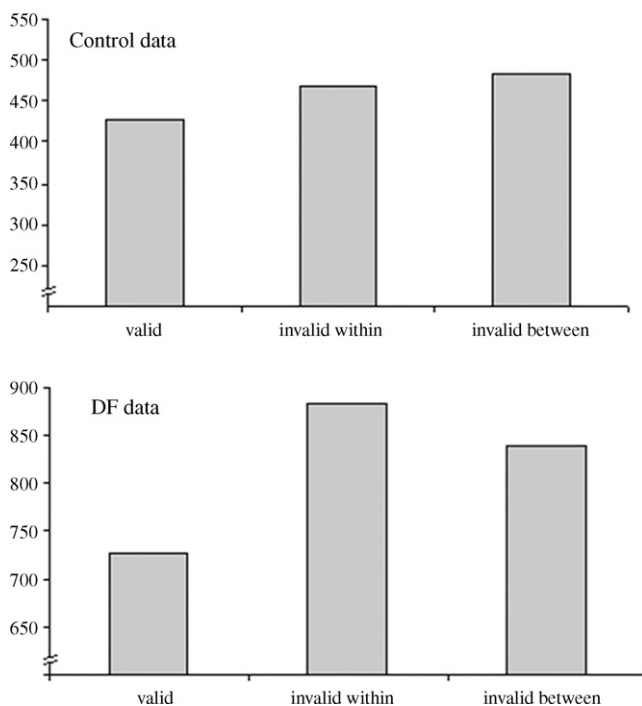


Fig. 2. Experiment 1. Reaction times (ms) for target discriminations across the three cueing conditions for a healthy control group and for patient D.F. Note the y-axis uses a different intercept for D.F. and the control sample.

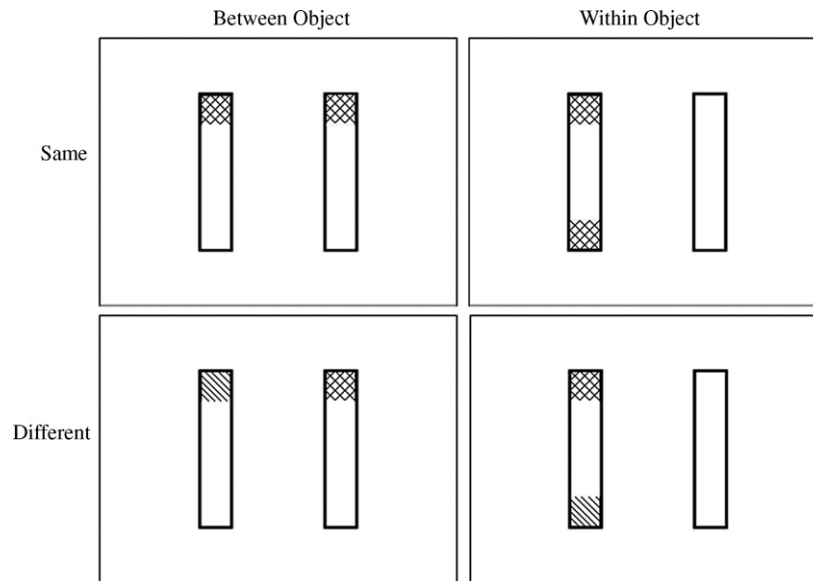


Fig. 3. Experiment 2. Illustrative stimuli used in the object-based two-item comparison paradigm (Experiment 2). The targets were red (shown as cross-hatched) or green (shown as dashed). The outline rectangles were white on a black background.

could either occupy opposite ends of the same rectangle, or homologous ends of the two different rectangles (Fig. 3).

The subject's task was to report whether the colours were the same or different using one of two buttons, again using the left index finger for one button and the right index finger for the other. The targets remained present on the screen until a response was made. There was a 1700 ms inter-trial interval during which the rectangles remained visible. Each participant completed 6 blocks of 96 trials. Each block contained equal numbers of same and different pairings and of within- and between-object trials. The presentation order was randomly counterbalanced within each block. Reaction times were trimmed for outliers and errors in the manner described in Experiment 1. This procedure removed 10% of trials as outliers.

