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RESEARCH ARTICLE

G. Schweigart · T. Mergner · G. R. Barnes

Object motion perception is shaped by the motor control mechanism of ocular pursuit

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Abstract It is still a matter of debate whether the control of smooth pursuit eye movements involves an internal drive signal from object motion perception. We measured human target velocity and target position perceptions and compared them with the presumed pursuit control mechanism (model simulations). We presented normal subjects (Ns) and vestibular loss patients (Ps) with visual target motion in space. Concurrently, a visual background was presented, which was kept stationary or was moved with or against the target (five combinations). The motion stimuli consisted of smoothed ramp displacements with different dominant frequencies and peak velocities (0.05, 0.2, 0.8 Hz; 0.2–25.6°/s). Subjects always pursued the target with their eyes. In a first experiment they gave verbal magnitude estimates of perceived *target velocity* in space and of self-motion in space. The target velocity estimates of both Ns and Ps tended to saturate at 0.8 Hz and with peak velocities >3°/s. Below these ranges the velocity estimates showed a pronounced modulation in relation to the relative target-to-background motion ('background effect'; for example, 'background with'-motion decreased and 'against'-motion increased perceived target velocity). Pronounced only in Ps and not in Ns, there was an additional modulation in relation to the relative head-to-background motion, which co-varied with an illusion of self-motion in space (circular vection, CV) in Ps. In a second experiment, subjects performed retrospective reproduction of perceived *target start and end positions* with the same stimuli. Perceived end position was essentially veridical in both Ns and Ps (apart from a small constant offset). Reproduced start position showed an almost negligible background effect in Ns. In contrast, it showed a pronounced modulation in Ps, which again was related to CV. The results were compared with simulations of a model that we have recently presented for velocity control of eye pursuit. We found that the main features of target velocity perception (in terms of dynamics and modulation by background) closely correspond to those of the internal drive signal for target pursuit, compatible with the notion of a common source of both the perception and the drive signal. In contrast, the eye pursuit movement is almost free of the background effect. As an explanation, we postulate that the target-to-background component in the target pursuit drive signal largely neutralises the background-to-eye retinal slip signal (optokinetic reflex signal) that feeds into the eye premotor mechanism as a competitor of the target retinal slip signal. An extension of the model allowed us to simulate also the findings of the target position perception. It is assumed to be represented in a perceptual channel that is distinct from the velocity perception, building on an efference copy of the essentially accurate eye position. We hold that other visuomotor behaviour, such as target reaching with the hand, builds mainly on this target position percept and therefore is not contaminated by the background effect in the velocity percept. Generally, the coincidence of an erroneous velocity percept and an almost perfect eye pursuit movement during background motion is discussed as an instructive example of an action-perception dissociation. This dissociation *cannot* be taken to indicate that the two functions are internally represented in separate brain control systems, but rather reflects the intimate coupling between both functions.

Keywords Visual system · Motion perception · Smooth pursuit eye movements · Motion illusion · Sensorimotor control · Action-perception dissociation · Model · Human

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G. Schweigart (✉) · T. Mergner
Neurological University Clinic, Neurocenter, Breisacher Strasse 64, 79106 Freiburg, Germany
e-mail: schweiga@nz.ukl.uni-freiburg.de
Tel.: +49-761-2705230
Fax: +49-761-2705416

G.R. Barnes
Department of Optometry and Neuroscience, UMIST, Manchester, UK

Introduction

When we estimate the motion of a visual object, we tend to foveate it with saccades and then track it with a smooth eye movement. As soon as eye tracking has reached a steady state, relative motion of the target on the retina becomes small. Yet, the target motion perception continues in essentially the same way and magnitude. Therefore, it is traditionally believed that pursuit-contingent target motion perception results mainly from a signal in the brain that represents the eye movement (often referred to as efference copy or corollary discharge). Conversely, however, target motion perception often has been considered to contribute to the control of eye pursuit. For instance, smooth eye pursuit can be performed with stabilised retinal images, provided there is a signal which initiates a target motion percept. The source of such a signal may be a vestibular input (Yasui and Young 1975), the effort to null a displacement error (Kommerell and Taumer 1972), a moving background (Wyatt and Pola 1979) or a shift in spatial attention (Barnes et al. 1995). Furthermore, subjects are able to pursue an imaginary target motion that perceptually is derived from, but is not directly related to retinal input (see, for example, Steinbach 1976). From such findings it has been suggested that target motion perception provides us with an internal drive signal by which we enhance eye pursuit performance (Yasui and Young 1975; Wyatt and Pola 1979; see Young 1977 for related earlier literature).

Generally, the pursuit system is considered to represent a closed-loop negative feedback system in which retinal target slip represents the input and the eye movement the output. Combining internally the retinal slip (error) signal with the aforementioned perceptual drive signal is thought to increase the overall (closed loop) gain of the system to a value close to unity, so that target tracking becomes very accurate. Originally, the perceptual drive signal was modelled as an internal positive feedback or feed forward loop in which the drive signal is derived from retinal target slip and then fed back to this signal (see Yasui and Young 1975; Wyatt and Pola 1979; Robinson et al. 1986; Barnes and Asselman 1991; Krauzlis and Lisberger 1994). It allows the incorporation of predictive mechanisms by which the rather long visual processing time at the beginning of a pursuit reaction can be overcome and the system's high frequency dynamics is improved (see Barnes and Asselman 1991). Furthermore, it allows the implementation of attentional mechanisms by which the pursuit mechanism (and the motion perception) selects one out of possibly several moving stimuli (see, for example, Worfolk and Barnes 1992; Ferrera and Lisberger 1995; Ferrera 2000). By the same token, it is thought to boost up the gain selectively for target pursuit, thereby leading to a dominance of pursuit over the optokinetic reflex and the vestibulo-ocular reflex (OKR and VOR, when target tracking is performed in the presence of a moving visual background and of head movements, respectively; see Schweigart et al. 1999).

The experimental evidence for the presumed internal drive signal for smooth eye pursuit so far is only indirect. It therefore would be desirable to test this notion by comparing the internal drive signal directly with target motion perception. Such an approach may possibly help also to better understand the pursuit-contingent target motion perception, because it is associated with a number of still enigmatic perceptual phenomena. For instance, the target appears to move more slowly if tracked with the eyes than if the eyes are held stationary and the target moves across the retina (Aubert-Fleischl phenomenon; Aubert 1886). Furthermore, a stationary visual stimulus in the background may appear to move counter to the eyes during tracking eye movements (Filehne illusion; Filehne 1922; for literature, see Post and Leibowitz 1985). These phenomena have led researchers in the past to the notion that the internal signal representing the eye pursuit is under-representing the movement, in line with reports of some loss of background position constancy during pursuit (for literature, see Mack and Herman 1978).

Interestingly, these perceptual phenomena appear to affect performance of eye pursuit only marginally. This is especially evident in a situation where subjects fixate a visual target that remains stationary while the background is moved. Perceptually, the stationary target appears as moving counter to the background ('Duncker's induced motion'; Duncker 1929). Despite this target motion perception, the eyes remain essentially stationary (Mack et al. 1982). Even though very tiny eye movements may occasionally occur, the motor and the perceptual effects are highly discrepant. Similarly, retinal background motion during pursuit of a moving target has only a minor effect on pursuit performance, but a dramatic one on the movement perception (Worfolk and Barnes 1992). Such dissociations have led some researchers to doubt that perception makes a considerable contribution to pursuit in normal situations (outside the laboratory). For instance, according to Mack et al. (1982) target motion perception acts as a stimulus for pursuit only when the 'perceptual target' has no retinal counterpart. Vice versa, also the importance of the pursuit efference copy for the target motion perception has repeatedly been questioned. For instance, Festinger et al. (1976) suggested that the internal representation of the pursuit movement contributes mainly to the direction of perceived target motion, but hardly to perceived speed.

It is true that many of the laboratory findings appear to be inconsistent with our experience in natural environments. Usually we can successfully grab a moving visual object while pursuing it with our eyes, independently of whether the visual background is stationary or moving. There have been numerous attempts to explain these and related discrepancies (see, for example, Mack and Herman 1978; Post and Leibowitz 1985; Wertheim 1994). Most of these studies focused exclusively on the perceptual aspects, however, not taking into account the feedback character of the pursuit control mechanism.

In the present study we measured human target motion perception to compare it with the presumed internal pursuit drive signal. We did this for situations in which the perception was congruent with, or dissociated from, the pursuit movement. To this end, we presented human subjects, in addition to the target, with a visual background that was either kept stationary or was moved with or against the target in a number of different stimulus combinations, while subjects always tracked the target with their eyes. In a first experiment, subjects gave magnitude estimates of perceived target velocity. The resulting estimation curves of target velocity were compared to curves obtained from a simulation of the presumed internal drive signal in a model which we recently suggested for the velocity control of target pursuit in monkey (Schweigart et al. 1999), which we adapted here for humans. In a second experiment we had our subjects reproduce, after presenting again the same stimulus combinations, the end and start positions of the target. This approach was based on the hypothesis that there exist two different perceptual ‘channels’, one encoding object speed and the other object position. The hypothesis relates to the earlier observation that target motion perception tends to be equivocal in the presence of a moving background. The impression is that a stationary object appears to move counter to the moving background, but *post hoc* its position has not changed appreciably (‘object motion paradox’; see Mergner and Becker 1990).

We performed the two experiments in both normal subjects and in patients with chronic loss of vestibular function. The main reason for involving the patients was that they, unlike normal subjects, experienced an illusory head motion (circular vection, CV) during the background motion stimuli, as we observed in pilot experiments of the present study. From this we hoped to learn how the perception of target motion in space combines with the perception of self-motion in space. The background is that our model also covers pursuit control during self-motion (Schweigart et al. 1999).

