Neuropsychologia 111 (2018) 1–7

Contents lists available at ScienceDirect

Neuropsychologia

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

Monocular channels have a functional role in endogenous orienting

William Saban[a,*], Liora Sekely[a], Raymond M. Klein[b], Shai Gabay[a,*]

[a] Department of Psychology and the Institute of Information Processing and Decision Making (IIPDM), University of Haifa, Israel
[b] Department of Psychology and Neuroscience, Dalhousie University, Halifax, Nova Scotia, Canada

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

* Corresponding authors.
E-mail addresses: williamsaban@gmail.com (W. Saban), shaigaba@gmail.com (S. Gabay).

https://doi.org/10.1016/j.neuropsychologia.2018.01.002
Received 15 May 2016; Received in revised form 25 December 2017; Accepted 4 January 2018
Available online 06 January 2018
0028-3932/

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 strengthen 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