Privileged visual processing of the straight-ahead direction in humans

Jean-Baptiste Durand
Université de Toulouse, Centre de Recherche Cerveau et Cognition, Toulouse, France; Centre National de la Recherche Scientifique, Toulouse Cedex, France

Damien Camors
Université de Toulouse, Centre de Recherche Cerveau et Cognition, Toulouse, France; Centre National de la Recherche Scientifique, Toulouse Cedex, France

Yves Trotter
Université de Toulouse, Centre de Recherche Cerveau et Cognition, Toulouse, France; Centre National de la Recherche Scientifique, Toulouse Cedex, France

Simona Celebrini
Université de Toulouse, Centre de Recherche Cerveau et Cognition, Toulouse, France; Centre National de la Recherche Scientifique, Toulouse Cedex, France

At any moment, the objects we face are endowed with a special behavioral status, either as potential obstacles during navigation or as optimal targets for visually guided actions. Yet, the gaze frequently jumps from one location to another when exploring the visual surroundings, so that objects located straight-ahead are often seen from the corner of the eyes. In the present study, we tested the hypothesis that peripheral vision might nevertheless ensure a privileged processing of these behaviorally important objects. Human subjects were asked to respond as fast as possible to the appearance of visual objects in their peripheral field of view while gazing successively in different directions. The visual objects formed similar images on the retina and differed only with respect to their egocentric location: either straight-ahead or eccentric with respect to the head/body midline. We found that straight-ahead objects elicit consistently shorter behavioral responses than eccentric objects (median difference of at least 10 ms). Additional experiments indicate that neither binocular visual cues nor full attentional resources play a fundamental role in this mechanism, and that it cannot be resumed to a simple preference for objects contralateral to the direction of gaze. These results are in agreement with recent electrophysiological findings showing that the early integration of gaze-related signals in the visual cortex of macaque monkeys lead to a higher neuronal sensitivity to the straight-ahead direction.

Keywords: primates, vision, spatial, gaze, location, reaction times

Introduction

In many circumstances, it would be wise to keep the eyes on what is right in front of oneself. This is particularly evident for actions in which the detection and avoidance of potential obstacles is crucial, for instance, when walking along a crowded sidewalk or when driving a car. But this holds for many other types of visually guided actions, which are performed optimally when both facing and gazing the target objects. The advantage in looking straight-ahead is that central vision, from which we extract fine-grained visual representations, covers this behaviorally important region. Yet, objects and events occurring in more eccentric locations with respect to the body midline can often capture the attention and attract the gaze for accurate processing in central vision. Each time this happens, the gaze is drawn away from the straight-ahead direction, and the objects located straight-ahead are then seen from the corner of the eye. As an adverse consequence, these behaviorally important objects are given a suboptimal processing in the peripheral vision (Berkley, Kitterle, & Watkins, 1975; Hess & Dakin, 1997; Kitterle, 1986; Poirier & Gurnsey, 2005; Westheimer, 1982). Thus, disengaging central vision from the straight-ahead direction seems to come at a behavioral cost.
Nevertheless, recent electrophysiological results (Durand, Trotter, & Celebrini, 2010) suggest that this adverse effect might somehow be alleviated by a privileged processing of the straight-ahead direction in peripheral vision. In that study, macaque monkeys maintained their gaze at different directions while the visual activity of neurons from the primary visual area was recorded. Because these neurons possess restricted sensory windows, i.e., their classical receptive fields (Hubel & Wiesel, 1962) which are anchored to the retina (Gur & Snodderly, 1997), they respond to a distinct portion of the surrounding space for each particular direction of gaze (Figure 1A). Although the same visual stimulation was delivered to the neurons’ receptive fields for all the directions of gaze tested, most of the neurons coding the peripheral field of view showed a marked preference for the straight-ahead direction; the level of evoked neuronal activity was the highest when both the stimuli and receptive fields were aligned with the straight-ahead direction, and it decreased progressively as the stimuli and receptive fields were brought farther away by changing the direction of gaze (Figure 1B).

