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VESTIBULAR CAPTURE OF THE PERCEIVED DISTANCE OF PASSIVE LINEAR SELF MOTION

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INTRODUCTION

The work of Pompeiano and Wilson has advanced our knowledge of the role of the vestibular system as a proprioceptive system for head movement (eg. (19, 26) and see (27) for a review of the earlier literature). A general principle of the operation of proprioceptors is that they signal information not about the absolute positions of parts of the body, but about the difference between what the motor signals instruct and what actually happens. Many proprioceptors, such as muscle spindles, remain essentially silent if the relevant body part is moving in a way consistent with the motor command. Activation of proprioceptors usually initiates a closed-loop response which seeks to cancel proprioceptor activity and restore the status quo.

Following this principle, we might expect the vestibular system, as a proprioceptive system, to be especially active during externally imposed whole-body motion. The signal for this function does not have to be calibrated against any external measure but merely need indicate the extent of disagreement between the actual and expected motions. However the vestibular system also provides an accurate quantitative signal that is available for a multitude of tasks including eye movement control (8) and perception (11). In this study we assessed the vestibular response to externally imposed whole-body motion. Is it a crude open-loop demand for action to restore the status quo or can vestibular responses be quantitatively informative about self motion?

The otoliths of the vestibular system, probably supplemented by somatic graviceptors (15), potentially provide quantitative information about linear self motion. The otolith system transduces only linear acceleration (13), so periods of constant velocity cannot be registered by this system, but, with this caveat, position relative to some initial state can be obtained by two integrations over time. People can use vestibular information to assess a position change (1, 4, 9, 12, 14, 17) and their direction of travel (16, 22).

The vestibular system rarely works alone. Information about whole-body motion is usually provided by other senses too. Normally when moving through a stable three-dimensional environment, the components of the retinal image stream across the retina and the resulting optic flow contains information about the direction and velocity of movement (3, 10, 20). People can use optic flow to assess their direction of travel (20, 24, 25) but, although it has been shown that honey bees can use optic flow to assess the absolute distance they have travelled (2), there have been no explicit claims that humans can do this.

The experiments reported here measure the relative roles of the visual and vestibular systems in the perception of linear motion. Measuring how far someone perceives themselves to have moved presents some interesting methodological considerations. Simply asking people to estimate how far they have moved requires them to make a relative judgement against an internal representation of some kind of yardstick. Distortions in the representation of the yardstick, such as stimulus compression or expansion (17, 21) when judging multiples of the yardstick, complicate the interpretation of such data. Asking subjects to reproduce previously travelled distances (1) is fraught with similar concerns since an inaccuracy or systematic bias in the perception of the initial distance will be matched by similar inaccuracies and bias in the measurement trials. The actual distance moved in the reproduction trial cannot provide the experimenter access to the perceived distance in terms of actual world distances. We have attempted to overcome these problems in this study by asking subjects to judge their motion relative to target distances presented through one of two modalities: either visually or by physical motion. Although visual motion to a visual target and physical motion to a physically-presented target distance are subject to the 'reproduction fallacy', cross-modal matching is not. Furthermore, trials in which bimodal stimuli (vision and physical motion) are matched to either visually or a physically presented targets allow us to access the relative contributions of the sensory modalities without needing access to absolute-distance judgements. Some of these experiments have been reported elsewhere in abstract form (6, 29).

METHODS

Subjects

Seventeen subjects took part in these experiments. Their mean age was 28.3 yrs and they had normal visual acuity and no history of vestibular or balance problems. Subjects were paid for their participation. Experiments were approved by the York Ethics Approval Committee.

Physical motion equipment

Subjects were subjected to physical motion by being strapped to a chair that was mounted on a mobile cart. The cart had low-friction, in-line skate wheels and ran on a smooth floor. The ensemble of subject, chair and cart was attached by a rope to a weight which could be dropped through a distance of 1.5 metres. By an arrangement of pulleys, this drop pulled the cart through a distance of up to 4.5 metres. When the weight was released it fell with a downward force of mass x gravity and pulled the cart at a constant acceleration (0.1 - 0.4 $m.s^{-2}$ depending on the mass of the weight and the mass of the subject). Cart position was transduced by running a thin, earth-fixed wire around the optical-encoder shaft of a mouse mounted on the cart. The signal from the mouse was sampled and stored by the computer. The system was calibrated by moving the cart through known distances by hand.

