Object-based attentional facilitation and inhibition are neuropsychologically dissociated

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Abstract

Salient peripheral cues produce a transient shift of attention which is superseded by a sustained inhibitory effect. Cueing part of an object produces an inhibitory cueing effect (ICE) that spreads throughout the object. In dynamic scenes the ICE stays with objects as they move. We examined object-centred attentional facilitation and inhibition in a patient with visual form agnosia. There was no evidence of object-centred attentional facilitation. In contrast, object-centred ICE was observed in 3 out of 4 tasks. These inhibitory effects were strongest where cues to objecthood were highly salient. These data are evidence of a neuropsychological dissociation between the facilitatory and inhibitory effects of attentional cueing. From a theoretical perspective the findings suggest that 'grouped arrays' are sufficient for object-based inhibition, but insufficient to generate object-centred attentional facilitation.

Introduction

Attention refers to a range of cognitive mechanisms that help select behaviourally relevant information for processing while suppressing the processing of irrelevant information. These attentional mechanisms can operate on spatial representations (e.g. Posner 1980), object representations (e.g. Duncan, 1984) and representations of individual features (e.g. Treisman & Gelade, 1980). The locus of attention can be guided in a consciously controlled way in response to our current goals and desires (Endogenous orienting), or in an unconscious, stimulus driven way in response to salient events in the environment (exogenous orienting) (Posner, 1980). This latter form of orienting is transient, with the maximal attentional facilitation occurring ~150ms after stimulus onset (Muller & Rabbitt, 1989). By ~300ms attention has been withdrawn from the salient location and is superseded by a sustained inhibitory effect. This inhibitory effect is characterised by slowed orienting to targets presented at the cued location (Inhibition of Return: IOR (Posner, Rafal, Choate, & Vaughan, 1985) and an impaired ability to make perceptual discriminations at the cued location (Inhibitory Cueing Effect: ICE, see Hilchey, Klein, & Satel, 2014). The facilitatory and inhibitory effects of attention are thought to be mediated by independent neural and cognitive systems (e.g. Posner et al., 1985).

In the lab, exogenous attentional facilitation and inhibition are typically studied using cueing tasks. In the canonical cuing task a participant is presented with a fixation point and some placeholders. A salient visual transient is then presented at one of the placeholders. The participant is then presented with a second stimulus to which they must make a response (e.g. press a button as fast as possible). This target stimulus appears with equal probability at the same location as the visual transient (the cued location) or at some other location (the uncued location). This manipulation ensures participants are not motivated to endogenously attend to the cued location. Attentional facilitation is operationalised as faster responding to targets at

the cued location. Inhibition is operationalised slower responding to targets at the cued location (relative to the uncued location).

These cueing tasks were originally developed to examine spatial attention but were subsequently adapted to study object-based attention. The seminal study (Egly, Driver, & Rafal, 1994) demonstrated that attention could also operate in an object-centred frame of reference. Participants were shown two rectangles on a screen. One end of one of the rectangles was cued with a luminance flicker. After a short delay a probe appeared at one of the 4 rectangle ends. RTs were fastest at the cued location. However, RTs to the uncued location *within the cued object* were also significantly faster than RTs to the uncued location opposite the cued location. Critically, these locations were equidistant from the location of the cue, so the RT difference could not be caused by differences in spatial attention. Egly et al., concluded that attention spread from the cued location throughout the cued object, demonstrating that attention could be influenced by the presence of objects in the scene. Jordan & Tipper (1999) subsequently demonstrated that inhibitory effects could also spread throughout cued objects. Further evidence of object based attentional processing comes from studies of moving objects. Specifically, Tipper and colleagues (Tipper, Driver, & Weaver, 1991; Tipper, Weaver, Jerreat, & Burak, 1994) presented participants with array of objects. One object was cued, then all the objects moved to a new position. Participants exhibited inhibitory effects when the target appeared at the spatial location of the cue (which was now occupied by a new object) and when the target appeared on the cued object, (which had moved to an uncued spatial location). This latter effect demonstrates that attentional inhibition can be encoded in an object-based frame of reference.

Interestingly, magnitude of object centred effects appears to be influenced by the identity of objects. For example, in a typical Posner-style cueing task Schendel, Robertson & Treisman (2001) showed that changing the shape of an object during a trial reduced the

magnitude of the inhibitory effect from ~18ms to ~8ms. Paul & Tipper (2003) used more complex stimulus arrays and reported that IOR was larger and more persistent for objects differentiated by colour, form and spatial location compared to objects differentiated by spatial location alone. In a related study Tipper and colleagues (Tipper, Grison, & Kessler, 2003) paired a peripheral cue with a highly recognisable stimulus presented at fixation (a face). Following a variable delay a second face stimulus was shown at fixation, along with a peripheral target. Inhibitory effects were only observed when the stimulus paired with the target was identical to that paired with the cue. This result was subsequently replicated and extended using real objects (Morgan, Paul, & Tipper, 2005) and abstract objects (Morgan & Tipper, 2007).

The behavioural characteristics of object-centred facilitatory and inhibitory cueing effects have been extensively reviewed (Reppa, Schmidt, & Leek, 2012; Scholl, 2001) but the *relationship* between object-based facilitation and object-based inhibition has received less interest. Indeed, it remains unclear to what extent object ICE depends on the same cognitive and neural structures as object-centred attentional facilitation. Recent studies examining the neural correlates of object-based attentional facilitation argue that the ventral visual system, and in particular the Lateral Occipital region (LO), is of critical importance for the attentional facilitation of objects. For example, LO is associated with attentional prioritization of an object (Fink, Dolan, Halligan, Marshall, & Frith, 1997; Hou & Liu, 2012; Murray & Wojciulik, 2004) and the automatic spread of attention with objects (Martinez et al., 2006). Furthermore, de-Wit and colleagues (de-Wit, Kentridge, & Milner, 2009) observed that object-based attentional facilitation was abolished in a patient with a bilateral ventral lesion which included area LO. Together, these studies offer compelling evidence that LO is a key neural substrate for object-centred attentional facilitation.

