Eye Position Affects Orienting of Visuospatial Attention

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Summary

The ability to detect an incoming visual stimulus is enhanced by knowledge of stimulus location (orienting of visuospatial attention [1]). Although the brain mechanisms at the basis of this enhancement are not yet fully clarified, there is evidence that orienting of attention is accompanied by the activation of oculomotor circuits [2-6]. It remains unclear, however, whether this oculomotor activity is an epiphenomenon or is functionally related to the attentional process. Attentional benefits are usually measured by the classical Posner paradigm [7]. When subjects fixate centrally and are requested to detect a visual stimulus that could appear in an attended or unattended location. they react faster to stimuli appearing in the attended one. Here, we demonstrate that in monocular vision visuospatial attention was significantly modulated by the position of the eye in the orbit. When the screen was placed 40° to the right or to the left of subjects' sagittal plane, attentional benefits for stimuli appearing in subjects' temporal spatial hemifield dramatically decayed, even if the retinal stimulation was exactly the same as in the classical paradigm. The finding that eyes and attention show a common limit stop point supports their close functional coupling.

Results and Discussion

In 1867, von Helmholtz [8] first reported that, while keeping the eyes at the center of a picture, an observer can perceptually enhance the details of any part of the scene if he "concentrates his attention ... simply by a conscious and voluntary effort." More recently, several brain-imaging studies aiming to describe the brain network underlying orienting of attention showed that, although subjects were required to keep their eyes still, orienting of attention determined a brain activation pattern largely coincident with that specific for eye movements [2-6]. This functional overlap between attention and eye movements has been further suggested by monkey electrophysiological experiments both during the recording of visual neurons in the superficial layers of the superior colliculus (enhancement effect [9]) and during the electrical microstimulation of oculomotor centers [10]. This last study shows an improvement in the perception of visual stimuli appearing in that portion of visual space represented by the stimulation site. The involvement of the oculomotor system during experiments in which subjects were explicitly requested to keep the eyes still appears at first glance quite bizarre. Cognitive theories of attention interpret the oculomotor activation as an epiphenomenon due to the inhibition of motor programs automatically generated to move the eyes toward the appearing stimulus [11]. An alternative interpretation considers orienting of attention as the result of the preparation of a saccadic eye movement toward the location to be attended [12].

Here we investigated the role of oculomotion in orienting of attention by dissociating perceptual from motor capabilities. If causal relationships link oculomotion and orienting of attention, any constraint limiting eye movements should abolish, or at least reduce, attentional benefits in the region of the spatial field barely reachable by the eye. On the contrary, if attention is a purely cognitive process, then no effects are expected to arise from oculomotor constraints. We decided to evaluate attentional benefits by using a classical Posner paradigm [7]. Although this method does not represent the only way to investigate visuospatial attention, it is one of the most diffused in this kind of literature. Fourteen naive university students participated in the experiment. In order to exclude possible influences of eye dominance on spatial attention [13], we included equal numbers of right and left ocular dominants in the sample. Subjects fixated the center of a computer screen in monocular vision. According to a central cue (see Figure 1), they oriented their attention toward one of two locations (5° to the right and 5° to the left of the fixation box) to detect a stimulus that could appear either in the attended or in the unattended location. The probability of stimulus appearance in the cued location (valid trials) was 70% and in the uncued location (invalid trials), 30%. While maintaining fixation, subjects had to signify detection of the stimulus as quickly as possible by pressing a switch.

Each eye was involved in two experimental conditions (see Figure 1). In the first condition, the screen was "canonically" placed in front of the subject (frontal condition). In the second condition, the screen was located at the same distance but was rotated 40° to the right of subjects' sagittal plane when the right eye was open or 40° to the left when the left eye was open (rotated condition). We selected the degree of screen rotation in order to keep the entire experimental display centered on the fovea and within the effective oculomotor range [14]. No perceptual differences were present between frontal and rotated conditions, as we assessed by testing subjects' visual acuity with an eye chart. Participants' reaction times (RTs) were calculated from stimulus appearance to the pressing of the switch. For both the frontal and the rotated conditions, RTs obtained from the left and right eye conditions were grouped according to the spatial hemifield in which the stimulus was presented (nasal and temporal). Data were standardized within subjects and submitted to two separate



Figure 1. Experimental Setup

(A) Illustration of the events occurring during a valid trial. The experiment took place in a sound-attenuated room, dimly illuminated by a halogen lamp. The stimulus display consisted of a central fixation box ($0.2^{\circ} \times 0.2^{\circ}$) and two empty circles (diameter 1^o). The direction of a thin line (cue, length 0.4°) attached to the central box indicated the circle in which the stimulus (a filled square, $0.15^{\circ} \times 0.15^{\circ}$) was most likely to appear. The timing of the stimulus responded to stimulus appear ance by pressing the spacebar of a keyboard placed in front of them.