Visual motion equipment

Subjects viewed a 84° x 65° display presented on a single-screen, Liquid Image MRG3 virtual reality helmet equipped with a six degrees-of-freedom Flock of Birds head tracker (Ascension

Technologies). The reference transmitter for the Flock of Birds was mounted on the cart and therefore the head tracker reported the position of the head relative to the cart. The image was displayed at optical infinity. The display simulated a virtual corridor 50m long, 2m wide and 2.5 m high, whose dimensions were roughly based on the dimensions of a typical corridor at York University. This is shown on the left of Fig 1. The walls of the corridor were "painted" with multicoloured vertical stripes 0.5m wide which changed colour on a random schedule. The flickering colour reduced the possibility that subjects merely tracked a visual stripe to assess where they were. The floor and ceiling were "painted" black. The visual position of the subject in the virtual corridor was derived from the vector sum of the physical position of the cart relative to the room (measured by the earth-fixed wire) and the subject's head position relative to the cart (measured by the Flock of Birds). Vision-only displays were created by recording the physical motion of the cart and using it later to drive the virtual reality display. This ensured that the visual conditions were the same in the vision-only and the vision-plus-vestibular conditions (cf. (7)).

Calibration of the visual display

It was important that the distances of features in the virtual reality display were correctly calibrated to the real world. To calibrate the optics of the display, subjects were presented in the helmet with a virtual target at a simulated distance. They then lifted the helmet and viewed a real-world target at the same distance. Subjects then raised and lowered the helmet while the simulated focal length of the virtual reality display was adjusted until the simulated and real targets appeared to be at the same distance. Subjects were encouraged to move their heads around during this exercise to generate parallax cues. The match was verified at several distances.

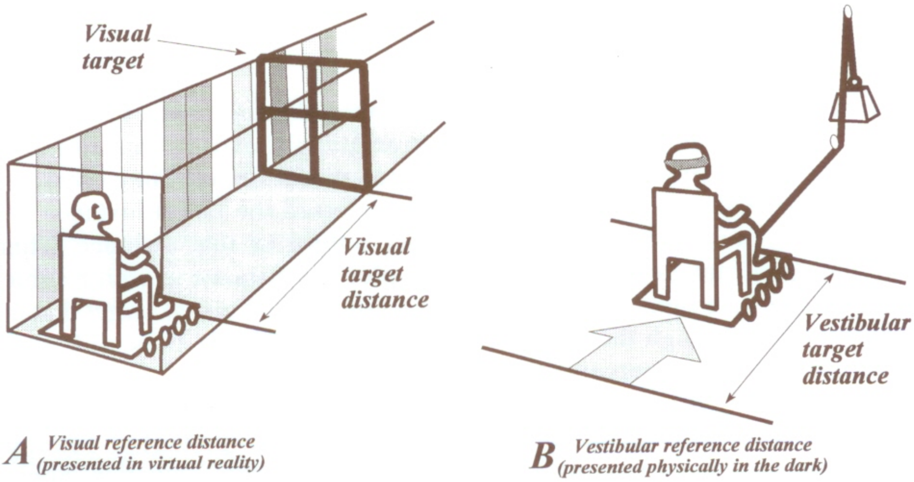

Fig. 1. - *Apparatus.*

Subjects wore a virtual reality helmet and sat on a cart which was attached by a rope to a weight hung from pulleys. When the weight was released it pulled the cart at a constant acceleration. The helmet displayed a virtual environment in which subjects were sitting in a corridor as illustrated in the left-hand panel (panel A). The walls of the corridor were painted with vertical stripes 0.5m wide which changed colour on a random schedule. The floor and ceiling were black. Visual targets consisted of a cross displayed at some distance down the corridor. To present targets vestibularly, subjects were moved through the target distance in total darkness at constant acceleration by dropping the weight attached to the cart (panel B). When the target distance was reached they were stopped suddenly and returned to the start position.

