Object-based attention involves subcortical neural mechanisms

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Abstract

Mechanisms of object-based attention (OBA) are commonly associated with the cerebral cortex. However, less is known about the involvement of lower visual pathways in these processes. In the current study, the classic double-rectangle cueing task (Egley et al., 1994) was implemented in a stereoscope, in order to differentiate between the involvement of lower (monocular) and higher (binocular) visual pathways in OBA processes. We found that there was a functional role for subcortical structures in two main aspects of OBA: in the process of exogenous orienting towards an object (Experiment 1; $N=34$); and in the process of attentional deployment within objects (Experiment 2; $N=32$). Thus, it seems that subcortical visual regions are not simply passing information to higher cortical areas but have a functional computational role in OBA. These findings emphasize the importance of subcortical regions in attentional processes and, more specifically, in OBA.

Introduction

The representational basis of attentional selection can be constructed upon spatial locations (space based attention; SBA), objects (object based attention; OBA), or other entities (e.g. features) (Egeth & Yantis, 1997). SBA involves attentional selection of a specific location in space. That is, attention facilitates responses to stimuli within a restricted area of the visual field (Posner, 1980). In SBA, attention is considered as a metaphoric spotlight that illuminates a region in space. Regions that fall within this spotlight are enhanced and afforded prioritized processing over those outside of it (Eriksen & Eriksen, 1974; Logan, 1996; Posner, 1980; Posner & Cohen, 1984; Treisman & Gormican, 1988). In contrast, OBA involves selection of a specific object and encompasses all of the features associated with that object (Kahneman & Henik, 1981; Neisser, 2014; Soto & Blanco, 2004). The double-rectangle cueing paradigm (Egley, Driver, & Rafal, 1994) has been used to simultaneously measure both SBA and OBA processes. In this task, two parallel rectangles are presented to participants. After a short period of time, one of the rectangle's edges are brightened briefly, providing an endogenous, predictive cue indicating the most likely location for target appearance. The participants are then required to detect a dark square (the target) which appears either within the cued rectangle (valid-cue condition) or in the uncued rectangle (invalid-cue condition). There are two types of invalid-cue trials: the target appears either at the uncued location within the cued rectangle (invalid-same object condition) or at the uncued rectangle (invalid-different object condition). Critically, these two invalid locations are equidistant from the cued location. As expected in cueing experiments, Egley et al. (1994) observed faster responses on valid-cue trials than invalid-cue trials; an instantiation of SBA. For invalid-cue trials, responses were faster for the same-object condition than for the different-object condition, indicating an instantiation of OBA often termed a 'same-object advantage'. The pattern of results demonstrated the existence of both components of attention simultaneously: SBA and OBA (Chen, 2012; Moore, Yantis, & Vaughan, 1998).

Visual attention processes are usually considered to be guided by a cortical network of frontoparietal regions (Pooresmaeili, Poort, & Roelfsema, 2014; Serences et al., 2004; Yantis & Serences, 2003; Kastner & Ungerlieder, 2001; Corbetta & Shulman, 2002) that provide biasing signals to visual cortex, indicating which stimuli should be attended and which should be ignored (Greenberg, Esterman, Wilson,

Serences & Yantis, 2010; Greenberg et al., 2012). Object perception is also considered to be a cortical function (i.e., LOC; Grill-Spector, 2003; Serre, Bileschi, Riesenhuber & Poggio, 2007). Nevertheless, attentional processes (both spatial and object-related) are adaptive for survival and are shared across many different species, some of which lack any cortical tissue (Krauzlis, Bogadhi, Herman & Bollimunta, 2018). One example comes from a study that examined the existence of exogenous and even endogenous spatial orienting of attention in the archer fish (Gabay, Leibovich, Ben-Simon, Henik, & Segev, 2013; Saban, Sekely, Klein & Gabay, 2017). The archer fish have an optic tectum but lack fully developed cortical structures. In these studies, archer fish were trained to perform a Posner cuing task, and demonstrated the typical pattern of results observed in humans: that is, both facilitation and inhibition of return (IOR). Thus, it seems that SBA can be performed without a fully developed cortex and relies upon subcortical visual pathways in addition to a cortical component.

