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Subjective Velocity Estimation During Conflicting Visual-Vestibular Stimulation

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Summary. Human subjects continuously estimated their position during and after steps of angular acceleration in complete darkness. These estimations were compared with the same vestibular stimulation in the light while subjects gazed at a striped cylinder which completely enclosed them and was mechanically fixed to the turntable. Rotation with such a fixed visual surround created a sensory conflict: the acceleration is sensed by the vestibular end organs, while the visual system senses no displacement. Accordingly, during the conflict stimulation, the estimation of rotational velocity and its duration is markedly reduced. These findings in humans compare well with nystagmus and single neuron recordings in the vestibular nuclei of alert monkeys.

Key words: Velocity estimation – Visual-vestibular conflict – Subjective velocity estimation – Vestibular stimulation.

Zusammenfassung. Versuchspersonen gaben kontinuierlich ihren Drehwinkel während und nach Winkelbeschleunigungen in völliger Dunkelheit an. Anschließend wurden die Versuchspersonen mit den gleichen Parametern im Hellen gedreht, wobei sie von innen auf eine gestreifte Trommel blickten, die den Drehstuhl vollständig umgab und mit ihm rotierte. Dies provozierte einen sensorischen Konflikt: während bei Beschleunigungen über das vestibuläre Endorgan eine Drehung gemeldet wird, wird visuell keine Bildverschiebung gesehen. Entsprechend sind bei der Konfliktreizung Dauer und Größe der Geschwindigkeitsschätzung herabgesetzt. Diese Ergebnisse entsprechen gut Messungen von Nystagmus und Einzelzellaktivität in den vestibulären Kernen bei wachen Affen, die unter identischen Versuchsbedingungen getestet wurden.

Schlüsselwörter: Geschwindigkeitsschätzung – Visuell-vestibulärer Konflikt – Vestibuläre Reizung.

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Introduction

When a subject is rotated about a vertical axis in complete darkness, he can easily recognize and estimate any angular acceleration. Thresholds for subjective sensation are between 0.1° and $1°/s^2$ and, with special testing, even lower values have been reported (Clarke and Stewart, 1968). An identical subjective sensation of self-rotation about a vertical axis can be induced by rotating only the visual surround. This is called circular vection (CV) and was first described by Mach (1875). Later it was investigated by Fischer and Kornmüller (1930) and by Dichgans and Brandt (1974, 1978).

The sensation of circular vection cannot be differentiated from true body motion, which prompted a series of investigations exploring the interaction between visual and vestibular inputs in the generation of motion sensation (Young et al., 1973) and nystagmus (Meiry, 1965; Koenig et al., 1978). A nonlinear interaction was proposed (Zaccharias and Young, 1980). The present study was undertaken to explore this interaction further: that is, during 'conflict stimulation,' and to compare the human data to single neuron recordings and nystagmus measurements in alert monkeys (Waespe and Henn, 1978). Therefore, care was taken to use identical stimulus conditions for the human as well as the animal series. For the human experiments presented here, the task was to estimate subjective velocity during angular rotation in the dark and then to compare it to the same vestibular stimulus with a fixed visual environment ('conflict stimulation,' i.e., the visual field fixed relative to the subject).

Methods

Ten healthy young adults participated; three of them repeated the test series four times. Subjects were seated on a servo-controlled turntable, which could be rotated around a vertical axis. A vertically striped cylinder (diameter 125 cm), which totally enclosed the subject, was mechanically coupled to the turnable. The cylinder was illuminated from within. Stimulation consisted of rotating the turnable with an angular acceleration between 0.5° and $20°/s^2$, followed by constant velocity rotation at 20° or 40°/s for at least 20 s, followed by decerleration. For pure vestibular stimulation, all rotation was carried out in complete darkness. For the conflict stimulation, rotation was performed while subjects gazed at the illuminated striped cylinder, which was mechanically fixed to the turnable and rotated with it.

Subjects indicated their position by turning a handle, which could be fully rotated over 360° and was coupled to a potentiometer. The instruction was to continuously indicate the instantaneous position. Horizontal eye position was measured with skin electrodes (electrooculogram). Care was taken that subjects were alert, and adequate rest periods were intercalated. All relevant data were written out on a 6-channel rectilinear oscillograph, from which further measurements were taken.

