NeuroReport 10, 3549–3553 (1999)

Visual mental imagery interferes with allocentric orientation judgements

Fred Mast,[CA] **Stephen M. Kosslyn and Alain Berthoz**[1]

Department of Psychology, Harvard University, William James Hall, 33 Kirkland Street, Cambridge, MA 02138, USA; [1] Laboratoire de la Physiologie de la Perception et de l'Action, CNRS et Collège de France, Paris, France

[CA] Corresponding Author

THE subjective visual vertical is determined when a subject judges the orientation of an indicator (e.g. a short line segment) as apparently vertical. The mechanisms that underlie this perceptual performance are usually assumed to be based predominantly on bottom-up processing of primarily vestibular and visual information. However, it is also possible that top-down processes play a role in such abilities. We used an interference paradigm in order to investigate the effects of mental images on the perception of the visual vertical. The results demonstrate for the first time that visual mental imagery can exert the same directional influence on the subjective visual vertical as a perception of the corresponding stimulus. *NeuroReport* 10:3549–3553 © 1999 Lippincott Williams & Wilkins.

Key words: Cognition; Field dependence–independence; Gravity perception; Head-down tilt; Imagination; Space perception; Vestibular system

Introduction

Most models of human spatial orientation include a top-down component, such as a central processor that weights sensory information according to certain *a priori* assumptions [1], or an internal model that specifies the spatial frame of reference [2,3]. These aspects of the models have rarely been addressed empirically, and thus there is only scant evidence that top-down processing does in fact affect human spatial orientation. Indeed, in many instances there is no data at all that support the existence of such processing. A case in point is the subjective visual vertical (SVV); in the usual laboratory procedure, the visual vertical is determined in complete darkness when a subject judges the orientation of a visual indicator as apparently vertical. No research has been conducted to discover whether the SVV is susceptible to top-down influences. On the contrary, most theorists have assumed that the perception of the visual vertical is based primarily on bottom-up processing of gravity-receptive sensory information [4,5]. The integration of vestibular, visual and (although less extensively documented) somatosensory information [6] in determining the SVV has been shown in the clinical literature (e.g. peripheral [7–9] and cortical [10] vestibular lesions systematically affect the SVV) as well as in numerous psychophysical findings (e.g. retinal cues for verticality influence the SVV [11–13]).

The present study addresses the question of whether top-down processing can affect the SVV. We used an experimental paradigm in which visual mental images could interfere with gravity-receptive sensory information. Interference between visual mental images and perceptual stimuli have been demonstrated previously [14,15] and neuroimaging studies have provided additional evidence that visual imagery and visual perception share common cerebral structures [16–18]. However, at present, this converging evidence from behavioral and neuroimaging studies has not motivated the investigation of the effect of mental images on allocentric orientation judgements. The SVV is considered an allocentric orientation judgement because subjects must indicate the direction of an indicator with respect to an external reference axis such as gravity.

The present study is the first to examine the influence of top-down processing on the SVV in general, and the influence of mental imagery in particular. In this study, we instructed the subjects to visualize gratings oriented at a fixed angle while judging the visual vertical. The aim was to determine whether these gratings influence the SVV in a similar way when they are perceptually present and when they are imagined. Therefore, we compared the effects of imagery to those in the corresponding perceptual situation.

Materials and Methods

Subjects: Twenty-four healthy subjects (12 female, 12 male, mean age 22, range 18–31 years) gave their informed consent prior to taking part in this study.

They were Harvard students or professionals from the Boston area. All subjects were naive as to the purpose of this study. The study has been approved by the Harvard committee on the use of human subjects in research.

Experimental stimuli and recording parameters: All the experiments were conducted while the subjects were lying horizontally on their right side (roll body tilt: 90°). The horizontal body position was appropriate because of the increased effect of the visual frame of reference in roll-tilted observers [11]. The subjects were lying on a smoothly padded platform and a pillow provided comfortable support of the head; the position of the head was secured by a chin rest. Before the experiment proper began, the subjects rested for 6 min in the horizontal body position in complete darkness in order to rule out postural adaptation effects [19]. A small keypad with push buttons controlled a motor that allowed subjects to adjust a visual indicator. The visual indicator consisted of three equally spaced LEDs on a rod (visual angle between the two outer LEDs: 21°), which could rotate in the frontal plane. The keypad could be disabled by means of a switch on the control unit operated by the investigator. The visual indicator also could be controlled by the investigator and its orientation was measured by means of a potentiometer (accuracy 0.1°). During the experiments, there were no interfering visual cues from inside the completely darkened room; the rod holding the LEDs was not visible to the participants. The middle LED was continously lit; it was in line with the axis of rotation and positioned at a distance of 80 cm, centered straight between the two eyes. A visual square wave grating (spatial frequency: 0.5°/cycle) was mounted on a disk (visual angle 20°), and served as a visual frame of reference for the perceptual condition; visual angles of similar size have been effectively used in previous perceptual [11] and imagery [20] studies. Imagery studies have shown that the maximal size of similar visual mental images extends to ~20°, and stimuli of this size have been effective in previous studies of the SVV. The disk could be rotated in the frontal plane while the three LEDs remained visible (the two outer LEDs were immediately outside the disk and the middle LED appeared through a small aperture in the center of the disk).