The involvement of subcortical structures in attentional orienting in humans has also been suggested. For example, in a study that examined the functional role of visual monocular pathways in exogenous facilitation and IOR, it was found that exogenous facilitation involves subcortical regions, as indexed by monocular visual channels (Gabay & Behrmann, 2014). In that study, a Posner exogenous, non-predictive cuing task was presented via a stereoscope, which enabled presentation of different visual information to each eye separately, allowing for segregation between monocular (mostly subcortical) and binocular (mostly cortical) visual pathways. Using this procedure, IOR was observed both when the cue and target were presented to the same monocular channel, and to different monocular channels. In contrast to the IOR effect, exogenous facilitation was only observed when the cue and target were presented to the same monocular channel. The main conclusion was that exogenous facilitation is primarily reliant upon subcortical levels of the visual pathways. Based on the above-mentioned findings, one can infer that SBA involves lower, subcortical regions.

Similarly to SBA, it is reasonable to assume that subcortical mechanisms are also involved in OBA processes, yet the empirical evidence for this claim is sparse. One example comes from a study that focused on the neural substrates of space-based and object-based deployment of spatial attention (Arrington et al., 2000). Participants' performance was measured in a variant of the Posner spatial cueing task in which both space-based and object-based cueing could be implemented. During functional

magnetic resonance imaging (fMRI), participants were instructed to discriminate between target letters and flanker stimuli. In the object-cueing condition, a geometric shape-cue was presented which encircled the target letters. In the spatial-cueing condition, a central arrow cue pointed toward the target letters. Every display contained both types of cues (arrow and shape) and the participants were informed as to which cue to attend in each block. The results revealed that cortical areas such as the superior frontal gyrus, medial frontal gyrus, extrastriate regions, parahippocampal gyrus, and subcortical areas such as the pulvinar nucleus and inferior cerebellum, were more activated for object-cueing compared to the spatial-cueing. Although subcortical regions showed activation during the object-cueing condition, it is somewhat tenuous to infer a causal role of brain regions from neuroimaging studies, which are fundamentally correlational.

The current study focuses on the functional role of subcortical structures in OBA. In order to investigate the involvement of subcortical regions in OBA, we employed a stereoscope, thus enabling us to manipulate the visual information presented to each eye separately. This technique allowed us to examine the involvement of monocularly segregated subcortical regions of the visual processing stream (Figure 1) and infer causality regarding their functions.

Figure 1: *Schematic illustration of the experimental apparatus and visual pathways from the eyes to the brain. Each monitor provided visual information to a different eye. From the eye, the visual information passes first through monocularly segregated subcortical regions (dashed lines left eye, solid lines right eye). This information is then projected to the lateral geniculate nucleus (LGN) and subsequently reaches striate and binocular extrastriate regions.*

The stereoscope method relies on the fact that visual input is monocularly segregated until it reaches extrastriate regions (Horton, Dagi, McCrane, & de Monasterio, 1990; Menon, Ogawa, Strupp, & Ugurbil, 1997). Through the optic nerve, visual information reaches the lateral geniculate nucleus (LGN) of the thalamus. The LGN contains axons that terminate in the striate cortex (V1). Each track is sensitive to monocular information, while neurons in the extrastriate cortex and higher cortical regions are primarily sensitive to binocular information (Byrne & Hilbert, 1997). Presenting different visual information to each eye separately is an effective method for isolating the involvement of monocular (mostly subcortical) neural channels. Hence, if monocular regions of the visual pathway are functionally involved in a process, dividing the visual information by eye should impair performance, since the visual information would be segregated between the two monocular channels. In contrast, if subcortical areas are not functionally involved in this process, segregating the visual information between the eyes should have no effect on performance.

