



Monocular channels have a functional role in endogenous orienting

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ARTICLE INFO

Keywords:

Endogenous attention
Monocular regions
Orienting
Cortex
Subcortical regions

ABSTRACT

The literature has long emphasized the role of higher cortical structures in endogenous orienting. Based on evolutionary explanation and previous data, we explored the possibility that lower monocular channels may also have a functional role in endogenous orienting of attention. Sensitive behavioral manipulation was used to probe the contribution of monocularly segregated regions in a simple cue – target detection task. A central spatially informative cue, and its ensuing target, were presented to the same or different eyes at varying cue-target intervals. Results indicated that the onset of endogenous orienting was apparent earlier when the cue and target were presented to the same eye. The data provides converging evidence for the notion that endogenous facilitation is modulated by monocular portions of the visual stream. This, in turn, suggests that higher cortical mechanisms are not exclusively responsible for endogenous orienting, and that a dynamic interaction between higher and lower neural levels, might be involved.

1. Introduction

Looking for your smartphone before you want to call a friend, or responding to a ringing smartphone when someone calls you, are both everyday situations in which humans orient their attention. Orienting of attention is defined as - allocation of attention to specific objects or locations in space. As described by many authors (see, e.g., Posner, 1980) orienting may be generated voluntarily (endogenously), or can be captured by an external stimulus (exogenously).

A common method for examining the two types of attentional orienting is by employing two versions of Posner's cuing task (Klein, 2005; Posner, 1980). When studying exogenous orienting of attention, a non-predictive peripheral cue is presented before the appearance of a target. The typical pattern of results in this task is an early facilitation followed by inhibition of return (IOR; Posner and Cohen, 1984). That is, reaction time (RT) for Valid trials (i.e., target appears at the cued location) is faster than for Invalid trials (i.e., target and cue appear at opposite locations) at short SOAs (stimulus onset asynchrony—the duration from cue onset until target onset) and slower for Valid than Invalid trials at longer SOAs. When studying endogenous orienting, a central predictive cue (e.g., central arrows, numbers or color patches) is presented before the appearance of a peripheral target. The typical pattern of results elicited in such conditions, is that RT for Valid trials is faster than for Invalid trials, and this pattern gradually emerges over SOAs.

Behavioral studies have demonstrated several differences between

exogenous and endogenous orienting (for a review, see Klein, 2009, p. 245–248). There are differences in the time course of facilitation, that is, endogenous orienting is slower to develop than exogenous orienting (Shepherd and Müller, 1989). There are differences in the automaticity of the effects, exogenous orienting is more automatic than endogenous orienting (Carrasco et al., 2006; Hein et al., 2006; Jonides, 1981; Yeshurun and Carrasco, 1998). There are also differences in the attentional components that are involved in the two tasks, although facilitation is observed in both forms of orienting, IOR is observed in the aftermath of exogenous but not endogenous orienting (Posner and Cohen, 1984; Rafal et al., 1989). In contrast to the general agreement in behavioral studies that the two attentional systems act independently (Berger et al., 2005; Berlucchi et al., 2000; Lupiáñez et al., 2004), as reviewed below, most imaging studies suggest that the two systems share similar neural substrates.

1.1. Does monocular channels have a functional role in attentional orienting?

Orienting of attention is often considered to be accomplished mostly by higher regions of the cortical visual system. Both exogenous and endogenous orienting of attention have been demonstrated to activate a fronto-parietal cortical network (Andersen et al., 1997; Kincade et al., 2005; Peelen et al., 2004; Rosen et al., 1999; Voytko et al., 1994; Yantis et al., 2002). According to one influential theory (Corbetta and Shulman, 2002), dorsal and ventral fronto-parietal networks (including

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the superior parietal lobe, temporal parietal junction, and frontal eye field) are responsible for orienting attention. Rosen et al. (1999) showed that both exogenous and endogenous orienting activated bilateral parietal and dorsal premotor regions, including the frontal eye fields.

Those theories focus mainly on higher cortical networks, somewhat neglecting lower visual areas and subcortical regions. The neural findings are rather inconsistent and a debate exists regarding the engagements of higher versus lower levels of the visual system in orienting of exogenous and endogenous attention. The tendency to implicate higher cortical involvement in attentional orienting, might not be surprising when considering some limitations of commonly used imaging techniques. For instance, functional magnetic resonance imaging (fMRI) experiments have a tendency to overemphasize cortical activation over subcortical structures (LaBar et al., 2001). Subcortical structures are smaller, and are more difficult to image because of the reduction in signal-to-noise ratio relative to cortical regions. In addition, it is not simple to ascribe direct causal relations between activation in brain areas and particular cognitive events, potentially leading to misinterpretations of epiphenomenal brain activations. Taken together, these limitations might obscure a full understanding of the cognitive-neural basis of exogenous and endogenous attention.

In contrast to the suggestion that higher visual regions are the main neural substrates involved in attentional orienting, recent studies demonstrated that the primary visual cortex (V1) is also involved in exogenous attentional orienting (Li, 2002; Zhang et al., 2012b). In addition, it was suggested that subcortical regions might also be involved in orienting of attention (Lovejoy and Krauzlis, 2009; McAlonan et al., 2008; Rafal et al., 1988; Voytko et al., 1994). It was suggested that the cholinergic system, arising in the basal forebrain, plays a critical role in attentional orienting, so lesions of the basal forebrain in monkeys interfere with orienting of attention (Voytko et al., 1994). In addition, it was previously proposed that the exogenous orienting system may be phylogenetically older than the endogenous orienting system, allowing us to automatically respond to environmental demands and react quickly to stimuli that are likely to provide behaviorally relevant information (Carrasco, 2011). Respectively, studies suggested that endogenous orienting might involve higher cortical regions (e.g., fronto-parietal), and that exogenous attention also recruits subcortical processing (Robinson and Kertzman, 1995; Zackon et al., 1999). Study on the macaque monkeys also demonstrated that a subcortical region (the Superior Colliculus; SC) is involved in exogenous orienting, but not in endogenous orienting (Robinson and Kertzman, 1995).