The instructions ensured that the subjects understood the task. (That is, adjust the indicator so that the upper LED appears right above the lower LED. If the upper LED were dropped it would directly collide with the lower LED). There was no time limit for the baseline measurements, when subjects adjusted the SVV by using the keypad until the LED's appeared gravitationally vertical. For all the other conditions, a two-alternative forced choice paradigm was used. The subjects pressed a button when they were ready, which caused the upper and lower LED to light up simultaneously for a duration of ~500 ms. They judged whether the upper LED appeared to the left or to the right of the vertical with regard to the lower LED. If they responded 'right' the indicator was subsequently rotated leftward by an increment of 2° before the LEDs were lit up again and, correspondingly, if they indicated 'left' the indicator was rotated rightward by the same increment of 2° prior to the next presentation of the LEDs. A transition point was determined according to the method of limits; specifically, the transition point was defined as the averaged inclination of the indicator when two successive judgements switched from right to left or *vice versa*. This method has been shown to reliably determine the SVV and has the considerable advantage of avoiding manual operations on the keypad that interfere with the two imagery conditions [21].

Perceptual condition: The grating was presented at an angle of 67.5° clockwise or counterclockwise with respect to the previous baseline adjustment of the SVV. In such an orientation between horizontal and diagonal, the grating does not appear perfectly horizontal but still within range of horizontality, and thus constitutes a biasing visual frame of reference. We used inclined gratings in order to bias the SVV as has been shown in previous studies [11–13]; we refer to this condition as *perception*.

Imagery conditions: The subjects were asked to perform two distinct imagery tasks. Prior to each, they underwent a training session during which they inspected the entire grating for 30 s. They were then asked to visualize the same grating as accurately as possible in complete darkness. When they reported having mentally generated and visualized it as accurately as possible, they were again shown the real grating and asked to correct their mental image if necessary. This procedure was repeated five times and the entire training session lasted ~5 min.

In the imagery condition that we refer to as *completion*, we occluded almost the entire grating except the outer line segments (visual angle 2°), as illustrated in Fig. 1. The subjects were instructed to visualize the entire grating by using visual mental imagery to fill in the occluded surface. They were instructed to visualize the grating as vividly as possible, as if they were seeing the entire pattern. While performing the imagery task they kept their gaze centered on the middle LED and pressed a button indicating that they had generated the mental

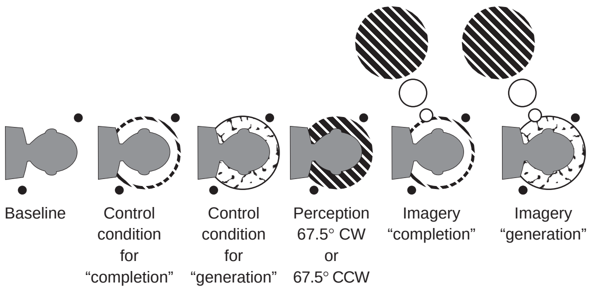

FIG. 1. Experimental paradigm. The subjects were lying horizontally on the side (roll body tilt: 90°) while they estimated the vertical by means of two briefly presented LEDs. The stripes were either oriented 67.5° counterclockwise, as illustrated here, or clockwise to the baseline SVV. These two orientations as well as the two imagery conditions were presented in a counterbalanced order over subjects. The baseline SVV measurements were recorded at the beginning of the experiment and prior to each perceptual condition. All control conditions were completed before the first imagery condition started.

image. Immediately after that, the two LED's lit up and the subjects gave their judgement as noted above.

We refer to the second imagery condition as *generation*. This condition differed from completion in that no oriented visual cues were visible. Thus, they could not simply attend to the fragments of the grating, but had to supply the entire stimulus via top-down processing. The subjects were asked to visualize the entire grating while they looked at a disk with randomly oriented line segments (maximal visual angle 2.5°) and small splotches (maximal visual angle 0.4°), as shown in Fig. 1. The two imagery conditions were presented in a counterbalanced order over subjects. The control conditions preceded the imagery conditions, and the subjects judged the SVV without any instruction to visualize while they viewed the disk with unstructured noise (this was a control for generation) and the disk with the peripheral visual cues (a control for completion). During the entire session, there were three blocks of repeated baseline measurements of the SVV, which served largely to control for possible adaptive processes. The SVV is moderately affected by adaptation when the tilted posture is maintained for a few minutes [19]. Therefore, the gratings and the visual cues were presented at a fixed angle of 67.5° (clockwise or counterclockwise) with respect to the last recorded baseline measurement.

