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RESEARCH NOTE

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Vestibular signals can distort the perceived spatial relationship of retinal stimuli

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Abstract The flash-lag phenomenon is an illusion that affects the perceived relationship of a moving object and a briefly visible one: the moving object appears to be ahead of the flashed one. In practically all studies of this phenomenon, the image of the object moves on the retina as the object moves in space. Therefore, explanations of the illusion were sought in terms of purely visual mechanisms. Here we set up a situation in which the object's motion in space is entirely produced by passive rotation of the subject. No motion occurred on the retina. The visual display (a continuously lit stimulus and a flashed one) was mounted on a vestibular chair. While the subjects fixated this display, they were rotated in the dark at a constant speed and suddenly stopped. Perceptual misalignment (flash-lag) was robust and consistent during both the initial phase of rotation and the postrotary period when neither chair, subject, nor stimulus was actually moving. As a vestibular signal can cause an illusory spatial dissociation in the visual domain, we conclude that the mechanism of the flash-lag must be more general than was thought up-to-now.

Key words Flash-lag · Illusion · Misalignment · Vestibular · Rotation

Introduction

In the absence of background cues, the spatial relationship between a moving object and a briefly illuminated one may be systematically distorted. This has long been known as the flash-lag illusion (MacKay 1958). Recently, Nijhawan (1994) renewed the interest in this phenomenon by designing an experimental set-up that demonstrates the misperception unambiguously and allows for its quantification. In Nijhawan's design, a light bar rotates at a constant speed (30 rpm) in front of the observer in the dark, and a light spot is briefly flashed exactly when the bar is passing at the level of the spot. Although the two stimuli are physically aligned, the moving one is perceived as clearly ahead of the flashed one.

Diverse hypotheses have been advanced to explain this illusion. Some invoke features of early visual mechanisms, like differences in visual persistence or visual latency (Puruschothaman et al. 1998; Whitney et al. 2000), spatiotemporal filtering involved in motion integration (Krekelberg and Lappe 1999), or more complex phenomena like the focusing of attention (Baldo and Klein 1995), priming and backward masking (Sheth et al. 2000). Other (top-down) hypotheses postulate that, somehow, the brain actively corrects its own perception, either on account of the past stimulus motion (Nijhawan 1994) or its future motion (Eagleman and Sejnowski 2000).

Let us note that all these studies of the flash-lag phenomenon were done under conditions in which visual stimuli actually moved on the retina. Indeed, retinal receptors were activated consecutively. However, is retinal motion really necessary to produce the illusion? Apparently it can occur as well when the perception that a stimulus is moving in space is generated entirely by the movement of the observer, the stimulus image remaining steady on the retina (Schlag et al. 2000). In the latter experiment, subjects wore a helmet on which bar and spot stimuli, similar to those used by Nijhawan (1994), were mounted 36 cm in front of the eyes. Subjects were asked to make sinusoidal 20–30° head movements horizontally in the dark. Although gaze was continuously fixed on the moving bar, the flash-lag illusion was produced: the moving bar appeared to be ahead of the flashing spot. We have now further investigated the illusion in the case in which the head and body rotation was passive: subjects were rotated in a chair at constant speed while fixating the stimuli mounted on the chair. These new results show that vestibular stimulation due to passive body ro-

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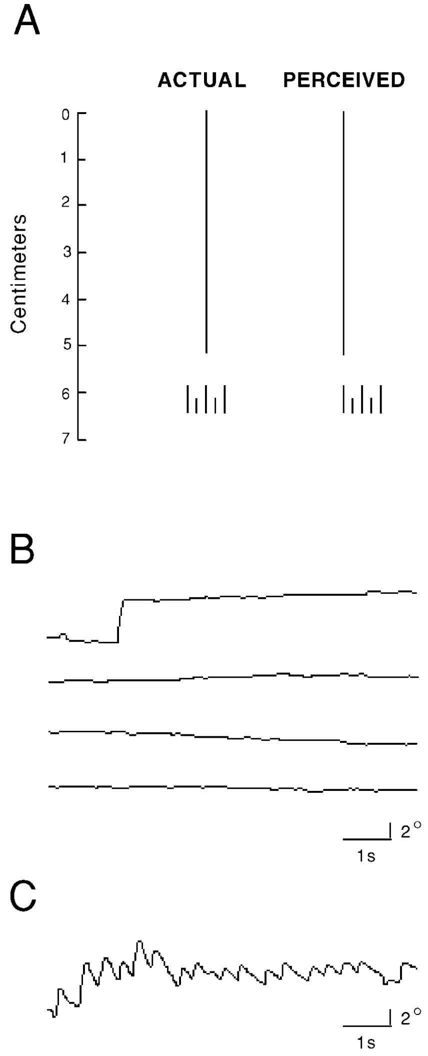