When different methods such as sensitive behavioral manipulations (Gabay and Behrmann, 2014; Self and Roelfsema, 2010); single cells recording (Dorris et al., 2002); patient study (Sapir et al., 1999) and examining the archer fish as a model for early evolutionary species (Gabay et al., 2013) were used to probe the contribution of subcortical areas, it was demonstrated that subcortical structures have a functional role in exogenous orienting.

An outstanding question is whether monocular channels are also involved in endogenous orienting. In contrast to most literature (Corbetta et al., 2000; Kincade et al., 2005; Peelen et al., 2004; Rosen et al., 1999), there is some data implying monocular involvement in endogenous orienting. First, by recording from neurons in attending macaque monkeys, it was demonstrated that attention modulates visual signals before they reach the cortex by increasing responses of neurons in the lateral geniculate nucleus (LGN). Those results suggesting sources of visual attention modulation in the LGN (McAlonan et al., 2008), and imply that subcortical mechanisms can be involved also in endogenous orienting of visual attention. Second, when high-resolution fMRI was combined with a threshold-contrast detection task to explore the role of the SC in endogenous visual attention, it was discovered that the SC exhibits a retinotopically selective, attention-related, response (Katyal and Ress, 2014). Third, when orienting of visual attention was studied

in patients with progressive supranuclear palsy (PSP), Rafal et al. (1988) showed that the midbrain retinotectal pathways are important not only for controlling eye movements, but also for orienting endogenous attention. In a recent study, we have demonstrated that the archerfish can also orient attention endogenously (Saban et al., 2017b), a finding which also strengthens the claim that subcortical structures might have a functional role in endogenous orienting. To summarize, there is some basis to surmise the involvement of lower monocular channels (subcortical regions and V1) in the process of endogenous orienting.

1.2. How to probe the contribution of monocular channels?

In contrast to the above mentioned methods used to implicate the involvement of subcortical structures in endogenous orienting, this question can also be addressed by employing a sensitive behavioral method. By controlling the visual information presented to each eye separately, one can examine the involvement of monocular portions of the visual system (subcortical regions and V1) in endogenous attentional orienting. Visual input, once received by the retina is monocularly segregated. The information is projected to the lateral geniculate nucleus (LGN) and subsequently reaches striate and binocular extrastriate regions (Horton et al., 1990; Menon et al., 1997). Extrastriate visual areas are mostly binocular and their activation is not eye-dependent. By using a stereoscope, it is possible to manipulate the visual information presented to different eyes separately. As such, manipulating the cue and target Eye-of-Origin provides a useful tool for isolating the involvement of monocular (mostly subcortical regions and V1) versus binocular (mostly cortical) neural channels (e.g., Saban et al., 2017a; Saban et al., in press).

As mentioned above, studies which examined exogenous orienting demonstrated that when the cue and target were presented to different eyes (versus the same eye), the onset of facilitation was delayed (Gabay and Behrmann, 2014; Self and Roelfsema, 2010). Based on the visual channels mechanism explained, the authors concluded that exogenous facilitation involves subcortical structures. Using the same method, in a binocular-rivalry paradigm, it was demonstrated that attending a monocular cue enhanced the competitive strength of a stimulus presented to the cued eye (Zhang et al., 2012a). This study examined the influence of endogenous cuing on information processing. However, the involvement of monocular portions of the visual stream in endogenous spatial attention have not been studied yet.

The goal of the current study was to apply the same method and logic to endogenous orienting. To do so, we used a simple detection task, in which a predictive central cue was presented before the appearance of a peripheral target. Using the stereoscope, we manipulated the eye to which the endogenous cue and target were presented: In the different eyes condition, the cue and target were presented to different eyes, and in the same eye condition, both were presented to the same eye. If the attentional dynamic is modulated by the cue and target Eye-of-Origin (same versus different eyes), this implies a functional role of monocular visual pathways in endogenous orienting.

2. Experiment 1

2.1. Method

2.1.1. Participants

32 participants (mean age 23.3; 25 females) volunteered to participate in exchange for payment or course credit. All had normal or corrected-to-normal vision. The study was approved by the ethics committee of the University of Haifa.

2.1.2. Stimulus and apparatus

Stimulus presentation was performed using a HP Z200 computer, operating with Windows 7 system. Stimuli were displayed on a

Samsung LCD monitor (model S24C650PL) with a recommended resolution of 1680 × 1050. Responses were made using DELL Hebrew-English Extended Keyboard (model RT7D50 SK-8115). The computer monitor was positioned 57 cm in front of a stereoscope (model ScreenScope LCD SA200LCD), blocking the participants' direct view of the monitor (see Fig. 1). The monitor presentation was divided into two halves (each half was presented to a different eye), and consisted of two rectangles (6°X17.8°) placed 10.3° from the center of the screen, and 20.6° from each other. Each rectangle contained 3 squares (2.8° each side) in a vertical alignment. The upper and lower squares were placed at 5.8° from the center of the screen and the central square was placed at its center. A central fixation cross comprised two lines (0.7° each), centered within the central squares. Cues consisted of red or green colors filling in the central square. An asterisk target (0.7°) was then presented, centered within one of the peripheral squares. Except for the cues, all stimuli were white figures against a black background.

2.1.3. Procedure

Typical experimental trials are depicted in Fig. 2. Each trial began with a fixation cross appearing for 500 ms. Two hundred ms after fixation disappeared, the central cue was presented for 100 ms. After a variable SOA of 100, 500 or 1000 ms, the target appeared for 3000 ms or until a response was detected. The target appeared at the cued location (Valid trial) or at the opposite location (Invalid trial). Each color was associated with a specific location (counterbalanced between participants), and the target appeared in the predicted location in 80% of the trials. Participants were informed about cue predictability. The cue and target were presented to the left or right eye with equal probability. There were four possible target locations that varied equally and randomly: Left eye-up, left eye-down, right eye-up, right eye-down. Participants were instructed to respond to target appearance by pressing the space bar of a keyboard with their dominant hand as fast as possible. After manual response an inter-trial interval of 1000 ms was introduced. Each participant had 16 practice trials before the experiment began. In 6.25% of the trials, no target appeared (i.e., catch trials) and the participant was instructed not to respond. Catch trials were dispersed randomly across the trials. Each participant completed a total of 512 experimental trials divided into four blocks. For each of the two Eye-of-Origin conditions, subjects performed 64 Valid trials for each one of the three SOAs, and 16 Invalid trials for each one of the three SOAs. All instructions were automated and presented on the screen. The different experimental conditions were randomly interleaved within each block.

