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Neuropsychologia

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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.

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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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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 (Bueti et al., 2013). The pathways giving rise to blindsight are still debated (Covey, 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 geniculostriate 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° × 6° (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 × 29 cm² 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.

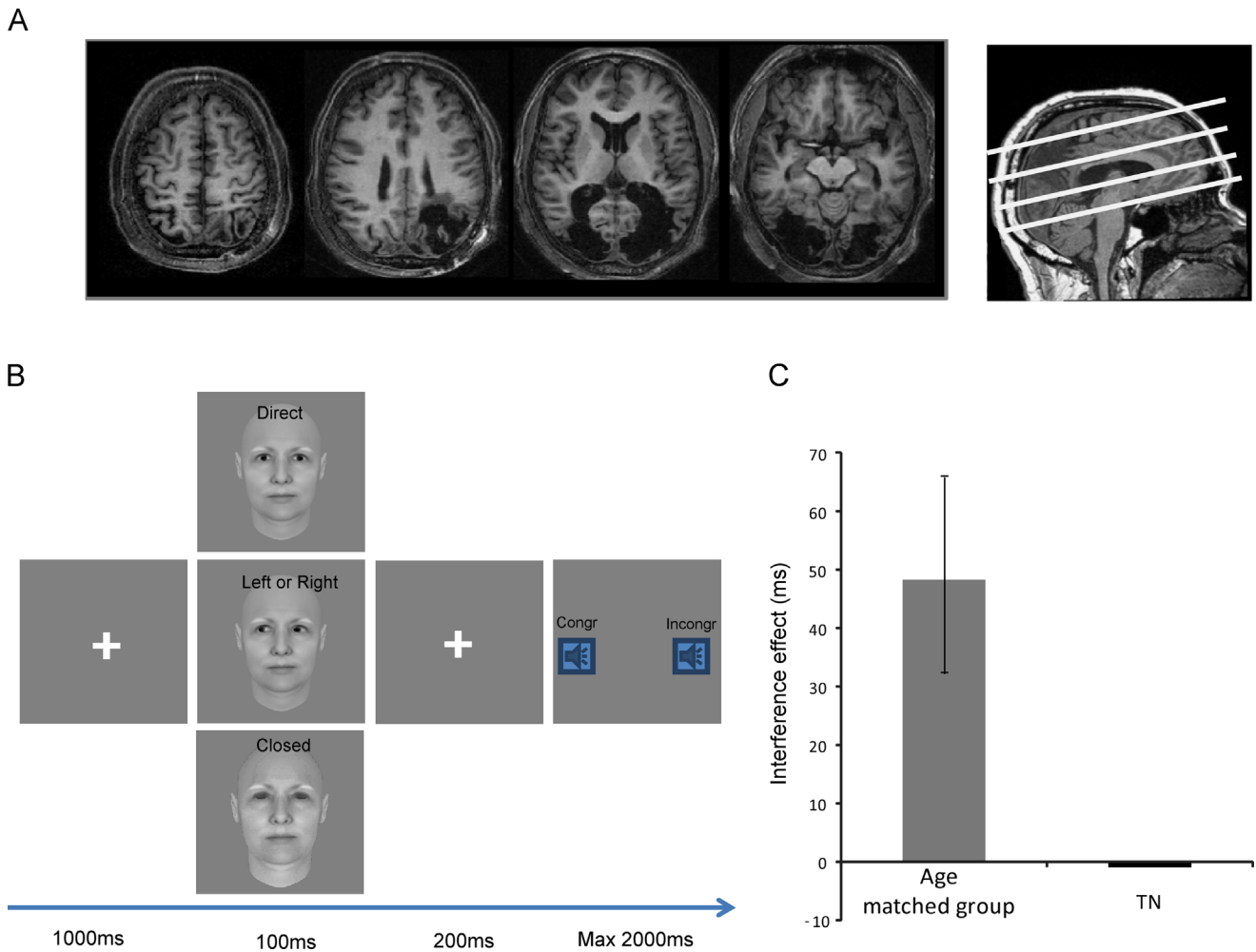


Fig. 1. (A) Structural T1 MRI images illustrating the lesioned areas. The left panel shows the horizontal sections of TN's brain at Talairach z coordinates 50, 30, 10 and -10 . The right panel shows the corresponding sagittal sections. The left hemisphere is represented on the right following radiological convention. (B) Experimental procedure. A face with different gaze position, straight, averted or closed was presented in the center of the screen and was followed by a lateralized sound of 50 ms. Then, the program waited 2 s for a response. The orientation of gaze was congruent or incongruent (50%–50%) with respect to the lateral sound location. Gaze was neutral when directed at the viewer or when the eyes were closed. (C) The mean interference effects (incongruent RT–congruent RT) for the age-matched group (min: 23, max: 123) and patient TN. The error bars indicate the 95% confidence intervals.

3. Results

Results were corrected for violation of sphericity using the Greenhouse–Geisser approach to epsilon correction of degrees of freedom, when appropriate.

3.1. TN

Median response times (RTs) for the congruent, incongruent, contact neutral and closed neutral conditions were 378, 377, 367, and 379 ms respectively. We tested the significance of these data using a univariate ANOVA. It did not reach the level of significance, $F(3,355)=.98$, $p=.4$, $\eta^2=.008$. TN did not show the expected effect of congruence (incongruent minus congruent RT: -1 ms). His accuracy to respond to the tone was of .96, .94, .94, and .94, respectively, $F(3,380)=.19$, $p=.9$, $\eta^2=.002$.

