NEW RESULTS IN MOTION CONSTANCY DURING SMOOTH PURSUIT EYE MOVEMENTS

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Abstract. Smooth pursuit eye movement adds a velocity field to the retinal image, in the direction opposite to that of the eyes. To correctly perceive the physical motion of objects, the visual system has to compensate for this self-induced motion. Compensation is usually assumed to involve combining the retinal signal with an extra-retinal estimate of eye velocity. How are these signals combined? According to the linear model, the estimated eye velocity is added to the retinal signal and the resulting motion is perceived as the physical motion of the stimulus. The linear model has largely been supported by studies using collinear motion, and velocities close to the pursuit target velocity. Furthermore, the pursuit target has typically been available as a visual referent, allowing the observer to judge object-relative rather than absolute motion. Because the movement of the pursuit target is generally similar to that of the eyes, such object-relative information would yield an egocentric bias in the responses. We studied the compensation problem using stimuli moving in different directions and with a wide range of speeds. Furthermore, we eliminated the pursuit target as a visual referent by relying on residual smooth eye movement after the pursuit target is extinguished. If we fit the linear model to our data, we obtain an extraretinal gain of 0.4, which is in agreement with the eye velocity underestimation reported in the literature. However, we find that compensation for eye movements varies dramatically as a function of retinal motion along the axis of eye movement: retinal motion is compensated when it is in the opposite direction as that of the eyes, but is perceived largely uncompensated for motion on the retina in the same direction as pursuit. These results contradict the linear model, and suggest that the compensation depends not only on the eye movement but also on retinal information such as the direction and speed of the stimulus. Thus, our data challenge the classical view that compensation is derived solely from extraretinal sources. We suggest instead that retinal motion is compensated by an eye movement estimate derived from a combination of extraretinal and retinal signals, the latter based on an assumption of target stationarity.

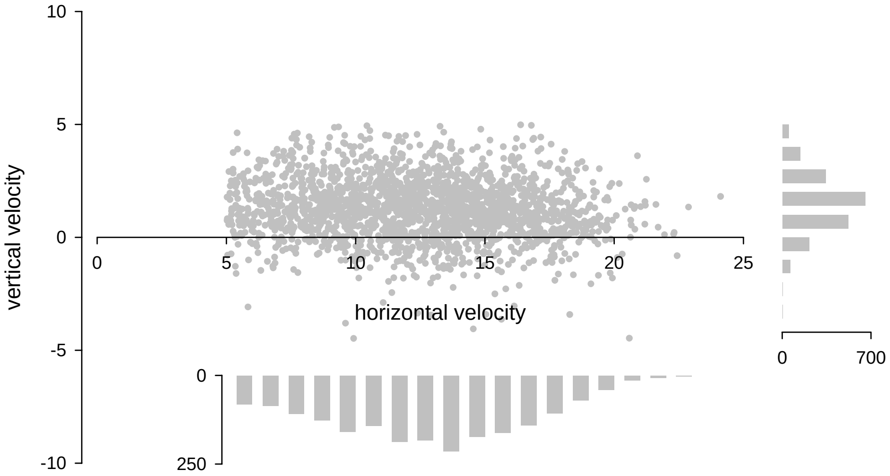

Figure 1. Vertical and horizontal eye velocities for each trial and their distribution. The clear cuts are due to selection conditions applied to the trials.

The general idea of our protocol is as follows: subjects pursued a target dot moving at 20°/s. After a variable duration, this target dot didappeared and the stimulus dot appeared moving in one of the variable directions from 5° to 75° with a speed between 5°/s and 72°/s during 100 ms. The stimulus motion was pratically defined by its horizontal and vertical speeds. The horizontal speed ranging from $-60°$/s to $+60°$/s and the vertical one from 0°/s to 40°/s. Motion in the pursuit direction is positive. During the presentation of the stimulus dot the eyes kept moving horizontally with a decent gain during the 100ms of the presentation of the stumulus as shown Fig. 1. The subjects task was to report the perceived direction of the stimulus dot by ajusting a line on the screen.