2.2. Results

Trials in which RT was longer than 2000 ms or shorter than 100 ms were excluded from the analyses (less than 1%). Participants responded during catch trials on less than 1% of the trials, and at less than 1% of the trials in which target appeared the participants didn't respond.

For each Eye-of-Origin condition (Same, Different), an analysis of variance (ANOVA) with SOA (100 ms, 500 ms or 1000 ms), and Validity (Valid, Invalid) as a within-subject factors was conducted with RT as the dependent variable. Fig. 3 presents RT as a function of Eye-of-Origin, SOA and Validity.

When the cue and target were presented to the same eye, the main effect of SOA was significant [$F(2, 62) = 34.2$, $MSE = 996$, $P < 0.001$], indicating faster RT with increasing SOAs. The main effect of Validity was also significant [$F(1, 31) = 15.7$, $MSE = 960$, $P < 0.001$], indicating a significant facilitation. The SOA × Validity interaction was not significant [$F(2, 62) < 1$, NS], indicating a significant facilitation at all SOAs [$F(1, 31) = 4.7$, $MSE = 1260$, $P < 0.05$; $F(1, 31) = 8.7$, $MSE = 688$, $P < 0.01$; $F(1, 31) = 5.66$, $MSE = 598$, $P < 0.05$, for the 100 ms, 500 ms and 1000 ms SOAs, respectively].

When the cue and target were presented to different eyes, the main

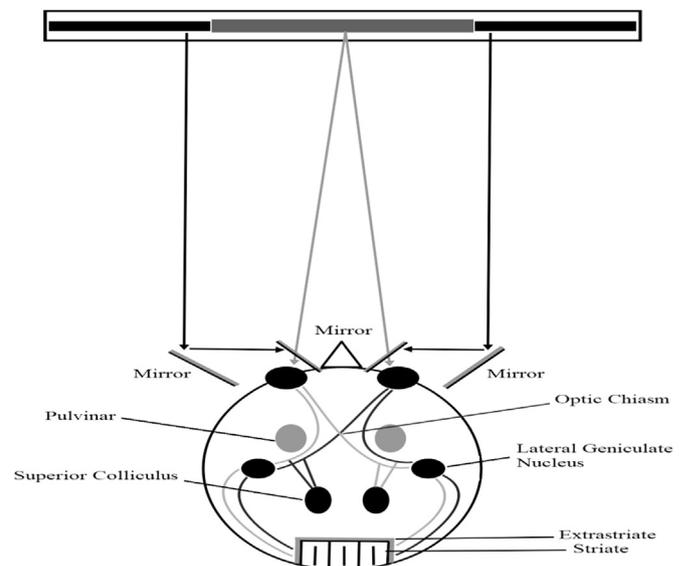


Fig. 1. Schematic illustration of the experimental apparatus and visual pathways from the eyes to the brain. Each side of the computer monitor provided visual information to a different eye. From the eye, the visual information passes first through monocularly segregated regions (dashed lines left eye,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

effect of SOA was significant [$F(2, 62) = 19.13$, $MSE = 1054$, $P < 0.001$]. The main effect of Validity was also significant [$F(1, 31) = 6$, $MSE = 1233$, $P < 0.05$]. In contrast to the same eye condition, the SOA × Validity interaction in the different eyes condition was significant [$F(2, 62) = 3.15$, $MSE = 617$, $P < 0.05$]. Further analyses of this interaction indicated that no facilitation was found at the 100 ms SOA, but at the two later SOAs a significant facilitation was observed [$F(1, 31) < 1$, NS; $F(1, 31) = 5.59$, $MSE = 884$, $P < 0.05$; $F(1, 31) = 5.22$, $MSE = 1212$, $P < 0.05$, for the 100 ms, 500 ms and 1000 ms SOAs, respectively].¹

2.3. Discussion

Early facilitation was observed at the 100 ms SOA in the same eye condition, but not in the different eyes condition. At the 500 ms and 1000 ms SOAs, facilitation was observed in both conditions. Thus far, the results demonstrate that relative to the condition in which the cue and the target are presented to different eyes, earlier facilitation in the same eye condition was found. This finding implicates the involvement of monocularly segregated regions in endogenous orienting.

3. Experiment 2

The following experiment was designed to better understand the time course of endogenous orienting, and to reveal the rise and fall of the endogenous facilitation dynamics. This experiment is similar to the first experiment, but used shorter set of SOAs. This was done in order to obtain a finer resolution of the gradually developing facilitation. To do so, we included a 500 ms SOA in order to replicate the results from the first experiment while including two shorter SOAs not used in the first experiment - 0 ms and an intermediate SOA of 300 ms.

¹ In a separate analysis we examined the interaction between Eye-of-Origin and Validity for the first SOA which resulted in a marginally significant effect [$F(1, 31) = 3.79$, $MSE = 800$, $P = 0.06$].