3.2. Age-matched control group

RTs for the control group were entered into a one-way ANOVA using the 4 experimental conditions as repeated-measures. A significant effect of condition was observed, $F(3,30)=19.2$, $p<.001$, $\eta^2=.56$. RTs were significantly shorter in the congruent condition

than in the incongruent condition for (373 vs. 422 ms), $t(10)=-6.4$, $p<.001$, confirming the effects of gaze direction on attention shifting in our task. The size of the congruency effect ranged between 23 and 123 ms. RTs in the control condition were situated between the congruent and the incongruent RTs (399 ms). The contact neutral condition (394 ms) failed to reach our threshold for significance compared to the closed neutral condition (404 ms), $p=.09$. This group confirmed the classic congruence effect, which is illustrated in Fig. 1C.

Accuracy was very high and no significant difference was observed between congruent and incongruent conditions, $F(1.29,12.94)=2.73$, $p=.103$, $\eta^2=.228$.

3.3. Comparisons

Using the method provided by Crawford and Garthwaite (2002), we measured whether TN's congruence effect of -1 ms was situated below the 95% confidence interval computed around the congruence effect of 49 ms for the control group. This proved to be the case, $t(10)=-1.81$, $p=.04$ (one-sided t -test). Further, the 95% confidence interval for the congruence effect was from 31 to 67 ms in the control group.

Taken together, the RT results suggest that TN is not influenced by gaze direction while the control group is.

4. Discussion

In this experiment, we used a crossmodal paradigm to test whether direction of gaze constitutes a spatial cue that can orient spatial attention and speed responses to a subsequently lateralized auditory target. More specifically, our primary aim was to determine whether awareness is necessary for gaze cueing to occur, by studying this effect in a patient with bilateral cortical blindness and comparing performances with an age and gender-matched control group.

Our data showed that the response times of healthy control participants were faster for targets appearing in a gaze-cued location, corroborating previous observations (Driver et al., 1999; Friesen & Kingstone, 1998; Hietanen, 1999; Vuilleumier, 2002). Importantly, this effect was not observed in patient TN, revealing that gaze cueing cannot occur without awareness.