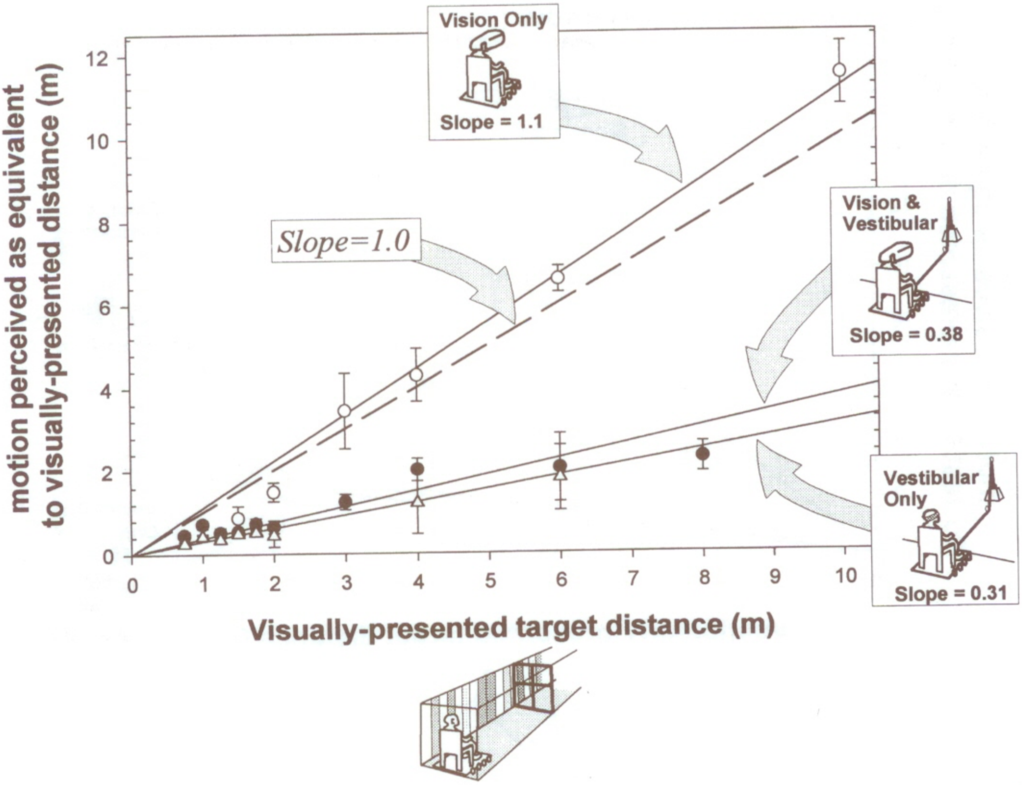

Fig. 2. - *Movements considered perceptually equivalent to a visually presented target distance.*

The vertical axis indicates the movement considered perceptually equivalent to the target distances indicated on the horizontal axes. Each symbol represents the average of all the subjects' data together with standard errors. The line plotted through the data are regression lines forced through the origin. The dashed line indicates a slope of 1, representing perfect performance. The open circles indicate the amount of visually induced vection required for the subjects to perceive that they had travelled through the visually presented target distance. Performance was quite accurate with a slope of 1.1. The open triangles indicate the amount of physical motion required to give the sensation of travelling through the visually presented target distance. The slope of 0.31 indicates that very much less physical motion was required to move through a given visual distance. When both visual and vestibular stimulation were given simultaneously, performance was very close to the vestibular-alone condition (filled circles: slope = 0.38), indicating a dominance of the vestibular response which we refer to as *vestibular capture*.

Matching physically-presented distances

Vestibular only. When target distances were presented by physical demonstration (see Fig. 1b), subjects were able to indicate accurately when they had travelled through the previously presented distances when they were moved passively in complete darkness. The slope of the regression line, forced through zero, of their actual movement versus their perceived distance (open triangles, Fig. 3) was 0.82 (s.e. ± 0.09).