However, it should not be assumed that what is true for facilitatory processes will also apply to inhibitory ones. In fact, there is considerable evidence that the facilitatory and inhibitory effects of *spatial* attention are mediated by separate mechanisms (Ivanoff & Klein, 2003; Mele, Savazzi, Marzi, & Berlucchi, 2008; Smith, Rorden, & Jackson, 2004; Smith, Rorden, & Schenk, 2012; Smith & Schenk, 2010; Tassinari, Aglioti, Chelazzi, Peru, & Berlucchi, 1994) and that object-centred IOR can be observed in the absence of attentional capture (Smith, Jackson, & Rorden, 2009). Indeed, although studies which explicitly examine the neural correlates of object-centred inhibition have reached the broad conclusion that object IOR is mediated by cortical, rather than subcortical neural systems (Possin, Filoteo, Song, & Salmon, 2009; Smith et al., 2009; Tipper et al., 1997), they do not appear to support the specific hypothesis that area LO forms the neural substrate for object-centred inhibition effects. More specifically, Vivas and colleagues (Vivas, Humphreys, & Fuentes, 2008) reported that patients with parietal lesions had deficient object IOR and concluded that object IOR was mediated by the parietal cortex (i.e. the dorsal visual system). Thus, the existing neurophysiological and neuropsychological evidence suggests a possible dissociation between object- centred attentional facilitation and object-centred inhibition, such that facilitation is mediated by LO, whereas inhibition is mediated by structures in the parietal cortex. However, to date no study has explicitly examined the extent to which object-centred facilitation and inhibition engage similar mechanisms within the same participants. Here, we address this issue by examining object-centred attentional facilitation and object-centred inhibitory cueing effects in patient DF. Patient DF has extensive bilateral damage to the ventral visual cortex, encompassing the lateral occipital gyri (LO) with signs of atrophy in other parts of the brain but largely sparing V1 and the fusiform gyri (James, Culham, Humphrey, Milner, & Goodale, 2003). If object facilitation and object ICE are indeed mediated by different neural and cognitive systems, such that facilitation relies on LO

whereas inhibition relies on parietal areas, DF should show disrupted object-centred attentional facilitation but may have preserved object-centred inhibitory cueing effects.

Participants

DF:

Patient DF is a 58 year old female with extensive bilateral damage to the ventral visual cortex caused by carbon monoxide poisoning in 1988. The lesion encompasses the lateral occipital gyri (LO) with signs of atrophy in other parts of the brain but largely sparing V1 and the fusiform gyri (James et al., 2003). DF also has a right inferior quadrantanopia with 5° of macular sparing (Hesse, Ball, & Schenk, 2012). DF performs at chance when asked to discriminate the shapes of different black polygons presented on a white background but her ability to discriminate luminance, colour and texture differences are normal (Milner et al., 1991).

Age Matched Controls:

Ten right-handed, age-matched controls (8 female, aged 49-63,) participated in Experiment 1. Eight age-matched control participants completed Experiments 2, 3 and 4 (7 female, aged 48-65), four of whom had also participated in Experiment 1.

Experiment 1

Stimuli & Materials

A fixation cross (5mm) was presented in the centre of the screen. The objects were black polygons (a square, a hexagon, an octagon) presented on a white background. Each object subtended 1.2° of visual angle at their widest point. Objects were presented on the circumference of an imaginary circle with a radius of 3.5° of visual angle. The objects were

separated by an arc of 120°. This setup ensured none of the stimuli appeared within DFs scotoma. The cue was a black outline of the object (width 2 pixels) filled with white. The probe was a red spot (0.35° of visual angle) that appeared at the centre of one of the objects. Objects were displayed on a 17" colour monitor. Responses were collected using a keyboard.

Procedure

Participants sat in a dark room with the head supported by a chinrest 80cm from the computer monitor. Trials began with the onset of the objects. Starting locations were counterbalanced across trials. After 1500ms one of the objects was cued for 100ms by replacing the solid symbol with a symbol that presented only the outline of the same symbol (see Fig. 1A). 100ms later the fixation point was cued for 100ms. After a further delay of 50ms the objects began to move in a clockwise direction at a speed of 63°/s for 112ms. 200ms after motion offset the target appeared and remained present until response or until 2500ms had elapsed. There was an inter-trial interval of 1500ms. Total SOA between cue and probe was 662ms. The probe appeared at the cued spatial location on 25% of trials (Valid Location trials), within the cued object on 25% of trials (Valid Object trials) and at the uncued object and location on 25% of trials (Invalid trials). The remaining 25% of trials were Catch trials (i.e., trials without a probe) and participants were instructed to withhold a response. DF completed 24 practice trials and 456 experimental trials. Breaks were given after each block. Controls completed 12 practice trials and two blocks of 72 experimental trials. Participants were instructed to fixate the centre of the display throughout each trial and to respond with a button-press as soon as they detected the onset of the target. Figure 1 illustrates the sequence of events.