The geometrical conséquences of pursuit on the projection of non-collinear motion in the retina is shown Fig. 2. The figure also shows the predicted responses of the classical linear model in case of perfect compensation and in case of incomplete compensation.

The results are shown in Fig. 3. This diagram shows, for the different conditions of stimulus velocities, the direction of the stimulus on the screen (in red), the direction of the retinal image of the stimulus averaged between subjects (in blue) and the response averaged between subjects (in grey). A general tendency emerges from those results : when the stimulus moves opposite to the eyes (left part of the figure) the response is very close to the direction of the stimulus on the screen,

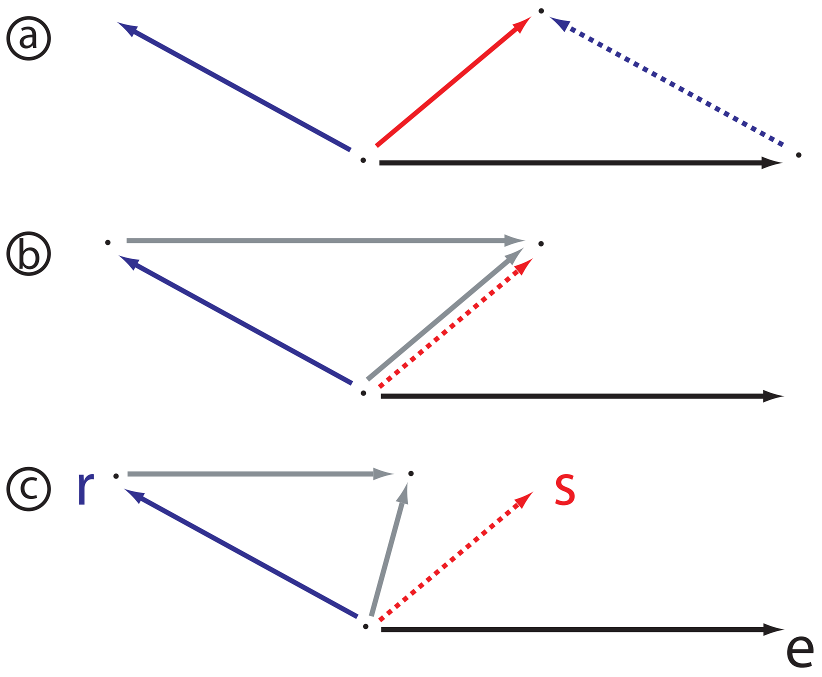

Figure 2. When we make a pursuit eye movement, the image on the retina undergoes a shift in the direction opposite to that of the eyes. Because of this geometrical modification, the angle of an object on the screen is different from its angle on the retina: a) Directions of the stimulus on the screen (s, in red) and corresponding retinal image (r, in blue) for a given eye movement (e, in black). b) Representation of perfect compensation, the visual system adds the eye velocity to the retinal projection (horizontal grey vector), and recovers the real direction of the stimulus on screen: the perceived direction (oblique grey vector) equals the real direction on the screen. c) Consequences of undercompensation, if the visual system underestimates the eye velocity, the perceived direction lies between the real direction on screen and the direction on the retina.

on the other hand, when the stimulus moves in the eyes direction, the response is much closer to the retinal direction. This general tendency is visible for all vertical velocities (vy). The visual system compensates more when the stimulus moves on the opposite direction than the eyes