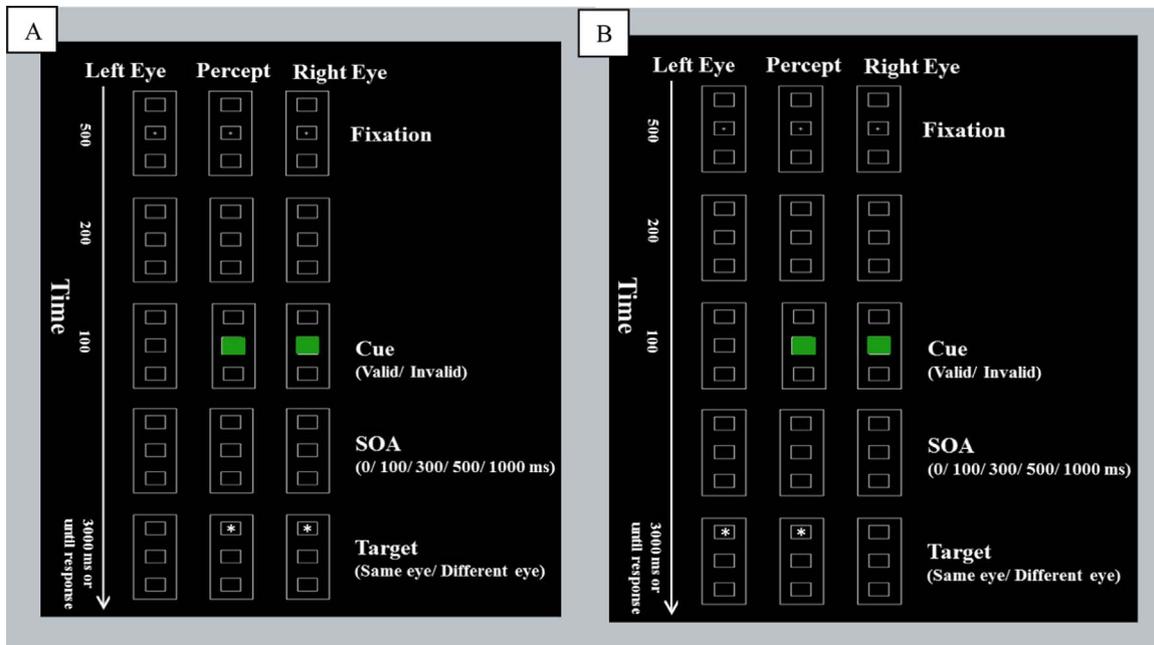


Fig. 2. Experiment in which a red cue predicts a target at the lower square while a green cue, predicts a target at the upper square. (A) A typical Valid, Same Eye condition trial in which the cue (green square) is presented to the right eye (right column) and the target is presented to the right eye (right column), at the upper square. The middle column represents the participant's fused perception. (B) A typical Valid, Different Eyes condition trial in which the cue (green square) is presented to the right eye (right column) and the target is presented to the left eye (left column), at the upper square. The middle column represents the participant's fused perception. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

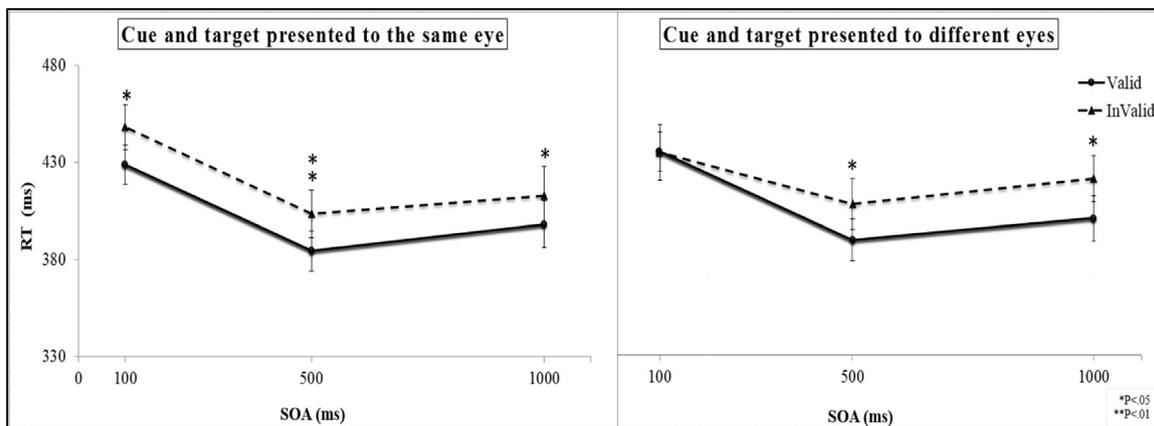


Fig. 3. RT as a function of SOA, depicted for each Eye-of-Origin condition, with Valid and Invalid trials plotted separately. Error bars represent one standard error from the mean.

3.1. Methods

With the following exceptions all of the methods were similar to those used in Experiment 1. 31 participants (mean age 20.6; 23 females) volunteered to participate in exchange for payment or course credit. All had normal or corrected-to-normal vision. The study was approved by the ethics committee of the University of Haifa. The SOAs used were 0 ms, 300 ms and 500 ms.

3.2. Results

Trials on which RT was longer than 2000 ms or shorter than 100 ms were excluded from the analyses (less than 1%). Participants responded during catch trials on less than 1% of the trials, and at less than 1% of the trials in which target appeared the participants didn't respond.

For each Eye-of-Origin condition (Same, Different), an analysis of variance (ANOVA) with SOA (0 ms, 300 ms or 500 ms), and Validity (Valid, Invalid) as within-subject's factors was conducted with RT as the dependent variable. Fig. 4 presents RT as a function of Eye-of-Origin,

SOA and Validity.

When the cue and target were presented to the same eye, the main effect of SOA was significant [$F(2, 60) = 88.49$, $MSE = 1717$, $P < 0.001$], indicating faster RT with increasing SOAs. The main effect of Validity was significant [$F(1, 30) = 9.35$, $MSE = 1385$, $P < 0.005$], indicating faster RT for Valid compared to Invalid trials. Although the $SOA \times Validity$ interaction was not significant [$F(2, 60) = 1.8$, NS] we continued to analyze the two-way interaction by examining the Validity effect for every SOA separately because no facilitation was predicted for the shortest SOA (0 ms). In line with this prediction, no facilitation was found in the 0 ms SOA condition [$F(1, 30) < 1$, NS]. In contrast, and in agreement with Experiment 1, significant facilitation was observed in the 300 ms and 500 ms SOA conditions [$F(1, 30) = 7.5$, $MSE = 1092$, $P < 0.05$; $F(1, 30) = 4.35$, $MSE = 2514$, $P < 0.05$, for the 0 ms, 300 ms and 500 ms, for each SOA respectively].