Results

The key finding is that both imagery conditions were able to deflect the SVV in a very similar manner as in the corresponding perceptual situation. Figure 2 illustrates the mean influence of the perceptual grating and the imagined grating for the completion condition for 24 subjects. Each data point

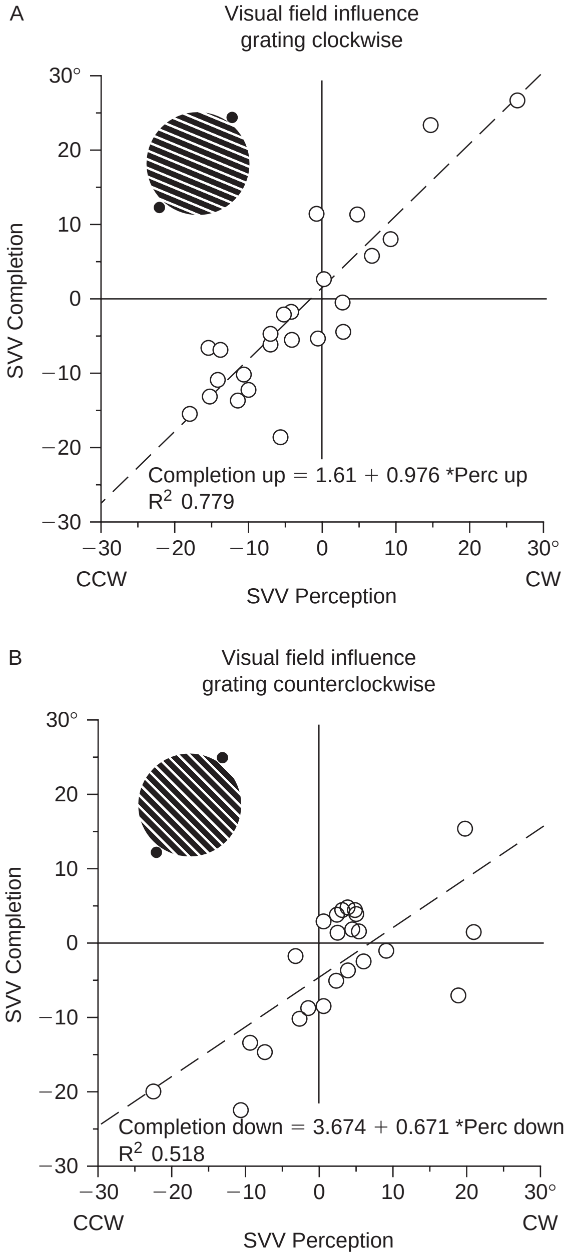

FIG. 2. Mean SVV measurements for the 67.5° clockwise (**A**) and counterclockwise (**B**) oriented grating in completion and perception conditions for 24 subjects. All data points are corrected for control by subtracting the mean SVV from the control condition.

represents the individual mean of eight SVV measurements in the completion (see ordinate in Fig. 2) and perception conditions (see abscissa in Fig. 2). Each measurement was corrected for any biasing effect induced by the control condition; that is, the mean SVV from the control condition was subtracted from the SVV measurements in completion and from the SVV measurements in perception. The individual s.d. were on average 2.3° (maximum s.d. 9.9°) for perception and 1.8° (maximum s.d. 4.5°) for completion. The Pearson correlation coefficients for perception *vs* completion were 0.88 ($p < 0.0001$) for clockwise presentation (Fig. 2A) and 0.72 ($p < 0.0001$) for the counterclockwise presentation (Fig. 2B). The clockwise presented grating in Fig. 2A biased 17 subjects to shift their SVV to the left (counterclockwise, negative values) in perception as well as in completion. The mean absolute biasing effect was 8.8° for perception (range 1.2–26.0°; three subjects $< 2^{\circ}$) and 9.4° for completion (range 1.4–27.0°; three subjects $< 2^{\circ}$). The counterclockwise presented grating in Fig. 2B biased 17 subjects to the right (clockwise, positive values) in perception and 11 in completion. The difference in perception for clockwise and counterclockwise oriented gratings was significant ($t = 2.11$, $df = 23$, $p < 0.05$). Figure 2 shows that the majority of subjects were biased to set the indicator perpendicular to the oriented stripes. The mean absolute biasing effect was 6.7° for perception (range 0.1–18.9°; five subjects $< 2^{\circ}$) and 6.9° for completion (range 0.7–15.9°; four subjects $< 2^{\circ}$). Table 1 shows that strong correlations could also be observed between perception and generation. The mean absolute biasing effect for generation was 7.7° (clockwise presented grating: range 0.4–24.1°; five subjects $< 2^{\circ}$) and 6.3° (counterclockwise presented grating: range 0.1–15.2°; five subjects $< 2^{\circ}$). The individual s.d. were on average 1.6° (maximum s.d. 2.6°). The mean baseline measurements of the SVV clustered around a mean of 15.6° (s.d. 7.4°, range 0.3–26.9°), and hence showed the typical A-effect (i.e. the phenomenon in which the visual indicator is set toward the own longitudinal body axis).