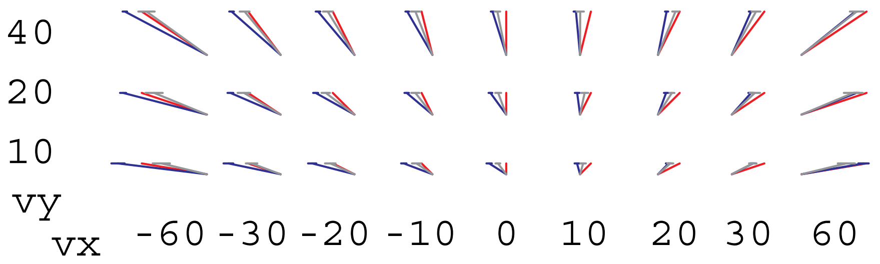

FIGURE 3. Angular responses in pursuit averaged across subjects (7) for the different conditions of horizontal and vertical stimulus velocities. The red line indicates the stimulus direction on screen, the blue line is the orientation of the retinal projection path, and the grey line is the perceived direction averaged across subjects. We can notice a general tendency in the responses, the faster the stimulus moves in the opposite direction than the eyes, the stronger is the compensation: the reponse direction is very close to the retinal direction in the right part of the figure and very close to the direction on the screen on the left part.

(backward) than when it moves with the eyes (forward). In terms of the classical linear model, it means that the eye velocity is estimated correctly or even overestimated (extraretinal gain κ around 1) when the stimulus moves opposite to the eyes and decreases toward 0 when it moves in the pursuit direction.

A first step to explore this theory of the influence of retinal velocity is to evaluate the influence of the stimulus parallel speed on the retina on the extraretinal gain κ. We separated the data in 7 subgroups of trials depending on the parallel retinal speed. The linear model was fitted for each of these subgroups. The function fitted derived from the general equation of the linear model:

$$\begin{aligned} p_x &= r_x + \kappa e_x \\ p_y &= r_y + \kappa e_y \end{aligned} \tag{1}$$

Thus, if θ' is the predicted response angle :

$$\theta' = tan^{-1} \frac{s_y + (\kappa - 1)e_y}{s_x + (\kappa - 1)e_x} \tag{2}$$

The κ's were estimated by fitting function 2 to the data by subgroups and then comparing the predicted θ' to the real response direction θ. The trials influence on the fit was weighted by the perceived speed.

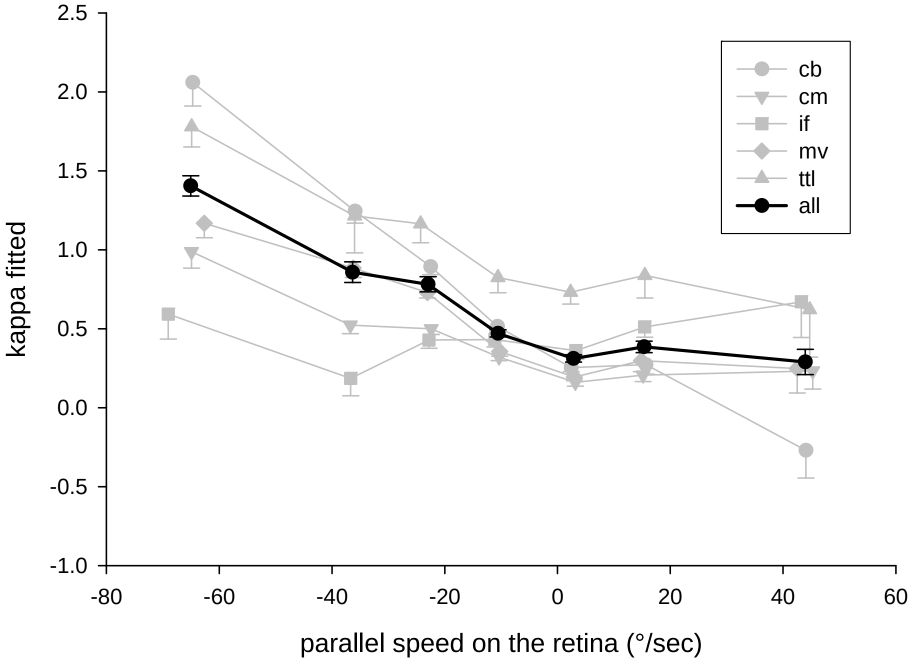

FIGURE 4. Influence of the retinal parallel speed on the values of κ obtained by fitting the linear model weighted by the values of the perceived speed (model 2). The κ values decrease as the retinal parallel speed increases. This effect is true for all subjects except one, and is visible when the model is fitted on the trials for all subjects. Error bars represent bootstrap calculated standard deviations.

