Neuropsychologia 92 (2016) 51–58

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Reprint of: Object-based attentional facilitation and inhibition are neuropsychologically dissociated

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ARTICLE INFO

Keywords:
Attention
Inhibition
Object
Space
Exogenous
Lesion
Lateral Occipital Cortex
Agnosia
Cueing
IOR
Ventral stream

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Salient peripheral cues produce a transient shift of attention which is superseded by a sustained inhibitory effect.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.

1. 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 and 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 ~150 ms after stimulus onset (Muller and Rabbitt, 1989). By ~300 ms attention has been withdrawn from the salient location and is superseded by a sustained inhibitory effect.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 et al., 1985) and an impaired ability to make perceptual discriminations at the cued location (Inhibitory Cueing Effect: ICE, see Hilchey et al. (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 et al., 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

DOI of original article: http://dx.doi.org/10.1016/j.neuropsychologia.2015.11.003
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http://dx.doi.org/10.1016/j.neuropsychologia.2016.11.002
Received 19 August 2015; Received in revised form 30 September 2015; Accepted 5 November 2015
Available online 15 November 2016
0028-3932/

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 and 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 et al. (1991, 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 et al. (2001) showed that changing the shape of an object during a trial reduced the magnitude of the inhibitory effect from ~18 ms to ~8 ms. Paul and 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 et al. (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 et al., 2005) and abstract objects (Morgan and Tipper, 2007).

The behavioural characteristics of object-centred facilitatory and inhibitory cueing effects have been extensively reviewed (Reppa et al., 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 prioritisation of an object (Fink et al., 1997; Hou and Liu, 2012; Murray and Wojciulik, 2004) and the automatic spread of attention with objects (Martinez et al., 2006). Furthermore, de-Wit et al. (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 and Klein, 2003; Mele et al., 2008; Smith et al., 2004, 2012a, 2012b; Smith and Schenk, 2010; Tassinari et al., 1994) and that object-centred IOR can be observed in the absence of attentional capture (Smith et al., 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 et al., 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 et al. (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 et al., 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.

2. Participants

2.1. 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 et al., 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).

2.2. 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.

3. Experiment 1

3.1. Stimuli and materials

A fixation cross (5 mm) 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.

3.2. Procedure

Participants sat in a dark room with the head supported by a chinrest 80 cm from the computer monitor. Trials began with the onset of the objects. Starting locations were counterbalanced across trials. After 1500 ms one of the objects was cued for 100 ms by replacing the solid symbol with a symbol that presented only the outline of the same symbol (see Fig. 1A). 100 ms Later the fixation point was cued for 100 ms. After a further delay of 50 ms the objects began to move in a clockwise direction at a speed of 63°/s for 112 ms. 200 ms after motion offset the target appeared and remained present until response or until 2500 ms had elapsed. There was an inter-trial interval of 1500 ms. Total SOA between cue and probe was 662 ms. The probe appeared at