4.2. Results

The control subjects took reliably longer to make discriminative responses when the targets were both located on different objects than when they were on the same object [$t(7) = 3.7, p < 0.01$; within-object mean RT 499 ms, between-object mean RT 511 ms].¹ Thus their results were clearly consistent with the operation of object-based attention in this paradigm. Again D.F.'s results showed a quite different pattern. She not only showed no cost for between- as opposed to within-object comparisons, but in fact took longer to make within-object comparisons [D.F. within-object RT 1287, between-object RT 1224]. Crucially, Crawford and Garthwaite's (2007) Bayesian inferential test showed that D.F.'s mean difference score (within-object minus between-object) differed significantly from that of the controls [$p < 0.001$] (Fig. 4).

Control subjects did not differ in accuracy on the between- and within-object trials (97.9% correct on both within and between trials), and Crawford and Garthwaite's inferential test on the difference scores shows that this pattern is not different from that shown by D.F. ($p = 0.219$, within 97.2%, between 95.5%).

4.3. Interim discussion

The results from this experiment again demonstrate that D.F.'s allocation of attention is not influenced by objects in the usual manner. As was seen in Experiment 1, D.F. responded if anything faster in

the between-object condition, a pattern opposite to that shown by the controls. Taken together, the results from Experiments 1 and 2 demonstrate that D.F. does not exhibit the normal effects of object-based attention. Before we can draw any meaningful conclusion from these findings, however, it is vital to establish that D.F.'s results

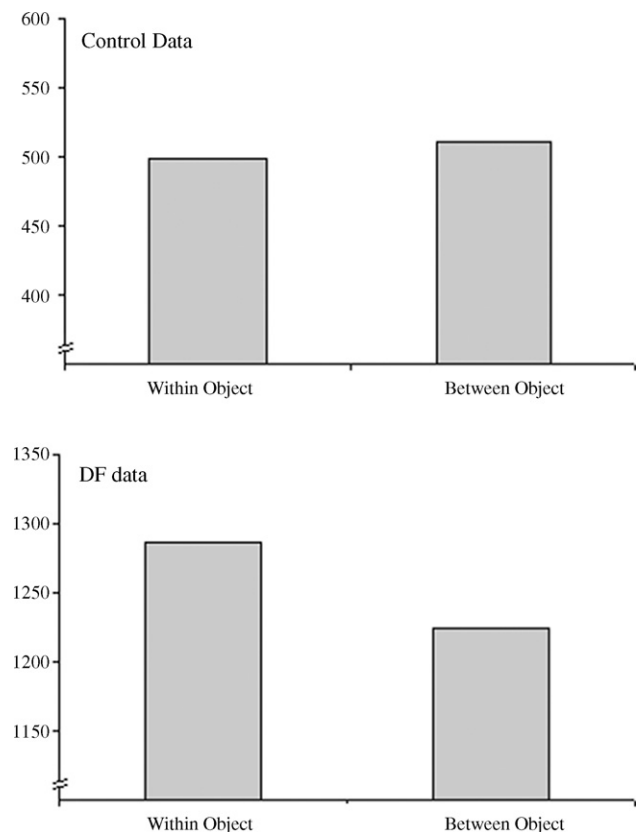


Fig. 4. Experiment 2. Data for a healthy control group and for patient D.F. Reaction times (ms) for same/different comparisons for pairs of stimuli appearing within the same object or between the two objects. Note the y-axis uses a different intercept for D.F. and the control sample.

¹ The first block of 96 trials for one of the control participants had to be removed because performance fell below 50% (i.e. below chance) in one of the conditions, suggesting that they had not learnt the correct key responses.

do not simply reflect a failure of attention *per se*, but are specific to object-based attention. Experiment 3 therefore examines simple covert spatial orienting in D.F., using the classic Posner spatial attention paradigm.