As noted in Section 1, gaze cueing has been reported to possess characteristics of exogenous attention, suggesting automatic attention orienting. For example, authors presented cues composed of schematic faces looking left, right or straight ahead (Friesen & Kingstone, 1998). These were followed by letters that the participants had to identify, localize or simply detect. Response times were faster when the targets were presented on the side the face was looking at. This occurred even though the participants were informed that the gaze was not predictive of target location. In a similar experiment using photographs of faces, Driver et al. (1999) also showed that response times were faster for letters situated on the side indicated by the gaze cues. This again arose when the subjects were informed that gaze did not predict the side of appearance of the target, but also when they were instructed to ignore the face. These findings suggest that gaze cues reflexively produce attention orienting as this arises when the subjects do not intend to follow the direction of gaze of the cue and even when they attempt to counteract the process. That attention is oriented in an obligatory and uncontrollable manner and indicates a certain degree of automatic processing.

These findings have been disputed by others who have reported that gaze-cueing may not share much similarity with exogenous cues and is less automatic than previously described. For example, in a neurological case report (Vecera & Rizzo, 2006), a patient with orbito-frontal lesions (MJ) was submitted to an attention shifting task with either exogenous or endogenous cues. Exogenous cues (the highlighting of peripheral boxes) produced lower reaction times for targets at the cued locations. On the other hand, endogenous cues (the words “left” or “right”) failed to produce a faster response at the corresponding locations. This indicated that damage to the frontal areas impaired voluntary, but not reflexive shifting of attention. More importantly however, MJ also failed to show quicker responses at gaze-cued locations. According to the authors, this suggests that gaze direction act as an endogenous cue that is modulated by intentions, rather than being an automatic process.

As outlined in Section 1 however, automaticity can encompass slightly different meanings (Driver et al., 1999) and in previous reports was examined mainly with respect to features such as controllability (see Bargh, 1994). Our study suggests that if the “unawareness” component of automaticity (Bargh, 1994) is present, gaze cues can no longer exert attention orienting, since our cortically blind patient was unaffected by gaze direction.

This conclusion may appear to be in contradiction with the findings in healthy controls, in whom awareness was manipulated using backward-masking procedures. Sato, Okada, and Toichi

(2007) cued locations using gaze-cues with schematic faces, as well as photographs of real faces. Healthy controls were asked to respond as fast as possible to targets appearing at congruent or non-congruent locations. Of particular significance here is the fact that the cues were presented supraliminally and subliminally. The authors found that the response times were shorter to stimuli appearing in a gazed-at location whether the faces were consciously seen or not. Consequently, they concluded that awareness was not necessary for the gaze cue to be effective. Again, these results seem to oppose our current data, and suggest on the contrary that gaze *can* orient spatial attention even when awareness is absent. This inconsistency however may simply reflect the limitations in comparing blindsight in patients, and *simulated* blindsight in healthy controls, obtained through experimental manipulations that limit awareness. Indeed, the mechanism through which awareness may be suppressed in the latter situation differs substantially from that in patient studies. In patients, brain damage obviously precludes any processing by V1 due to the lack of functional tissue in this region. By contrast, when awareness is suppressed perceptually, electrophysiological recordings in monkey V1 show that the activity of neurons in this area is in fact unaffected (for a review see Leopold, 2012; see for example Leopold & Logothetis, 1996; Maier et al., 2008). This points to different mechanisms producing unawareness in blindsight and in visual masking, which could in turn explain divergences between the results in our study and in that of Sato et al. (2007).

We cannot rule out the possibility that TN may have been insensitive to gaze cueing before his lesion, as it is well known that not all individuals respond to gaze cues (for a review see: Landry & Parker, 2013). This of course restricts the scope of our interpretation. Notwithstanding this limitation, the lack of response might appear discrepant in view of the fact that TN *did* process eye-contact non-consciously, showing an amygdala response for direct gaze compared to averted gaze (Burra et al., 2013), yet failed to show attention orienting in response to gaze-cueing. In our view, amygdala activation in this patient occurs most likely through a direct colliculo-pulvino-amygdalar pathway that bypasses V1, and evidence exists showing “automatic” gaze processing is linked to the amygdala (Okada et al., 2008). Furthermore, the superior colliculus has been shown to produce attention orientation in cortical blindness (Rafal, Smith, Krantz, Cohen, & Brennan, 1990). Why then should not his subcortical pathway allow non-conscious, gaze-cued orientation of spatial attention?