Numerous other studies had already reported a modulatory influence of gaze direction on neuronal activity in the visual cortex (Andersen & Mountcastle, 1983; Bremmer, 2000; Bremmer, Distler, & Hoffmann, 1997; Bremmer, Ilg, Thiele, Distler, & Hoffmann, 1997; Bremmer, Pouget, & Hoffmann, 1998; Galletti & Battaglini, 1989; Galletti, Battaglini, & Fattori, 1995; Guo & Li, 1997; Li, Tanaka, & Creutzfeldt, 1989; Nowicka & Ringo, 2000; Rosenbluth & Allman, 2002; Trotter & Celebrini, 1999; Weyand & Malpeli, 1993). However, this modulatory influence was implicitly considered as (a) showing no bias for a particular spatial location at the neuronal population level (e.g., Bremmer, 2000) and (b) being dedicated to coordinate transformations by which visual objects, initially encoded in a retino-centric frame of reference, can be localized with respect to the head (Andersen, Essick, & Siegel, 1985; Andersen, Snyder, Li, & Stricaine, 1993; Pouget, Fisher, & Sejnowski, 1993; Pouget & Snyder, 2000; Zipser & Andersen, 1988). Indeed, localizing visual objects with respect to oneself requires integrating information about where we are gazing, in addition to visual information about where the objects’ images fall on the retina.

The fact that most neurons coding the peripheral field of view in the primary visual area have a marked preference for the straight-ahead direction (Durand et al., 2010) implies that the same object, forming the same image on the peripheral retina, evokes a higher level of neuronal activity when it is located straight-ahead than when it occupies a more eccentric location with respect to the body midline. This property may serve an important and previously unexpected function: compensating the disengagement of central vision from objects located straight-ahead by boosting their visual processing in peripheral vision. As such, the privileged processing of the straight-ahead direction might...
represent an attentional mechanism enlightening the processing of a behaviorally relevant region of the surrounding space. Attentional mechanisms are known to increase the level of neuronal activity for the attended locations or features (Luck, Chelazzi, Hilliard, & Desimone, 1997; Motter, 1993) and to decrease the behavioral reaction times for these attended locations or features (Posner, Snyder, & Davidson, 1980).

We tested the hypothesis of a privileged straight-ahead processing in human subjects by asking whether objects appearing in the peripheral field of view elicit faster behavioral responses when those objects are located straight-ahead rather than eccentric with respect to the head/body midline. Our results demonstrate that human subjects actually respond faster to straight-ahead objects than to eccentric objects when both are seen from the corner of the eyes (cf. “main binocular task”) and that this straight-ahead preference cannot be accounted for by fixation error during asymmetric gazing (cf. “fixation control”). Moreover, further experiments indicate that neither binocular visual cues (cf. “monocular task”) nor full attentional resources (cf. “dual task”) are required for a privileged processing of the straight-ahead direction in human peripheral vision. Finally, a last experiment (“tuning task”) shows that the effects reported here do not simply reflect a preference for targets in opposite direction with respect to gaze direction, but rather a real tuning centered on the straight-ahead direction. These results are thus in good agreement with the predictions drawn from electrophysiology in macaque monkeys. They support the view that, in primates, the straight-ahead direction is monitored with special care even during disengagements of central vision.

Materials and methods

Subjects

Twenty-one subjects (15 males and eight females; mean age = 24.8 years, Standard Deviation = 6.3 years) participated in the first experiment (“main binocular task”). Among them, nine were also involved in the second experiment (“monocular task”), and 11 participated in the third experiment (“dual task”). Finally, eight subjects were involved in the fourth experiment, including five subjects from the first experiment. All subjects had normal vision or corrected to normal with contact lenses for six of them. One subject was excluded for wearing corrective lenses that could have partially occluded visual stimuli in the peripheral field of view. Subjects volunteered and gave written informed consent for participating in psychophysical experiments. (They were nevertheless naive regarding the specific purpose of these experiments.) All experiments met the requirement of the ethical principles of the Declaration of Helsinki and those of the local ethic committee.