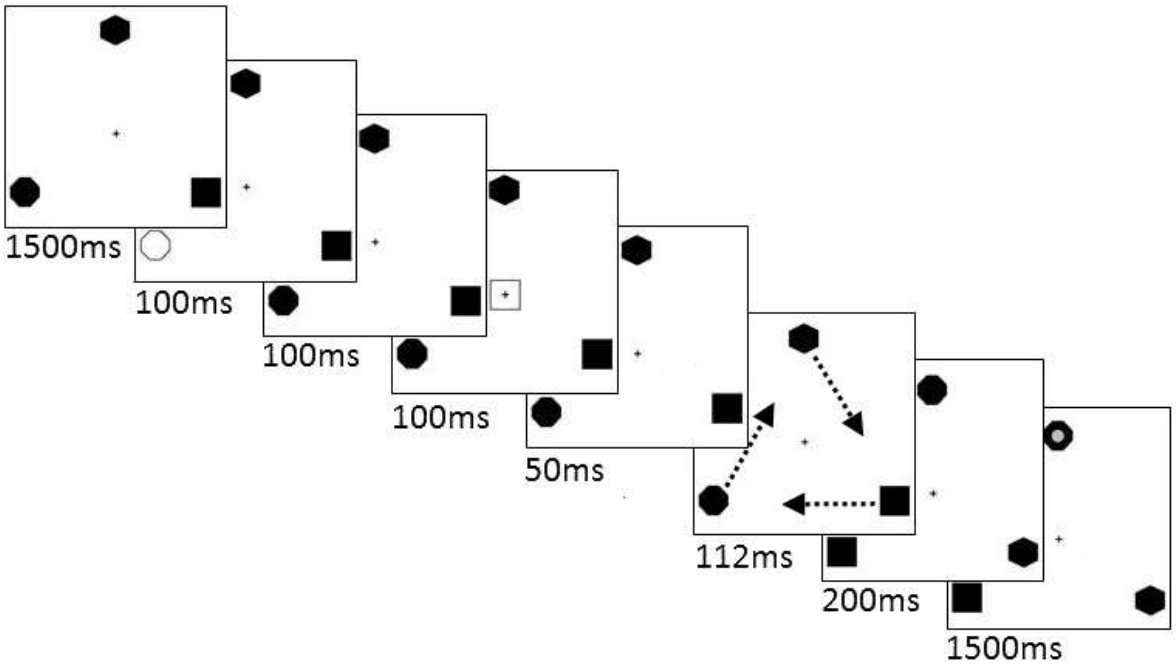

Figure 1: Procedure for Experiment 1. The figure shows the sequence of events and presentation times, starting with the panel in the top left corner. The dotted arrows represent the direction of motion.

Results & Discussion

Data from DF were filtered to remove catch trials, misses (n= 14) and anticipations (RT < 100ms; n = 2). DF reported false alarms on 10% of catch trials. One way ANOVA on the reaction times revealed a main effect of Validity ($F_{(321)} = 3.28$, $p < 0.05$). Planned comparisons revealed significant slowing of RT during Valid Object trials compared to Invalid trials ($t_{(213)} = 2.44$, $p < 0.05$; d=0.33) and a trend towards significant slowing of RT during Valid Location trials compared to Invalid trials ($t_{(214)} = 1.9$, $p = 0.059$; d=0.26). Figure 2 shows the mean reaction times in the different conditions. Accuracy data were analysed using a one-way ANOVA with a factor of Validity (Valid Location, Valid Object & Invalid). This analysis revealed no main effect of Validity ($F_{(2,337)} = 1.4$, $p = 0.245$).

Data from the control participants were filtered to remove catch trials, misses (n=2), anticipations (RT <150ms, n= 9) and responses that were more than 3 standard deviations longer than an individual's mean reaction time (n=11). One way ANOVA on the reaction times revealed a main effect of Validity ($F_{(2,18)} = 3.7$, $p < 0.05$). Planned comparisons (t-tests) revealed a significant object-centred ICE (9.3 ms; $t_{(9)} = 3.04$, $p < 0.05$; d=0.1) and a significant location ICE effect (7.4 ms; $t_{(9)} = 2.44$, $p < 0.05$; d=0.l). Figure 2 illustrates these effects.

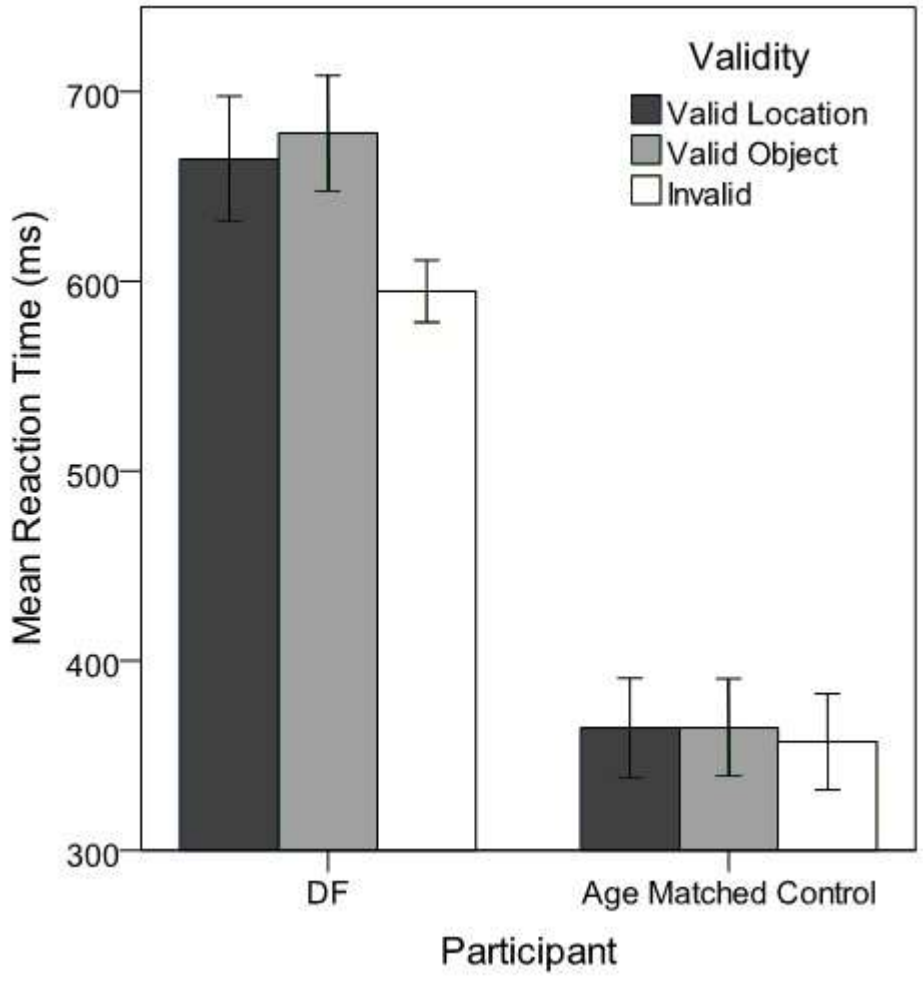

Figure 2: Experiment 1: Mean response times for age-matched controls (left bars) and DF (right bars). Error bars show +/-1 SEM

The magnitude of the ICE experienced by DF was compared to that of the control group using the modified t-test for single-case neuropsychology proposed by Crawford & Garthwaite (2002). The analysis indicated that DF experienced significantly larger object-centred ICE (83ms vs 7.5ms; t=7.5, p <0.01) and location-centred ICE (68ms vs 7.4ms, t=5.68, p <0.01) than the age-matched controls. However, it is clear from the data that DF's response times are much slower than those of controls. We therefore z-transformed the RT data from DF and controls (Faust, Balota, Spieler, & Ferraro, 1999) and conducted a second Crawford & Garthwaite t-test. This analysis revealed no significant difference between DF and the control group on either Object ICE (t=0.28, p>0.05) or location ICE (t=0.12, p>0.05). These results indicate that the apparent exaggeration of ICE in DF is actually an artefact of her prolonged and relatively noisy RTs.