Fig. 1 **A** *ACTUAL* Visual stimuli used for quantification of the illusion. The *long bar* was continuously lit while the five *short bars* were flashed for 6 ms every 1.5 s. Subjects reported alignments as zero and misalignments as 1, 2, or greater than 2. *PERCEIVED* As an example, apparent misalignment that would be reported as a 2 (and plotted as 22 minutes of arc in Fig. 2). **B** Four consecutive horizontal electro-oculographic traces during the initial 30 s after clockwise rotation had stopped, while the subject fixated the stimulus. **C** Horizontal record from the same subject showing the initial postrotary nystagmus in complete darkness without the stimulus

tation – and its abrupt cessation – affects the visual perception of spatial visual relations in much the same way as retinal motion does. Furthermore, the results here demonstrate that objective stimulus motion in space is not required. A subjective sense that things are moving in space is all that is needed to generate the flash-lag phenomenon.

Materials and methods

Six subjects (two na) with normal vision, or corrected to normal, served in this study. They sat in a vestibular chair in complete darkness, head immobilized by a head band, facing a visual display mounted on the chair 42 cm in front of the eyes. We used two displays successively. The initial display consisted of a vertical LED bar (25.5×1.3 mm). One centimeter below the bar and aligned with it was another vertical LED bar (12.7×1.3 mm) which flashed for 6 ms every 2 s. This display was modified to allow quantification of the illusory misalignment. All the LEDs were narrower (51×0.4 mm) and, instead of one lower LED bar, there were five parallel LED bars (three long: 4.5×0.4 mm and two short: 2.25×0.4 mm; see "*ACTUAL*" in Fig. 1A) all flashing every 1.5 s. The right-hand drawing "*PERCEIVED*" in Fig. 1A shows the illusory perception when subjects started rotating to the left (counterclockwise) or when they were immobile just after rotation to the right (clockwise).

A session consisted of four consecutive trials: (1) chair rotation in one direction, (2) stop, (3) chair rotation in the opposite direction, and (4) stop again. Each trial lasted 1 min and subjects were forewarned a few seconds prior to starts and stops of rotation. Speeds were constant, ranging from 60 to 180°/s. Rotation was started and stopped abruptly (velocity step). Subjects were instructed to fixate the lower extremity of the continuously lit bar, that is, the end closest to the flashing LEDs (see Fig. 1A). In the initial experiments with the first display described above, subjects had only to report when the moving and the flashing stimuli appeared misaligned and the direction of the perceived misalignment. With the second display, subjects verbally reported, every 1.5 s, which of the five flashing LEDs (see Fig. 1A) appeared aligned with the continuously lit bar. An infrared video camera attached to the chair was used to monitor eye movements. In six sessions, electro-oculographic (EOG) recordings were made of the eye movements of three subjects, first, with the stimulus display turned on (as in Fig. 1B) and, second, in complete darkness without any point of fixation (as in Fig. 1C). The experimental protocol was approved by the UCLA Office for the protection of research subjects.

Results

The six subjects participated in 28 sessions (112 trials). In all trials, the continuously lit bar was reported to be ahead in the direction of rotation when rotation started, and behind in the direction of the previous rotation when this rotation had stopped. Vestibulo-ocular reflex (VOR) suppression was complete up to 120°/s of rotation speed. No nystagmus was observed on the video screen or the EOG recorded in three subjects (Fig. 1B), except for the few initial seconds at speeds of 120–180°/s. At those speeds, brief stimulus misalignments of varying sizes or even reverse direction were occasionally reported. Such misalignments could be due to the chance occurrence of flashes presented near reset or catch-up saccades. To avoid such ambiguities, data obtained at speeds larger than 100°/s were not included in this report.