Discussion

The effect of static visual cues on the SVV, as it was tested in this study, has been accounted for by purely bottom-up processing of the weighted input from orientation-selective feature detectors [11,12]. This study clearly shows that the mechanisms underlying the SVV are also susceptible to top-down influences, via visual mental imagery.

Both imagery conditions demonstrated that mental images can stand in for perceptual stimuli and exert the same directional influence on the SVV as in the corresponding perceptual situation. A major requirement in imagery studies is to ensure that the subjects used visual mental imagery during the task. In principle, the effect of visual mental imagery in the completion condition could be attributed to an attentionally mediated influence that increases the biasing effect of the outer line segments. However, these line segments were absent in the generation condition but, nevertheless, the biasing influence of mental imagery remained. Thus, the observed effect cannot be ascribed simply to increased attention to the line fragments around the periphery. Similarly, it appears unlikely that memory effects underlie the high correlations between the effects in the completion, generation and perception conditions. In each case, the LEDs were lit for only a very brief duration, and, particularly in the generation condition, there were no visual cues that could serve as fixed landmarks.

In general, the presence of the visual and imagined frame of reference exerted a bias to shift the SVV towards an orthogonal orientation with respect to the grating. However, as Fig. 2 illustrates, a small number of subjects showed a reverse bias; these subjects tended to shift their SVV towards the orientation of the stripes even though they were presented at a relatively large angle of 67.5° to the SVV. Such a tendency is consistent with previous findings showing interindividual differences in weighting the axis that determines the visual influence on the SVV [11]. However, and this is the crux of the matter, such a reverse bias is consistently evident in both the imagery and perception conditions. The small number of subjects who were less susceptible to visual field influences also turn out to have had a small influence when the grating was imagined.

The fact that visual mental imagery strongly interferes with the SVV is consistent with neuroimaging findings that early visual cortex is activated when people visualize (e.g. sets of stripes [18]). Futhermore, repetitive transcranial stimulation applied to medial occipital cortex disrupted performance in imagery tasks, which demonstrates that the

Table 1. Pearson correlation coefficients for the perceptual and imagery conditions

	Condition	r	p
Counterclockwise presented grating	Perception *vs* imagery completion	0.88	< 0.0001
	Perception *vs* imagery generation	0.88	< 0.0001
	Imagery completion *vs* imagery generation	0.97	< 0.0001
Clockwise presented grating	Perception *vs* completion	0.72	< 0.0001
	Perception *vs* imagery generation	0.70	< 0.0001
	Imagery completion *vs* imagery generation	0.88	< 0.0001

activation of early visual areas is functionally involved during visual mental imagery [18]. In the present context, it is not known which brain areas are specifically associated with the interaction of static visual and vestibular information. Recent findings demonstrate the role of the parieto-insular vestibular cortex, a multisensory cortical area, and the corresponding human brain areas are activated in neuroimaging studies during vestibular stimulation. This area could well be principally associated with the perception of the vertical, however, the cortical representation of the static vestibular input from the otoliths is still controversial [22]. Alternatively, the interaction of static visual and gravity-related sensory information could also involve earlier levels. Recent neurophysiological findings have shown that a portion of neurons in the occipital area V2 shift their orientation specificity from retinal to gravity related coordinates during roll tilts [23].

Conclusions

We have demonstrated for the first time that visual mental imagery affects the perception of the visual vertical. Visual mental images can stand in for perceived visual stimuli, exerting a corresponding influence on the perception of verticality. The results show that even a phenomenon as apparently simple and fundamental as the perception of the vertical can be influenced by top-down mechanisms.

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ACKNOWLEDGEMENTS: F.M. is supported by grants from the Swiss National Science Foundation, the Research Committee of the University of Zurich (Switzerland), the Human Frontiers Science Program, and the Holderbank Foundation (Switzerland). We thank Walter Schmid for technical assistance.

Received 1 September 1999; accepted 17 September 1999