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An intact eye-movement system is not required to generate inhibition of return

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Abstract

AI is unable to make eye-movements and has a deficit of reflexive attention (Smith, Rorden, & Jackson, 2004). Here, we demonstrate that despite these deficits AI exhibits Inhibition of Return (IOR) for peripherally cued objects and locations. These data suggest that an intact oculomotor system is not required for the generation of either object-based or location-based IOR, and are consistent with the view that the early, facilitatory effects of peripheral cues and late IOR effects are mediated by different mechanisms.

Introduction

Salient peripheral events trigger a reflexive shift of attention which, under certain circumstances, is superseded by a sustained Inhibition of Return effect (IOR: Posner, Rafal, Choate, & Vaughan, 1985). The most common explanation for IOR is that it prevents the observer from re-inspecting already attended objects or locations, thus facilitating visual search (Klein & MacInnes, 1999). This ‘foraging facilitation’ account of IOR is widely accepted as the ‘why’ of IOR, but the ‘how’ of object and location-based IOR remains highly controversial. Several studies have shown that patients with lesions to parts of the oculomotor system such as the superior colliculus (SC) present abnormal or abolished patterns of IOR (Danziger, Fendrich, & Rafal, 1997; Sapir, Soroker, Berger, & Henik, 1999; Sereno, Briand, Amador, & Szapiel, 2006), and Transcranial Magnetic Stimulation (TMS) over the Frontal Eye Fields (a cortical structure involved in visual processing and saccade control) also disrupts IOR (Ro, Farne, & Chang, 2003), suggesting that an intact oculomotor system is necessary for the production of IOR.

However, other studies are not consistent with this idea. Sumner, Nachev, Vora, Husain, & Kennard, (2004) have shown that IOR can be generated in response to stimuli which cannot be processed by the SC, indicating that IOR can be generated independently of the oculomotor system. Similarly, in a previous report we have demonstrated that AI (a unique single case who has a congenital oculomotor palsy, a condition which means she is unable to make eye-movements) does not show early reflexive attention shifts in response to a peripheral cue, but in one of our experiments there appeared to be evidence of an IOR effect (Smith et al., 2004).

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These studies appear to support the view that IOR can be generated independently of the oculomotor system. However the conclusion that an intact eye-movement system is not required for the generation of IOR may be premature. IOR can be attached to both locations and moving objects (Tipper, Driver, & Weaver, 1991; Tipper, Weaver, Jerreat, & Burak, 1994; Weaver, Lupianez, & Watson, 1998). The SC can respond to moving stimuli but it cannot code direction of movement, rendering it incapable of being directly involved in the generation of IOR attached to mobile objects (Tipper et al., 1994). To account for these data they have hypothesised that location-based IOR is mediated by the midbrain visuomotor pathways responsible for eye-movements and object-based IOR mediated by a newer, cortical system.

The studies of Smith et al., (2004) and Sumner et al., (2004) used only static stimuli (i.e. object and location were never decoupled). If object and location are confounded the possibility that disruption to location-based IOR (which could depend on an intact oculomotor system) was masked by an intact object based IOR cannot be ruled out.

In the current study we used a modified version of the object based IOR paradigm described by Tipper et al., (1994) to decouple object and location based IOR effects in AI. If location-based IOR depends on an intact oculomotor system but object based IOR depends on a different, perhaps cortical, mechanism AI should show abnormal or abolished location-based IOR, but may retain intact object-based IOR.

Methods

Participants

At the time of testing AI was a 26 year old female university graduate in full-time employment. Two previous reports describe AI's condition in detail. Gilchrist, Brown, & Findlay, (1997) provided the original case study, and the aetiology and functional characteristics of AI's ophthalmoplegia have been described by Gilchrist, Brown, Findlay, & Clarke, (1998). These studies indicate that the ophthalmoplegia has been present since birth. Consequently, AI has never made an eye movement. A medical examination of AI's eyes revealed thin and fibrotic extra-ocular muscles, a finding which was consistent with a diagnosis of oculofibrosis syndrome of unknown aetiology. Ultrasonic imaging of the affected muscles demonstrated no changes in their size or shape when AI attempted to make eye movements. AI was also tested for the presence of an optokinetic nystagmus response, which is often taken as an indication of the presence of residual eye movement functions. No such response was seen, although some highly restricted drift movements were recorded (at most $\pm 0.5^\circ$). These drifts were not linked to stimulus motion.