5. Experiment 3

5.1. Methods

Experiment 3 employed a variant of the Posner (1980) peripheral spatial cueing paradigm. The participant was presented with a background against which two low contrast placeholders (each represented by the corners of a square) were displayed. These placeholders subtended a visual angle of 10.68° , and were located from centre to centre 15.4° either side of fixation. The lines making up the placeholders were 0.15° thick. They remained present on the screen throughout each experimental session. At the onset of each trial, one of the placeholders would brighten for 30 ms as a spatial cue (see Fig. 5, top right). On cue-offset there was an interval of either 90, 120 or 150 ms before target presentation. The target was a red or green square subtending 7.84° , which appeared either on the same side as the cue (valid target) or on the opposite side to the cue (invalid target). There were equal numbers of valid and invalid trials.

The participant identified the target's colour as quickly and accurately as possible using one of two buttons, again using the left index finger for one button and the right index finger for the other. Following the response there was a 1500 ms inter-trial interval during which the placeholders remained visible. Participants were instructed to maintain fixation on the cross in the centre of the screen throughout each experimental trial. The stability of fixation was monitored using an infra-red camera. Testing was conducted in 6 blocks of 96 trials. The order of stimulus type (red, green) cue type (valid, invalid) and cue-target interval (90, 120 or 150 ms) were independently randomized within each block. The reaction times were trimmed for outliers and errors in the manner described for Experiment 1. This procedure removed 6% of trials as outliers.

5.2. Results

D.F. showed a normal pattern of spatial orienting, with validly cued targets (i.e. appearing on the same side as the cue) being identified significantly faster than targets appearing on the opposite side to the cue [$t(470) = 2.38, p = 0.018$, valid mean RT 752 ms, invalid mean RT 793 ms]. A group analysis revealed the same effect for the

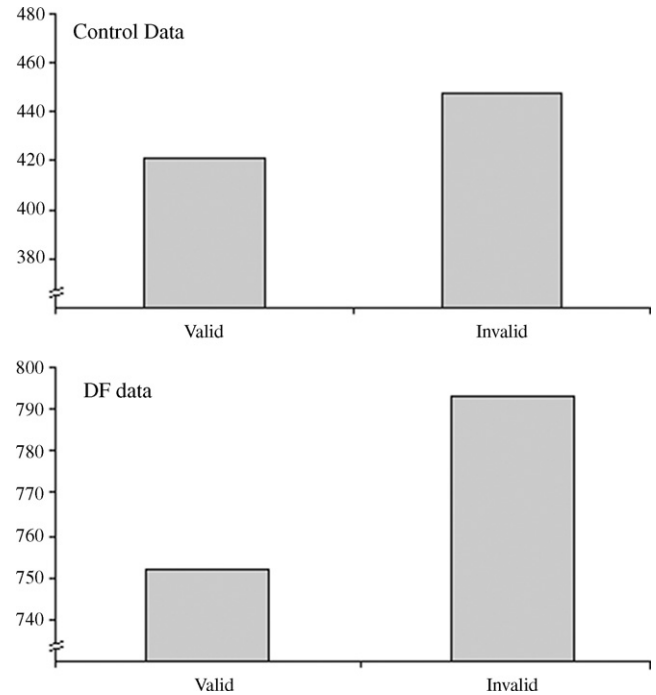


Fig. 6. Experiment 3. Reaction times (ms) for target discriminations following valid and invalid spatial cues. Note the y-axis uses a different scale for D.F. and the control sample.

control subjects [$t(7) = 5.51, p < 0.001$, mean RT for validly cued targets 421 ms, mean RT for invalidly cued targets 448 ms]. Crawford and Garthwaite's (2007) Bayesian inferential test revealed that D.F.'s shift costs (invalid minus valid mean RTs), although quantitatively greater, did not differ significantly from those of the controls [$p = 0.335$]. Indeed, allowing for her longer reaction times, the proportionate shift costs were very similar to those of controls (Fig. 6).