Apparatus

Subjects sat in a chair, legs uncrossed and both feet on the floor, in a dimly lit room. Their heads were stabilized within a chin rest and constrained mechanically to avoid rotation. Both hands were aligned on a computer keyboard in front of them. The chair/chin rest/keyboard positioning was set to ensure a fine alignment between the subjects’ head and trunk axes. Subjects were asked to keep this positioning as constant as possible during the experiment. Postural corrections were applied when necessary between successive blocks of trials. Subjects faced a computer screen at a viewing distance of 40 cm. The screen subtended 35.6° × 26.8° of visual angle and was set to run with 100 Hz refresh rate at 1024 × 768 pixels resolution. The experiments were programmed in Matlab (MathWorks®, Natick, MA) using the Psychophysics Toolbox (Brainard, 1997) on a standard Microsoft Windows computer system. For a subset of subjects (N = 7), eye movements were recorded with a video-based eye tracker (iView Hi-Speed, SMI, Berlin, Germany) while they performed the main binocular task (see following). This was done to ensure that subjects could maintain accurate asymmetric fixation (±10°) for several minutes.

Visual stimuli

In all the experiments, subjects were asked to maintain their gaze on a white fixation cross (0.5° × 0.5°) displayed at the center of the screen on a gray background. Visual objects were presented in their peripheral field of view (10° of retinal eccentricity) for 60 ms with a random interstimulus interval between 1 and 4 sec. The visual objects were vertically oriented Gabor patch subtending 2° of visual angle (1 cycle per degree; 30% contrast; mean luminance equal to that of the gray background: 20 Cd/m²).

Experimental design

The experimental design common to the first three experiments is shown in Figure 2. This is a 2 × 2 factorial design with gaze direction (10° left/10° right) and objects’ location in the peripheral field of view (10° left/10° right) as main factors. Importantly, combining these factors produces two conditions in which the objects are aligned with the head/body axis (straight-
In the last experiment, gaze direction was varied between trials across five directions along the horizontal meridian (−10°, −5°, 0°, +5°, +10° relative to the straight-ahead direction), and peripheral objects were systematically presented 10° above the fixation cross.

**Behavioral tasks**

In all the experiments, subjects were asked to maintain their gaze while responding as fast as possible to the appearance of a visual object in the peripheral field of view by pressing the “space” key of a keyboard with their dominant hand.

In the main binocular task, subjects (N = 21) saw the peripheral objects with both eyes. In the monocular task, subjects (N = 9) were involved in the same task, except that it was performed under monocular viewing conditions, so as to discard any binocular visual information. An eye patch was placed over the right eye during blocks of leftward gazing and shifted over the left eye during blocks of rightward gazing. In the dual task, subjects (N = 11) performed the same peripheral detection task (under binocular conditions), but in addition, they were also instructed to respond with the same “space” key when the central fixation cross dimmed slightly. So, subjects were involved in a dual task: central dimming task and peripheral detection task. Finally, in the tuning task, subjects (N = 8) were involved in the same dual task, but rather than maintaining the gaze either 10° left or 10° right during a block of trials, the fixation cross jumped pseudorandomly across five positions along the horizontal meridian (−10°, −5°, 0°, +5°, +10°) between successive trials.

In all these tasks, subjects were first involved in a training session (10–40 trials) and subsequently performed four or five test blocks with alternating gaze directions (±10°). In the main binocular task as well as in the monocular task, each block included 100 trials (50 objects left and 50 objects right; randomly interleaved) and lasted ~4 min. In the dual task, blocks contained 150 trials (50 objects left, 50 objects right, and 50 central, dimming; randomly interleaved) and lasted ~6 min. In the tuning task, each block contained 100 trials (~4 min) with 10 repetitions for each of the 10 conditions (five gaze directions × two types of event, i.e., central dimming or peripheral target in the upper visual field).