In two experiments, we aimed to understand the subcortical involvement in two aspects of OBA. The first process we investigated was the deployment of attention towards an object as the result of an attentional cue. Specifically, we wanted to examine whether the cuing of an object involves lower monocular channels. That is, whether the cue and the object must be presented to the same monocular channel in order to produce the typical OBA effect. The second process we examined was the influence of attentional deployment within a cued object on the detection of a target. That is, whether the cued object must be presented to the same monocular channel as the target in order to produce the typical OBA effect.

Experiment 1

The purpose of Experiment 1 is to isolate the involvement of monocular channels in the process of exogenous orienting towards an object, and to investigate participants' propensity to prioritize the processing of a cued versus uncued object. By segregating the cue from the objects and targets (see figure 2), we can examine our main hypothesis that cuing an object in order to create the OBA effect involves monocular (subcortical) visual channels.

Figure 2: An example of a typical trial in Experiment 1. The figure depicts a valid object, dichoptic condition trial. The left column represents the presentation to the left eye, the right column is the presentation to the right eye and the center column is the participants' perception.

Method

Participants. Thirty-four participants (11 males; 24.8 ± 3.9 years) consented to participate. All participants had normal or corrected-to-normal vision (i.e., only corrective lenses, no spectacles). We reimbursed participants for their time either via payment (30 NIS) or course credit. The Institutional Review Board (IRB) of the University of Haifa approved the experimental protocol.

Stimuli. For each participant the viewing distance was 45 cm. All stimuli were presented on a black background using a 22" CRT monitor with a $1,680 \times 1050$ screen resolution and a 59-Hz refresh rate. We used two rectangles as objects. Each rectangle measured 2.27° high x 11.48° wide, and was oriented either vertically or horizontally in a block design. The rectangles were formed by a white outline of thickness 0.5° . The

cues were introduced by increasing the width of the object's frame at the cued location from 0.5° to 1.1° . The target was the letter 'O' or 'Q' (Ariel Bold font, 0.501°) rendered in white. The screen was divided into 2 parts, so each half of the screen was presented to a different eye through the use of a stereoscope (Figure 2). On each side of the screen a large rectangle was presented to one of the eyes (and was also used to enhance convergence between the eyes). All visual stimuli were presented within the large rectangular frames.

Procedure. Each trial began with the appearance of two parallel objects. Objects were oriented either horizontally or vertically in different blocks, and the order of blocks was counterbalanced between participants. This initial screen lasted for 1000 ms, and was followed by a peripheral cue for 100 ms. The target was presented after a variable stimulus onset asynchrony (SOA) of 100 or 200 ms in one of three possible locations: (1) the same location as the cue (i.e., valid trial), (2) different location within the same object as the cue (i.e., invalid same object trial), or (3) in a different object than (but equidistant to) the cue (i.e., invalid different object trial). Targets were present until participants responded and RTs were recorded. The invalid same object and different object locations were equidistant from the valid position. The cue validity was 33%; that is, the cue was exogenous and non-predictive of the target location. We employed exogenous cues pursuant to the finding that exogenous, non-predictive cues yield stronger object-based selection (Goldsmith & Yeari, 2003). Participants were instructed to respond according to the target's identity by pressing either 'p' or 'q' (counterbalanced between participants) on a bilingual computer keyboard as quickly and accurately as possible. On half of the trials, the cue, target, and object were presented to a single eye (single eye presentation). On the other half of trials, the cue was presented to one eye and the target and object to the other eye (dichoptic presentation; see Figure 2). The factors manipulated in this task were target Eye Presentation (monoptic, dichoptic), Cue Validity (valid, invalid same object, invalid different object), Object Orientation (horizontal, vertical), and SOA (100 ms, 200 ms). Participants performed 4 experimental blocks. Each block contained 140 trials.