Apparatus

Stimuli were displayed on a 19 inch Illyama Vision Master Pro 454 with a refresh rate of 80 Hz. The stimuli were generated using a Dell Inspiron 2650 laptop running E-Prime software. AI's head was supported by a chinrest located 57cm away from the monitor. Responses were collected with a computer keyboard.

Stimuli

The stimuli consisted of four coloured boxes (i.e. coloured outlines with a white centre; red [RGB 255,0,0], blue [65,0,255], green [0,128,0] and black [0,0,0]) and a black fixation point presented on a white background. The boxes were arranged in a cross formation with the centre of each box 80 from fixation. Each box had an area of $2.4^\circ \times 2.4^\circ$. In 50% of trials the boxes were aligned along the horizontal and vertical midlines. In the other 50% of trials the boxes were aligned along the 45° diagonals. Cues consisted of a $2.3^\circ \times 2.3^\circ$ colour patch

which appeared in one of the peripheral boxes. The colour of the cue matched the colour of the box in which it appeared. The probe was a black spot (0.5° diameter).

Procedure

Trials began with the appearance of four coloured boxes and the fixation point. After 1000ms the array began to rotate at $33^\circ/\text{s}$. Ninety-nine ms into the rotation the array paused for 100ms and a cue appeared in one of the peripheral boxes for 100ms. Rotation resumed for 99ms. A central cue then appeared around the fixation point for 33ms. Rotation continued for 132ms then stopped. After a variable SOA (170 or 470ms) a probe appeared in one of the boxes on 67% of trials. On the remaining 33% of trials no probe appeared and AI was instructed to withhold her response (catch trials). The total cue-target SOA was either 600ms or 900ms. The probe could appear in a square occupying the same spatial location as the cue (valid location trials), within the square which was the object that had been cued (valid object trials) or within one of the boxes which was neither the cued object nor the cued location (invalid trials). The probe had an equal probability of appearing in any of the 4 coloured squares. AI was instructed to respond to probes by pressing a key as fast as possible. AI was given 16 practice trials followed by 480 experimental trials (80 valid-object, 80 valid-location, 160 invalid and 160 catch).

Results

The data were filtered to remove responses of $< 100\text{ms}$ (anticipations) and responses that were > 2.5 SDs greater than AI's mean response time. This procedure resulted in the exclusion of 4 trials. AI also responded to 5 catch trials.

Reaction time data were subjected to an univariate ANOVA with factors of SOA (600 and 900ms) and Validity (valid location, valid object and invalid) revealed a main effect of Validity ($F(2) = 4.7$, $P < 0.01$) but no effect of SOA and no SOA $\times$ Validity interaction. For the remainder of the analysis data were collapsed across both 600 and 900ms SOAs. Planned contrasts revealed that response times were significantly faster when probes appeared at an uncued location compared to a validly cued object ($t(238) = 2.64$, $P < 0.025$) and a validly cued location ($t(237) = 2.29$, $P < 0.025$). There was no significant difference between valid object and valid location trials ($t(157) = 0.36$, $P = 0.79$). Figure 1 illustrates these effects.

Discussion

We observed significant object and location based IOR effects in AI, indicating that an intact oculomotor system is not required to generate either location or object based IOR. It is of interest to note that AI's head movements are qualitatively similar to the ocular saccades of normal participants (i.e. AI's head saccades are facilitated during the gap-paradigm, are delayed by the remote distractor effect, are slower when making antisaccades and produce saccadic suppression) indicating that AI has compensated for her inability to make ocular saccades by making head-saccades instead (Gilchrist et al., 1998). If this is the case it may suggest that IOR requires an intact saccadic system, rather than an intact oculomotor system per se. Indeed, this would be consistent with the view that IOR acts as a foraging facilitator which prevents the re-inspection of attended locations.

However, in one respect our results are counter to the notion of IOR as a foraging facilitator. Specifically, we have previously shown that AI does not reflexively attend to peripheral cues (although she did exhibit an IOR effect at 900ms; Smith et al., 2004). When considered in the light of our current data, this result suggests that AI develops IOR to locations and objects which have not yet been attended (in a sense this makes the term "Inhibition of Return" something of a misnomer for AI). The inhibition of processing at potentially

interesting, but unexplored, locations would not lead to efficient search. Furthermore, the observation of IOR in the absence of reflexive attention indicates that IOR emerges independently of a reflexive shift of attention rather than being a consequence of reflexive shift of attention.

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Figure 1. Response times in different cueing conditions. Dark grey bars show validly cued object trials, light grey bars show validly cued location trials and white bars show invalid trials. Error bars show ± 1 SEM.