**Data analysis**

On a trial per trial basis, reaction times were computed as the time elapsed between the appearance of the left or right peripheral target and the button...
press. Reaction times (RTs) less than 150 ms were considered as anticipatory responses and were excluded from the analysis. RTs greater than 800 ms were considered as attentional errors and were also excluded from the analysis. Note that such “band pass” filtering preserved the vast majority of trials (99.3% of the trials in the binocular task, 98.3% in the monocular task, and 98.4% in the dual task). Median RTs were calculated for each subject as a function of target visual location (±10° relative to the fixation point) and gaze direction (±10° relative to the straight-ahead direction). Confidence intervals at 90% were calculated using nonparametric bootstrap. For statistical tests, the median RTs were analyzed using two-way repeated measures (RM) ANOVA in the first three experiments with gaze direction and objects’ visual location as within-subjects factors. In the last experiments, one-way RM ANOVAs were used for both central dimming and peripheral objects presentation. Note that in the two-way RM ANOVA, the specific influence of objects’ egocentric location (either straight-ahead or eccentric) on the median RTs was assessed by the interaction term between gaze direction and visual location (\( p_{\text{gaze} \times \text{visual}} \)).

**Results**

**Main binocular task**

In the main task, subjects (\( n = 21 \)) maintained their gaze on a fixation cross either 10° to the left or 10° to the right and were required to produce speeded hand responses following the appearance of visual objects 10° left or 10° right from the fixation cross. Figure 3A shows the median RTs of the individual subjects in response to the appearance of left objects versus right objects while they maintained their gaze to the left. The fact that most points lie below the identity diagonal indicates that a vast majority of subjects (19/21) responded faster for objects to the right of the fixation cross. Interestingly, a symmetrical pattern of results was obtained when the same subjects were gazing to the right (Figure 3B). Most subjects (18/21) were faster when responding to left objects. The fact that shorter RT are found for right objects during leftward gazing and for left objects during rightward gazing suggests that, irrespective of gaze direction and visual location, straight-ahead objects are processed faster than eccentric objects.

Statistically, the two-way RM ANOVA confirmed that neither gaze direction nor visual location, per se, had significant effect on the median RT (\( p_{\text{gaze}} = 0.72, p_{\text{visual}} = 0.25 \)). However, the interaction term was highly significant (\( p_{\text{gaze} \times \text{visual}} < 10^{-4} \); see Table 1), revealing a strong influence of the objects’ location with respect to the head/body axis. Across subjects, median RTs were found to be about 10 ms shorter for straight-ahead objects than for eccentric objects (median RT for straight-ahead objects = 300.2 ms; median RT for eccentric objects = 314.9 ms; median \( \Delta \text{RT} = -10.6 \text{ ms} \), 90% confidence interval: −15.0 ms, −7.1 ms).

**Fixation control**

It is important to control that the advantage for straight-ahead objects over eccentric objects actually depends on their egocentric location and not on the location of the images they form on the retinas. Both types of objects are set to share the same retinal eccentricity (10°) with the assumption that subjects actually gaze accurately at the fixation cross. Yet,
unequal retinal eccentricity for straight-ahead and eccentric objects might arise if subjects fail to maintain their gaze on the fixation cross located at ±10° relative to the head/body axis. Notably, a recentering drift of the eyes toward their primary position (i.e., the straight-ahead direction) might cause an average fixation error, reducing the retinal eccentricity of straight-ahead objects and increasing that of eccentric objects (Figure 4A and 4B). Although such drifts occur mainly in darkness (when the fixation target is extinguished) and for more eccentric gaze directions than those used in the present study (Becker & Klein, 1973; Skavenski & Steinman, 1970), we nevertheless addressed this point by recording eye movements for seven of the 22 subjects while they performed the binocular task.