The results suggest that dynamic object-centred ICE is preserved following damage to the ventral visual cortex, indicating that the ventral visual system is not required to generate object-centred ICE in dynamic displays. Given that DF has previously been shown to have a deficit of object-centred attentional facilitation (de-Wit et al., 2009), it is tempting to conclude that a neuropsychological dissociation exists between object ICE and object facilitation. However, strong conclusions are premature as the current experiment utilised moving objects, whereas previous studies examined attention and inhibition using static displays. To examine whether a dissociation between object facilitation and object ICE could be observed in static displays we examined object-centred attentional facilitation and ICE in 3 further experiments.

Experiment 2

Stimuli & Materials

Experiment 2 used an adaptation of the cueing paradigm devised by Egly et al. (1994). The objects were two vertically oriented, white outline rectangles (17° x 3.6° of visual angle) presented on a black background. The centre of the objects was 6.5° of visual angle to the left or right of fixation. The cue was a grey square (3.6° x 3.6° of visual angle) which appeared at the end of one of the bars. The target was a red or green coloured square (3.6° x 3.6° of visual angle) which appeared at the end of one of the bars. There was also a central cue used to orient attention back to fixation. This reorienting cue was a white ring with a diameter of 2° of visual angle. The experiment was generated using e-prime 2. Responses were collected with an e-prime response box.

Procedure

Participants sat in a dark room with their head 57cm away from the computer monitor. Trials began with the onset of the objects. After 1500ms the cue appeared at the end of one of the objects for 200ms. On 50% of trials the target appeared immediately following cue offset (200ms SOA). On the other 50% of trials there was a delay of 50ms, after which the re-orienting cue appeared at fixation for 100ms. The target then appeared 850ms after re-orienting cue offset (1200ms SOA). The target remained present until response or until 2500ms had elapsed. Twenty-five percent of trials were validly cued (i.e. cue and target appeared at the same location), on 25% of trials the target appeared within the cued object ($Invalid_{within}$), on 25% of trials the target appeared in the object opposite the cue ($Invalid_{between}$) and on 25% of trials the target appeared diametrically opposite the cue ($Invalid_{Diagonal}$). Cue position did not predict target location. Participants were asked to press a button corresponding to the colour of the target as quickly as possible. DF completed one block of 64 practice trials and 15 blocks of 64 experimental trials. Age matched controls

completed one block of 32 practice trials and three blocks of 64 experimental trials. Figure 3 illustrates the procedure.

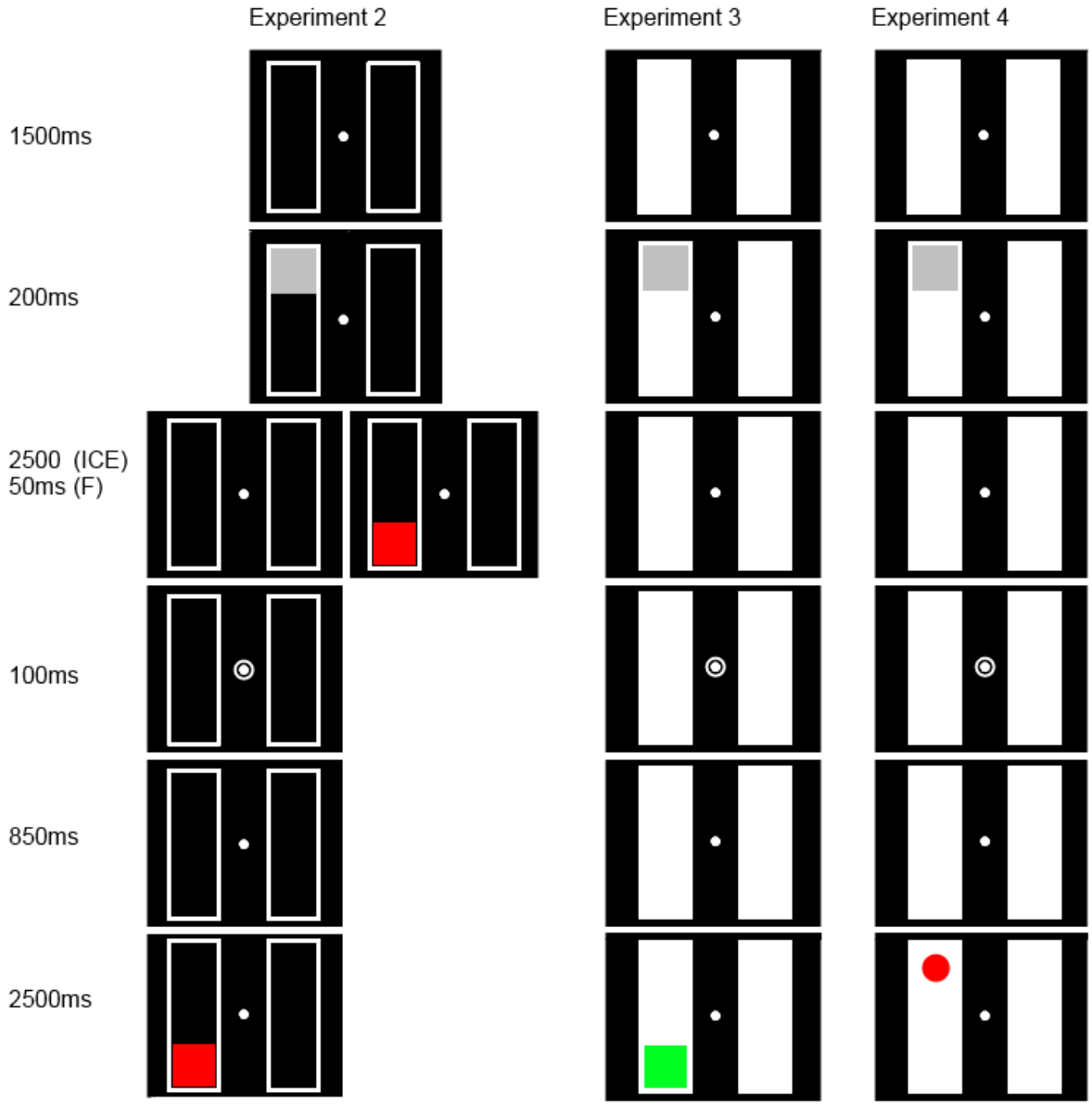

Figure 3: *Stimuli and procedure employed in Experiment 2, 3 & 4. For Experiment 2 the leftmost branch of the figure shows the sequence of events on trials measuring inhibitory cueing effect (ICE) and the right branch shows the sequence of events on trials measuring attentional facilitation (F). An* $Invalid_{within}$ *trial is illustrated for Experiments 2 and 3. Experiment 4 illustrates a Valid trial.*