Generally, we make in our study an attempt to fuse two commonly held concepts from different research fields into one coherent picture, one concept being held by many oculomotor physiologists (target motion perception represents a decisive constituent of the smooth pursuit control mechanism) and the other by visual psychophysicists (pursuit-contingent perception of target motion involves an internal representation of the eye movement, which is erroneous during background motion, however). Our study also tries to explain why motor performance is essentially correct even during background motion conditions where the perception of target motion is clearly erroneous.

Experiment 1: velocity estimation

Materials and methods

Subjects

Six normal subjects (four males and two females; age 21–53 years) and three patients with bilateral loss of vestibular function (males; 25, 36 and 37 years) participated in the study. All subjects were naïve to the conditions of the experiment. Vestibular dysfunction was assessed by clinical examination (for example, balancing problems when standing on foam rubber with eyes closed), electronystagmography (absence of caloric nystagmus and of rotation-evoked VOR) and case histories (meningitis and ototoxic medication in childhood). Apart from hearing problems, patients showed no neurological symptoms. In compliance with the Helsinki declaration (1964), all subjects gave their informed consent to the study which was approved by the local ethics committee.

Apparatus and stimuli

Subjects were seated on a rotation chair which was kept stationary, however, except during sparsely interspersed sham trials. Subjects' heads were fixed by side and rear supports. The chair was surrounded by a cylindrical screen (vertical axis, r=1 m). A target (red spot luminance, ca 20 cd/cm^2; diameter, 0.5° of visual angle; Fig. 1a) was projected onto the screen at eye level. The target could be rotated in the horizontal plane by a mirror galvanometer (TS *target rotation in space*). In addition, an optokinetic (‘background’) pattern could be projected onto the screen and could be rotated about the same axis (BS *background rotation in space*). It consisted of a pattern of black-and-white patches, apart from a horizontal dark stripe of 5° width, on which the target was moved (Fig. 1a). The axis of target and background rotation passed through the intersection of the interaural and naso-occipital lines of subjects' heads. Subjects' ears were plugged to minimise auditory orientation cues. Subjects were monitored by a remote infrared video system.

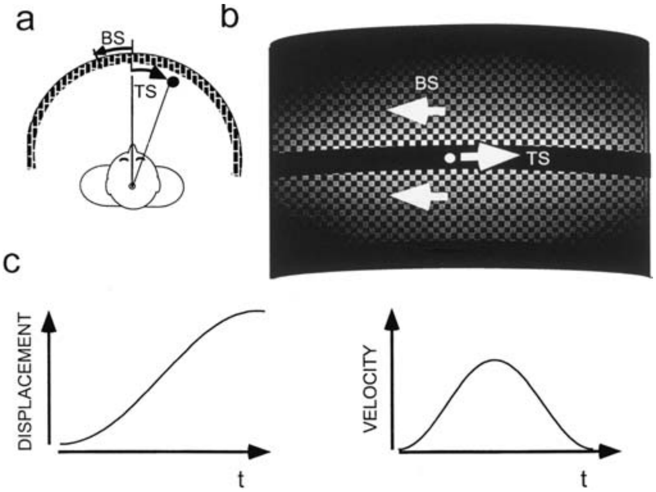

Fig. 1a–c Experimental set-up. **a** Top view of a subject pursuing with the eyes a target moving in space, *TS*. In the example shown, there is a simultaneous motion of a visual background in space, *BS*, of same magnitude, but in counter direction. **b** Subject's view of the stimulus combination (*arrows* indicate movement direction). Elliptical luminance gradient of background is taken to indicate subjects' shrunken visual fields at the very low luminance level used (by this, subjects no longer saw the shadows of their orbital rims, despite dark adaptation). **c** Displacement and velocity profiles of motion stimuli

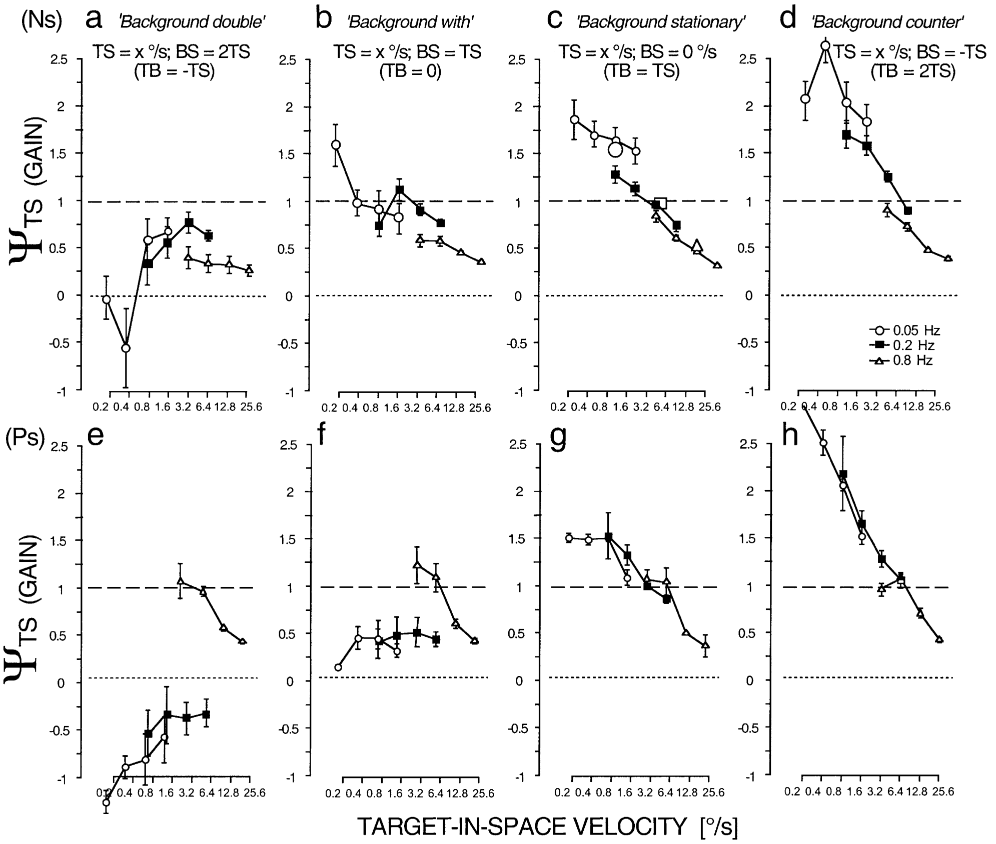

Fig. 2 Velocity estimates of target motion in space (*TS*) for different background motion conditions in normal subjects (*Ns*; **a–d**), and vestibular loss patients (*Ps*; **e–h**). Gain of estimated peak TS velocity (means ±1 SE) is plotted against the actual velocity (abscissae, logarithmic scale, in °/s) for the three stimulus frequencies indicated. While TS was the same across all panels, background in space motion (*BS*) was modified from left to right panels as indicated above each panel. Veridical estimates would yield a gain of unity (*dashed horizontal lines*). *Large symbols* in **c** (BS=0°/s condition) give the gain values of the 'across-frequency' runs, to which the results of the 'within-frequency' runs (interconnected mean estimates) were referenced. In this 'background stationary' condition, estimates are approximately veridical in the midvelocity range, while larger velocities led to underestimation and smaller velocities to overestimation. Note clear modulation of estimation curves by BS motion in **a–d** (Ns) and, more pronounced, in **e–h** (Ps). Ψ Perception

Special care was taken to prevent subjects from seeing relative motion cues between target or background and their own bodies, since they may show a facilitating effect on self-motion perception (see Mergner et al. 2000a, b). To achieve this, possibly visible apparatus and body parts were covered by black cloth. Furthermore, the experiment was conducted with the subjects in a dark-adapted state and with a low level of background luminance. In this condition the background still remained clearly visible and CV could still be evoked in both normals and patients when tested with constant velocity motion stimuli (compare Leibowitz et al. 1979).

All rotational stimuli were smoothed position ramps (to the left or right) that had a 'raised cosine' velocity profile ('cosine bell'; Fig. 1c), represented by the equation:

$$v(t) = -A * f * \cos(2\pi f * t) + A * f;\ 0 < t < 1/f$$

with t denoting time and A the peak angular displacement. This stimulus has the advantage of being a transient motion that contains a single frequency (f) and a well-defined peak velocity. In view of the fact that the ocular pursuit system shows both low-pass frequency *and* high velocity saturation characteristics (see Schweigart et al. 1999), we used three different stimulus frequencies (f=0.05, 0.2 and 0.8 Hz) each with four different angular displacements (A=2°, 4°, 8°, or 16°; durations, 1.25, 5, and 20 s, respectively). The corresponding peak velocities ranged from 0.2°/s (0.05 Hz, 2°) to 25.6°/s (0.8 Hz, 16°) and can be read from the abscissae in Fig. 2.

Stimulus conditions. Target and background could be rotated either in isolation or in combination. With the combined rotations, they had either the same direction or opposite directions (under computer control which ensured appropriate timing and dynamics; position accuracy <0.5%). A negative sign in the stimulus conditions given below indicates counter direction. Six different stimulus conditions were used:

A. *'Background stationary'*. BS=0°; TS=2, 4, 8 or 16°. Target displacement relative to background, TB=TS.
B. *'Background counter'*. The background was rotated by the same amount as the target in space, but in the opposite direction (BS=–TS; for example TS=8°, BS=–8°, TB=16°).
C. *'Background with'*. The background was rotated by the same amount and in the same direction as the target in space, so that essentially no relative motion occurred (BS=TS, TB=0°).
D. *'Background double'*. The background was rotated in the same direction as the target in space, but with double the amplitude, so that relative target-to-background motion became reversed (BS=2×TS, TB=–TS).
E. *'Background-only (Duncker's)'*. The target remained stationary, while the background was rotated in space and alone deter-

mined the relative target-to-background motion (TS=0°, BS=2, 4, 8 or 16°=–TB).