Indeed, if we hypothetize a gaussian noise on the perceived direction of motion (resulting from noise on the perceived direction on the retina and on the estimated eye velocity) the resulting uncertainty on the response direction will be higher for trials with a slower perceived speed. It should be noted that we performed the fits weighted and non-weighted and that the we get the same qualitative influence of retinal parallel speed on the κ's. The resuting fitted κ's for the 7 subgroups of trials are shown in Fig. 4.

Here we can see that the extraretinal gain decreases when the retinal velocity increases (for 4 subjects on 5).

The influence of the retinal speed of the stimulus on the eye velocity estimation contradict the linear model where the eye velocity estimation is dependant only on the eye velocity (κ is constant).

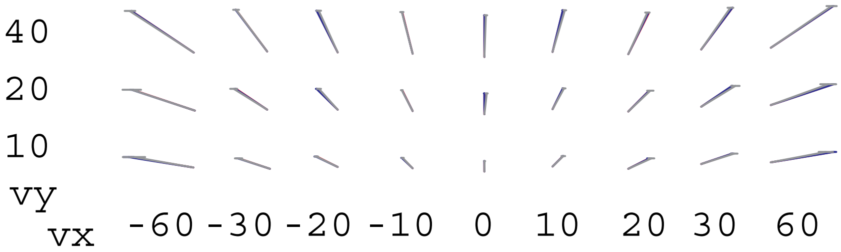

Figure 5. Angular responses in fixation averaged across subjects (2) for the different conditions of horizontal and vertical velocities. The red line indicates the stimulus direction on screen, the blue line the orientation of the retinal projection's path, and the grey line the perceived direction averaged across subjects.

To ensure that this effect of retinal speed is not the reflect of a simple response bias we run a control experiment in fixation. Indeed, the general tendancy in the response could also be viewed as an "attraction" toward the vertical. This bias toward the vertical could arise if the subjects reponses were more vertical than the perceived direction, or if they tended to perceived directions more vertical than they are on screen.

To test the existence of such a bias we run a control experiment similar to the main experiment except for the eye movements. Subjects were fixating a stationnary dot while the stimulus (same stimulus conditions as in the main experiment) was presented, then they reported the perceived direction. Results in this condition (shown in Fig.5) does not show any special bias, the subjects are very accurated in reporting the stimulus direction.

Several explanation can be proposed to account for our results.

1) One of them is that the stimulus dot does not have the same status when it goes forward or backward. When it goes forward, the visual system might consider that it is a tracking target and could keep the information on the motion of the dot in retinal coordinate which are more usefull to program eye movements. On the other hand, when the stimulus moves backward, it could be considered as a normal background dot and the transformation of coordinate (the compensation) would normally operate.

2) The second interpretation is that the retinal slip is used by the visual system (in addition to the extraretinal information) to evaluate the eye velocity, in combinaison with an hypothesis of stationnarity

of the background. When the stimulus moves in the same direction as the eyes, the effective retinal slip would be much slower than the expected one. In this case, the visual system might correct its extraretinal estimation of the eye velocity by taking into account this retinal information, considering that the eyes are moving slower. It would then compensate for this new value of eye velocity, and the angular responses would be very close to the retinal direction, as has been found. On the other hand, when the retinal sleep is fast on the opposite direction than the eyes, the visual system would estimate the eye velocity as faster than the one indicated by extraretinal signals, and then compensate more.

We conducted an additional experiment to test those two hypothesis. The results show that the second interpretation is more likely.