Results

Trials from DF's lower-right visual field, where she has a scotoma, were excluded. We also excluded trials where the probe appeared diametrically opposite the cue. In this case

the spatial separation between cue and target is smaller on $Invalid_{within}$ trials than on $Invalid_{Diagonal}$ trials, making it hard to interpret any RT differences (see Egly et al., 1994). The data were then filtered to remove errors (N = 7) anticipations (RT<100ms) and RTs > 3SD from the mean RT (n=24) DF's mean reaction times were subjected to a 2 (SOA: 200ms, 1200ms) x 3 (Validity: Valid, $Invalid_{within}$, $Invalid_{between}$) ANOVA. The analysis revealed no main effects or interactions (SOA F=0.68; Validity F= 0.74; SOA x Validity F=0.57). Table 1 summarises the reaction times.

			Invalid Between	Invalid Within	Valid	Object-based cueing	Position based cueing
Experiment 2	DF	200ms	669 (151)	707 (184)	690 (132)	-38	-21
	Controls	200ms	501 (52)	493 (47)	497 (41)	7	4
Experiment 3	DF	200ms	651 (131)	726 (153)	650 (138)	-75†	1†
	Controls	200ms	497 (45)	474 (60)	482 (57)	26*	15
Experiment 2	DF	1200ms	692 (182)	695 (159)	720 (190)	-3	-28
	Controls	1200ms	468 (51)	489 (52)	477 (65)	-21*	-9
Experiment 3	DF	1200ms	633 (148)	649 (136)	617 (123)	-16†	18†
	Controls	1200ms	475 (63)	492 (71)	468 (60)	-17*	7
Experiment 4	DF	1200ms	417 (77)	493 (124)	465 (117)	-76*	-49*
	Controls	1200ms	293 (41)	299 (39)	304 (36)	-6*	-11*

Table 1: *Mean reaction times for each condition in Experiments 2-4. Object based cueing effects were calculated by subtracting $Invalid_{within}$ from $Invalid_{between}$. Position based cueing effects were calculated by subtracting Valid from $Invalid_{between.}$ Standard deviations are shown in parentheses. Negative numbers show an ICE effect. * = $p < 0.05$. † = cueing effect not tested for significance because the SOA x Validity interaction was not significant.*

Reaction time data from age matched controls were also filtered to remove anticipations (RT<100ms) and RTs > 3SD from the mean RT (n=12). Planned comparisons (paired t-tests) showed no significant within-object facilitation effect at the 200ms ($t_{(7)} = 0.92$) but a significant within-object ICE effect at 1200ms SOA. ($t_{(7)} = 2.6$, $p < 0.05$), see Table 1.

Discussion

Consistent with de-Wit et al. (2009), there was no evidence of within-object attentional facilitation in DF. However, the result from our study must be interpreted with caution as the age-matched controls also failed to show within-object facilitation. In contrast, the age matched controls did exhibit a small but significant within-object inhibitory effect at long SOAs whereas DF showed no such effect. On first inspection this result suggests that DF's preserved object-ICE is specific to displays in which objects are moving. However, this conclusion may be premature for three reasons. Firstly, the object in this experiment was a contour and the cues and targets appeared within the contour. Although healthy participants tend to treat the space within the contour as belonging to the object, there is another way of interpreting the scene. Specifically, the contour itself could be perceived as the object, and the space within the contour as background. In this case, the cue and target could be interpreted to have appeared on the background, not the figure. In this case, a failure to observe facilitation/inhibition at a location bounded by a contour would not constitute evidence that object-based attentional processes were disrupted. Secondly, there is considerable evidence that object-based attention is modulated by the salience of the cues to objecthood. For example, object ICE effects are smaller for illusory contours than real contours (Jordan & Tipper, 1999) and for hollow compared to filled rectangles (Reppa & Leek, 2003, 2006). Given that DF has a problem perceiving visual objects, it may be that stronger cues to objecthood are required to observe object-based attention effects in this patient. Finally, the magnitude of ICE shown by DF fell within the range of the control group, making it hard to draw a strong conclusion regarding the absence of ICE in DF. In Experiment 3 we addressed these issues by changing the object to solid forms to provide more powerful cues to objecthood and make it unambiguous that the cues and targets appeared on the figure, rather than the background.

Experiment 3

Stimuli & Materials

Stimulus properties were as described in Experiment 2, with the exception that filled white rectangles were used as objects (see Fig. 3).

Procedure

The procedure was identical to that described in Experiment 2.

Results

Data from DF were filtered to remove lower RVF trials, $Invalid_{Diagonal}$ trials, errors (n=5), time-outs (n= 24) anticipations (n= 1) and trials with RTs > 3 SD from the mean RT (n=12). Mean reaction times were subjected to a 2 (SOA: 200ms, 1200ms) x 3 (Valid, $Invalid_{within}$, $Invalid_{between}$) ANOVA. The analysis revealed a main effect of SOA (F = 6.66, p <0.05) and a main effect of Validity (F = 4.02, p <0.05) but no Validity x SOA interaction (F = 1.06). Analysis of simple main effects revealed that RTs on $Invalid_{within}$ trials were significantly slower than RTs on Valid (687 vs 634; $t_{(202)}$ = 2.7, p <0.05) and $Invalid_{between}$ (687 vs 642; $t_{(164)}$ = 2.02, p <0.05) trials.