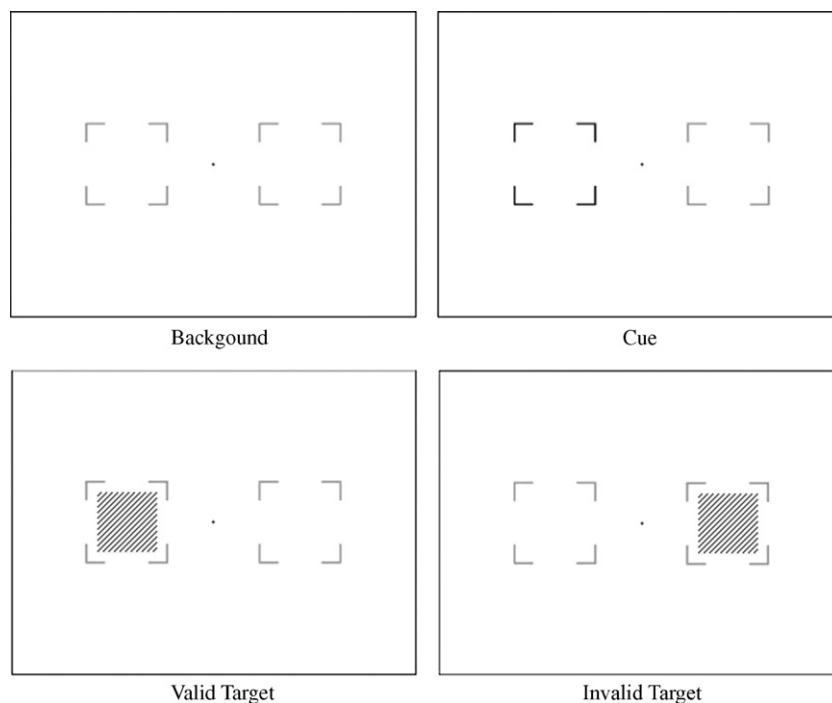


Fig. 5. Experiment 3. Illustrative stimuli for the Posner spatial cueing paradigm. The placeholder frames and fixation cross were white on a black background. The dashed pattern is used to illustrate the target, which could be either green or red.

Cue validity did not affect accuracy for control subjects [$t(7)=0.113$, valid mean 98.1%; invalid mean 98.2%] and Crawford and Garthwaite's inferential test showed no difference between D.F. and the controls in terms of accuracy [$p=0.669$, valid 99.6%, invalid 99.2%].

6. Experiment 4

In Experiments 1 and 2, D.F. not only showed no cost for shifting attention between objects but, if anything, appeared to shift her attention more quickly between objects than within them. A possible explanation for those findings, however, is that in both of those experiments, the rectangles were always presented in a vertical orientation, so that between-object shifts were made horizontally whereas within-object shifts were made vertically. In another experiment currently in progress in our laboratory, we recently observed that healthy participants respond faster to targets following a horizontal shift in a variation of the Egly et al. (1994) paradigm in which the cue and targets were visible but the objects were not. It might be, therefore, that D.F.'s contrary pattern of performance in our object-based attention paradigms emerged totally independently of the presence of the rectangles on the screen. That is, D.F.'s performance is completely explicable if horizontal shifts can be achieved more rapidly in this task when the outline rectangles do not exert any influence. In Experiments 1 and 2 any such effect will have been masked for normal observers because of the influence of the objects. In Experiment 4 we sought to test this idea directly by retesting healthy controls using the procedures of Experiment 1, but in the absence of the rectangular shapes. With the rectangles absent we predicted that normal observers would show the same pattern of performance as D.F. showed, when the rectangles actually were present.

6.1. Methods

The procedure for Experiment 4 was identical to Experiment 1, except that the participants (healthy controls only) completed only one block of 96 trials. The cue and target stimuli were identical to Experiment 1, but they were presented on a blank screen, without the rectangular shapes. Responses were made and recorded in the same way as before. The results were trimmed for outliers and errors in the same manner as described for Experiment 1. This procedure removed 5% of trials as outliers.

6.2. Results

When the rectangles were absent from the screen, our healthy control participants showed the same pattern of performance as D.F. had done in Experiment 1. Participants showed a general cueing effect, with responses to validly cued targets being significantly faster than those to invalidly cued targets ($t(5)=-7.59$, $p=0.001$, valid mean RT 382.5, invalid mean RT 426). More critically their RTs to invalidly-cued targets requiring a horizontal shift of attention (corresponding to 'between-object' trials in Experiment 1: mean RT 416 ms) were significantly faster than those to targets requiring a vertical shift of attention (correspond to 'within-object' trials: mean RT 436 ms). Notably, while this difference across 'between' and 'within' object trials is significant [$t(5)=3.4$, $p<0.05$], it does not differ, in terms of Crawford and Garthwaite's (2007) Bayesian inferential test, from the performance of D.F. in Experiment 1 ($p=0.238$) (Fig. 7).