Results

In our paradigm, subjects were rotated together with the visual surround. The conflict is that there is vestibular stimulation, but no displacement of the visual world. Some relative motion of the visual field can be experienced, but only if

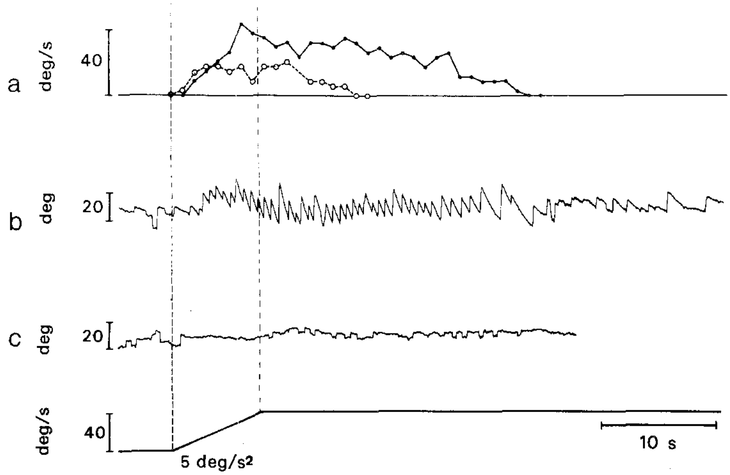

Fig. 1a—c. Velocity estimation and nystagmus are compared during vestibular stimulation in darkness and the conflict situation. **a** Velocity estimation, *filled circles* during vestibular stimulation, *open circles* during conflict; **b** and **c** are the nystagmus recorded during vestibular stimulation (**b**), and during conflict stimulation (**c**). The profile of the vestibular stimulation, the same in both cases, is shown in the bottom trace. For vestibular stimulation, the velocity estimation during acceleration approximately corresponds to the actual velocity and declines with a time course which is shorter than the accompanying nystagmus. During the conflict stimulation, velocity estimation is attenuated and shorter in duration, whereas nystagmus is totally absent. Note, however, that during the first few seconds during the conflict stimulation, velocity estimation was slightly enhanced

vestibularly induced nystagmus is not completely suppressed. The conflict and vestibular stimulation in the dark were performed in random sequence immediately following each other. The data obtained from each subject under the two different conditions with identical rotational stimuli were then compared. The conflict attenuated peak subjective velocities, and shortened the time constants of postacceleration decay of velocity sensation. Figure 1 shows a typical example. Absolute measurements of nystagmus and velocity estimation varied considerably, not only between subjects, but between trials of the same subject. Often subjects realized their changing responsiveness and ascribed it to declining alertness and/or slight nausea. Therefore, all measurements will be given as relative values, the full response or 100% being equal to individual values obtained during vestibular stimulation in the dark.

Latency. The time between the start of acceleration and its detection changed with the value of acceleration. With 0.5°/s^2, latency was on the average 25 s (SD 11 s) for vestibular stimulation and 28 s (SD 11 s) for the conflict stimulation. With an acceleration value of 20°/s^2, this latency was 0.7 s (SD 0.1 s) under both conditions. Also, for all intermediate values of acceleration, latencies in the two experimental conditions did not differ significantly.

Threshold. On average, every subject detected the acceleration of 0.5°/s^2, both as vestibular stimulation and in the conflict situation. Velocity estimation during the