The illusory misalignment lasted 12–30 s at rotation speeds from 60 to 100°/s. This duration corresponds to the period during which subjects had a clear sensation of their body rotation, at both start and stop. In the example of Fig. 1 (subject B), the illusion lasted for the duration of the first three record traces but not the fourth one (22.5–30 s). Note that there were no differences in eye fixation between these early and late periods. The misalignment also corresponds to the period during which nystagmus was observed and recorded in control sessions (as seen in Fig. 1C), i.e., when the subjects were in

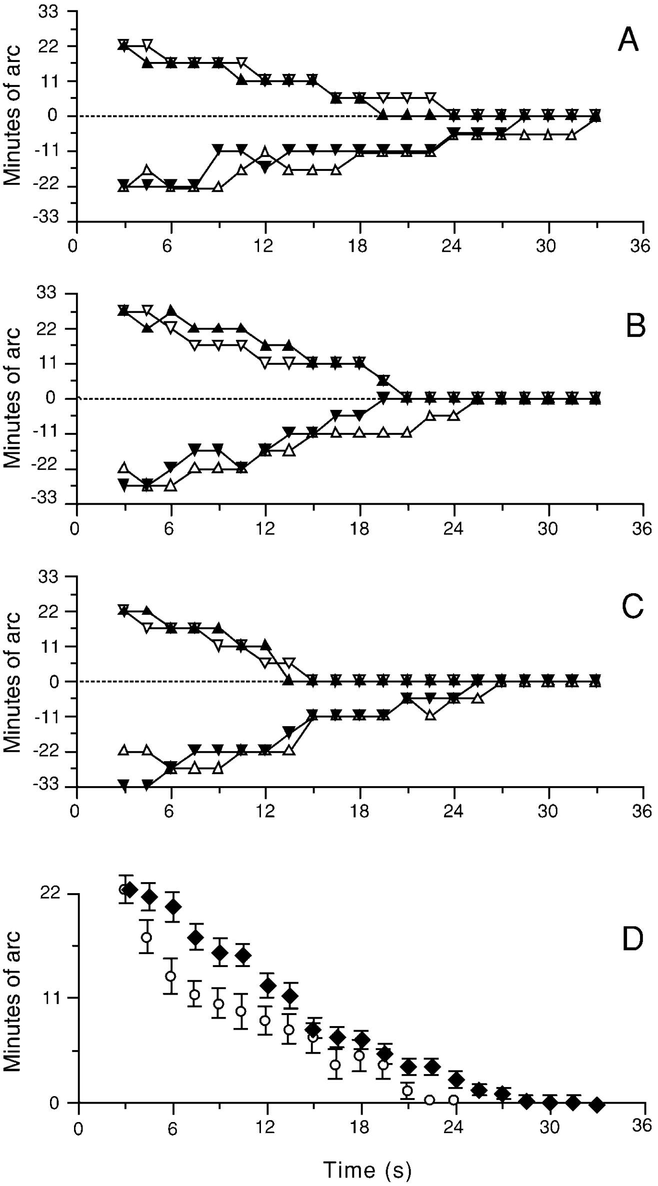

Fig. 2 **A–C** Misalignments reported by three subjects every 1.5 s in sessions of rotation at 100°/s. Each point is the average of two sessions per subject. Symbols code each type of trial: ▲ clockwise rotation, ▼ clockwise stop, △ counterclockwise rotation, ▽ counterclockwise stop. **D** Overall comparison of misalignment data obtained for three subjects at 100°/s (◆; each point is the mean of 32 trials) and 60°/s (○; each point is the mean of 12 trials). *Bars* show the standard error. The *ordinate scale* represents the visual angle of perceived misalignment (11 minutes of arc between adjacent *flashed bars*)

complete darkness with no point of fixation to block the VOR.