Previous studies have confirmed that the amygdala (Kawashima et al., 1999) plays an important role in processing the direction of gaze, along with the superior temporal sulcus (STS) (Hoffman & Haxby, 2000). Using a PET analysis in healthy controls, Kawashima et al. (1999) found that when participants judged the direction of gaze of a person on video, the (left) amygdala was activated relative to a control condition in which gaze did not vary. Elsewhere, Okada et al. (2008) reported that the amygdala was essential for reflexive shifts of attention in response to gaze cues. They studied a control group, as well as 7 epileptic patients, who had undergone left or right medial temporal lobectomy that included large portions of the amygdalar region, and in whom the visual field was intact. Nonpredictive gaze cues were presented to the visual field contralateral or ipsilateral to the intact hemisphere. Responses to subsequent targets were faster when they appeared at the cued location for controls, as well as in patients providing they were presented to the intact hemisphere. By contrast, no effect of gaze was found when the cues appeared contralaterally to the side of surgery. This suggests that the amygdala plays a key role in reflexive attention shifting in response to gaze. However, the “reflexive” quality of the cues was defined on the basis of their uncontrollability, as the fact that they were non-predictive. Thus, although these findings confirm

that the amygdala might play a role in automatic attention orienting, automaticity in this case does not include unawareness as a feature. The findings therefore confirm that the amygdala is necessary, though not sufficient, to produce attention orientation.

The superior colliculus is known to be critical for eye movements in reflexive, non-conscious orienting of attention (Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988; Rafal et al., 1990). Rafal et al. (1988) specifically tested the role of the superior colliculus in non-conscious processing by presenting stimuli to the hemianopic fields of 3 patients. Retino-tectal projections are predominantly from the temporal rather than the nasal visual field. Consequently, by presenting stimuli either in the temporal or the nasal field under monocular viewing conditions, the investigators were able to establish the contribution of the superior colliculus to reflexive saccades. The results showed that saccadic movements towards targets situated in the intact visual field were inhibited by distracters in the temporal but not the nasal hemianopic field. Since the superior colliculus receives a greater input from the temporal field, it can be concluded that exogenous, as well as unconscious attention-shifting relies on this structure.

In our patient, structural MRI reveals that damage affects posterior brain areas but spares the retino-thalamic and retino-tectal projections. In addition, a previous study in TN showed that he responds above chance to exogenous peripheral cues in a pointing task (Buetti et al., 2013). The preserved superior colliculus in TN, associated with his sensitivity to exogenous peripheral cues suggests that this subcortical structure may indeed allow non-conscious attention shifting. Nevertheless, this effect was not observed for gaze cueing suggesting that collicular involvement is insufficient to produce gaze-cued attention orienting and thus providing further evidence of differences between the two types of cues.

To conclude, although direct gaze contact is processed non-consciously by TN's amygdala, most likely through a collicular route (Burra et al., 2013), the current data suggest that non-conscious processing does not lead to attentional orientation in response to averted gaze cues. If gaze-cueing qualifies as automatic on some counts, this does not include unawareness as a constituent component. This may be due to the fact that direct gaze represents an imperative behavioral signal for the organism, operating at a fundamental level of neural processing that does not initially require awareness but causes it to arise more readily (Chen & Yeh, 2012). By contrast, when gaze is averted, processing of direction and attentional orientation may require the activation of a more diffuse network that extends beyond the amygdala and includes the primary visual cortex, as well as the parietal and STS regions (Nummenmaa, Passamonti, Rowe, Engell, & Calder, 2010), part of which are damaged in this patient.

Acknowledgments

This investigation was supported by the Swiss National Science Foundation for Scientific Research (Grant nos. #320030-144187 and PDFMP1_129459).

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