In Figure 4C, the horizontal error bars indicate the range of horizontal angular positions (relative to the fixation cross) to which each individual subject gazed for 95% of the time when looking either leftward (in green) or rightward (in red). It can be seen that subjects do not show any tendency in spending more time to the right of the fixation cross during leftward gazing and more time to the left of the fixation cross during rightward gazing (Wilcoxon paired signed-rank test, \( p = 0.81 \)). Moreover, no correlation is found between those median angular positions and the difference in reaction times for left and right objects (Spearman correlation: \( \rho = 0.28, p = 0.56 \) for leftward gaze; \( \rho = -0.34, p = 0.23 \) for rightward gaze). Importantly, the shortening of reaction times for straight-ahead objects in this subgroup of subjects is comparable to that found for the whole group (two-way RM ANOVA: \( p_{\text{gaze}} = 0.61, p_{\text{visual}} = 0.20, p_{\text{gaze} \times \text{visual}} < 10^{-2} \); median ART = −16.4 ms, 90% CI: [−31.3, −10.2] ms). Thus, the shorter RT elicited by straight-ahead objects cannot be accounted for by a recentering drift of the eyes.

### Monocular task

In order to assess the potential influence of binocular visual cues in this egocentric bias, nine of the subjects involved in the binocular task performed the same task under monocular viewing condition (monocular task). An eye patch was placed over the right eye during blocks of leftward gazing and shifted over the left eye during blocks of rightward gazing.

Overall, the subjects showed longer reaction times in the monocular task than in the binocular task (monocular task: median RT = 331.1 ms, 90% CI = [327.7, 348.4] ms; binocular task: median RT = 311.3 ms, 90% CI: [301.4, 323.2] ms; Wilcoxon paired signed-rank test, \( p < 0.01 \)). However, as was the case in the binocular task, most subjects still exhibited shorter RT for right objects when gazing to the left (6/9 subjects;
Figure 5A) and for left objects when gazing to the right (8/9 subjects; Figure 5B), suggesting that the preference for straight-ahead objects over eccentric objects is preserved under monocular viewing condition.

To address this point statistically, we performed a two-way RM ANOVA over the nine subjects with the direction of gaze (left/right) and the objects’ visual location (left/right) as main factors. As previously discussed, the interaction between gaze direction and visual location was highly significant ($p_{gaze \times visual} < 10^{-2}$), confirming that objects’ location with respect to the head/body axis exerts a strong influence on visual RTs (Table 1). These results indicate that the preference for straight-ahead objects occurs independently of the particular viewing conditions (binocular or monocular). Actually, net differences in RTs between straight-ahead and eccentric objects for the nine subjects involved in both tasks were comparable under monocular and binocular viewing (median RT = 305.8 ms, 90% CI: [280.0, 331.6] ms; binocular task: median RT = 298.7 ms, 90% CI: [280.0, 312.6] ms; Wilcoxon signed-rank test, $p < 10^{-3}$). However, as shown in Figure 6, most of the subjects were still faster for responding to right objects during leftward gazing (9/11 subjects; Figure 6A) and to left objects during rightward gazing (8/11 subjects; Figure 6B).

As was the case for the monocular task, a two-way RM ANOVA showed that, despite an overall influence of the dual task on subjects RTs, there was still a marked preference for straight-ahead over eccentric objects ($p_{gaze \times visual} < 10^{-2}$). Thus, the preference for straight-ahead objects was not affected by introducing the central dimming task. Once again, net differences in RTs between straight-ahead and eccentric objects in the dual task were comparable to those measured in the binocular task for the 11 same subjects (dual task: median $\Delta$RT = 9.8 ms, 90% CI: [20.1, 6.4] ms; binocular task: median $\Delta$RT = 10.9 ms; 90% CI: [16.3, 2.8] ms; Wilcoxon signed-rank test, $p = 0.27$).

Thus, even when spatial attention is at least partially recruited by a central dimming task, RTs in response to peripheral visual objects continue to show a comparable shortening for straight-ahead objects. Note, however, that this experiment cannot rule out the implication of visuospatial attention in the egocentric bias. It rather indicates that the bias for the straight-ahead region of space does not require full attentional resources.