F. *'Dark'*. The target was rotated in a dark environment (background extinguished).

General instructions. Whenever the target was presented, subjects were required to foveate it and to track it when it moved. They were instructed to direct their full attention to the target and its motion in space.

Target presentation. Prior to each trial the background was displayed, being stationary. Then the target appeared at the straight ahead position and remained stationary for 400 ms, before being moved (together with the background, according to the aforementioned stimulus combinations). Then target and background remained stationary for another 400 ms before being extinguished. After a brief period of darkness the stationary background reappeared and the subjects were required to make estimates as detailed below. In the 'dark' condition stimulus presentation was as described above, but there was no background during target presentation.

Estimation procedure. The subject's task was to verbally estimate perceived peak velocity of the target in space. Each experiment started with training sessions. During these sessions first a standard stimulus was repeatedly presented, which consisted of target rotations of a given peak velocity (see below), randomly to the left or right, with the background always being stationary. Subjects assigned, after cessation of the stimulus, a number of their own choice, between 10 and 100, to the perceived peak velocity of the target (*'modulus'*). Then subjects learned to express perceived peak velocity of other stimuli (test stimuli) as fractions or multiples of the modulus (*'magnitude estimation'*; Stevens 1956). In a previous study on the perception of self-motion we had shown that the results obtained with this verbal estimation procedure closely resemble those acquired with a concurrent indication procedure (Mergner et al. 1991).

Stimulus presentation. The trials were always presented in blocks. Each block began with the standard stimulus (known to the subjects) which was followed by three test trials. These trials could contain a 'hidden' repetition of the standard stimulus. The order of the test trials was random, but with the constraint that extreme changes in velocity (factor >4) and in background motion (stimulus combinations B and D) from one to the next trial were avoided. The aim was to minimise ceiling, floor and anchor effects (see Poulton 1968).

Subjects always had to give two velocity estimates per trial, which should encompass the lower and the higher end of their 'uncertainty range' (a high degree of subjective certainty would be expressed by giving the same value twice). In 98.5% of the trials the difference between the two estimates was 25% or less and the average of the two values was taken. The remaining trials (difference >25%) were repeated. In addition to the velocity estimates, subjects also had to indicate the direction of perceived TS motion (left or right). This was compared to actual TS motion and the estimate was given a positive/negative sign when its direction was the same/opposite of TS motion (exception: in the Duncker's condition the sign was referenced to TB).

Design of runs. The range of presented peak velocities was too broad to be covered in one and the same experimental run with the magnitude estimation method (see above, ceiling and floor effects). We therefore performed two different sets of runs:

1. *Within-frequency runs.* Separately for each stimulus frequency (0.05, 0.2 and 0.8 Hz), we compared estimates across different peak target velocities and background conditions. In each run, a total of 48 test trials were presented for each frequency [6 background conditions × 4 velocities × 2 directions (leftward, rightward)]. Each frequency run was repeated twice. Overall, the six runs were performed in separate sessions on different days. The standard stimulus was 0.8°/s (8°) in the 0.05-Hz run, 3.2°/s (8°) in the 0.2-Hz run and 12.8°/s (8°) in the 0.8-Hz run.
2. *Across-frequency runs.* In these runs we compared the estimates across the three frequencies. This was performed for one target velocity value per frequency (0.8°/s at 0.05 Hz, 3.2°/s at 0.2 Hz and 12.8°/s at 0.8 Hz) with the background always stationary. Each run comprised a total of six test trials (2 directions × 3 frequencies) and was repeated six times (one session). Only one standard stimulus was used (0.2 Hz/3.2°/s/8°).

Using the 0.2 Hz/3.2°/s/8° standard stimulus in both sets of runs allowed us to cross-reference the data of the within-frequency runs with those of the across-frequency runs (see Results).

Derivation and validation of 'perceptual gain'

Based on a previous study in which we measured object motion perception by means of a nulling procedure (Mergner et al. 1992), we assumed that perceived target velocity with the 0.2 Hz/3.2°/s/8° standard stimulus is approximately veridical. By veridical we mean here that the magnitude of a response matches the magnitude of the stimulus. In order to validate this stimulus-response matching in the present experiments, we performed a control experiment in which normal subjects were presented with this standard stimulus and, after storing the perceived motion into memory, produced an arm movement that reproduced the target movement (by moving in complete darkness with the outstretched right arm a pointer with the same trajectory and speed as the previously seen target). Reproduced peak velocity averaged 3.09°/s, which indeed is very close to the presented value of 3.2°/s (error <4%), while larger errors (>15%) were found with analogous tests at 0.05, 0.1, 0.4 and 0.8 Hz.

Because there was this close correspondence between the standard stimulus and the corresponding perception-derived motor response, we equated the magnitude of the velocity estimate with a 'perceptual gain' of 1 and referenced all other estimates to this value (see Results). For instance, the estimation curves in Fig. 2 are expressed in terms of velocity gain values, a way in which normally the characteristics of pursuit eye movements are displayed (compare Discussion where pursuit performance is compared to perception).

After having delivered the estimates of target velocity in space and its direction, subjects gave an estimate of perceived peak self-velocity in space, in relation to the modulus (i.e. to perceived peak target velocity during the standard stimulus). The data obtained were evaluated in the same way as described above for perceived target velocity. The test trials contained sparsely intermingled sham trials in which, in addition to target and background, the chair was rotated.

Control eye movement recordings

It is well known (see, for example, Barnes 1993; Lindner et al. 2001) that subjects tend to keep their eyes very accurately on target during pursuit even in the presence of a stationary or moving background, unless the dynamic limits of the pursuit system are exceeded. A continuous eye movement recording was not deemed feasible during the demanding and rather long lasting psychophysical measurements. We therefore confirmed these previous findings for the stimuli described above in only two normals and one patient. We used both an infrared eye movement recording system ('Iris'; Skalar, Delft; which restricted subjects' visual field, however) and EOG recordings (no visual field restriction; DC, 30 Hz low pass filtered, 200 Hz sampling rate, spatial resolution ca 0.5°). These recordings showed that the background modulates pursuit by <10% when compared to the dark, in accordance with previous studies (see, for example, Collewijn and Tamminga 1984; see also Worfolk and Barnes 1992). The effect of the background was considerably less than that previously observed in monkeys (Schweigart et al. 1999).

Statistics and model

We pooled the responses for leftward and rightward target motion, since they showed no statistically significant differences. Values outlying more than three standard deviations from the mean value were considered as outliers and were rejected. Statistics was performed by the commercial software SPSS (SPSS, Chicago, Ill., USA).

Results were compared to simulations of a recently developed model of pursuit–OKR interaction of monkey (Schweigart et al. 1999), which was adapted for humans (see Discussion). Simulations were performed with the commercial software Matlab/Simulink (MathWorks, Natick, USA).

Results

Across-frequency runs

The estimates of the across-frequency runs are shown in Fig. 2c (background stationary). The mean values are given in the form of large open symbols (*circle* 0.05 Hz, *rectangle* 0.2 Hz, *triangle* 0.8 Hz). The data are normalised to the modulus of the 0.2 Hz/3.2°/s/8° standard stimulus (assumed to yield an essentially veridical estimate; see Materials and methods). The estimates to the 0.2 Hz/3.2°/s/8° test trial (‘hidden standard stimulus’) well reproduced the modulus (0.94). In contrast, velocity of the 0.8°/s stimulus at 0.05 Hz was overestimated by a factor of 1.54 and that of the 12.8°/s stimulus at 0.8 Hz was underestimated by a factor of 0.51. We used these factors in the following section to obtain a normalisation of the results in the within-frequency runs.

Within-frequency runs

To explain the normalisation in the within-frequency runs, consider again Fig. 2c. The results are plotted separately for the three stimulus frequencies used (as indicated by small interconnected symbols; mean ±1 SE). The standard stimulus used for the 0.2-Hz run (*filled squares*) was equal to that in the across-frequency runs, but here peak velocity for a given frequency was varied. The response to the 0.2 Hz/3.2°/s/8° test trial (‘hidden standard stimulus’) was essentially the same as before and reproduced the normalised modulus (unity), as indicated in the diagram. The responses decreased with increasing peak velocity (6.4°/s stimulus) and increased with decreasing velocity (1.6°/s and 0.8°/s stimuli). Thus, the resulting estimation curve for 0.2 Hz is inversely proportional to the logarithm of peak TS velocity (note logarithmic scale on abscissae). Similar estimation curves were obtained for the 0.05- and 0.8-Hz runs. The results of these runs (*small open circles* and *triangles*) were referenced to those obtained in the 0.2-Hz run by multiplying them with the factors obtained in the across-frequency runs (1.54 and 0.51 for the 0.05-Hz run and 0.8-Hz run, respectively; see above). In other words, all values in the diagram are referenced to the 0.2 Hz/3.2°/s/8° standard stimulus. The same referencing was performed also for the results obtained in the different conditions with a moving background and in the dark condition.

These results are described in the following for normals (Fig. 2a–d).

‘Background stationary’. The results obtained for this most natural condition where the target was moved against the stationary background are briefly repeated here, since they serve as a basis of comparison with the other background conditions. Note that the perceptual gain was close to unity in the midvelocity range (around 3.2°/s), while normals overestimated peak velocity at low velocity and frequency and underestimated it at high velocity and frequency (Fig. 2c).

‘Background counter’. When the background was moved with the same velocity as, but in the opposite direction to the target (note that target-to-background, TB, is now doubled), the rise in gain with decreasing velocity was more pronounced than in the previous combination (Fig. 2d). In contrast, gain remained anchored at the high velocity end of the estimation curves at values similar to those above (G=0.40 at 25.6°/s) and the same was true for the other stimulus conditions to be described below.

‘Background with’. When the background was moved in synchrony with the target, the 0.2- and 0.05-Hz estimation curves levelled at approximately unity gain (exception with smallest velocity used, 0.2°/s; Fig. 2b).