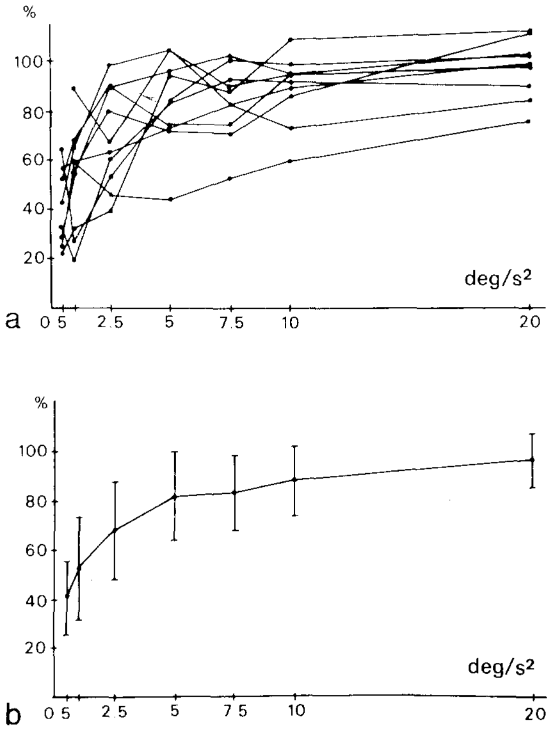

Fig. 2a and b. Maximum velocity estimate during visual-vestibular conflict stimulation, plotted separately (**a**) and averaged (**b**). Ordinate is response as a percentage of the velocity estimation during acceleration in the dark. Abscissa gives value of acceleration. Vertical bars in **b** indicate standard deviation. With low acceleration values, the stationary visual surround greatly attenuates velocity estimation, whereas with higher acceleration this effect becomes smaller

conflict was, on the average, attenuated. Often, however, immediately after the start of the conflict stimulation higher velocity estimates were made. If a higher velocity estimation was made, it was only present for about 5 s, after which the velocity estimation was always attenuated in all subjects. With the low acceleration values, some subjects could differentiate between an initial jitter or instability of the visual surround which was similar, but not identical to a proper velocity sensation. Other subjects did not make such a distinction and only experienced an angular displacement.

Maximum Velocity Estimation. If the maximum velocity estimate during acceleration in the dark is set at 100%, then during conflict stimulation, the velocity estimate is always attenuated. With small accelerations this effect is greatest and gradually becomes smaller with higher accelerations (Fig. 2). In terms of percentage of the vestibular response in the dark, the velocity estimation during the conflict stimulation is 40% at $0.5°/s^2$, and rises to 95% at $20°/s^2$ (single values, averages, and standard deviations are shown in Figure 2).

Time Course of Velocity Estimation. During the acceleration period, the time course has already been characterized in terms of latency, threshold, and maximum. The velocity sensation outlasting the acceleration period was very short in the conflict situation. It was shortened in every case, typically by about 50%, corresponding to an absolute value of less than 10 s (Fig. 1).

Nystagmus. During vestibular stimulation, nystagmus was present in every case. Its slow phase velocity was clearly related to increasing velocity, and therefore also to subjective velocity sensation. During the postacceleration period, slow-phase velocity declined, as did subjective velocity. Typically, however, nystagmus outlasted subjective sensation (Fig. 1). Nystagmus was absent in the conflict stimulation. In a few trials single beats could be observed, but never continuous nystagmus.

Discussion

Experiments were performed to measure how a visual environment which is stationary relative to the subject, influences the magnitude of the sensation of velocity during angular acceleration. Two oppositely-directed effects were found: the overall velocity estimate during the conflict stimulation was reduced in every case; however, during the initial acceleration period, some subjects experienced an increased velocity sensation. The overall reduction in velocity estimation runs parallel to the reduction in nystagmus. However, nystagmus is more attenuated. In our series of experiments, it is reduced so much that, apart from a few beats at high acceleration, it was no longer measurable.

The sensation of motion is conveyed centrally via several peripheral sensory systems, the vestibular and visual systems playing a dominant role. The peripheral vestibular system is generally considered to convey high acceleration values, whereas the visual system is better tuned to convey low acceleration or constant velocity signals. The combination of inputs via these different sensory systems should then relay information about the true velocity over a wide range: from constant velocity to high accelerations (Waespe and Henn, 1979).

If under laboratory conditions the two inputs are chosen to contradict each other, one would expect each channel to dominate the response over its natural working range. For the vestibular organ, this is the high acceleration range ($> 10°/s^2$); for the visual system, the low acceleration range ($< 2°/s^2$). In between, the two ranges overlap ($2°$—$10°/s^2$). This was also found in the experiments described above.

Psychophysics. Our results reflect the hypothesis that the central vestibular system receives information from different peripheral sense organs, each specifically tuned to a certain working range: during low acceleration the visual input dominates the overall velocity sensation, whereas with higher acceleration values the vestibular input dominates during the acceleration phase. In the postacceleration period, the sensation is strongly shortened whenever the visual input signals zero velocity.