Data from age matched controls were filtered to remove errors (n=60) and trials with RTs > 3SD from the mean RT (n=16). Mean reaction times were subjected to a 2 (SOA: 200ms, 1200ms) x 3 (Valid, $Invalid_{within}$, $Invalid_{between}$) repeated measures ANOVA. The analysis revealed a Validity x SOA interaction (F = 6.54, p <0.05). Paired t-tests confirmed a within-object advantage at 200ms SOA ($Invalid_{within}$ 475ms; $Invalid_{between}$ 597ms; $t_{(7)}$ = 2.84, p <0.025) and a within-object inhibition at 1200ms SOA ($Invalid_{within}$ 493ms; $Invalid_{between}$

475ms; $t_{(7)}$ =2.88, p <0.025). Figure 4 illustrates these effects.

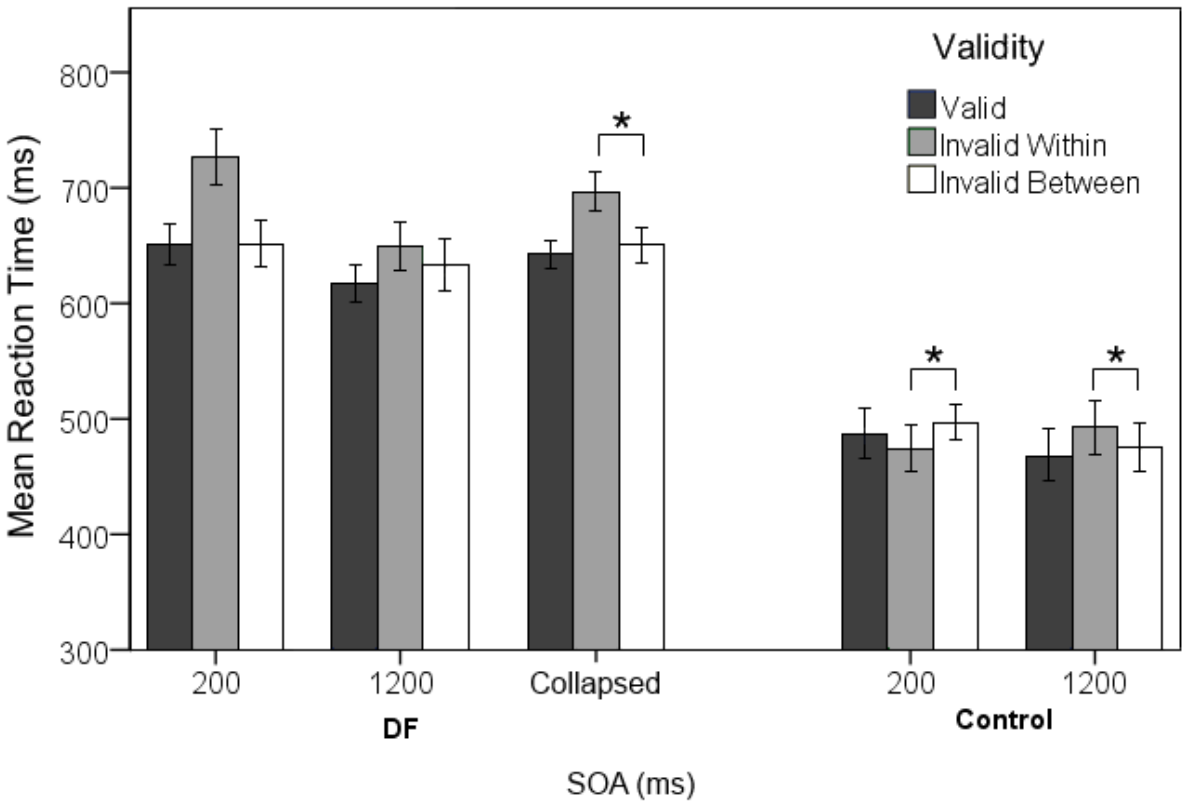

Figure 4*: Experiment 3. The three sets of bars on the left show data from DF. The data from each SOA (leftmost sets of bars) are shown to facilitate comparison between DF and the controls, but please note there was no SOA x Validity interaction for DF. The central set of bars shows the data collapsed across SOA, illustrating the main effect of Validity observed in DF. The two sets of bars on the right show the SOA x Validity interaction observed in age matched controls. Error bars show +/-1 SEM.. . * = p <0.05.*

Discussion

As with Experiment 2, DF showed no evidence of object-based attentional facilitation. There was a main effect of validity, such that RTs were slower when the target appeared at the cued $Invalid_{within}$ condition, relative to the $Invalid_{between}$ condition, consistent with the presence of an object-centred inhibitory cueing effect. In contrast, the age matched controls showed the typical biphasic pattern of object-centred facilitation followed by inhibition. The most likely explanation for the discrepancy between Experiment 2 and 3 is that the display in Experiment 3 contained more salient information about which elements should be parsed into objects, thus enhancing within-object attentional effects in the control

group (Reppa & Leek, 2003). Increasing the salience of the information about objecthood did not enhance within-object attentional facilitation in DF. Indeed, the object ICE effects were much larger at the short SOA. It is tempting to explain the early onset of object ICE in the following way. In the intact brain the onset of the cue triggers parallel, competing processes of facilitation and inhibition. For the first few hundred milliseconds the facilitatory process are dominant and RTs are quicker when probes appear at cued objects. However, at longer intervals inhibition is dominant and RTs are slower at cued locations. In the case of DF, the object-based facilitation is impaired but the inhibitory processes are not. As a consequence, the inhibitory effect which is typically masked by facilitatory effects at short SOAs can be observed in DF. Regardless of the cause of the early onset of ICE, this experiment suggests that DF's lack of within-object attentional facilitation is not driven by a perception that the cue appeared on the ground rather than the figure.

In Experiment 3 object ICE was observed when cues to objecthood were made more salient. In Experiment 4 we examined whether this effect would generalise when the response required was a simple detection task rather than a discrimination task.