‘Background double’. When the background was rotated in the same direction, but with double the velocity of the target, the relative target-to-background motion became opposite to target-in-space motion (TB= –TS). As a consequence, the 0.2- and 0.05-Hz estimation curves developed a decrease with decreasing stimulus velocity (Fig. 2a). At peak velocities ≤0.4°/s, the direction of perceived target-in-space motion even reversed (indicated here by negative gain values).

The results of normals obtained in the two additional stimulus conditions are shown in Fig. 3a, b. The ordinal scaling is the same as before (gain, referenced to the TS 0.2 Hz/3.2°/s/8° standard stimulus).

‘Background-only’ (‘Duncker’s induced motion’). The results are plotted as a function of peak target-to-background velocity (accordingly, estimates received a positive sign because perceived target motion is in the direction of this relative motion; Fig. 3a). Noticeably, gain in the 0.8-Hz estimation curve is close to zero. It increased considerably with the 0.2-Hz stimuli and even more so with the 0.05-Hz stimuli, reaching a maximum of G=1.07 at 0.4°/s.

‘Dark’ (no background). The results (Fig. 3b) resemble those obtained with the background stationary (compare Fig. 2c). For example, perceived target velocity was overestimated at low velocities (G=1.63 at 0.4°/s,

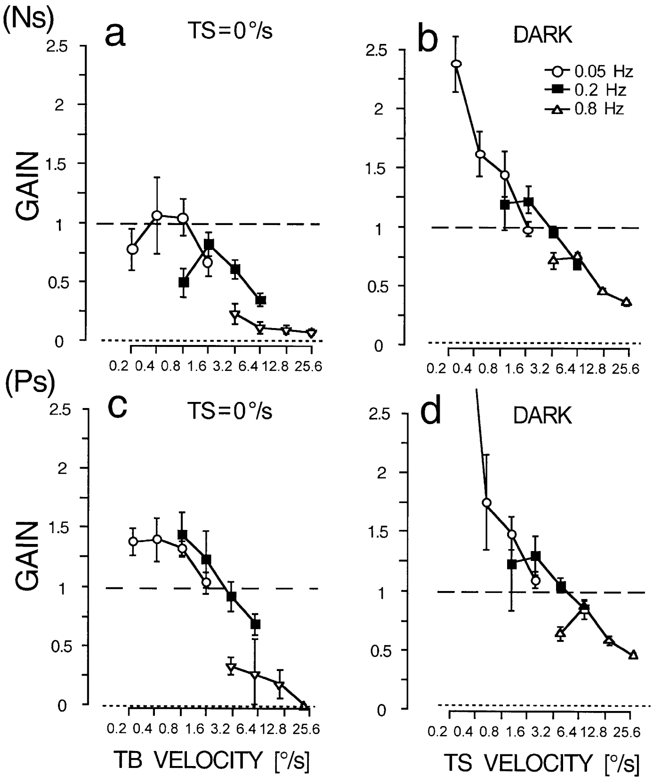

Fig. 3 Velocity estimates of target-in-space (*TS*) motion in normals (*Ns*; **a**, **b**) and patients (*Ps*; **c**, **d**) in the remaining stimulus conditions. **a**, **c** 'Target stationary' condition (TS=0°/s). The background was moved, while the target was kept stationary, with the relative target-to-background motion (*TB*) yielding an illusion of TS motion (Duncker's induced motion). Presentation as in Fig. 2, but estimation curves give perceived TS velocity with respect to background in space velocity (on *abscissae*). **b**, **d** 'Dark (no background)' condition

0.05 Hz), almost veridical at midvelocities (G=0.96 at 3.2°/s, 0.2 Hz) and underestimated at high velocities (G=0.36 at 25.6°/s, 0.8 Hz).

Response variability. In terms of gain values as displayed in Fig. 2, both intrasubject and intersubject variability of the estimates tended to increase with decreasing frequency as well as with decreasing velocity (note that this trend would be reversed if the data were considered in absolute values in degrees per second, instead of gain). Furthermore, the two variabilities depended on stimulus condition, being smallest in the 'background stationary' condition and largest in the 'background double' condition. For instance, upon trial repetition in the 'background stationary' condition, the gain values of normal subjects' varied, on average, by 0.13, 0.27 and 0.60 for the 0.8 Hz/6.4°/s, 0.2 Hz/1.6°/s and 0.05 Hz/0.4°/s stimuli, respectively, while the corresponding values for the 'background double' condition were larger, amounting to 0.18, 0.47 and 1.47 (mean of six intrasubject SD values, each from four values, 2 trial repeats × 2 stimulus directions). There was a similar, but stronger trend for the intersubject SD values ('background stationary'; 0.16, 0.39 and 0.34; 'background double': 0.52, 0.73 and 0.78; SD of six mean values, one per subject). The latter finding suggests that there exist considerable intersubject idiosyncrasies of the background effect on perceived target velocity.

Patients' estimates of target velocity

Patients' estimates of target velocity are shown in Figs. 2e–h and 3c, d. At 0.8 Hz and the highest velocities, the anchoring of the estimation curve at low values was similar to that in normals in all conditions. Noticeably, also with 'background stationary' (Fig. 2g) the estimation curves for 0.2 and 0.05 Hz resembled those of normals, with respect to both the gain increase at low velocities and the gain decrease at high velocities. The same applied to the 'dark' condition (Fig. 3d). In all other conditions, in contrast, background motion had a stronger effect than in normals. This was especially evident in two conditions: (a) in 'background with' (Fig. 2f), the 0.2-Hz estimation curve and, even more so, the 0.05-Hz curve showed gain values clearly below unity and (b) in 'background double' (Fig. 2e), perceived target motion in space was counter to its actual motion (as indicated by negative gain values) at 0.2 Hz and, even more so, at 0.05 Hz. With 'background counter' (Fig. 2h) the (negative) slopes of the three estimation curves became slightly steeper than in normals. Also in the 'background-only' (Duncker's) condition (Fig. 3c), the increase of the patients' estimates curves with decreasing frequency and velocity was more pronounced than in normals, starting from approximately G=0 at 0.8 Hz/25.6°/s. The increase reached gain values >1, but tended to saturate at the lowest velocities (0.4 and 0.2°/s).

Characteristics of the background effect

To better visualise the background effect on perceived target velocity, we replotted part of the data of Fig. 2 in Fig. 4a (normals) and Fig. 4b (patients), arranging the combinations on the abscissae according to target-to-background velocity (TB=–1/0/1/2×TS) and background-in-space velocity (BS=2/1/0/–1×TS). As guides in Fig. 4a, b, we indicate veridical target-in-space velocity (TS lines, slope=0) and complete dependence on background motion (TB lines, slope=1). Results are given for only two velocities per stimulus frequency, while those for the other two velocities are omitted for clarity.

Note that in the top panel of Fig. 4a (0.05 Hz) the estimation curve for 0.4°/s approximately parallels the TB line with an offset that corresponds approximately to the TS line. Thus, perceived target velocity with these stimulus parameters appears to reflect the sum of TS and TB velocities. With the 1.6°/s stimulus at 0.05 Hz, the background (TB) effect is still present, but less pronounced (smaller slope). Even less background effect is seen with the curves obtained at 0.2 Hz and it is essentially absent at 0.8 Hz (where, in addition, the effect

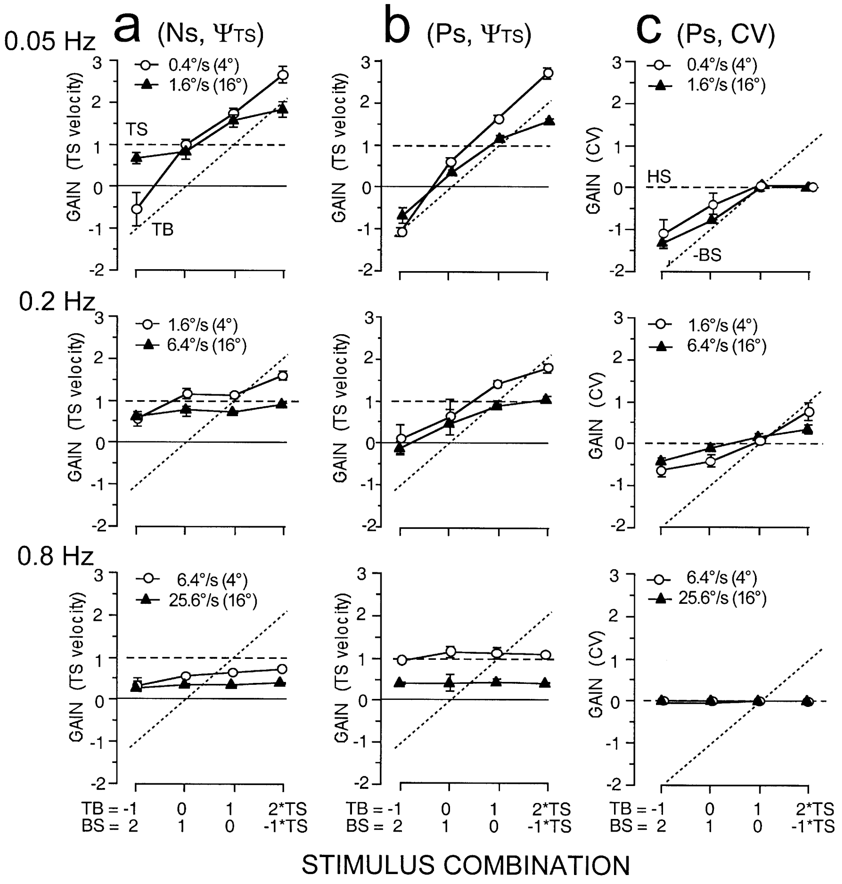

Fig. 4 a, **b** Replot of velocity estimates of normals (*Ns*; **a**) and patients (*Ps*; **b**) from Fig. 2 across different background motion conditions (relative target-to-background, TB=–1×TS, TB=0×TS, TB=1×TS, TB=2×TS; cf. Fig. 2a–d and e–h, respectively). In addition, the corresponding background-in-space motions is given [BS=2×TS, 1×TS, 0×TS (i.e. stationary) and –1×TS]. For the sake of clarity, only the data of two stimulus velocities per frequency are plotted, as indicated. The gain curves show little dependency on background motion at 0.8 Hz [they approximately parallel the horizontal TS lines which indicate 'ideal' (meaning veridical) performance], a moderate background effect at 0.2 Hz and a pronounced background effect at 0.05 Hz (the slopes become similar to that of the TB lines which represent complete dependency on the relative motion stimulus). The modulation by the background is clearly larger in patients than in normals. **c** Self-motion estimates of patients (circular vection, *CV*). CV velocity was estimated using same modulus and standard stimulus (CV gain=1, if CV is equal to, and in same direction as actual TS; negative sign indicating opposite direction). Normals never consciously experienced CV with the stimuli used

of TS velocity decreases). The results in patients (Fig. 4b) resembled those of normals, apart from a somewhat steeper slope (see next section).