Results

Trials in which participants responded incorrectly were discarded (less than 10%). For each participant, responses in which RTs were faster or slower than 2

standard deviations from the mean of all participants and experimental conditions were also discarded (4.9%). A 4-way analysis of variance (ANOVA) was conducted on RT in the discrimination task, with Eye Presentation (same, different), Cue Validity (valid, invalid same object, invalid different object), Object Orientation (horizontal, vertical) and SOA (100 ms, 200 ms) as repeated measures factors. All main effects were significant. A significant main effect of Cue Validity was observed, [$F(2, 66) = 105.6$, $p < .001$, $\eta^2 = .76$]. Planned contrasts demonstrated significantly shorter RTs for the valid compared to both the invalid same object [$F(1, 33) = 119.27$, $p < .001$, $\eta^2 = .78$] and invalid different object conditions [$F(1, 33) = 146.48$, $p < .001$, $\eta^2 = .82$]. There was no significant difference between the invalid same and invalid different object conditions [$F(1, 33) = 3.62$, n.s.]. A significant main effect of Eye Presentation was observed, [$F(1, 33) = 23.5$, $p < .001$, $\eta^2 = .41$], indicating shorter RTs for the single eye ($M = 539.67$ ms, $SD = 18.34$) compared to the dichoptic condition ($M = 551.28$ ms, $SD = 18.04$). We observed a main effect of Object Orientation, [$F(1, 33) = 25.5$, $p < .001$, $\eta^2 = .43$], with shorter response times in the horizontal condition ($M = 531.1$ ms, $SD = 17.12$) than in the vertical condition ($M = 559.9$ ms, $SD = 19.45$). We also observed a main effect of SOA, [$F(1, 33) = 19.6$, $p < .001$, $\eta^2 = .37$], with shorter response time in the 200 ms condition ($M = 542.03$ ms, $SD = 18.34$) than in the 100 ms condition ($M = 548.93$ ms, $SD = 17.98$).

Moreover, there was a significant interaction between Object Orientation and SOA, [$F(1, 33) = 34.7$, $p < .001$, $\eta^2 = .51$]. Planned contrasts revealed that RTs for the 100 ms SOA were slower than for the 200 ms SOA only in the horizontal condition [$F(1, 33) = 60.35$, $p < .001$, $\eta^2 = .64$]; while there was no difference in the vertical condition [$F(1, 33) = .56$, n.s.].

Of primary importance, we observed a significant interaction between Cue Validity and Eye Presentation, [$F(2, 66) = 6.8$, $p < .001$, $\eta^2 = .23$]. As can be seen in Figure 3, planned contrasts revealed that the space based effect (difference between valid and invalid same object condition) was significant, both in the single eye presentation condition [$F(1, 33) = 100.12$, $p < .001$, $\eta^2 = .75$]; and in the dichoptic presentation condition [$F(1, 33) = 50.16$, $p < .001$, $\eta^2 = .6$]. The object based effect (difference between invalid same object and invalid different object conditions) was significant in the single eye presentation condition, [$F(1, 33) = 4.98$, $p < .05$, $\eta^2 = .13$]; but not in the dichoptic condition [$F(1, 33) = .32$, n.s.].

No other interactions were significant.

Figure 3: Experiment 1 results. The graph shows reaction time (RT) and error rate for Eye Presentation conditions as a function of Cue Validity; $F(2, 66) = 4.91$, $p = .01$, $\eta^2 = .13$. As can be seen, the object based effect (the difference in RTs between invalid same object and invalid different object conditions), was significant only in the single eye presentation condition. $*P < 0.05$; $**P < 0.01$.

Discussion

Experiment 1 focused on the involvement of lower visual pathways in attentional deployment towards an object, as a result of a spatial cue. The main finding showed that the OBA effect was exhibited only in the single eye presentation condition, whereas the SBA was found in both monoptic and dichoptic conditions. These results suggest a functional role of subcortical regions in the deployment of object based attention following an exogenous spatial cue; but no role of subcortical regions in the deployment of spatial attention.

Experiment 2

In the second experiment we aimed to examine the involvement of monocular channels in the attentional deployment within objects (see Figure 4). If subcortical mechanisms are functionally involved in the influence of attention deployed within an

object on the detection of the target, we would expect the eye-of-origin manipulation of target location to influence the OBA effect.