When the cue and target were presented to different eyes, the main effect of SOA was significant [$F(2, 60) = 90.17$, $MSE = 1711$, $P < 0.001$], indicating faster RT with increasing SOAs. In contrast to the same eye condition, the main effect of Validity was not significant

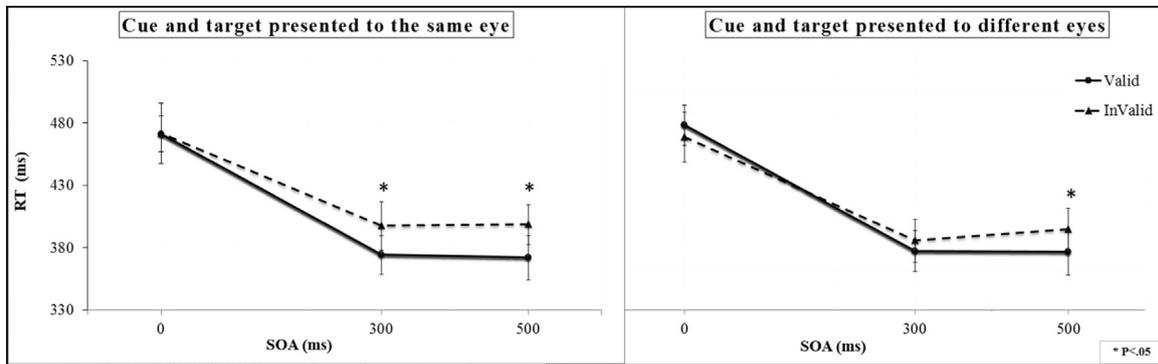


Fig. 4. RT as a function of SOA, depicted for each Eye-of-Origin condition, with Valid and Invalid trials plotted separately. Error bars represent one standard error from the mean.

[$F(1, 30) = 1.63$, NS]. Although the $SOA \times Validity$ interaction was also not significant [$F(2, 60) = 2.11$, NS] we continued to analyze the two-way interaction by examining the Validity effect for every SOA separately because, in accordance with Experiment 1, facilitation was predicted when the SOA was 500 ms. As expected, at SOA 0 ms no facilitation was found [$F(1, 30) = 1.27$, NS]. The Validity effect was also not significant at the 300 ms SOA [$F(1, 30) = 1.27$, NS]. Replicating the finding from Experiment 1, however, the validity effect was significant when the SOA was 500 ms [$F(1, 30) = 6.7$, $MSE = 718$, $P < 0.05$].

4. General discussion

By employing a simple endogenous orienting detection task, we tested whether the endogenous facilitation is modulated by the Eye-of-Origin manipulation. To reveal the microgenesis of endogenous facilitation, Fig. 5 shows the aggregated results across the multiple SOAs

from the two experiments. The data demonstrates that the onset of facilitation was modulated by the Eye-of-Origin manipulation. Facilitation was observed over the full range of non-zero SOAs tested (from 100 to 1000 ms) in the same eye condition. In striking contrast, in the different eye condition facilitation was not significant until the 500 ms SOA. An alternative way to describe this difference is that endogenous orienting was observed at the 100 and 300 ms SOAs in the same eye condition, whereas it was not observed at these SOAs in the different eye condition. These findings provide converging evidence for the notion that monocular portions of the visual stream have a functional role in endogenous orienting.

4.1. Involvement of monocular versus binocular visual channels

As indicated in the introduction, similar to subcortical regions, V1 also has monocularly segregated neurons that might be responsible for the differences between the two eye-of-origin conditions. V1, which

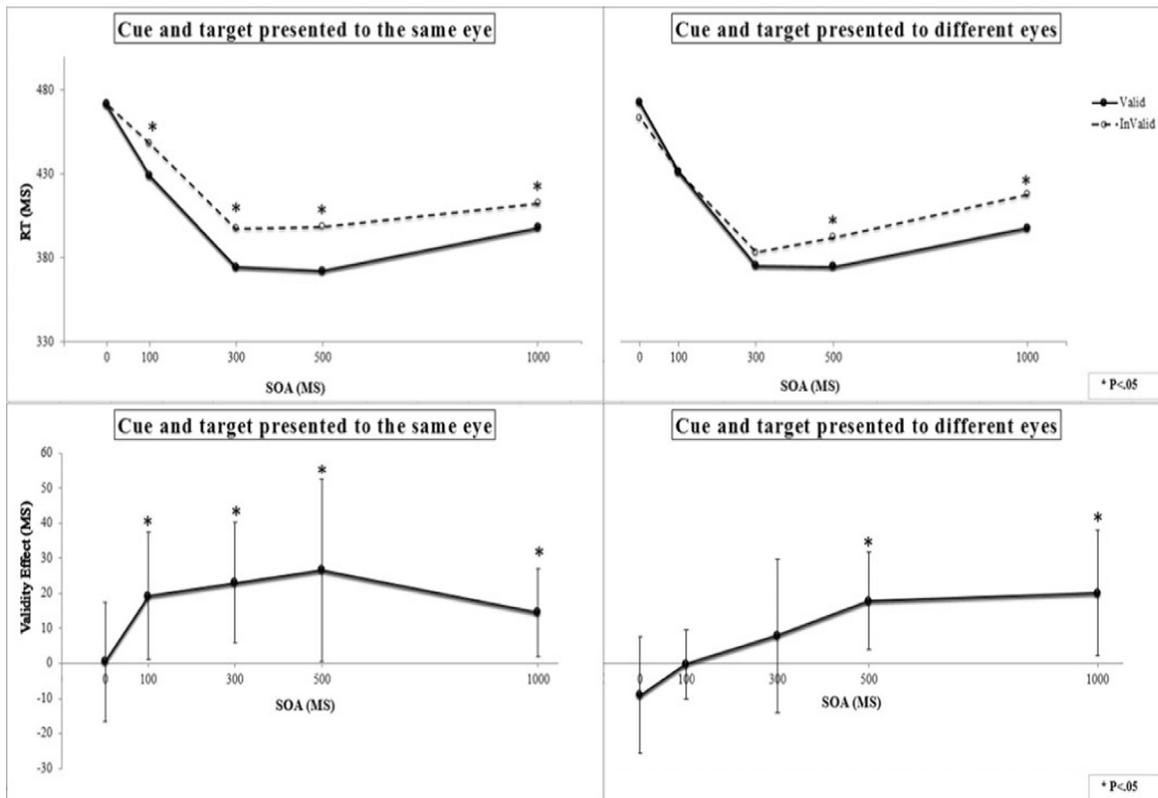


Fig. 5. Data collectively assembled from the two experiments to reflect the attentional dynamics over time. The upper panels show RT in the Valid and Invalid conditions, and the lower panels show the Validity effect (Invalid RT minus Valid RT). Ninety-five % confidence intervals are shown in the error bars. The RT and Validity effect, presented as a function of SOA and depicted for each Eye-of-Origin condition.