Vision only. When subjects were given only visual movement and asked to

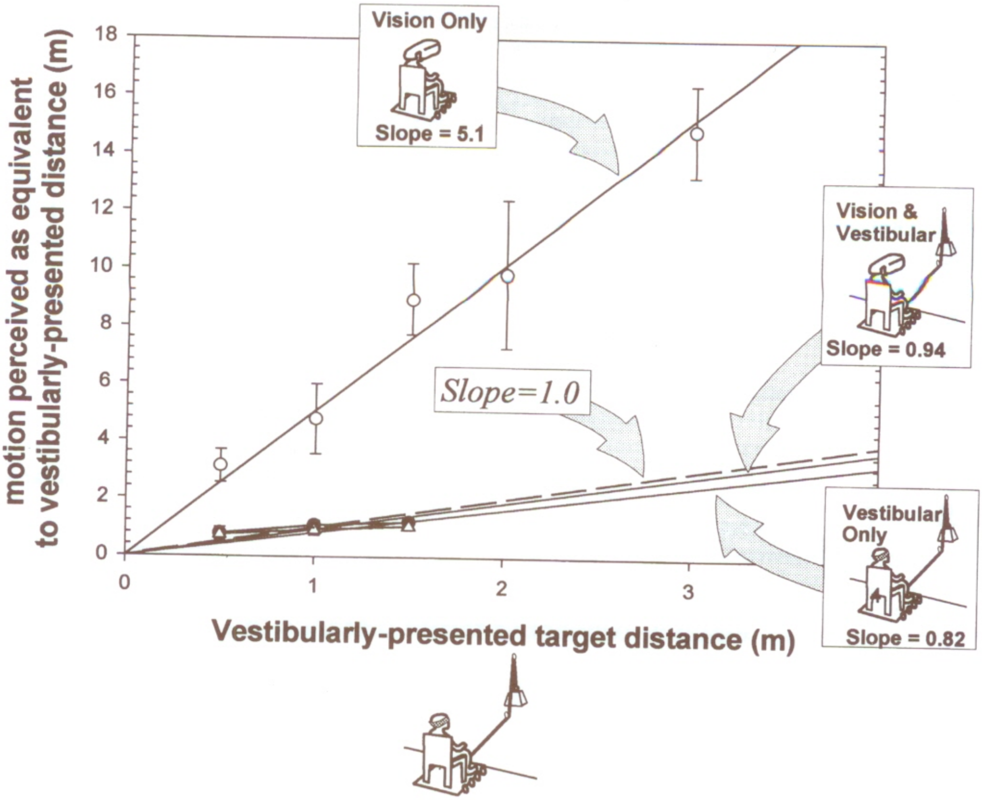

Fig. 3 - *Movements considered perceptually equivalent to a vestibularly presented target distance.*

Conventions as for Figure 2. Note that the scales of Figures 2 and 3 are different. The ability to match physical motion in the dark to a previously presented physical motion was quite accurate (open triangles; slope = 0.82). Very much more visual motion was required, however, to produce the sensation of moving through this physically-presented distance (open circles; slope = 5.1). When both physical and visual motion were presented together, again a dominance of the vestibular signal was seen and the slope is similar to the vestibular-alone trials (filled circles; slope = 0.94).

indicate when they had moved by vection down the corridor by the amount of the previously presented physical motion, they needed to travel a long way down the virtual corridor, well beyond the target distance, before they *perceived* they had travelled through that distance. This is shown by the open circles of Figure 3. The regression line for the visual movement versus the perceived distance, forced through zero, was 5.1. That is subjects needed five times as much visual movement to match the previously presented physical motion.

Vision and vestibular together. When subjects were presented with simultaneous visual and vestibular cues to self motion and asked to match it to a previously presented physical motion they were dominated by the vestibular response and virtually ignored the visual information. Similar to what happened when subjects matched visually presented targets, their performance when both cues were available was very close to their performance in the dark. The slope of the regression line, forced through zero, was 0.94 (closed circles Fig. 3) which was much closer to the vestibular-only performance than the visual-only performance.

DISCUSSION

The experiments described in this paper used a subject's self motion itself as a direct measure of perceptual equivalence. By reporting when they have travelled through a certain perceptual distance, subjects indicated that this sensation was perceptually equivalent to the given target distance. Our experiments demonstrated that (*i*) the perceived distance of motion evoked by optic flow was accurate relative to a visual target but (*ii*) was perceptually equivalent to a shorter physical motion. (*iii*) The perceived distance of physical motion in the dark was accurate relative to a previously presented physical motion but (*iv*) was perceptually equivalent to a much longer visually presented distance. (*v*) The perceived distance of self motion when both visual and physical cues were present was perceptually equivalent to the *physical* motion experienced and not the simultaneous visual motion even when the target was presented visually. These perceptual equivalences are summarised in Table 1.