Figure 4: *An example of a typical trial in Experiment 2. The Figure depicts the invalid same object, dichoptic condition. The left column represents the presentation to the left eye, the right column is the presentation to the right eye and the center column is the participants' perception.*

Method

Participants. Twenty-three participants (5 males; 28.68 ± 4.2 years) consented to participate in the experiment. All participants had normal or corrected-to-normal visual acuity (i.e., only corrective lenses, no spectacles). Participants were reimbursed for their time either via payment (30 NIS) or course credit. The Institutional Review Board (IRB) of the University of Haifa approved the experimental protocol.

Stimuli. The stimuli were identical to those used in experiment 1.

Procedure. The procedure was similar to that used in experiment 1, with the following exception: the objects and cue were presented to a single eye, whereas the target was presented either to the same or different eye.

Results

Trials in which participants responded incorrectly were discarded (less than 10%). For each participant, responses in which reaction times (RTs) were faster or

slower than 2 standard deviations from the mean of all participants and experimental conditions were also discarded (5.1%). A 4-way analysis of variance (ANOVA) was conducted on RTs for correct trials as the dependent variable and Eye Presentation, Cue Validity, Object Orientation, and SOA as repeated measures factors. Three of the main effects were significant. A significant main effect of Cue Validity was observed, $[F(2, 44) = 15.21, p < .001, \eta^2 = .41]$. Planned contrasts demonstrated significantly shorter RTs for the valid compared to both the invalid same object $[F(1, 22) = 16.14, p < .001, \eta^2 = .42]$ and the invalid different object conditions $[F(1, 22) = 16.37, p < .001, \eta^2 = .43]$. There was no significant difference between the invalid same and invalid different object conditions $[F(1, 22) = 1.28, n.s.]$. A significant main effect of Eye Presentation was observed, $[F(1, 22) = 20.75, p < .001, \eta^2 = .49]$, which resulted from shorter RTs for the single eye presentation condition ($M = 553.5$ ms, $SD = 14.36$) than for the dichoptic condition ($M = 587.8$ ms, $SD = 18.84$). A significant main effect of Object Orientation also was observed, $[F(1, 22) = 4.92, p < .05, \eta^2 = .18]$, indicating shorter RTs in the horizontal condition ($M = 562.31$ ms, $SD = 16.15$) compared to the vertical condition ($M = 579$ ms, $SD = 17.33$).

Moreover, there was a significant interaction between Object Orientation and Cue Validity, $[F(2, 44) = 7.63, p < .005, \eta^2 = .26]$. Planned contrasts revealed that the Space-based Effect (the difference in RTs between valid and invalid same object conditions) was significant, both in the vertical condition $[F(1, 22) = 25.35, p < .001, \eta^2 = .53]$; and in the horizontal condition $[F(1, 22) = 4.65, p < .05, \eta^2 = .17]$. In contrast, the Object-based Effect was only observed in the horizontal (but not vertical) condition. RTs for the invalid same object condition were significantly faster than for the invalid different object condition, when objects were oriented horizontally, $[F(1, 22) = 17.1, p < .001, \eta^2 = .43]$; yet a significant opposite pattern was observed in the vertical condition $[F(1, 22) = 4.57, p < .05, \eta^2 = .17]$.

The 3-way interaction of Object Orientation, Eye Presentation, and SOA was significant $[F(1, 22) = 5.1, p = .035, \eta^2 = .19]$. This interaction resulted from a smaller difference between the two Eye Presentation conditions at the first SOA compared to the second SOA in the horizontal Object Orientation condition $[F(1, 22) = 6.49, p < 0.05, \eta^2 = 0.23]$, while no difference was observed in the vertical Object Orientation condition $[F(1, 22) = 1.62, n.s.]$.

Most importantly, as predicted, there was a significant interaction between Cue Validity and Eye Presentation, [$F(2, 44) = 3.87, p = .028, \eta^2 = .15$]. As can be seen in Figure 5, planned contrasts revealed that the space based effect was significant, both in the single eye presentation condition [$F(1, 22) = 27.39, p < .001, \eta^2 = .55$]; and in the dichoptic condition [$F(1, 22) = 5.1, p < .05, \eta^2 = .18$]. In contrast, the object based effect was significant only in the single eye presentation condition, [$F(1, 22) = 5.38, p < .05, \eta^2 = .19$] while in the dichoptic condition it was not, [$F(1, 22) = .31, n.s.$]¹.