**Dual task**

The objective of this third experiment was to assess the implication of visuospatial attention in the straight-ahead preference evidenced in peripheral vision. Eleven of the subjects involved in the binocular task performed the same task under dual task condition. In one-third of the trials, target appearance in the peripheral field of view was replaced by a slight dimming of the central fixation cross. Subjects were instructed to respond as fast as possible by a button press to both peripheral objects’ appearance and central dimming.

Adding a central dimming task had a detrimental effect on peripheral performances across the 11 subjects, marked by an overall lengthening of the RTs in response to peripheral objects (dual task: median RT = 340.1 ms, 90% CI: [325.9, 361.9] ms; binocular task: median RT = 298.7 ms, 90% CI: [280.0, 312.6] ms; Wilcoxon signed-rank test, $p < 10^{-3}$). However, as shown in Figure 6, most of the subjects were still faster for responding to right objects during leftward gazing (9/11 subjects; Figure 6A) and to left objects during rightward gazing (8/11 subjects; Figure 6B).

Figure 5. Results of the “Monocular Task.” Median reaction times (RT) for the individual subjects ($N = 9$) as a function of objects’ visual location (left versus right). Horizontal and vertical error bars show the 90% confidence intervals for the median RT. Results are shown separately for leftward (A) and rightward (B) gazing blocks. Red and gray areas, above or below the identity line, indicate regions of shorter reaction times for straight-ahead (red areas) and eccentric (gray areas) objects.
Tuning task

The aim of this last experiment was motivated by the need to assess whether the results presented so far might simply reflect a preference for visual objects appearing contralateral to the direction of gaze rather than a real tuning around the straight-ahead direction. Eight subjects (among which five were involved in the binocular task) performed a dual task similar to that previously described. Subjects were instructed to respond as fast as possible by a button press to either peripheral objects’ appearance or central dimming. However, the location of the fixation cross was varied pseudorandomly between each trial among five positions along the horizontal meridian (−10°, −5°, 0°, +5°, +10°), and the peripheral objects were always presented 10° above the fixation cross (Figure 7A). Thus, although peripheral objects can occupy different locations with
Discussion

In this study, we investigated whether objects seen from the corner of the eye receive privileged processing when they are located straight-ahead compared to those occupying more eccentric locations with respect to the head/body midline. This hypothesis was drawn from results of a previous electrophysiological study performed in macaque monkeys (Durand et al., 2010) showing that the visual sensitivity of many neurons in the primary visual area increases as their receptive fields are brought closer to the straight-ahead direction by changing the direction of gaze. If this mechanism is at work in the human visual cortex, then the objects one faces could elicit stronger neuronal responses than eccentric objects and should thus evoke faster behavioral responses.

In the main (binocular) task, the experimental design allowed disentangling the respective contribution of gaze direction (left/right), objects’ location in the visual field (left/right), and objects’ egocentric location (straight-ahead/eccentric) on visuomotor reaction times. Our results demonstrate that, across subjects, reaction times are significantly affected neither by gaze direction nor by objects’ location in the visual field. By contrast, we found that, in most human subjects, straight-ahead objects actually trigger faster visuomotor responses than eccentric objects. By recording eye movements in a subset of subjects, we could rule out an explanation based on the quality of fixation.

Results of the monocular task indicate that binocular visual cues, and particularly vertical disparity, between the left and right retinal images, are not required for privileged processing of objects located straight-ahead. Vertical disparity arises as soon as objects are closer to one eye than to the other (Howard & Rogers, 1995), which is the case for eccentric objects, but not for straight-ahead objects in our experiments. Neuronal sensitivity to vertical disparity has been documented in the primary visual area (Cumming, 2002; Durand, Zhu, Celebrini, & Trotter, 2002; Gonzalez, Relova, Perez, Acuna, & Alonso, 1993) and particularly in the peripheral representation of the visual field (Durand et al., 2007). At the population level, the distribution of preferred vertical disparity seems to be Gaussian-shaped and centered on a null vertical disparity, implying that most neurons prefer objects with small or no vertical disparity. Thus, the preference for straight-ahead objects might be explained by the fact that these objects contain less vertical disparity than eccentric objects. However, the fact that straight-ahead objects still elicit faster visuomotor responses when seen from one eye only indicates that vertical disparity does not play a crucial role in this effect. Note that a similar conclusion was reached concerning the neuronal preference for the straight-ahead direction in macaque primary visual area, which was also found with monocular stimuli (Durand et al., 2010).