Experiment 4

Stimuli & Materials

Stimulus properties were as described in Experiment 3, with the exception that the target was a red disk (diameter 3° of visual angle)

Procedure

The procedure was similar to that described in Experiment 2 with the following exceptions. Firstly, there was no 200ms SOA condition. Secondly, on 10% of trials no target was presented and participants were instructed to withhold their response. Thirdly,

participants responded to the appearance of the target by pressing a button on the response box as quickly as possible. Finally, DF completed one block of 36 practice trials and 5 blocks of 72 experimental trials. Age matched controls completed one block of 10 practice trials and 3 blocks of 72 experimental trials.

Results & Discussion

One participant withdrew before completing the experiment. Data from DF were then filtered to remove trials where targets appeared diagonally opposite the cue, trials from the lower right VF and trials with RTs > 3SD from the mean RT (n=8). DF's mean reaction times were subjected to a one-way ANOVA with a factor of Validity (Valid, $Invalid_{within}$, $Invalid_{between}$). The analysis revealed a main effect of Validity ($F= 5.20$, $p <0.05$) such that $Invalid_{within} < Valid < Invalid_{between}$. T-tests revealed a significant difference between $Invalid_{between}$ and $Invalid_{within}$ ($t_{(83)}=3.536$, $p<0.025$), consistent with the presence of Object ICE. There was also a significant difference between Valid and $Invalid_{between}$ ($t_{(103)}=2.34$, $p<0.025$), indicating the presence of a spatial ICE.

Data from age matched controls were filtered to remove trials where targets appeared diagonally opposite the cue, trials with RTs > 3SD from the mean (n=6) and misses (n=1), then subjected to a repeated measures ANOVA with a factor of Validity (Valid, $Invalid_{within}$, $Invalid_{between}$). The analysis revealed a main effect of Validity ($F= 5.23$, $p <0.05$), such that $Valid < Invalid_{within} < Invalid_{between}$ (see Table 1), consistent with the presence of both spatial and within-object ICE in age matched controls. A planned comparison (1 tailed t-test) confirmed the presence of a small but significant within-object ICE ($Invalid_{within}$ 299ms; $Invalid_{between}$ 293ms; $t_{(6)} =2.07$, $p <0.05$). Figure 5 illustrates these effects. As with Experiment 1 the within-object ICE observed in DF was significantly larger than that of the control group (76ms vs 6ms, $t=4.9$, $p < 0.01$) when compared using a t-test for single-case

neuropsychology (Crawford & Garthwaite 2002). As with Experiment 1 we applied a z transformation to the RT data and reanalysed the ICE effects with a Crawford & Garthwaite t-test. The test just failed to reach significance (t=1.89, p = 0.054).

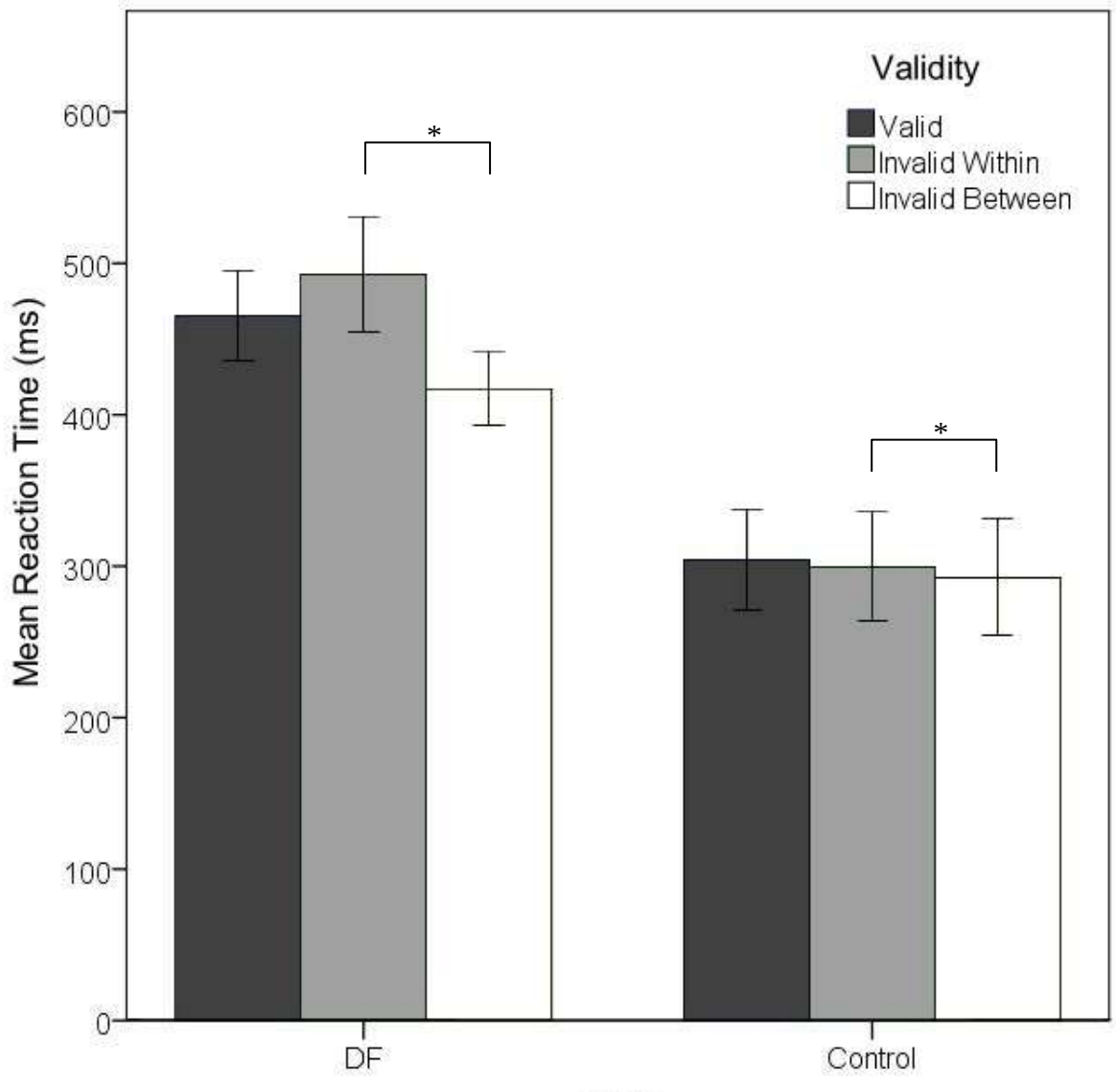

***Figure 5**: Experiment 4. The bars show the main effect of Validity observed in DF and control participants. Error bars show 95% confidence intervals. * = p <0.05*