There were no differences in accuracy across 'between' and 'within' object trials in the subjects tested [$t(5)=0.963$, invalid 'within' mean 98.5%, invalid 'between' mean 97%], and again Crawford and Garthwaite's inferential test shows that this pattern is not different from that of D.F. in Experiment 1 [$p=0.989$].

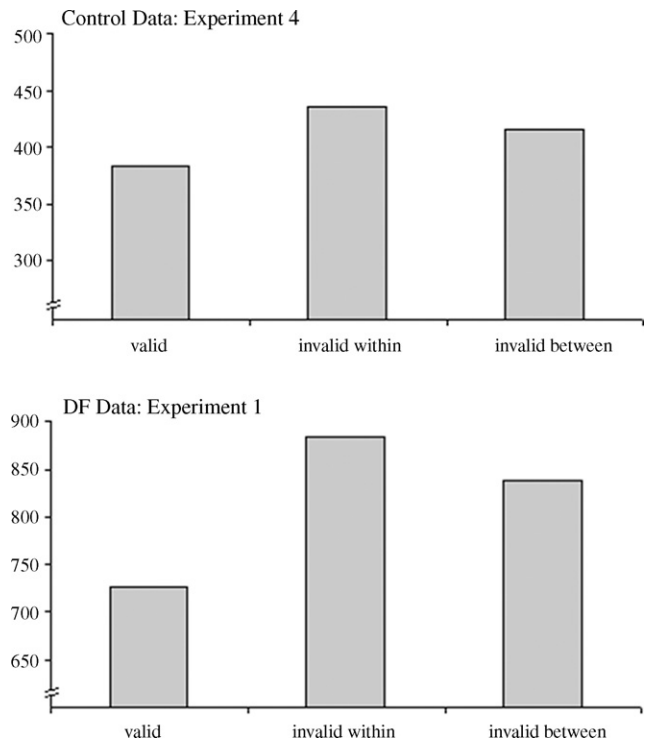


Fig. 7. Experiment 4. Reaction time data (ms) for control subjects on a target discrimination task in the equivalent of the three cueing conditions used in Experiment 1, but without the outline shapes. Thus the "invalid-within" data refers to vertical attention shifts, while the "invalid-between" data refers to horizontal shifts. D.F.'s data is reproduced from Experiment 1. Note the y-axis uses a different intercept for D.F. and the control sample.

7. Discussion

Despite D.F. clearly showing normal covert spatial attention effects (as reported in Experiment 3) we have found, using two different object-based attention paradigms (Experiments 1 and 2), that there was no evidence that the deployment of her attention was sensitive to the presentation of objects. In fact her performance was so insensitive to the presence of objects in the display that it matched that produced by healthy participants performing the task when no objects were present at all (Experiment 4). In their recent paper Martinez et al. (2006) argue that object-based attention effects emerge because object representations are highlighted by spatial attention. In these terms, our data indicate that in D.F., despite normal spatial attention, there are no 'objects' to highlight.

Given D.F.'s severe form perception deficit, the inability of visual form representations in the ventral stream to influence attention could be argued to give little cause for surprise. Recent theorizing about object-based attention (Driver et al., 2001) has, however, emphasized that object representations *per se* might not be influencing the allocation of attention. Rather, the spread of attention might be modulated by the segmentation processes that parse the visual scene prior to the construction of object representations. Basic segmentation processes operating within in the primary visual cortex are likely to be still intact in D.F., given her ability to carry out simple visually guided acts of object grasping quite normally, and given that these acts are accompanied by normal patterns of dorsal-stream activation in the object-grasping area AIP (James et al., 2003). Indeed D.F. is able to differentiate figures from their background and give accurate perceptual reports of the number of items presented on a display (Carey et al., 2006). Our results show, however, that these early stages of figure-ground segmenta-

tion are not able to influence the spread of attention. At the same time, our results do not demonstrate that attention is influenced solely by ‘high level’ object representations. Whilst D.F. is clearly impaired in recognizing objects on the basis of shape or form, this does not imply that the representations underpinning perceptual recognition are the locus at which shape influences attention. Although D.F. can perform some perceptual tasks not requiring object recognition (figure-ground segmentation) there are other aspects of visual processing, also not requiring object recognition, that are disrupted in D.F. She is, for example, insensitive to a number of gestalt cues to perceptual grouping that normally influence perception (Goodale et al., 1994). It may be the case that processes such as these are intrinsically linked to the genesis of object-based attention.