These behavioral results in humans are thus in full agreement with the hypotheses drawn from electrophysiological results in macaque monkeys. They show that the human visual system is particularly sensitive to the region of space one directly faces, even when it is seen from the corner of the eye.

This privileged processing of the straight-ahead direction can be seen as an attentional mechanism involved in filtering and selecting behaviorally relevant information. However, results of the dual task show that the introduction of an attention-demanding central task lengthens the reaction times for peripheral objects, but does not interact with the preference for straight-ahead objects, which still elicit shorter reaction times. Thus,
this mechanism is at least partially dissociated from those involved in classical visuospatial attention (Colby & Goldberg, 1999; Posner, 1980). We propose that this particular attentional mechanism emerges from the early integration of visual and postural signals in an automatic and hard-wired fashion. In natural conditions, visuospatial attention and gaze behavior are tightly linked (Rizzolatti, Riggio, Dascola, & Umiltà, 1987), and the former is generally a guide for the latter when exploring a visual scene. The fact that focusing both the attention and the gaze away from the straight-ahead direction does not impair the preference for that particular direction is a strong argument for considering that the role of this mechanism is to alleviate the behavioral cost of drawing away these resources from the objects one faces. Importantly, the 10-ms decrease in reaction times we observed for straight-ahead versus eccentric objects, even when performing a demanding central dimming task, is close in comparison to the increases in reaction times that have been reported when objects are drawn away from the center of gaze (Marzi & Di Stefano, 1981; Marzi, Mancini, Metitieri, & Savazzi, 2006) or from the attentional spotlight (Coull & Nobre, 1998; Posner, 1980; Posner et al., 1980).

Beyond allowing a constant attentional focus on the straight-ahead direction, the early integration of eye-position signals might also help to understand two important issues: (a) how attention toward egocentric locations can emerge within the retinotopic areas that constitute most of the visual cortex (Wandell, Dumoulin, & Brewer, 2007) and (b) why such integrations are so pervasive across the visual cortex (Andersen & Mountcastle, 1983; Bremmer, 2000; Bremmer, Distler et al., 1997; Bremmer, Ilg et al., 1997; Bremmer et al., 1998; Galletti & Battaglini, 1989; Galletti et al., 1995; Guo & Li, 1997; Li et al., 1989; Nowicka & Ringo, 2000; Rosenbluth & Allman, 2002; Trotter & Celebrini, 1999; Weyand & Malpeli, 1993).

Importantly, the tuning task experiment shows that the preference for straight-ahead objects cannot be reduced to a simple preference for contralateral versus ipsilateral directions with respect to the direction of gaze. With peripheral objects presented along the vertical meridian (thus neither ipsilateral nor contralateral), a real tuning centered around the straight-ahead direction was demonstrated, echoing that evidenced at the neuronal level in macaque primary visual area (Durand et al., 2010).

This last task also allows ruling out another potential confound linked to the retinal “blind spot” (or optic disk). In humans, the blind spot is a vertically ovoid region (~4° × 6°) at about 15° of eccentricity, slightly below (2°) the horizontal meridian in the nasal retina (e.g., Awater, Kerlin, Evans, & Tong, 2005). Based on this definition, peripheral objects in the first three experiments were completely away from the blind spot (10° eccentricity along the horizontal meridian, 2° size). Nevertheless, due to anatomical variability, we cannot firmly exclude a small fraction of overlap with the blind spot in some subjects, which could have influenced performances. However, in the last task, peripheral objects were presented far away from the blind spot along the vertical meridian. Thus, proximity with the blind spot can be excluded as an explanation for the straight-ahead preference.

