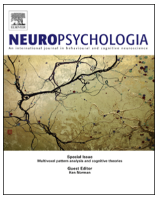
Neuropsychologia 58 (2014) 75–80

Contents lists available at ScienceDirect

Neuropsychologia

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



Lack of automatic attentional orienting by gaze cues following a bilateral loss of visual cortex

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ARTICLE INFO

Article history:
Received 13 January 2014
Received in revised form
28 March 2014
Accepted 4 April 2014
Available online 13 April 2014

Keywords:
Blindsight
Gaze
Attention
Amygdala

ABSTRACT

In social interactions, the location of relevant stimuli is often indicated by the orientation of gaze. It has been proposed that the direction of gaze might produce an automatic cueing of attention, similar to what is observed with exogenous cues. However, several reports have challenged this claim by demonstrating that the behavioral gain that arises with gaze cueing could be explained by shifts of attention, which are intentional and not automatic. We reasoned that if cueing by gaze was truly automatic, it should occur without awareness and should be sustained by subcortical circuits, including the amygdalae, independently of the main geniculo-striate visual pathway. We presented a cross-modal version of the Posner cueing paradigm to a patient (TN) with bilateral lesions of occipital cortex (Burra et al., 2013; Pegna, Khateb, Lazeyras, & Seghier, 2005). TN was asked to localize a sound using a key press. The location of the sound was congruent or incongruent with the direction of gaze of a face-cue. In groups of healthy young and age-matched participants, we observed significantly longer response times for incongruent than congruent sounds, suggesting that gaze direction interfered with processing of localized sounds. By contrast, TN's performance was not affected by sound-gaze congruence. The results suggest that the processing of gaze orientation cannot occur in the absence of geniculo-striate processing, suggesting that it is not automatic.

1. Introduction

Numerous studies have demonstrated that the direction of gaze is a social cue that produces shifts of spatial attention and it has been argued that these shifts in attention are involuntary, reflexive responses that involve exogenous covert attention (Driver et al., 1999). In the attention shifting paradigms developed by Posner and colleagues (see for example Posner, 1980; Posner & Cohen, 1984), exogenous cues are distinguished from endogenous cues. In the latter, the cues are centrally-presented symbolic cues such as arrows that indicate the most likely side of appearance of the target. Here, attention shifting depends on the subjects expectations and is under voluntary control, hence the term endogenous. In the case of exogenous cues, attention shifting is determined by a peripheral visual cue (e.g., a flickering box) appearing prior to the target. These cues are considered reflexive or automatic as they produce shifts of attention even when they do not predict the subsequent appearance of the target and that participants are made aware of this fact, or are asked to disregard the cues (Jonides, 1981; Spence & Driver, 1994)

Automaticity is not easy to define and the term can encompass slightly different meanings (Driver et al., 1999). Furthermore, no process can be considered either completely automatic or wholly intentional (Bargh, 1994). Nevertheless, research on gaze cues has attempted to determine their automaticity by studying their similarity with exogenous cues, and by investigating whether certain characteristics composing automaticity appear. For instance, studies have suggested that the temporal dynamics of attention orienting in response to gaze cues are similar to exogenous cues. Indeed, the peak of the attentional effects appears early in time, occurring already within 100 ms after the onset of the cues, as for exogenous cues (Friesen & Kingstone, 1998). Other component features of automaticity, such as unintentionality (i.e., whether or not the participant intends to follow the direction of gaze of the cue) and uncontrollability (i.e., whether or not a participant can counteract the influence of the cue) (see Bargh, 1994) have been observed for gaze cues. For example, even when participants are explicitly informed that gaze will not be used as a predictor of stimulus location or are apprised of the fact that gaze predicts target location

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http://dx.doi.org/10.1016/j.neuropsychologia.2014.04.003
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only very weakly, faster responses continue to be observed for targets appearing at the gazed-at location (Driver et al., 1999). Moreover, the allocation of attention in the direction of gaze occurs with very brief presentation times (Hietanen & Leppanen, 2003), again suggesting automatic processing of gaze direction.

However, substantial differences also exist between exogenous cueing and gaze cueing (Wiese, Zwickel, & Müller, 2013). Involuntary shifts of attention following the presentation of exogenous cues in the periphery are observed up to 300 ms after cue onset (e.g., Posner & Cohen, 1984), whereas gaze cues produce effects of much longer duration, lasting at least up to 700 ms after cue onset (Friesen & Kingstone, 2003). In addition, the slowing of response times that is observed at longer cue-target intervals, called "inhibition of return" (IOR), is consistently observed for peripheral cues, but not for gaze cues (Friesen & Kingstone, 2003), although IOR may be observed for gaze cues with more sensitive methods (Frischen, Bayliss, & Tipper, 2007; Frischen & Tipper, 2004).

One important, yet less investigated feature composing automaticity is awareness (Bargh, 1994). If participants can be made unaware of the presence of a gaze cue but remain nevertheless influenced by it, this should provide additional proof of the automaticity of attention orientation in responses to gazes. Awareness can be prevented in healthy participants through different experimental manipulations, such as backward masking (e.g., Pegna, Landis, & Khateb, 2008), but neuropsychology provides alternate means to address this question. One typical situation is that of hemianopic patients who suffer from lesions in their occipital cortex and who consequently become blind in the contralateral visual hemifield. Despite this cortical blindness, some visual abilities are preserved and patients may be able to "guess" certain visual characteristics of the stimulus that they cannot see with a probability above chance. This phenomenon has been called "blindsight" (Weiskrantz, Warrington, Sanders, & Marshall, 1974). In some rare cases, both occipital cortices can be injured. This unfortunate condition arose in patient TN, who is the subject of the present study. TN suffered two consecutive strokes within 36 days that successively destroyed first his left, then his right occipital regions, subsequently rendering him cortically blind.