No other interactions were significant.

Figure 5: Results from Experiment 1. The graph shows reaction time (RT) for both Eye Presentation conditions as a function of Cue Validity; $F(2, 44) = 3.87, p = .028, \eta^2 = .15$. Results show that the object based effect (the difference in RTs between invalid same object and invalid different object conditions) was significant only in the single eye presentation condition. * $P < 0.05$; ** $P < 0.01$.

Discussion

Experiment 2 examined the involvement of lower visual pathways in the influence of attention deployed within an object on detecting a target. In order to manipulate attention within objects, in the dichoptic condition, the target was presented to a different eye than the cue and object. The typical pattern of results (i.e. OBA and SBA effects) was replicated when the objects were horizontally oriented in the single

¹ This pattern was also observed when examining only the horizontal condition.

eye presentation condition. However, in the dichoptic condition, we only observed the SBA effect. This pattern of results is in agreement with previous findings of OBA effects only in the horizontal orientation (Pilz et al., 2012). One explanation is that attention may be allocated more easily along the horizontal meridian than along the vertical meridian. That is, for horizontal rectangles, attention on the invalid-same object trials was allocated along the horizontal meridian of the visual field, whereas on invalid-different object trials attention was allocated along the vertical meridian. The hypothesis that information processing is facilitated along the horizontal meridian is consistent with the results of studies of visual search (Carrasco & Chang, 1995; Mackeben, 1999) and object-based attention (Al-Janabi & Greenberg; 2016; Barnas & Greenberg, 2016; 2019).

Orientation effects notwithstanding, as in experiment 1, these results again suggest a role of subcortical mechanisms in the deployment of object based attention. In experiment 1, attentional deployment to an object (following an exogenous spatial cue) depended on monocular channels; whereas in experiment 2, attentional deployment within an object (following appearance of the target) depended on monocular channels. In both instances we observed no role of subcortical regions in the deployment of spatial attention.

General Discussion

The present study provides new insights regarding the neural substrates of OBA. In two experiments, we have demonstrated the involvement of early levels of the visual pathway in attentional deployment both within, and towards, an object. Our findings that OBA involves lower portions of the visual system, fits well within an evolutionary framework of attentional control. The involvement of subcortical mechanisms in OBA might not be surprising when considering the similar (to humans) benefit that less evolved organisms would gain from prioritizing objects when scanning the visual field. OBA seems to be an adaptive and strategic process (Greenberg & Gmiendl, 2008; Shomstein, 2012) and as such might also be evident in other less evolved species. Object perception has previously been demonstrated in lower order species such as pigeons (Cook, Shaw & Blaisdell, 2001) and fish (von der Emde, 2006).

In the current study, a modulation of OBA as a function of Eye Presentation was observed, but no modulation of SBA was demonstrated. This dissociation might

be explained by the specific SOAs used in this study. In a study which examined the involvement of monocular channels of the visual system in SBA, it was demonstrated that exogenous facilitation is delayed when cue and target were presented to different eyes, only in very short SOAs (e.g., 100 ms) but not for longer SOAs (e.g., 225 ms). In the current study the shortest SOA was 200 ms which is long enough for the SBA to be manifested also in the dichoptic condition (Gabay & Behrmann, 2014).

To summarize, the experiments reported in this study support the notion that object-based attention processes are generated in lower subcortical regions as opposed to spaced-based attention processes. The tendency to study and relate cognitive processes mainly to cortical regions is evident in many fields within cognitive neuroscience, and the tendency to assign most of the cognitive abilities to cortical mechanisms impairs our understanding of the neural basis of cognition. In the current study, we demonstrated for the first time (to our knowledge) that OBA processes also involve monocular visual channels.

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