Further experiments are nevertheless required to firmly conclude that the privileged processing of the straight-ahead direction observed in humans relies on a neuronal mechanism similar to that described in the monkey visual cortex. Both psychophysical (Nieman, Hayashi, Andersen, & Shimojo, 2005; Nishida, Motoyoshi, Andersen, & Shimojo, 2003) and fMRI studies (Andersson, Joliot, Perchez, & Petit, 2007; DeSouza, Dukelow, & Vilis, 2002) have provided indirect evidences that the direction of gaze influences neuronal activity in human visual cortex. Yet it remains to be demonstrated that this influence leads to a higher sensitivity for the straight-ahead direction in human primary visual area. To address this issue, we are planning a parallel human/monkey functional imaging (fMRI) study (Orban, 2002; Vanduffel et al., 2001) in which cortical activations produced by straight-ahead and eccentric objects will be compared across visual areas in both primate species. If the same mechanism is at work in both species, straight-ahead objects should elicit stronger activations in the primary visual area (and probably beyond, in extrastriate visual areas) in both humans and monkeys.

Another important point that will deserve attention is whether the preferred straight-ahead direction is that defined by the head axis, the body (i.e., trunk) axis, or a complementary action of both. Previous studies have highlighted the importance of the body axis as a reference for the egocentric representation of the surrounding visual space and as an anchor for visuospatial attention (Karnath, Schenkel, & Fischer, 1991; Ventre, Flandrin, & Jeannerod, 1984). Most of these evidences emanate from studies in unilateral neglect patients, in which it has been shown that rotating the patients’ trunk toward the contralesional space can increase the ability to explore and detect events in that otherwise neglected part of space (Karnath, Christ, & Hartje, 1993; Karnath et al., 1991). In healthy subjects, results are more controversial (Grubb & Reed, 2002; Hasselbach-Heitzeg & Reuter-Lorenz, 2002; Rorden, Karnath, & Driver, 2001). Recently, it has been reported that objects presented along the body axis should actually elicit shorter visuomotor responses, but only when subjects are walking, not when they remain still (Grubb, Reed, Bate, Garza, & Roberts, 2008). This result is in apparent contradiction with our results, because the preference for the straight-ahead direction reported here was evidenced in subjects sitting on a chair. This difference might be due to the fact that we manipulated gaze direction by
asking subjects to move their eyes toward the fixation target (head and body aligned) while subjects from that previous study were asked to turn their head toward the fixation target (head and body not aligned). This would suggest that both the head and trunk axes participate in constructing an internal representation of the straight-ahead direction. Although a lot remains to be done for reaching a more global understanding of this straight-ahead preference and the conditions in which it arises or not, the present study support the view that visual perception is an “embodied” process, which depends on postural information.

Conclusions

To conclude, we have shown that, even when looking elsewhere, the objects one faces are still processed preferentially in peripheral vision. This effect, evidenced at the behavioral level in human subjects, echoes that previously described at the neuronal level in macaque monkeys. It is likely to reflect the special behavioral status of objects located straight-ahead, either as potential obstacles during navigation or as optimal targets for other types of visually guided actions.

Acknowledgments

We thank S. Rima for English proofreading. This work was supported by grants from the Fondation de France (B. Fouassier), the Fyssen foundation, and the Centre National de la Recherche Scientifique (CNRS)

Durand, Trotter, and Celebrini conceived and designed the experiments; Durand, Celebrini, and Camors performed the experiments; Durand and Camors analyzed the data; and Durand, Trotter, and Celebrini wrote the paper.

Commercial relationships: none.
Corresponding author: Jean-Baptiste Durand.
Email: jbdurand@cerco.ups-tlse.fr.
Address: Université de Toulouse, Centre de Recherche Cerveau et Cognition, Toulouse, France; Centre National de la Recherche Scientifique, Toulouse Cedex, France.

References


Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. Journal of Neuroscience, 18(18), 7426–7435.


changes in performance with eccentricity modeled by multiple eccentricity-dependent limitations. *Vision Research, 45*(18), 2436–2448.