General Discussion

The goal of our study was to examine the functional role of Lateral Occipital Cortex in object based attentional facilitation and inhibition. Firstly, it is clear that subtle variations

in experimental conditions significantly modulated the presence of facilitation and inhibition effects (see Reppa et al., 2012). This observation is certainly true for healthy participants but in part also for DF. More specifically, we found robust inhibition for both space and objects in DF and healthy participants when a dynamic display coupled with a single speeded response paradigm was used. However those effects were substantially weakened and in the case of DF completely abolished when a static display with contour-defined objects and a choice RT paradigm was employed. Effects recovered somewhat with the introduction of solid forms instead of a contour-based object and persisted when a static display was combined with solid forms and a detection paradigm. These data suggest that both the nature of the experimental stimuli and the nature of the response influenced ICE effects, with the most reliable effects being observed when there are clear cues to objecthood and the task is a speeded detection task. Table 2 illustrates the pattern of results across the different experimental conditions.

			Reference Frame			
Experiment	**Stimulus properties and response type**	**Attentional Effect**	**Space**		**Object**	
			DF	**Healthy**	**DF**	**Healthy**
1	Dynamic, Solid object, Single RT	Facilitation	—	—	—	—
		Inhibition	✓	✓	✓	✓
2	Static, Contour defined object , Choice RT	Facilitation	✗	✗	✗	✗
		Inhibition	✗	✗	✗	✓
3	Static, Solid object, Choice RT	Facilitation	✗	✗	✗	✓
		Inhibition	✗	✗	✓	✓
4	Static, Solid object, Single RT	Facilitation	—	—	—	—
		Inhibition	✓	✓	✓	✓

Table 2: Pattern of attentional cueing effects across different experimental setups.

Despite these variations in performance a number of interesting observations can be made. For DF (and also for healthy observers) a significant object-ICE was found in three out

of four experiments. These findings suggest that the damaged ventral stream structures do not form an irreplaceable part of the mechanisms underlying object-based ICE effects. In contrast to object-based ICE, facilitation effects were found in none of the experiments with DF, consistent with the findings of de Witt et al., (2009). In this respect we observed a dissociation between DF and healthy observers since healthy observers but not DF produced a significant object-facilitation effect in Experiment 3. It is tempting to argue that LOC and other damaged parts of the ventral stream may be critical for object-based facilitation but not for object-based IOR effects. This line of argument could certainly help explain why DF tended to show a larger ICE effect compared to controls in the static detection task (Experiment 4). Specifically, if it is assumed that ICE and attentional facilitation act in competition, it might be argued that the absence of attentional facilitation in DF allowed the ICE effect to emerge earlier and more powerfully.

However, we do not think our data provides conclusive evidence for such a statement. The main problem is that we did not obtain reliable position-based facilitation effects in either DF or in our healthy participants. One explanation for the weakness of the facilitation effect is that the discrimination task may have been so easy that it was relatively insensitive to the effects of attention, particularly for control participants. There is good evidence that attention influences perception by altering the sensitivity of the cortex to incoming sensory information. Attentional facilitation enhances the signal-to-noise of attended signals (Carrasco, 2011; Carrasco, Ling, & Read, 2004) and inhibition reduces the signal to noise (Sapir, Jackson, Butler, Paul, & Abrams, 2014; Smith, Ball, & Ellison, 2012). If the test-task is too easy, attending / inhibiting the cued location or object may not actually have produced a sufficiently large boost in the signal-to-noise to produce a detectable difference in choice RT performance. Irrespective of the precise reason for the weakness of facilitatory effects, it seems clear that our experimental paradigms were not perfectly suited to produce position-

based facilitation effects. This means that we do not know whether DF's lack of facilitation effects is specific to object-based paradigms or may in fact reflect a more general inability to benefit from attentional facilitation. However, De-Wit et al.'s (2009) finding of intact spatial facilitation effects in DF seem to argue against such a generalized facilitation deficit. Our own observation in Experiment 3, where DF showed inhibitory effects already with short SOAs suggests instead that the general slowing of visual processes in DF might mask early facilitation effects. In this case one might expect that the critical variable that determines whether DF shows facilitation effects may be the ease with which the required visual stimulus can be processed within the affected ventral stream, as opposed to the distinction between spatial versus object-based cueing. However, this question certainly requires further research.

The second dissociation between DF and healthy observers relates to Experiment 3. In this experiment contour-defined objects were used. These objects were clearly sufficient to produce object-based ICE effects in healthy observers but not in DF. It thus seems that DF's ability to use object-information to guide attention depends on the features that are used to define objecthood. Clearly, DF requires more salient features than healthy observers. The observation that attention in DF is influenced by surface but not contour is also consistent with the claim that LO is the key cortical substrate for contour integration (Volberg & Greenlee, 2014)

Taken together our findings suggest that LOC and surrounding areas are not critical for object-based ICE per se, but may contribute cues for the perceptual grouping process that allows observers to identify a group of visual stimuli as belonging to one object. Such a view can explain why DF is subject to object-based ICE in some conditions but not others. This view is also broadly consistent with the grouped array hypothesis (Hollingworth, Maxcey-Richard, & Vecera, 2012; Vecera & Farah, 1994) This hypothesis states that object-based

attention reflects attention to a number of spatial locations that have been grouped together by perceptual organization processes occurring early in the visual process (i.e. grouping by proximity, colinearity, shared contours etc.). The hypothesis states further that those spatial locations are coded in an egocentric spatial frame of reference. This last assumption fits well with our earlier observation that DF is particularly impaired in tasks that require allocentric coding while producing relatively normal performance when egocentric coding is required (Schenk, 2006).

To summarise, we found preserved object-based attentional inhibition in a patient with bilateral damage to parts of the ventral stream. This inhibitory effect appeared to be modulated by the ease with which visual stimuli could be grouped into objects. We conclude that the ventral stream does not provide the essential mechanism for object-based ICE but probably contributes perceptual cues that support the grouping of spatial locations that is needed to select and focus on visual objects.

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