projects monosynaptically to the SC and thus provides a source of cortical inputs to the SC, could play a role in guiding attention. Indeed, recent experimental evidence supports the idea (Li, 2002) that V1 creates a bottom-up saliency map that plays a role in guiding attention exogenously (Zhaoping, 2008). As Zhaoping suggests, if V1, through its SC connections, is involved in exogenous attention, it is possible that the same low-level neuronal mechanisms also guide endogenous orienting of attention.

In a recent fMRI/ERP study, Zhang et al. (2012b) demonstrated that when observers are unable to perceive a cue that nevertheless generates exogenous orienting, it is V1, rather than the parietal and frontal areas, that is activated by the cue. This finding allows for the possibility that the typical activation of fronto-parietal regions by exogenous cues (which are usually perceptible) does not reflect a functional role of these areas in generating the orienting, but rather is associated with awareness of the cue. It is possible that the same logic can explain the results from previous endogenous orienting studies.

Nevertheless, and in line with most literature, these - low level structures - may be necessary but not sufficient, to elicit endogenous orienting. Since the visual system has many feedback connections (Bullier, 2001; Lamme et al., 1998), dynamic interactions between cortical and lower monocular regions might be involved in the process of endogenous orienting. The delayed facilitation in the different eye condition might result from the involvement of such feedback connections.

Our findings have also implications for recent general theories of attention, such as the biased competition or the normalization models of attention. The finding that the facilitation effect appears earlier at monocular channels (vs. binocular channels) can be explained by the normalization model of attention (Reynolds and Heeger, 2009), that was initially suggested as a way of implementing biased competition (Desimone and Duncan, 1995). It should be noted that in order to fit with our findings, the attention field and stimulation field multiplication (which results in the behavioral benefit for attended locations), should be accomplished earlier at monocular portions of the visual system. This is in accordance with Motter (1993) who recorded neuronal responses in macaque areas V1, V2, and V4 to stimuli that varied in orientation, and demonstrated that directing attention to the stimulus in the receptive field often increased neuronal firing rates.

Note, several previous studies have examined the involvement of V1 in general attention processes, such as selective and contextual effects of attention (e.g., Buffalo et al., 2010; Ito and Gilbert, 1999; Lakatos et al., 2008; Motter, 1993; O'Connor et al., 2002; Roelfsema et al., 1998). Overall, as far as we know, no previous study has examined the involvement of lower neural systems in endogenous attentional orienting, using the well-studied Posner cuing task. The distinction between different attentional systems is highly important for the understanding of attention. Each system has its unique behavioral effects and neural substrates (see Klein and Lawrence, 2012; Posner and Petersen, 1990; Petersen and Posner, 2012, for a detailed taxonomy of attention), and hence, from the study of one attentional system one should not draw conclusions about the cognitive and neural structures involved in another attentional system. In addition, most of the aforementioned studies have only demonstrated a correlation between V1 and attentional processes, whereas our study suggests a causal relation.

4.2. Some evolutionary speculations

As mentioned above, in contrast to the general agreement from behavioral studies, that the exogenous and endogenous systems act independently, most imaging studies suggest that the two systems share, at least partially, similar neurophysiological substrates (Andersen et al., 1997; Kincade et al., 2005; Peelen et al., 2004; Rosen et al., 1999; Voytko et al., 1994; Yantis et al., 2002). Zhaoping (2016) has suggested that reflexive cuing effects observed in humans should also be present in lower vertebrates. Accordingly, it was previously

demonstrated that the archerfish, which possesses an optic tectum, but lacks fully developed cortical structures, demonstrated attentional reflexive abilities similar to those observed in human participants (Gabay et al., 2013). Zhaoping has also suggested that in primates, V1 creates a saliency map of the visual world. In lower vertebrates, such as fish, V1 is absent and the SC (the optic tectum in fish) receives most of the retinal input. Hence, it is possible that through evolution this saliency map of the visual world migrated from the optic tectum to V1 (Zhaoping, 2016). The current study indicates that, similarly to exogenous attentional orienting (Gabay and Behrmann, 2014), monocular channels are involved in endogenous orienting in humans. Therefore, it is plausible that both modes of orienting (exogenous and endogenous) are guided by a saliency map in V1 or in lower visual areas.

It is possible that during evolutionary development, higher neural substrates took control over lower mechanisms in order to manifest volitional attentional abilities. This assumption is in accordance with many recent theories suggesting that neural circuitry can be recycled and tuned for different purposes either phylo - or ontogenetically (Anderson, 2007a, 2007b, 2010; Dehaene, 2005; Dehaene and Cohen, 2007; Gallese, 2008; Gallese and Lakoff, 2005; Hurlley, 2008). Thus, brain organization is subject to strong anatomical and connective constraints inherited from evolution. New abilities (e.g., endogenous orienting) find their “neuronal niche”, a set of circuits that are sufficiently close to the required function, and sufficiently flexible as to reorient a significant fraction of their neural resources to this novel use. As evolutionarily older function is invaded by a novel one, its prior organization is never entirely erased. Thus, prior neural constraints exert a powerful influence on brain organization (Dehaene, 2005). Accordingly, neural circuits which were once established for one purpose (e.g., detect sudden changes in the environment – exogenous orienting) can be exploited during the evolutionary development for other uses (e.g., orient attention volitionally on the basis of predictions and expectations – endogenous orienting).