We conducted a repeated measures ANOVA in both normals and patients for each target frequency, with the main factors being TS and TB velocity (TB normalised with respect to TS, yielding TB=–1/0/1/2×TS, corresponding to our stimulus conditions 'background double'/'with'/'stationary'/'counter', respectively). There was a significant linear effect of the relative motion stimulus (TB) at all frequencies ($P<0.001$). This notion was confirmed when we conducted linear regression analyses on the data at each target velocity and determined the slope as a measure of the effect of background motion. The slopes were close to unity in normals and slightly larger in patients at 0.4°/s and declined with both increasing velocity and frequency, as evidenced in Fig. 4a, b.

The linear dependence of perceived target velocity on background conditions suggested that there might be a summation of TS and TB effects taking place (with additional non-linear effects, such as the saturation at high target velocities, for instance).

Self-motion perception

The self-motion estimates of our normal subjects were always zero. On retrospective request, they always considered themselves as stationary during the stimuli. Only at 0.05 Hz they occasionally experienced some uncertainty in this respect. Thus, we can largely exclude that CV represents a major source for the modulation of perceived target velocity by the background motion in normals.

In contrast, patients did report CV with the 0.05- and 0.2-Hz stimuli (except with the smallest, i.e. the 2°

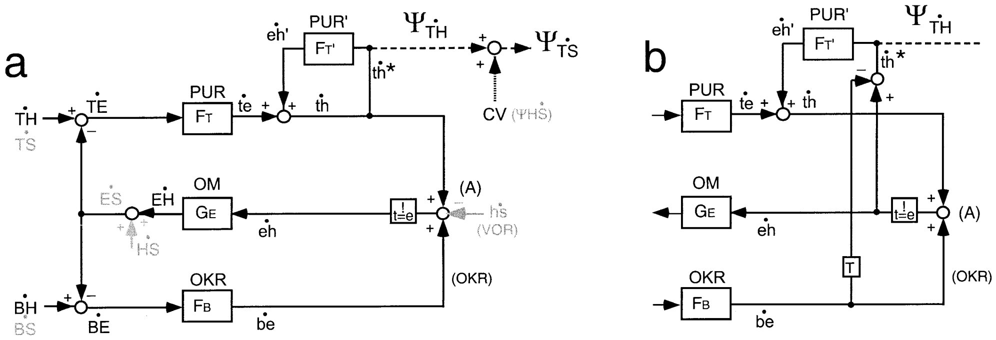

Fig. 5a, b Model of pursuit-contingent target motion (velocity) perception. **a** The basis is a model of ocular pursuit in the presence of a visual background, originally designed to describe pursuit–optokinetic reflex (*OKR*)–vestibulo-ocular reflex (*VOR*) interaction in monkey (Schweigart et al. 1999). It was adapted here to humans and extended to include target motion perception with respect to the head ($\Psi\dot{T}H$) and in space ($\Psi\dot{T}S$). The *box PUR* (pursuit system) contains a delay (60 ms) and a first-order low pass filter (corner frequency, 2.6 Hz). Then this signal pathway branches into two paths, one containing only a gain element of 0.4, and the other a saturation of ±5°/s and a gain of 0.6. The signals of the two pathways are summed prior to the output side of the PUR box. The *box OKR* (optokinetic system) contains the same delay and low pass filter and again an intermittent pathway branching. One branch contains a saturation of ±0.3°/s and a gain of 0.4, and the other branch a saturation of ±0.5°/s, a gain of 1.6 and an additional low pass filter (0.015 Hz). The *box OM* represents the oculomotor plant (gain GE=1). The *box t=!e* represents the sensorimotor transformation (of $\dot{t}h$ into $\dot{e}h$; no transfer characteristics). *$\dot{B}E$*, *$\dot{B}H$*, *$\dot{B}S$* Velocity of background-to-eye, -to-head, -in-space, respectively, *$\dot{E}H$*, *$\dot{E}S$* eye-in-head, -in-space, *$\dot{H}S$* head-in-space, *$\dot{T}E$*, *$\dot{T}H$*, *$\dot{T}S$* target-to-eye, -to-head, -in-space. The corresponding *lower case letter pairs* give the internal representations of these external signals. All space-referenced signals (for example, $\dot{T}S$) are *grey shaded*. *F_T*, *F_B* Transfer functions of visual feedback for the target and background, respectively (see above), *$F_{T'}$* internal model of F_T. **b** Repetition of part of the model with different topology, but functional equivalence. The signal pathway $-\dot{b}e$ is given a small threshold (T, 0.02°/s) to simulate the sharp bends of the estimation curves at the lowest stimulus velocity (0.2°/s)

stimuli). Their estimates are given in Fig. 4c after analysing and presenting them in a form analogous to the target velocity estimates. Note that we give in this figure, instead of the TS and TB lines, an indication of actual head-in-space velocity which was zero (HS lines) and of ‘full vection’ (CV reflecting exactly the reverse of BS velocity; –BS lines). From this it is evident that patients’ CV changed as a function of BS (see abscissae). At 0.05 Hz, there was a positive slope which was slightly less than BS, yet indicating strong CV. The slope was somewhat smaller at 0.2 Hz. In contrast, no CV was evoked at 0.8 Hz.

We therefore put forward the hypothesis that patients’ estimation curves of TS (Fig. 4b) reflect the sum of their CV (Fig. 4c) and an estimate of TS that is similar to that of normals (Fig. 4a). This hypothesis holds, at least qualitatively. We calculated the slope values from the regression lines of normals’ and patients’ perceived target velocity as a function of TB (Fig. 4a, b) and evaluated the difference between patients and normals. This difference between slopes resembled the slopes of patients’ CV curves (correlation, r= 0.90, P<0.001).

Discussion

As mentioned in the Introduction, there is a need for a unifying hypothesis for the relationship between target motion perception and the sensorimotor control of smooth pursuit. The hypothesis should be able to explain the dissociations which may occur between perception and motor control under certain stimulus conditions. In our experiments we have established a set of stimulus conditions in which such dissociations occurred. We posited that this approach might reveal the internal coupling between the perceptual and motor functions. In the following we therefore discuss the results in the light of current concepts of pursuit motor control.

It is clear from the data presented in Figs. 2 and 3 that the perception of target velocity is not related in a simple way to ocular pursuit (close to ideal in the mid- to low velocity range) as expected if it were a straightforward efference copy of the oculomotor output. As we will now show, the characteristics of perception actually bear a close resemblance to the presumed internal premotor signal related specifically to the target (‘drive signal for target pursuit’). In the presence of the background this target-related premotor signal differs markedly from the final motor signal that is responsible for producing the eye movement. These effects are best considered by reference to our pursuit model (Schweigart et al. 1999), which originally was developed for monkey and here is adapted to humans (by improving the pursuit signal and weakening the optokinetic signal; for details, cf. legend of Fig. 5a). It resembles most previous models of the velocity control of target pursuit, but is unique in that it includes a part that accounts for the interaction with the moving visual background.

The model in Fig. 5a represents the target pursuit control which consists of a closed-loop negative feedback system with target retinal slip (target-to-eye velocity, $\dot{T}E$) representing the input and the eye movement (eye-in-head velocity, $\dot{E}H$) the output (*grey symbols*, indicating a space referencing of pursuit, and the slightly modified version of

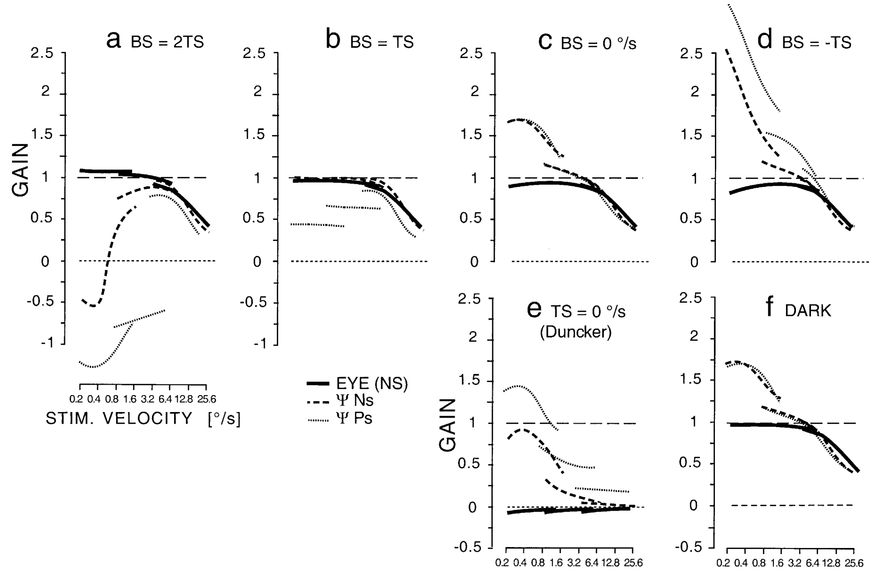

Fig. 6a–f Simulation results obtained with the model in Fig. 5b for the ocular pursuit in normals (*EYE*) and perceived target velocity in normals and patients (Ψ*Ns* and Ψ*Ps*, respectively). Stimulus conditions are those in Figs. 2 and 3

the model in Fig. 5b will be discussed further below). Internally, T˙E is processed by a visuomotor system for target pursuit eye movements (*box PUR*, which contains the dynamic characteristics; see legend of Fig. 5a). The internal representation of T˙E (t˙e) is transformed into a premotor eye-in-head signal e˙h. It is widely recognised that, in order to achieve a pursuit gain close to unity, whilst maintaining stability in a system which contains delays in visuomotor processing, it is necessary to have a special means of boosting the internal gain of the system. This boost of t˙e gain is usually implemented in the form of a local positive feedback loop that is restricted to the t˙e signal (see, for example, Barnes and Hill 1984; Robinson et al. 1986; Leigh and Zee 1999)[1]. This internal signal (e˙h') is derived from the t˙h signal in the model of Fig. 5a (t˙h*).