Although TN no longer possesses any primary visual cortex, he shows remarkable residual capacities including affective blindsight (Pegna, Khateb, Lazeyras, & Seghier, 2005), residual navigation by locomotion (de Gelder et al., 2008) and above chance guessing to exogenous peripheral cues (Buetti et al., 2013). The pathways giving rise to blindsight are still debated (Cowey, 2010; Pessoa & Adolphs, 2010; Sahraie, Hibbard, Trevethan, Ritchie, & Weiskrantz, 2010; Tamietto & de Gelder, 2010), but it is likely that it relies at least partly on subcortical projections to the superior colliculus (Sahraie et al., 2010) and in the case of affective blindsight (i.e., above-chance guessing for emotional stimuli) through a colliculo-pulvinar projection to the amygdala (Tamietto & de Gelder, 2010). Recently, we found that photographs of faces looking directly at the patient produced an increase in right amygdala activity when compared to faces with an averted gaze (Burra et al., 2013). This arose despite the absence of any awareness of the stimuli. In view of these findings, we decided to investigate whether gaze cues could orient attention non-consciously, and to determine whether the subcortical projections to the amygdala that process eye-contact could also process direction of gaze and produce attention orienting.

To assess this with TN, we created a cross-modal version of the gaze-cueing paradigm in which the cue remained a gaze but the target was a lateralized sound. We compared the interference effect in TN to that in an age-matched control group.

Considering that unawareness is a component of automaticity (Bargh, 1994), we surmised that if gaze cues orient attention in TN, this would provide further proof that they are processed automatically and in the absence of any conscious, voluntary control. By contrast, if gaze does not orient attention in TN, we should conclude that these cues require awareness, as well as the integrity of the primary visual cortex and the geniculo-striate pathway, for adequate processing.

2. Methods

2.1. Population

Eleven age-matched male adults (mean age: 55 years; range: 48–66) were recruited as a control group. Participants were naïve as to the purpose of the experiment. The local ethics committee had approved the study and informed consent was obtained from participants prior to the experiment.

2.2. Patient TN

Patient TN was a male physician, aged 60 years. His first stroke occurred in the left parieto-temporo-occipital cerebral area, producing right hemiplegia and transcortical sensory aphasia, which receded rapidly, but also a persistent right homonymous hemianopia. The second hemorrhage occurred in the right occipital lobe and produced the loss of vision in his remaining (left) visual field. The lesion in the left hemisphere includes most of the occipital lobe, with minimal sparing of the medial ventral part of the inferior occipital gyrus and anterior part of the lingual gyrus. The lesion extends anteriorly to the middle part of the fusiform gyrus leaving the parahippocampal gyrus grossly intact. Laterally, the lesion extends to the medial inferior temporal gyrus. Dorsally, the hemorrhage reached the superior parietal lobule and spared the ventral part of the precuneus. The right hemisphere lesion is smaller and includes most of the occipital lobe, with limited sparing of the medial part of the posterior lingual gyrus and medial part of precuneus. The anterior border stretches to the middle part of the fusiform gyrus and included the posterior inferior and middle temporal gyri, but spared the parahippocampal gyrus. More dorsally the superior temporal gyrus, as well as the inferior and superior parietal lobule appeared relatively intact (see Fig. 1). Finally, a thin layer of cortex appears to remain in the occipital region, however a previous investigation using diffusion tensor investigation (DTI) failed to show the presence of any fibers inputting this tissue and furthermore no activity was produced in response to visual stimulation suggesting that this region is non-functional (de Gelder et al., 2008).

2.3. Stimuli

Six different identities (3 males/3 females) were created using FaceGen Modeller 3.4, a software that has been used in previous studies on gaze perception (for instance Ethofer, Gschwind, & Vuilleumier, 2011). The avatars were de-saturated and equalized for their facial luminance. Presented on a gray background, each picture had 512×512 pixels, subtending approximately $6^\circ \times 6^\circ$ (width × height). Gaze deviation was 50% of the maximal deviation. Gaze was averted with equal probability to the left or right. A sound of 440 Hz was presented via a headphone to the left and right ear. Viewing distance was 85 cm and the screen dimensions were $37 \times 29\ \text{cm}^2$ with a resolution of 1024×1280 pixels.

We used the Cogent toolbox (www.vislab.ucl.ac.uk/Cogent2000) for Matlab to present the stimuli. Gaze was directed either towards the location of the sound (congruent), or towards the opposite location (incongruent). Two neutral conditions were used, one in which the gaze was directed straight ahead (contact neutral condition) and one in which the eyes were closed (closed neutral condition). For each trial type, there were 96 trials, divided into 8 blocks for a total of 384 trials. The head position was maintained with a chinrest in order to keep the eyes oriented towards the screen. Participants had to respond to the location of the sound by pressing a corresponding left or right key. An eye tracker could not be used with TN due to the technical impossibility of calibrating the setup (TN could not fixate any points on the screen due to his blindness). The investigators therefore visually monitored TN's eyes throughout the experiment. Participants (both TN and the healthy controls) were allowed rest periods between blocks. The same sound volume was used for all participants, but we ascertained that all participants perceived the sound easily. A fixation cross was displayed for 1000 ms. Then, the visual cue was presented for 100 ms. After an inter-stimulus-interval of 300 ms, the lateralized tone (50 ms) was presented through headphones. This ISI has been chosen because effects are strongest and less influenced by gender (Bayliss & Tipper, 2005). Participants had 2 s to respond while time was unlimited for TN. The next trial was initiated 1 s after the response, if TN accurately fixated the center of the screen. When this did not happen, he was asked to orient his gaze straight ahead, subsequently to which the experimenter initiated the trial manually.