Acknowledgments

This research was supported by the Israel Science Foundation (Grant no. 1124/14) to SG. All authors declare no conflict of interest pertaining to the present manuscript.

References

- Andersen, R.A., Snyder, L.H., Bradley, D.C., Xing, J., 1997. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annu. Rev. Neurosci.* 20 (1), 303–330.
- Anderson, M.L., 2007a. Evolution of cognitive function via redeployment of brain areas. *Neuroscientist* 13 (1), 13–21.
- Anderson, M.L., 2007b. The massive redeployment hypothesis and the functional topography of the brain. *Philos. Psychol.* 20 (2), 143–174.
- Anderson, M.L., 2010. Neural reuse: a fundamental organizational principle of the brain. *Behav. Brain Sci.* 33 (4), 245.
- Berger, A., Henik, A., Rafal, R., 2005. Competition between endogenous and exogenous orienting of visual attention. *J. Exp. Psychol.: General.* 134 (2), 207.
- Berlucchi, G., Chelazzi, L., Tassinari, G., 2000. Volitional covert orienting to a peripheral cue does not suppress cue-induced inhibition of return. *J. Cogn. Neurosci.* 12 (4), 648–663.
- Buffalo, E.A., Fries, P., Landman, R., Liang, H., Desimone, R., 2010. A backward progression of attentional effects in the ventral stream. *Proc. Natl. Acad. Sci. USA* 107 (1), 361–365.
- Bullier, J., 2001. Integrated model of visual processing. *Brain Res. Rev.* 36 (2), 96–107.
- Carrasco, M., 2011. Visual attention: the past 25 years. *Vision. Res.* 51 (13), 1484–1525.
- Carrasco, M., Loula, F., Ho, Y.X., 2006. How attention enhances spatial resolution: evidence from selective adaptation to spatial frequency. *Percept. Psychophys.* 68 (6), 1004–1012.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3 (3), 201–215.
- Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P., Shulman, G.L., 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat. Neurosci.* 3 (3), 292–297.
- Dehaene, S., 2005. Evolution of human cortical circuits for reading and arithmetic: the “neuronal recycling” hypothesis. In: Dehaene, S., Duhamel, J.R., Hauser, M.D., Rizolatti, G. (Eds.), *From Monkey Brain to Human Brain*. MIT Press, Cambridge, MA, pp. 133–157.