In the model, t˙h competes at junction A with a second retinal slip signal from a different visual stimulus, which here is given by background-to-eye velocity (B˙E, internally b˙e). This is processed by another visuomotor system that alone would produce an OKR (*box OKR*), also with a negative feedback via e˙h and E˙H. Fundamental to the understanding of the interaction that takes place between the target and background is the hypothesis that the balance between them is controlled by selectively boosting the gain of t˙e, so that eye velocity is dominated by target velocity and not by background velocity (Worfolk and Barnes 1992; Schweigart et al. 1999).

Our assumption is that a version of the t˙h signal (the t˙h* signal) not only yields the internal drive for target pursuit (e˙h'), but in addition represents the source of the target velocity perception (ΨT˙H). The reason for this assumption is that it represents a signal which can be modified by attentional and predictive mechanisms (see Barnes 1995; Fig. 5 in Schweigart et al. 1999, 'gain enhancement and prediction loop'). This hypothesis was tested by simulations of the model, comparing the t˙h* signal with the measured target velocity estimates as well as with the eye movements across the different background conditions we used.

The results of the simulations are shown in Fig. 6a–f (presentation as in Figs. 2a–d, 3a, b) together with the gain of the smooth component of eye velocity predicted by the model. The predicted perception corresponds closely to the experimental data. To start with, we refer to the decline in ΨT˙H observed at 0.8 Hz. The model effectively simulates the decline in ΨT˙H as target velocity increases (>3°/s) across all the background conditions used (both in normals and in patients). It also largely parallels the decline in gain of the pursuit eye movement. Both effects are brought about mainly by the velocity saturation characteristics of the visuomotor pursuit system (in *box PUR*).

For the responses obtained with the 0.2- and 0.05-Hz stimuli, we would like to point out that there is a clear perceptual overestimation already in the 'normal' situation of a stationary background (BS=0°; *panel c* in the figures), although this is small in terms of absolute velocity (see abscissae). In contrast, gain of the pursuit eye movement tends to show a slight decrease. These effects stem from the fact that the eye movement, when crossing the stationary background, creates an opposing background-to-eye signal (b˙e). The increase in perceptual gain originates from the negative T˙E feedback and the boosting of the t˙h signal. This boosted t˙h signal is responsible for suppressing the opposing b˙e signal at summing junction A and thus reducing any effect of the background on pursuit eye velocity.

The findings in the other stimulus conditions can be explained in an analogous way. In the condition BS=TS (Fig. 6b), the gain of the predicted ΨT˙H corresponds

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[1] We like to mention that it is not clear at present whether the gain boost of the premotor signal of target pursuit is implemented in the brain in the form of an internal positive feedback loop. However, we hold that our arguments and our view would apply also to other forms of such a gain boost, given they are functionally equivalent to the one assumed here

closely to that of ocular pursuit because there is no opposing background signal. When the background moves in the opposite direction to the target (BS=–TS; Fig. 6d), predicted $\Psi T^{\cdot}H$ is raised even further than for BS=0° because the opposing background signal is twice as large. In contrast, when the background moves in the same direction as the target at twice the speed (BS=2×TS; Fig. 6a), the gain of $\Psi T^{\cdot}H$ is less than that of pursuit, as found experimentally, because the background motion is no longer opposing but acting synergistically.

The same mechanism can also explain the illusory target velocity perception in 'Duncker's condition' and the very low eye velocity gain (see simulation results in Fig. 6e). Qualitatively, at least, a summation of the Duncker's effect with the curves in *panel b* (no TB motion) yields the findings in *panels a*, *c* and *d*, in line with the corresponding statistics given in the Results. However, it is evident that the summation hypothesis does not apply so well in *panel a* (background motion double of TS); there the background effect at low frequency/velocity is more pronounced than expected from a simple summation in both the predicted and experimental data (Figs. 6a and 2a, respectively). This appears to result from the non-linear velocity saturation characteristics of visual feedback operating within a closed-loop system.

Noticeably, the estimation curves obtained in the 'dark' condition (Fig. 6f) are similar to those in the 'background-stationary' condition, rather than resembling the ones in the 'background-with' condition where there is no relative background motion. We therefore asked our subjects retrospectively to describe their experience in the dark condition. They reported that they saw the target as moving with respect to a 'dark background' which they experienced as stationary. This led us to assume that, perceptually, perceived target motion always tends to be related to a reference and that here, in the absence of a visual one, an internal notion of space is taken as a default reference. In the simulations we therefore represented this by a stationary visual background.

Our study also aimed to test the possibility that the perception of target velocity contains a considerable contribution from CV which might result from the optokinetic stimulus (background-to-head motion). We accounted for this possibility by having our subjects estimate target velocity in space, by using sham trials with actual body rotation, and by having subjects estimate self-motion in space. Furthermore, we included vestibular loss patients into the study, having learned in pilot experiments that they show a strong tendency to experience CV with the stimuli used.

Our normal subjects did not experience CV in these experiments, at least consciously (see Discussion of experiment 2). In contrast, the patients experienced CV with the 0.05- and 0.2-Hz stimuli; this occurred consistently in the BS=TS and BS=2×TS conditions, less consistently in the BS=–TS condition and not at all in the BS=0°/s condition (Fig. 4c). We explained the difference between normal and patients with a vestibular-visual interaction mechanism for self-motion perception, which is missing in the patients (see Mergner et al. 2000b). As shown in the Results, patient's target velocity estimates essentially reflect the sum of an estimate of TS that is similar to that of normals and their CV. We corroborated this notion by adding to the $\Psi T^{\cdot}H$ in our model (Fig. 5a) a corresponding CV component, yielding simulation results for patients that closely resembled the experimental ones (*dotted estimation curves* in Fig. 6a–f).

We legitimised this approach by referencing the model to space (instead of to the head). In fact, in our original model of pursuit eye movements (Schweigart et al. 1999), pursuit was referenced to space (gaze pursuit) by including head-in-space movements and the VOR. In the model, pursuit overrides not only the OKR, but during superimposed head rotations also the VOR. (N.B. This applies to low frequencies/velocities, while at high frequencies/velocities the VOR takes over.) The space-referencing of the model in Fig. 5a is indicated by *grey symbols*. In this extended model, externally a head-in-space velocity ($H^{\cdot}S$) is added to the eye-in-head velocity and internally a corresponding VOR premotor signal is subtracted ($h^{\cdot}s$, to yield a compensatory response to $H^{\cdot}S$; the vestibular system, and other VOR-related aspects are omitted here for clarity)[2].

Noticeably, the presence of head velocity signals in the mechanism is another important reason for only boosting the gain of the selected target feedback, since all the attributes that are common to pursuit, such as prediction, velocity saturation, etc. that are also seen in VOR suppression are then explained without having to invoke another similar mechanism for VOR suppression (see Barnes and Grealy 1992 or Barnes 1993 for an explanation of this). $\Psi T^{\cdot}S$ (formerly $\Psi T^{\cdot}H$) then contains a component that reflects the rotation of the head in space, as repeatedly shown before (see, for example, Mergner et al. 1992). Correspondingly, an estimate of head-in-space rotation ($\Psi H^{\cdot}S$) is added to $\Psi T^{\cdot}H$, here in the form of the CV of the patients.

Experiment 2: position reproduction

Since velocity is nothing else but the change of position over time, one might expect that also the target velocity percept shows a simple relation to perceived target position. However, as mentioned in the Introduction, there appears to exist a clear dissociation between the two percepts in the presence of a moving background ('object motion paradox'), which led us to measure the target position percept for comparison.

Materials and methods

Stimulus presentation

Stimulus combinations were the same as in experiment 1, except that the 2° amplitude stimulus was omitted. Also stimulus presentation was similar, with two exceptions:

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[2] Note that for simulations of the VOR in complete darkness not only the boxes PUR and OKR have to be disabled, but also PUR'

1. Target presentation at the onset of each trial was not centred at subjects' straight ahead position, but was varied randomly within a range of ±12° with respect to this position.
2. The periods with stationary target prior to, and immediately following the target motion stimulus lasted 1.6 s; during these periods subjects were to store target start and end position into memory. These periods were preceded and followed, respectively, by dark periods (3 s) during which target and background positions were randomly varied to prevent carry-over of relative (target with respect to background) and absolute (target and background with respect to subject and space) position information.