Besides the overall strong attenuating effect, several subjects experienced an increased velocity sensation immediately at the start of acceleration. This increased sensation never lasted more than a few seconds. A few subjects further differentiated this initial sensation and were able to separate a proper velocity sensation from the experience of jitter of the visual surround. This description also gives a clue for possible interpretation. A consequence of any rotatory acceleration is a compensatory eye movement via the vestibulo-ocular reflex (VOR). In our case, as the visual environment does not move relative to the subject, the eye movement induced by the VOR does not stabilize vision and is perceived as a jitter of the surround. A majority of subjects do not differentiate between this visual jitter and self-motion and, therefore, describe it as self-motion. Similar results, i.e., an increased velocity sensation during low accelerations, have been obtained by Travis (1929), Marshall (1967), and Huang (1979). Huang and Young (submitted for publication, 1980) specifically investigated this phenomenon. Similar to our experiments, the subjects were accelerated with and without a stationary visual field. The basic effect of adding the visual field was to increase the initial sensation of velocity and to reduce the latency for perception of the acceleration. These effects were strongest with small accelerations, i.e., with small visual-vestibular conflict.

Eye Movements. During the conflict, nystagmus was almost totally suppressed with the accelerations applied. This is one of the many examples of dissociation between subjective velocity sensation and presence or absence of nystagmus in humans. If a little nystagmus could be detected, it was only at high acceleration values. This shows that although visual-vestibular interaction for the generation of nystagmus and motion sensation occur through similar mechanisms, these phenomena can be separated and definitely have different quantitative characteristics in terms of threshold, strength, and duration.

The presence of vestibularly-induced eye movements without the expected motion of the visual environment induces some motion of the visual frame that many subjects readily interpret as self-motion. This phenomenon, described above as jitter, has some analogy to the oculogyral illusion in which a small object, usually a fixating light; is seen as moving during a near threshold vestibular stimulation (Graybiel and Hupp, 1946). Typically, the light is seen in motion at acceleration values below those which induce a clear sensation of self-motion. Huang and Young (submitted for publication, 1980) compared the results of adding a large peripheral field vs a small fixating spot during the acceleration. They explain their experimental results with the oculogyral illusion. We made no attempt to correlate eye movements with this illusion, since our method of eye movement recording does not have a high enough resolution.

Animal Experiments. Originally, the question which these experiments have attempted to answer were suggested by the results of animal experiments (Waespe and Henn, 1978). In the conflict situation monkeys, like humans, almost completely suppress nystagmus with accelerations up to $10°/s^2$. Recordings in the vestibular nuclei revealed that during the conflict stimulation neuronal activity is attenuated, and the effect is most pronounced at low levels of acceleration. This attenuation, although qualitatively similar in all neurons, shows marked quantitative variability in different neurons, with little effect on some and almost complete inhibition in others. Time constants of decay of neuronal activity after the acceleration period are shortened.

These findings can be closely related to the phenomena of nystagmus and even psychophysical measurements in man. The presence of neurons with different thresholds and different susceptibility to these phenomena of visual-vestibular interaction support the notion of different types of cells, some projecting to the oculomotor system being part of the vestibulo-ocular reflex, others projecting via thalamocortical pathways to cortical areas, a necessary input for subjective information processing, as for all other sensory systems.

Modeling. It had been shown that visual-vestibular interaction follows a nonlinear course with vestibular input dominating at high levels of acceleration, and visual input dominating at low levels. Such interaction, in which weighting factors vary with values of input parameters, probably require nonlinear models. One such model specifically developed to describe psychophysical phenomena of visual-vestibular interaction was recently proposed by Zaccharias and Young (1980) and Huang and Young (submitted, 1980). Other models, having the advantage of offering more detailed description of actual neuronal connections (Robinson, 1977; Raphan et al., 1977), have not been tested in detail.

Conclusion

The present experiments were undertaken to measure human subjective sensation in an experimental paradigm identical to a previous study using Rhesus monkeys. Human subjective response, nystagmus in man and monkey, and single neuron recordings in monkeys show a very close correspondence which extends to the details of quantitative analysis. We take this as encouragement for further experiments.

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