Figure 2A–C illustrates the progressive decay of the illusion magnitude for three subjects. The ordinate indicates the visual angle of misalignment in terms of angular distance (multiples of 11 minutes of arc) between the flashed bars. Each point is the average of two identical sessions at 100°/s on separate days. Data are shown separately for each of the four types of trials: clockwise at start and after stopping, counterclockwise at start and after stopping. One of the subjects (C) showed a consistent asymmetry in the duration of the illusion, related to the perceived direction of rotation.

As all individual trials showed a monotonous decay of the illusion over time, we pooled data from all conditions (start and stop of clockwise and counterclockwise rotations, ignoring the sign) for all subjects in an attempt to estimate the effect of speed on the illusion. Figure 2D presents these overall data for the 100 and 60°/s speeds. The same proportion of trial types was included in this analysis. It is clear that the magnitude of the illusion was greater at and after 100°/s rotation than at and after 60°/s rotation.

Discussion

In this study, vestibular signals were the only possible source of the visual illusion reported. Because the head was immobilized, neck proprioceptive excitation was limited, at most, to the couple of seconds (that we discarded) at the start and stop of body rotation. Internal signals accompanying active head rotation could have been involved in a previous experiment (Schlag et al. 2000) but not here. Very likely, the vestibular input was provided by the semicircular canals, known to be responsible for rotary nystagmus and a subjective sense of rotation (Honrubia et al. 1992). In our experiments, the visual illusion waned down with a similar time course as these known vestibular effects. The internal signal producing a sense of stimulus movement probably has the decay characteristics of the signal blocking the VOR. Interestingly, as indicated by Belton and McCrea (1999), the mechanism for suppressing the VOR may be different in active and passive head movements. It is thus possible that the mechanism of the present illusion may also differ when head movements are active (as in Schlag et al. 2000) and when they are passive (this report).

The present results provide further evidence that retinal motion is not a necessary condition to induce a spatial illusion that is in all aspects similar to the one originally known as flash-lag. We established that vestibular stimulation triggered by passive body rotation – and its abrupt cessation – is adequate to influence the perception of spatial relationships between a moving and a flashed stimulus. The vestibular-induced effects were probably in the same range as the retinal motion induced effects, although it is difficult to match conditions that would allow a precise comparison. For instance, the stimulus image in the present experiment always remained foveal whereas, in all other studies (see, for example, Nijhawan 1994), the stimulus swept across the retina, i.e., through regions of variable visual resolution. Allowing for such differences, the largest misalignments that we observed were greater than 22 minutes of visual angle whereas, for instance in their study with a retinal moving stimulus, Whitney et al. (2000) reported misalignments of about 30 minutes of visual angle.

The common point between the present experiment and the classic flash-lag phenomenon is the perception that a stimulus moves in space. As the same illusion is generated in both cases, we suggest that it depends on the perception that a stimulus moves in space, whether the mechanism of this perception is retinal or vestibular. Of particular interest is the postrotary flash-lag illusion, when both the subject and the stimulus were immobile and yet the subject still had the sensation that both were rotating. Thus, objective stimulus motion in space is not required. A subjective sense that things are moving in space is already sufficient to generate the flash-lag phenomenon. This fits well with another observation of illusory stimulus motion, in this case, produced by visual motion aftereffect (Snowden 1998). This is also consistent with the notion that the perceived spatial relationship of retinal stimuli can be distorted by extraretinal signals (Cai et al. 1997; Ross et al. 1997). It is likely that the illusion reported here belongs to a more general category of perceptual phenomenon. It seems that such illusions occur when there is a continuous change in a sensory dimension (not only spatial, but also luminance or color; see Sheth et al. 2000). In such cases, the instantaneous state simultaneous with a sudden external event is erroneously determined, probably because the brain does not continuously record on line predictably evolving states.

Although the neural origin of the misperception is still unknown, possible candidates are brain structures in which neurons are said to “encode the direction of target motion in space-centered coordinates by integrating inputs reflecting retinal image motion plus eye and head movement” (Thier and Erickson 1992 about area MST-1). Neurons with similar properties have also been found in the frontal eye field (Fukushima et al. 2000) and in the cerebellum of monkeys (Kase et al. 1979).

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