Reproduction procedure

Following the stimulus presentation, the target and the background reappeared at random positions and subjects reproduced start and end position of the target in space from short-term memory ('*intrasensory delayed match-to-sample*' task; cf. Fig. 7). Reproduction was performed with the same light spot that earlier had served as target. To this end, subjects adjusted the turning knob of a hand-held remote control (which had neither a mechanical stop nor any other tactile landmarks and therefore delivered no position cues; visual control of knob was excluded, see precautions in experiment 1). The signal was fed into the galvanometer that was used to control target position. The galvanometer received, in addition, a computer-generated signal for stimulus presentation. As shown before (Maurer et al. 1997; Mergner et al. 2001), this reproduction procedure allows intrasensory matching without considerable distortions by subjects' sensory-to-motor transformation and motor performance.

Reproduction of target start position and end position was performed during the same trial. There were two series. In one, first the start and then the end position was reproduced. In the second series, the order of reproduction was reversed. A total of 432 trials were presented, with the two series and two repeats of the 108 stimulus combinations (6 background conditions × 3 frequencies × 3 amplitudes × 2 directions). They were presented over several sessions on different days, randomly alternating between the two series. The position experiments were interleaved with the velocity estimations of experiment 1.

Recording and evaluation

Position readings of target (galvanometer output), background (potentiometer of pattern projector) and remote control (potentiometer) were sampled at 100 Hz and stored in a laboratory computer for off-line analysis. Start and end positions of the target during stimulation and during the response were evaluated by an interactive computer program (cf. Maurer et al. 1997). The difference between stimulus and response data yielded measures of signed position errors (in degrees; positive/negative sign, error in same/opposite direction as target motion). The responses for leftward and rightward target motion showed no statistically significant differences and therefore were pooled.

Self-motion perception

After subjects had delivered the target position estimates, they were asked whether or not they experienced self-motion during the preceding stimulus presentation; no attempt was made to quantify the magnitude of perceived self-motion.

Results

An instructive example of a normal subject's reproduction responses is shown in Fig. 7. In this example, target motion (4° at 0.05 Hz) is to the right (upward) with respect to the start position (*s* in Fig. 7) and is associated with a background motion to the left (downward) of the same amplitude ('background-counter' condition, BS= –TS). After a poststimulus dark period in which target and background positions were varied (*a*), the subject first reproduced target start position in space (Ψs'). He set the target too far to the left by an amount similar to the background displacement. After another dark period (*b*) with further random changes of background and target positions, target end position (*e*) was reproduced rather accurately (Ψe'). Thus, noticeably, the subject's short-term memory of target start position was affected by the background motion, unlike that of target end position.

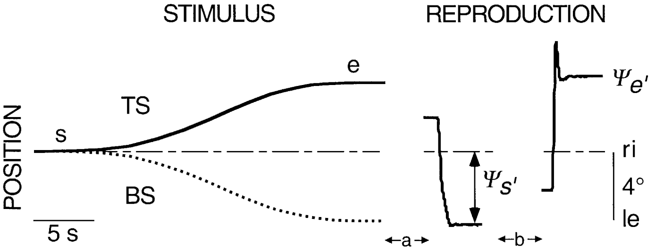
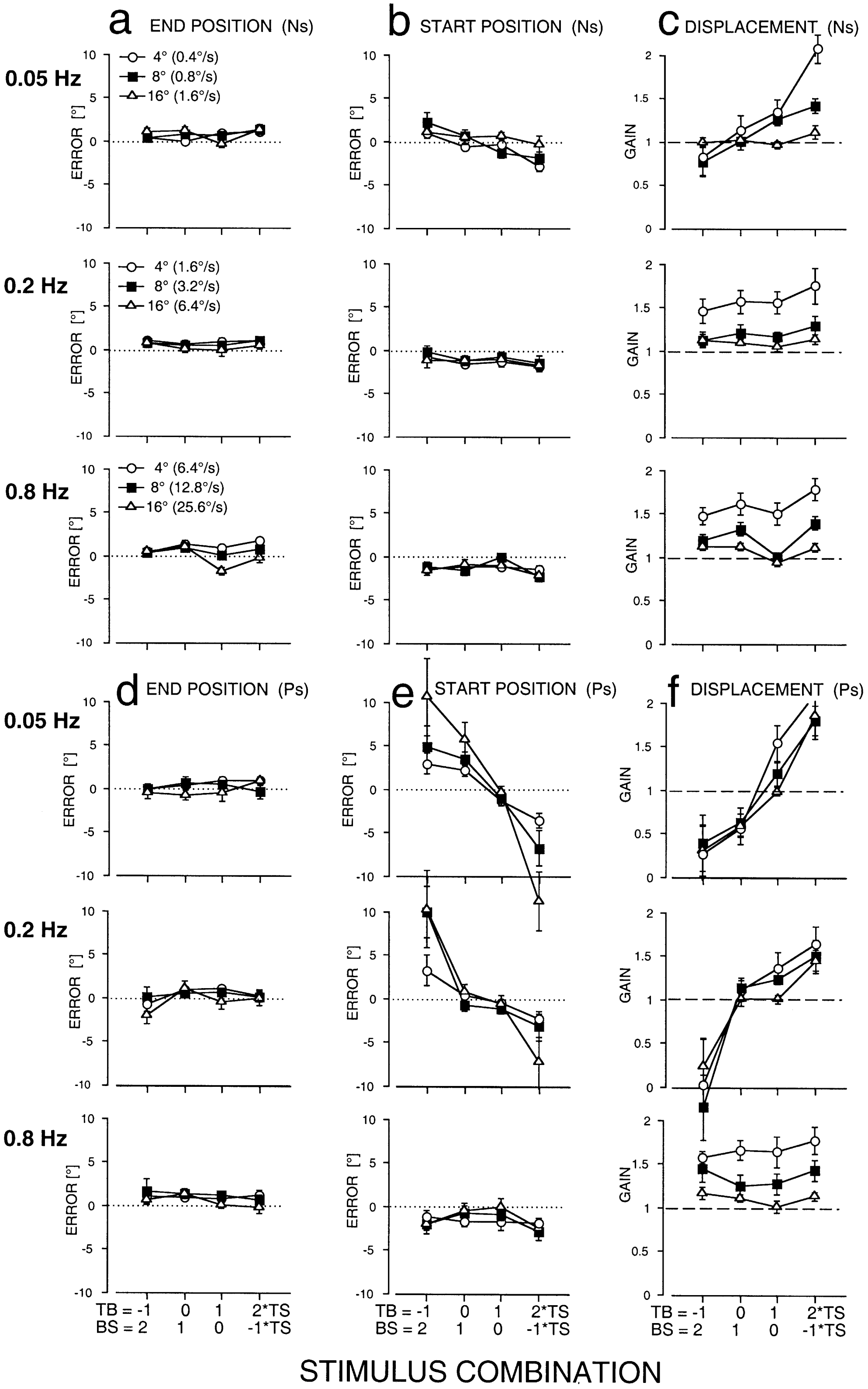


Fig. 7 Example of reproductions of target start and end position from a normal subject. During stimulus presentation (*STIMULUS*) target in space (*TS*) was moved within 20 s from a start position (*s*) by 4° to an end position (*e*) to the right (upward), while the background simultaneously was moved to the left by the same amount. After achieving the new positions, target and background were extinguished. During this dark period (*a*) their positions were randomly varied, independently of each other. Then they reappeared (background always stationary, omitted), indicating the beginning of the reproduction period (*REPRODUCTION*). The subject shifts the target, by means of a remote control, first to its remembered start position (Ψ*s*'). There follows a second dark period (*b*), again with random changes of target and background positions, after which the subject shifts the target on the remembered end position (Ψ*e*')

The averaged results across all normals and trial repeats are given in Fig. 8a, b. The figure gives the means of the signed errors (±SE) for end position and start position as a function of stimulus combination. Mean reproduction of end position (Fig. 8a) showed no variation in relation to background motion. It was rather accurate, apart from a slight offset which was independent of background motion, stimulus velocity and frequency (ca 1°, on average, in the direction of the target motion). Mean reproduction of start position (Fig. 8b) showed an offset of similar magnitude (ca –1°), but counter to target motion. In addition, it showed a small background effect. To better visualise this effect, we calculated from the difference between end and start positions a measure of perceived target displacement and expressed it in terms of displacement gain curves (Fig. 8c). The slopes of these curves represent the basis for comparison with the previous velocity data (cf. Fig. 4a). The slopes can be viewed as 'gain' of the effect of background motion on target displacement perception across the different stimulus combinations.

Fig. 8 Estimates of target end position (**a**, **d**) and start position (**b**, **e**) as well as displacement gain values derived thereof (**c**, **f**) of normals (*Ns*; **a–c**) and patients (*Ps*; **d–f**; means ±1 SE). The data are plotted across different background motion conditions (abscissae as in Fig. 4), separately for the three stimulus frequencies used. Estimated position values in **a**, **b** and **d**, **e** are given in terms of signed errors (in degrees) for the three different target displacements (i.e. the difference between stimulus start and end positions, 4°, 8°, 16°; as indicated). Displacement gain values in **c** and **f** were calculated by relating estimated to actual target displacements. **a**, **d** Reproduction of end position is essentially independent of background motion, both in normals and patients, but shows a slight constant offset in the direction of target motion (positive sign), on average. **b**, **e** Reproduced start position is modified by the background at low frequency (0.05 Hz in normals and, more pronounced, at 0.05 and 0.2 Hz in patients), with errors in the direction of background motion in space (*BS*, see abscissae). In addition, there is a small offset of the responses counter to the direction of target motion (negative sign), most evident at 0.8 Hz in both normals and patients. The offsets also show in the displacement gain curves (**c**, **f**), with the frequency-dependent background effect (slopes) superimposed



These curves exhibited slopes related to background motion only at 0.05 Hz, and this only for the 4° and 8° stimuli (slopes, 0.45 and 0.38, respectively; they were significantly greater than zero, $P<0.003$). For all other stimulus parameters (16° stimulus at 0.05 Hz and all stimuli at 0.2 and 0.8 Hz) the slopes in the displacement data were not significantly different from zero.