- Dehaene, S., Cohen, L., 2007. Cultural recycling of cortical maps. *Neuron* 56 (2), 384–398.
- Desimone, R., Duncan, J., 1995. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* 18 (1), 193–222.
- Dorris, M.C., Klein, R.M., Everling, S., Munoz, D.P., 2002. Contribution of the primate superior colliculus to inhibition of return. *J. Cogn. Neurosci.* 14 (8), 1256–1263.
- Gabay, S., Behrmann, M., 2014. Attentional dynamics mediated by subcortical mechanisms. *Atten. Percept. Psychophys.* 76 (8), 2375–2388.
- Gabay, S., Leibovich, T., Ben-Simon, A., Henik, A., Segev, R., 2013. Inhibition of return in the archer fish. *Nat. Commun.* 4, 1657.
- Gallese, V., 2008. Mirror neurons and the social nature of language: the neural exploitation hypothesis. *Social. Neurosci.* 3 (3–4) (317–333–33).
- Gallese, V., Lakoff, G., 2005. The brain's concepts: the role of the sensory-motor system in conceptual knowledge. *Cogn. Neuropsychol.* 22 (3–4), 455–479.
- Hein, E., Rolke, B., Ulrich, R., 2006. Visual attention and temporal discrimination: differential effects of automatic and voluntary cueing. *Vis. Cogn.* 13 (1), 29–50.
- Horton, J.C., Dagi, L.R., McCrane, E.P., de Monasterio, F.M., 1990. Arrangement of ocular dominance columns in human visual cortex. *Arch. Ophthalmol.* 108 (7), 1025–1031.
- Hurley, S., 2008. The shared circuits model (SCM): How control, mirroring, and simulation can enable imitation, deliberation, and mindreading. *Behav. Brain Sci.* 31 (01), 1–22.
- Ito, M., Gilbert, C.D., 1999. Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron* 22 (3), 593–604.
- Jonides, J., 1981. Voluntary versus automatic control over the mind's eye movements. In: Long, A.D. (Ed.), *Attention and Performance IX*. Erlbaum, Hillsdale, NJ, pp. 187–203.
- Katyal, S., Ress, D., 2014. Endogenous attention signals evoked by threshold contrast detection in human superior colliculus. *J. Neurosci.* 34 (3), 892–900.
- Kincade, J.M., Abrams, R.A., Astafiev, S.V., Shulman, G.L., Corbetta, M., 2005. An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *J. Neurosci.* 25 (18), 4593–4604.
- Klein, R.M., 2005. On the role of endogenous orienting in the inhibitory aftermath of exogenous orienting. In: Mayr, U., Awh, E., Keele, S. (Eds.), *Developing Individuality in the Human Brain: A tribute for Michael I. Posner*. APA Books, Washington, DC, pp. 45–64.
- Klein, R.M., 2009. On the control of attention. *Can. J. Exp. Psychol.* 63, 240–252.
- Klein, R.M., Lawrence, M.A., 2012. On the modes and domains of attention. *Cogn. Neurosci. Atten.* 11–28.
- LaBar, K.S., Gitelman, D.R., Mesulam, M.M., Parrish, T.B., 2001. Impact of signal-to-noise on functional MRI of the human amygdala. *Neuroreport* 12 (16), 3461–3464.
- Lakatos, P., Karmos, G., Mehta, A.D., Ulbert, I., Schroeder, C.E., 2008. Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science* 320 (5872), 110–113.
- Lamme, V.A., Super, H., Spekreijse, H., 1998. Feed forward, horizontal, and feedback processing in the visual cortex. *Curr. Opin. Neurobiol.* 8 (4), 529–535.
- Li, Z., 2002. A saliency map in primary visual cortex. *Trends Cogn. Sci.* 6 (1), 9–16.
- Lovejoy, L.P., Krauzlis, R.J., 2009. Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nat. Neurosci.* 13 (2), 261–266.
- Lupiáñez, J., Decaix, C., Siéhoff, E., Chokron, S., Milliken, B., Bartolomeo, P., 2004. Independent effects of endogenous and exogenous spatial cueing: inhibition of return at endogenously attended target locations. *Exp. Brain Res.* 159 (4), 447–457.
- McAlonan, K., Cavanaugh, J., Wurtz, R.H., 2008. Guarding the gateway to cortex with attention in visual thalamus. *Nature* 456 (7220), 391–394.
- Menon, R.S., Ogawa, S., Strupp, J.P., Uğurbil, K., 1997. Ocular dominance in human V1 demonstrated by functional magnetic resonance imaging. *J. Neurophysiol.* 77 (5), 2780–2787.
- Motter, B.C., 1993. Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J. Neurophysiol.* 70 (3), 909–919.
- O'Connor, D.H., Fukui, M.M., Pinsk, M.A., Kastner, S., 2002. Attention modulates responses in the human lateral geniculate nucleus. *Nat. Neurosci.* 5 (11), 1203–1209.
- Peelen, M.V., Heslenfeld, D.J., Theeuwes, J., 2004. Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *NeuroImage* 22 (2), 822–830.
- Petersen, S.E., Posner, M.I., 2012. The attention system of the human brain: 20 years after. *Annu. Rev. Neurosci.* 35, 73–89.
- Posner, M.I., 1980. Orienting of attention. *Q. J. Exp. Psychol.* 32, 3–25.
- Posner, M.I., Cohen, Y., 1984. Components of visual orienting. *Atten. Perform. X: Control Lang. Process.* 32, 531–556.
- Posner, M.I., Petersen, S.E., 1990. The attention system of the human brain. *Annu. Rev. Neurosci.* 13 (1), 25–42.
- Rafal, R.D., Calabresi, P.A., Brennan, C.W., Sciolto, T.K., 1989. Saccade preparation inhibits reorienting to recently attended locations. *J. Exp. Psychol.: Human. Percept. Perform.* 15 (4), 673.
- Rafal, R.D., Posner, M.I., Friedman, J.H., Inhoff, A.W., Bernstein, E., 1988. Orienting of visual attention in progressive supranuclear palsy. *Brain* 111 (2), 267–280.
- Reynolds, J.H., Heeger, D.J., 2009. The normalization model of attention. *Neuron* 61 (2), 168–185.
- Robinson, D.L., Kertzman, C., 1995. Covert orienting of attention in macaques. III. Contributions of the superior colliculus. *J. Neurophysiol.* 74 (2), 713–721.
- Roelfsema, P.R., Lamme, V.A., Spekreijse, H., 1998. Object-based attention in the primary visual cortex of the macaque monkey. *Nature* 395 (6700), 376–381.
- Rosen, A.C., Rao, S.M., Caffarra, P., Scaglioni, A., Bobholz, J.A., Woodley, S.J., et al., 1999. Neural basis of endogenous and exogenous spatial orienting: a functional MRI study. *J. Cogn. Neurosci.* 11, 135–152.
- Saban, W., Gabay, S., Kalanithroff, E., 2017a. More than just channeling: the role of subcortical mechanisms in executive functions—evidence from the Stroop task. *Acta Psychol.*
- Saban, W., Sekely, L., Klein, R.M., Gabay, S., 2017b. Endogenous orienting in the archer fish. *Proc. Natl. Acad. Sci. USA* 114 (29), 7577–7581.
- Saban, W., Klein, R.M., Gabay, S., 2018. Probabilistic versus "pure" volitional orienting—a monocular difference monocular difference. *Atten. Percept. Psychophys* (in press).
- Sapir, A., Soroker, N., Berger, A., Henik, A., 1999. Inhibition of return in spatial attention: direct evidence for collicular generation. *Nat. Neurosci.* 2, 1053–1054.
- Self, M.W., Roelfsema, P.R., 2010. A monocular, unconscious form of visual attention. *J. Vis.* 10, 4.
- Shepherd, M., Müller, H.J., 1989. Movement versus focusing of visual attention. *Percept. Psychophys.* 46 (2), 146–154.
- Voytko, M.L., Olton, D.S., Richardson, R.T., Gorman, L.K., Tobin, J.R., Price, D.L., 1994. Basal forebrain lesions in monkeys disrupt attention but not learning and memory. *J. Neurosci.* 14 (1), 167–186.
- Yantis, S., Schwarzbach, J., Serences, J.T., Carlson, R.L., Steinmetz, M.A., Pekar, J.J., Courtney, S.M., 2002. Transient neural activity in human parietal cortex during spatial attention shifts. *Nat. Neurosci.* 5 (10), 995–1002.
- Yeshurun, Y., Carrasco, M., 1998. Attention improves or impairs visual performance by enhancing spatial resolution. *Nature* 396 (6706), 72–75.
- Zackon, D.H., Casson, E.J., Zafar, A., Stelmach, L., Racette, L., 1999. The temporal order judgment paradigm: subcortical attentional contribution under exogenous and endogenous cueing conditions. *Neuropsychologia* 37 (5), 511–520.
- Zhang, P., Jiang, Y., He, S., 2012a. Voluntary attention modulates processing of eye-specific visual information. *Psychol. Sci.* 23 (3), 254–260.
- Zhang, X., Zhao, L., Zhou, T., Fang, F., 2012b. Neural activities in V1 create a bottom-up saliency map. *Neuron* 73 (1), 183–192.
- Zhao, L., 2008. Attention capture by eye of origin singletons even without awareness—a hallmark of a bottom-up saliency map in the primary visual cortex. *J. Vis.* 8 (5) (1–1).
- Zhao, L., 2016. From the optic tectum to the primary visual cortex: migration through evolution of the saliency map for exogenous attentional guidance. *Curr. Opin. Neurobiol.* 40, 94–102.