(B) Schematic illustration of frontal and rotated conditions here performed by the left

eye, with a patch covering the right eye. Each experimental session comprised 100 trials. Eye position was continuously monitored during the task. Break of fixation, eye drifts, and anticipation and retardation errors were very rare and equally distributed across conditions. They were discarded from analysis.

analyses of variance, one for the frontal and one for the rotated condition. Stimulus location (nasal versus temporal) and validity (valid versus invalid trials) were the within-subject factors.

Experimental data are shown in Figure 2. In the frontal condition, subjects were faster in valid trials than in invalid ones for a stimulus appearing both in nasal and temporal spatial hemifield (main factor validity, F(1,13) = 10.74, p <0,01; Newmann-Keuls post-hoc test, p < 0.05). Neither the factor stimulus location nor the interaction between stimulus location and validity was statistically significant. In the rotated condition, the validity factor was not statistically significant. By using the Newmann-Keuls post hoc test, we studied the interaction stimulus location \times validity (F(1,13) = 2.03, p = 0,18). The pairwise comparisons revealed a statistically significant difference between valid and invalid trials for nasal conditions only. All in all, the present results suggest that attentional benefits are always present in the frontal condition but not in the rotated one; it is evident from Figure 2 that, in the latter, valid trials were significantly faster than invalid trials for the nasal but not for the temporal condition.

Why is there a difference in attentional performance between nasal and temporal spatial hemifields for the rotated condition? One possibility is that eye rotation somehow affects perceptual capability. However, three strong arguments seem to go against this hypothesis. First, clinically assessed visual acuity was not influenced by eye's orbital position. Second, the retinal representation of presented stimuli with respect to the fovea was exactly the same in all conditions. Third, there was an absence of significant differences between temporal and nasal invalid trials. An alternative interpretation is that the lack of attentional benefits for temporal stimuli in the rotated condition was due to factors related to motor control. In this condition, the eye was kept at an extreme position in the orbit, and this position limited the execution of a saccade toward the temporal hemifield, whereas it allowed saccadic execution toward the nasal hemifield. This motor limitation appears to be the only plausible explanation of the present findings; attention cannot be directed toward spatial locations that are difficult for the eyes to access. This interpretation fits well with the premotor theory of attention [12], in which the perceptual enhancement consequent to orienting of attention is said to result from the preparation of a saccadic eye movement toward the to-be-attended location. A causal relation between eye movements and orienting of visuospatial attention necessarily implies the presence of attentional deficits when oculomotion is impaired. Although studies investigating attentional capabilities in cortical [15], subcortical [16], or peripheral [17] oculomotor lesions in patients suggest that such a relation might exist, they do not draw a congruent picture, probably because of the pathology-specific compensatory mechanisms.

Here we show clear evidence of the strict dependence of attention on oculomotor processes in neurologically healthy subjects. We obtained such evidence by having subjects orient their attention while they were affected by an experimentally induced "oculomotor deficit." Therefore, we interpret the perceptual enhancement consequent to orienting of visuospatial attention as the consequence of the backward activation (from executive frontal/premotor areas to perceptual parietal/occipital ones) of the same circuits used by the brain to generate a saccadic response toward a visual stimulus. This hypothesis might explain the role of oculomotor involvement during visuospatial attentional tasks, both in humans and monkeys, making the postulation of the existence of supramodal attentional centers unnecessary.

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Figure 2. Standardized Mean RTs to Stimulus Presentation Panels show frontal (A) and rotated (B) conditions' standardized RTs. Data for the attended (V, valid) and the unattended (I, invalid) location both in temporal and nasal hemifields are shown. Thin lines above each histogram indicate standard error of mean. Asterisks indicate the presence of a statistically significant difference between valid and invalid trials (p < 0.05). Ordinates are z scores. The mean RT values were 329.5 ms for the frontal condition and 329.6 ms for the lateral condition.

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