Another difference between velocity and displacement data concerns the responses to the high as compared with the low frequency/velocity stimuli. While the gain of the velocity perception dropped with increasing frequency/velocity to a value of less than 0.4 with the 0.8 Hz/16°/25°/s stimulus (Figs. 2a–d, 4a), the gain of the displacement perception for this stimulus remained close to unity (Fig. 8).

Patients' reproduction curves for target end positions (Fig. 8d) were very similar to those of normals. However, there was a clear difference in their reproduction of the start position at 0.05 and 0.2 Hz (Fig. 8e). The latter showed a clear background effect, as evident also in the corresponding displacement gain (Fig. 8f). Statistically, patients' data showed significant background effects on target start position and on the displacement gain at 0.05 and 0.2 Hz ($P<0.035$).

Offsets of start and end positions similar to those described for all other conditions were also observed in the dark condition (average in normals, –1.51° and 1.16°; patients, –1.15° and 1.06°, respectively). Only in the Duncker's condition (TS=0°/s) these offsets were clearly smaller (0.53° and 0.24° in normals and –0.34° and 0.08° in patients, respectively). In the latter condition, the background effect on the reproductions of start and end position was negligible at 0.8 Hz, while it was present for start position, unlike for end position, at 0.05 and 0.2 Hz (averages, 1.97° in normals and 5.24° in patients). From this we conclude that the background effect was again rather small in normals, but pronounced in patients.

When indicating presence or absence of self-motion perception after each trial, patients reported CV at 0.05 and 0.2 Hz in those stimulus combinations in which the background was rotated in space, whereas at 0.8 Hz they always considered themselves stationary. In contrast, normals always considered themselves stationary, as in experiment 1.

Discussion

These results confirm our notion that target position perception is distinct from the corresponding velocity perception, in that it does not show the decline in gain at high frequency/velocity that was observed with the velocity estimates and in that it is essentially veridical during background motion. The fact that the decline at high frequency/velocity was missing accords with the difference between the control of eye position and that of smooth eye velocity during pursuit. At frequencies of 0.8 Hz and above, the smooth eye velocity gain decreases, but the saccadic system maintains position control so that eye displacement gain remains close to unity even with considerably higher target frequencies (see Barnes 1993).

More important is the finding that the perception of target end position is not affected by the background motion, and this also at low frequency/velocity. It is essentially veridical in both normals and patients, except for the small constant offset in the direction of target motion, which is in the order of the accuracy of the stored eye position signal of approximately 0.8° (see Mergner et al. 2001). We deem it unlikely that this finding is related to the psychophysical procedure we used (retrospective indications, possibly allowing for some cognitive corrections), since a similar finding has been reported before with a concurrent indication procedure (see below). Rather we assume that the position perception is correct because it builds primarily on an internal position signal of the eye movements, which is largely freed from the background effect by the pursuit velocity control described above, and a retinal position error signal of the target.

There remains to be explained the effect of the background on perceived target start position. The effect was present in normals only at 0.05 Hz, but clearly more pronounced and extending to 0.2 Hz in patients. In patients the slopes of the estimation curves were clearly centred at the BS=0° condition (Fig. 8c), which we take to indicate that the effect is brought about by the CV they experienced (i.e. when reconstructing target start position in space, they combined the estimate of target-to-head displacement with one of a head-in-space displacement). The much smaller effect in normals at 0.05 Hz also appeared to be centred at the BS=0° condition (Fig. 8b). Correspondingly, we assume that there was an effect of CV also in normals at 0.05 Hz, although very small and not consciously perceived (despite an occasional uncertainty at this frequency, normals considered themselves as stationary during the stimuli).

To confirm the conclusions reached so far, we simulated normals' results of Fig. 8c by deriving from the pursuit model in Fig. 5 an eye position signal (by mathematically integrating the $\dot{e}h$ signal) and by adding a retinal target position error (assumed to have ideal transfer characteristics); an essentially veridical perception of target position resulted. This concept accords with Helmholtz's (1962) theory concerning the use of efference copy information to preserve the stability of the visual world during saccades. When adding to it the weak subconscious CV effect and the constant offset signals observed in the experimental data, gain estimation curves very similar to those in Fig. 8c resulted (not shown).

Our notion of a veridical percept of target position is supported by the findings of Smeets and Brenner (1995). These authors had their subjects trying to hit a virtual spider while this moved across a moving background. They found that background motion did not affect target hitting position to any considerable degree, but it did affect the arm movement velocity.

General discussion

Our findings shed a new light on visual perception of target motion and its linkage to pursuit eye movements. In particular, the successful description of the findings in the form of a dynamic model allows us to relate the perceptual phenomena to properties of the eye pursuit control mechanism (see Discussion of experiment 1). In the following we briefly consider how these findings relate to earlier psychophysical work on pursuit-contingent target motion perception, restricting ourselves to studies which considered an eye movement efference copy a decisive constituent of the perception. We then suggest possible reasons for the background effect on perceived target velocity, before addressing the background-related dissociation between target velocity percept (erroneous), on the one hand, and position percept and motor performance, on the other hand (essentially accurate; ‘action-perception dissociation’).

Efference copy in pursuit-contingent target motion perception

There is an enormous amount of psychophysical literature on this topic, which is, however, very inhomogeneous in many details concerning mainly the methodological approach. Yet, most of these studies appear to agree on an under-representation of the eye movement in the efference copy signal for the perception (it is considered to have a gain clearly below unity; for a review, see Bridgeman 1995). A previous study which comes closest to ours in its methodological approach stems from Pola and Wyatt (1989). These authors related perceived target motion in an open-loop condition, where the retinal slip was zero, to that in a closed-loop condition during oscillatory pursuit at 0.5–2 Hz. The differential gain measured in the open-loop condition at 0.5 Hz was in the order of 0.82 and continuously decreased at higher frequencies (along with the eye movement amplitude). These authors agreed with the previous notion of the efference copy having a gain <1, but we would conclude from their and our data that at lower frequencies/amplitudes its gain would approach unity (this applies in our model of Fig. 5a not only to the gain of e˙h, but also that of e˙h'). In fact, most of the previous work was performed in a frequency/velocity range where target velocity perception was affected by the limited dynamics of the pursuit system in our study.

It should be noted, however, that the target motion perception in our model (Fig. 5a) is not directly derived from the oculomotor efference copy (e˙h), but from a source (t˙h*) that also yields the premotor drive signal specific for target pursuit (e˙h'). The evidence for this is that e˙h' incorporates the background effect seen with the perception, unlike the e˙h signal and the evoked pursuit velocity. Only when there is no relative background motion, i.e. when the background is moving in fixed register with the target, becomes e˙h' equal to e˙h. This relation between the perception and the e˙h signal becomes more explicit when the model of Fig. 5a is transformed into a topologically slightly different, but functionally equivalent form (Fig. 5b). In this form, the t˙h* signal, from which both e˙h' and the perception are derived, results from e˙h–b˙e. Equivalence with the other version is given, since e˙h=t˙h+b˙e (at summing junction A), so that t˙h* equals t˙h. In this version it is also quite evident that both e˙h' and the perception contain the background effect (in the form of –b˙e) and that by this the e˙h signal is essentially freed of it at summing junction A.

Possible reasons for the background effect on perceived target velocity

In the mid- to low frequency and velocity range, perceived target velocity accurately reflects the actual target velocity only in situations where the background is moving with the target, while in all other situations it is ’distorted’ in the way described. As mentioned before, this also applies when the background is stationary (overestimation, although small in absolute terms). It raises the question why the system is not optimised (i.e. perceptually appropriate) for the overlearned condition of a stationary background. In other words, why is the target velocity control not freed of the background effect in some other way, for instance by suppressing the background signal early at the input site. We cannot give a definitive answer, but conceive of the following explanation. We assume that it is of high behavioural relevance to have the retinal signals from other, non-target visual stimuli continuously available at high perceptual levels. This allows us to make those stimuli the pursuit target at any moment when appropriate. In the model, such a switch to pursue the background rather than the target would be obtained by boosting the gain associated with the background rather than the target. In contrast, a suppression of non-target retinal signals would restrict the behavioural flexibility of the system, whereas the envisaged mechanism has this flexibility.

Action-perception dissociation

Consider again the Duncker situation: the eyes are kept quite well on the stationary target, although this is perceived as moving. Observations of such dissociations are occasionally taken to postulate that action and perception are represented in the brain in separate control systems (see, for example, Bridgeman et al. 2000). Our findings point to just the opposite: in our concept the background effect in target velocity perception reflects the mechanism by which eye pursuit is largely freed from this effect. Thus, although phenomenologically showing a clear dissociation, action and perception are intimately interrelated in this concept. We assume, in fact, that the perception is linked to the attention and effort required to produce the appropriate action (by assuming that a high level of attention and effort is required to bring the gain of the t˙h* signal in our model close to unity).

Having eye pursuit velocity largely free of the background effect and the saccadic system coping with remaining position errors and the limited dynamics of the pursuit system, eye position overall is always rather accurately reflecting target position, at least for frequencies below ca 1 Hz (Barnes 1993). Correspondingly, an efference copy of eye position can be taken to yield an essentially veridical estimate of target position and to use this signal for the control of other visuomotor tasks, for example arm movements in the spider hitting task mentioned above (Smeets and Brenner 1995). Future experiments will have to show whether our concept can be extended so as to explain, in addition to this action-perception dissociation, the perceptual 'incongruencies' associated with target pursuit mentioned in the Introduction (Filehne illusion, partial loss of background position constancy) and possible effects when attention is dissociated from target pursuit (for example, by having subjects estimate background motion during target pursuit, as was done in some of the earlier psychophysical studies).

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