The findings of James et al. (2003) allow us to relate the clear bilateral disruption to the object-selective area LO to D.F.’s visual form agnosia. First, her lesions overlap almost completely with area LO as determined in healthy controls through subtracting fMRI activations caused by viewing line drawings from those caused by viewing scrambled versions of those drawings. More tellingly still, a similar subtraction in D.F. yielded no net ventral-stream activation at all (James et al., 2003). In the context of this disruption of form processing in area LO, the lack of any influence of visual structure upon D.F.’s attention is clearly consistent with the suggestion of Martinez et al. (2006) that this area plays a critical role in object-based attention. Again, however, it would be premature to conclude that our data prove that LO is essential for object-based attention, as the damage to D.F.’s ventral stream is not solely restricted to LO. We are currently attempting to test the specificity of LO involvement in object-based attention by studying the effects of transcranial magnetic stimulation over LO in healthy participants.

Viewed in the context of D.F.’s established abilities in calibrating manual actions to selected visual objects, the present data demonstrate that classic perceptual object-based attention effects are not required for guiding manual actions. This finding is consistent with the theoretical framework of Milner and Goodale (1995) and reinforces the idea that not only is form processing in each stream computed separately but that it serves different functions. Our results, however, can only address the influence of one stream upon the other in one direction: specifically, they argue against ventral-stream object-based attention effects being required for the visual guidance of manual actions. Humphreys and Riddoch (2007) have suggested that computations in one stream might influence the other in the opposite direction. Specifically, they argue that the “objects” that influence attention are not solely perceptual entities: their nature and attentional status is also influenced by the manner in which one acts upon those objects. They argue that this influence manifests itself even when specific actions are only planned, and have not yet been executed. The results of the current study demonstrate that ventral-stream form representations are not able to influence the spread of attention in D.F., thus providing an ideal opportunity to test whether object representations localized solely within the dorsal stream might be able to influence attention. We therefore plan to explore the possibility that when D.F. is acting upon an object the representations subserving that action might be able to influence the perceptual allocation of attention within and between object (cf. Schenk & Milner, 2006).

In conclusion, although D.F. is able to show perfectly intact covert orienting of visuospatial attention, her allocation of attention seems to operate in a manner that is independent of the typical influence of visual structure. That is, her attentional shifts appear to depend solely on the spatial constraints of the task, and not at all on any configurational constraints. This result shows that the basic figure-ground segmentation that is intact in D.F. is not able to influence the spread of her visual attention. The absence of object-based

attention in D.F., together with her clear bilateral lesion to area LO, is consistent with the idea that LO plays a key role in object-based attention (Martinez et al., 2006). Viewed in the context of D.F.’s ability to guide manual actions with respect to selected objects, this finding suggests that classic perceptual object-based attention effects are not required when acting upon visual objects, and strengthens the view that form processing in the two streams is not only distinct but serves different functions.