Table 1. - *Summary of perceptual equivalences.*

	Physical motion only	Visual motion only	Visual and physical motion
Match to a visual target	0.31	1.1	0.38
Match to	0.82	5.1	0.94

Each number is the slope of the graphs presented in Figures 2 and 3 and indicates the actual motion that was perceptually equivalent to the target distance. This table shows two things. Firstly that very much less vestibular stimulation than visual stimulation is needed to evoke a perception of movement through a given distance. The vestibular response is between about 300% and 500% as powerful as the visual response. Secondly the table illustrates the dominance of the vestibular response when both visual and vestibular motion cues are present simultaneously: the last column is much closer to the first column (response to vestibular motion) than it is to the second column (response to visual motion).

Miscalibration between visual and non-visual self motion systems

Our observations reveal an unexpected miscalibration between the sensory systems involved in transducing passive, linear self motion. Optic flow is an unscaled variable: the optic flow alone contained in a visual stimulus cannot provide unambiguous cues to distance or velocity. An important source of calibration comes from the high-level cognitive expectations of the subject. Vestibular cues provide a potential calibration relative to 'g' and to previous experience. But under *passive* motion conditions the vestibular system indicates a mismatch between expected (nothing) and perceived (actual) motion which seems to lead to an exaggerated response. This overestimate of distance travelled has also been reported under active motion conditions (12) although there it was much less dramatic.

Comparison with other studies

There have been no other studies investigating the relationship between optic flow and the perceived distance of evoked linearvection. Other studies comparing physical motion with physically presented target distances have confirmed that such motions can be accurately matched (1). Israel et al. (9) matched a visually presented target distance with physical motion over short distances and found that subjects needed less physical motion (0.24 m) to match a visual distance (0.8 m). This overestimation, by a factor of between 3 and 5 for acceleration values around 0.5 $m.s^{-2}$, was also found when subjects were asked to estimate displacement in metres (5) perhaps reflecting a visualized comparison. The overestimation has also been confirmed for motion in the z-axis (28). Pavard and Berthoz (18) demonstrated that visual motion sensitivity could be reduced during combined visual and physical motion. The reduction in the use of visual movement cues under our vision-plus-vestibular condition might represent another example of this phenomenon.

Vestibular capture

When different senses report different amounts of self motion, one solution is to ignore the information coming from all except one of them. Sometimes the domination of that one chosen sense is so complete that information from the subordinate senses, even when it is different from the dominant sense, *appears* to agree with the information from that sense. This is known as *sensory capture*. A classic example of sensory capture is exploited by ventriloquism (23). In this case vision is the capturing sense and sounds are perceived as coming from the visually determined direction even though the auditory cues indicate it is coming from elsewhere. What we have described here is a very unusual example of intermodal capture. First, it is unusual to show the visual system being dominated by any other sense in humans. Second, it is unusual because in previous examples of capture, a subject had two senses that gave different information. Here we have an example of one sense capturing another even when both could, theoretically, indicate the same thing: that the person has travelled a certain distance. The capturing phenomenon was only revealed by the fact that judgements of self motion in the dark are in such glaring error.

SUMMARY

The relative role of visual and vestibular cues in determining the perceived distance of passive, linear self motion were assessed. Seventeen subjects were given cues to constant acceleration motion: either optic flow, physical motion in the dark or combinations of visual and physical motion. Subjects indicated when

they perceived they had traversed a distance that had been previously indicated either visually or physically. The perceived distance of motion evoked by optic flow was accurate relative to a visual target but was perceptually equivalent to a shorter physical motion. The perceived distance of physical motion in the dark was accurate relative to a previously presented physical motion but was perceptually equivalent to a much longer visually presented distance. The perceived distance of self-motion when both visual and physical cues were present was perceptually equivalent to the physical motion experienced and not the simultaneous visual motion even when the target was presented visually. We describe this dominance of the physical cues in determining the perceived distance of self motion as "vestibular capture".

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