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References

- Avrami, N. (1999). Objects of attention, objects of perception. *Perception & Psychophysics*, *61*, 1604–1612.
- Carey, D. P., Dijkerman, H. C., Murphy, K. J., Goodale, M. A., & Milner, A. D. (2006). Pointing to places and spaces in a patient with visual form agnosia. *Neuropsychologia*, *44*, 1584–1594.
- Chen, Z. (1998). Switching attention within and between objects: The role of subjective organization. *Canadian Journal of Experimental Psychology*, *52*, 7–17.
- Crawford, J. R., & Garthwaite, P. H. (2002). Investigation of the single case in neuropsychology: Confidence limits on the abnormality of test scores and test score differences. *Neuropsychologia*, *40*(8), 1196–1208.
- Crawford, J. R., & Garthwaite, P. H. (2005). Testing for suspected impairments and dissociations in single-case studies in neuropsychology: Evaluation of alternatives using Monte Carlo simulations and revised tests for dissociations. *Neuropsychology*, *19*(3), 318–331.
- Crawford, J. R., & Garthwaite, P. H. (2007). Comparison of a single case to a control or normative sample in neuropsychology: Development of a Bayesian approach. *Cognitive Neuropsychology*, *24*(4), 343–372.
- Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex*, *13*, 486–499.
- Driver, J., Davis, G., Russell, C., Turatto, M., & Freeman, E. (2001). Segmentation, attention and phenomenal visual objects. *Cognition*, *80*, 61–95.
- Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology-General*, *113*, 501–517.
- Egley, R., Driver, J., & Rafal, R. D. (1994). Shifting visual attention between objects and locations: Evidence from normal and parietal lesion subjects. *Journal of Experimental Psychology-General*, *123*, 161–177.
- Goodale, M. A., Jakobson, L. S., Milner, A. D., Perrett, D. I., Benson, P. J., & Hietanen, J. K. (1994). The nature and limits of orientation and pattern processing supporting visuomotor control in a visual form agnostic. *Journal of Cognitive Neuroscience*, *6*, 46–56.
- Goodale, M. A., & Milner, A. D. (2004). *Sight unseen: An exploration of conscious and unconscious vision*. Oxford: Oxford University Press.
- Humphreys, G. W., & Riddoch, J. (2007). How to define an object: Evidence from the effects of action on perception and attention. *Mind & Language*, *22*, 534–547.
- James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: An fMRI study. *Brain*, *126*, 2463–2475.
- James, T. W., Humphrey, G. K., Gati, J. S., Menon, R. S., & Goodale, M. A. (2002). Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. *Neuron*, *35*, 793–801.
- Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science*, *293*, 1506–1509.
- Lamme, V. A. F. (1995). The neurophysiology of figure ground segregation in primary visual-cortex. *Journal of Neuroscience*, *15*, 1605–1615.
- Lehky, S. R., & Sereno, A. B. (2007). Comparison of shape encoding in primate dorsal and ventral visual pathways. *Journal of Neurophysiology*, *97*, 307–319.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., et al. (1995). Object-related activity revealed by functional magnetic-resonance-imaging in human occipital cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(18), 8135–8139.
- Marino, A. C., & Scholl, B. J. (2005). The role of closure in defining the “objects” of object-based attention. *Perception & Psychophysics*, *67*, 1140–1149.
- Martinez, A., Teder-Salejari, W., Vazquez, M., Molholm, S., Foxe, J. J., Javitt, D. C., et al. (2006). Objects are highlighted by spatial attention. *Journal of Cognitive Neuroscience*, *18*, 298–310.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action* (2nd ed.). Oxford: Oxford University Press.
- Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*, 774–785.

- Milner, A. D., & Heywood, C. A. (1989). A disorder of lightness discrimination in a case of visual form agnosia. *Cortex*, 25, 489–494.
- Milner, A. D., Perrett, D. I., Johnston, R. S., Benson, P. J., Jordan, T. R., Heeley, D. W., et al. (1991). Perception and action in visual form agnosia. *Brain*, 114, 405–428.
- Müller, N. G., & Kleinschmidt, A. (2003). Dynamic interaction of object- and space-based attention in retinotopic visual areas. *Journal of Neuroscience*, 23, 9812–9816.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32, 3–25.
- Schenk, T., & Milner, A. D. (2006). Concurrent visuomotor behaviour improves form discrimination in a patient with visual form agnosia. *European Journal of Neuroscience*, 24, 1495–1503.
- Scholl, B. J. (2001). Objects and attention: The state of the art. *Cognition*, 80, 1–46.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.
- Zemel, R. S., Behrmann, M., Mozer, M. C., & Bavelier, D. (2002). Experience-dependent perceptual grouping and object-based attention. *Journal of Experimental Psychology-Human Perception and Performance*, 28, 202–217.