

## RESEARCH ARTICLE

Claudio de'Sperati · Natale Stucchi

**Visual tuning to kinematics of biological motion: the role of eye movements**

Received: 17 October 1994 / Accepted: 20 March 1995

**Abstract** The visual system is particularly sensitive to the covariation between velocity and curvature that constraint biological motion. Previous work showed that, when this biological constraint is satisfied, simple elliptical motion of a dot looks constant, although its velocity is highly non-uniform. This paper addresses the hypothesis that such a dynamic illusion is dependent upon smooth pursuit eye movements. Subjects had to adjust the kinematics of a dot moving along elliptical trajectories until they perceived a constant velocity. Different pursuit and fixation conditions were tested. The research shows that the dynamic illusion is largely independent of eye movements, suggesting that the visual system has access to implicit knowledge of motor constraints regardless of the concurrent oculo-motor commands.

**Key words** Perceptuo-motor interactions · Eye movements · Visual perception · Implicit knowledge · Motor control

**Introduction**

In their general form, motor theories of perception claim that our perceptual systems take into account some features of the motor system. It is known, for example, that the visual system is particularly well attuned to human movement (Johansson 1977; Cutting 1981), and it has been suggested that unlearned motor schemata interact with visual processing (Bertenthal et al. 1987). In particular, the hypothesis that our visual system is constrained by implicit knowledge of some human motor capabilities has been put forth (Beardworth and Bukner 1981; Shiffrar and Freyd 1990; Viviani and Stucchi 1992).

A principle common to both motor and visual systems is the relationship between geometry and kinematics of movement. The human motor system cannot produce spontaneous movements in which curvature and velocity are independent (Viviani and Terzuolo 1982; Viviani and Schneider 1991). Instead, these two parameters covary, and in simple movements like drawing ellipses, their relationship is well described by the empirical relation

$$A(t) = KC(t)^{1-\beta} \quad (1)$$

where  $K$  is a constant which depends on the type of movement. This equation implies that the angular velocity  $A(t)$  and the curvature  $C(t)$ , which are logically independent parameters, are in fact strictly related. Such a relationship has been termed the two-thirds power law because in adults the exponent  $\beta$  is close to  $1/3$  (Viviani and Terzuolo 1982). The skeletomotor system cannot escape this rule even in a reflex-like movement such as oculo-manual pursuit tracking, in which the velocity of the moving target largely departs from that prescribed by the two-thirds power law (Viviani and Mounoud 1990). This result excludes the higher level of motor programming as the source of this constraint. On the other hand, on both theoretical and experimental grounds (Viviani and Terzuolo 1982; Massey et al. 1992), a peripheral biomechanical on-line origin of this constraint has been excluded. Therefore, it appears that the two-thirds power law is embodied in the intermediate stages of our motor neural circuitry.

The visual system is particularly sensitive to covariation between velocity and curvature. In a recent experiment (Viviani and Stucchi 1989), a dot was moved along a circular trajectory with a velocity that decreased at around 3 o'clock and at around 9 o'clock. The deceleration was the same that would have been necessary to trace a horizontal elliptical trajectory with a kinematics specified by the two-thirds power law. Under this condition, the subjects perceived an elliptical path, as if the geometry of the figure defined by the

C. de'Sperati (✉) · N. Stucchi  
Dipartimento di Psicologia, Università di Torino,  
via Lagrange, 3, I-10123 Turin, Italy;  
Tel.: +39-11-549475/Fax No.: +39-11-549653/  
E-mail: DESPERAT@PSYCH.UNITO.IT

moving dot were influenced by some implicit knowledge about the kinematic rules.

This suggestion is further supported by another experiment reporting a novel dynamic illusion (Viviani and Stucchi 1992). The perceptual task consisted in producing a constant-velocity motion of a dot moving on elliptical trajectories. Velocity was perceived as constant only when velocity and curvature covaried accordingly to the two-thirds power law rule; yet, this condition corresponded to an objective highly non-uniform velocity. Taken together, these findings have led to the hypothesis that the visual system has access to an internal representation of movement of which the two-thirds power law is one operating rule.

How does the visual system acquire such sensitivity to the regularities expressed by the covariation between geometry and kinematics? We can conjecture that the visual system has access to the constraint-related information through a readout of the motor commands. Actually, the above-mentioned dynamic illusion is accompanied by smooth pursuit eye movements (Viviani and Stucchi 1992). These may convey the motor information used by the perceptual system in order to formulate the constant-velocity estimate and hence could be responsible for the illusion. The present study is aimed at verifying whether the misperception of constant velocity depends on a readout of smooth pursuit oculomotor commands. The strength of the illusion has been therefore assessed in conditions where no eye movements were allowed.

## Materials and methods

### Subjects

Thirty-one undergraduates plus five members of staff (23 men and 13 women) participated in the experiments. They had normal or corrected-to-normal vision and were unpaid volunteers. Out of these, 22 subjects took part in the first experiment (experiment 1) and 14 in the second one (experiment 2).

### Stimuli

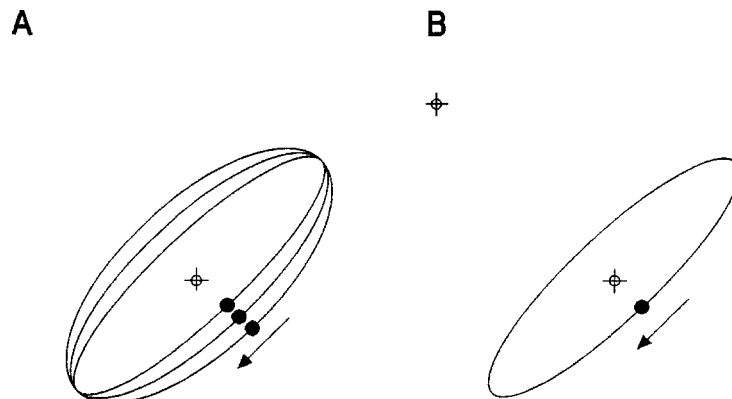
The experiments were run on an 80486-based computer equipped with a 12-in. color monitor with a resolution of  $640 \times 480$  pixels.

In experiment 1, a blue dot (diameter 1.2 mm) was continuously moved on one of three different elliptical trajectories (eccentricities of 0.968, 0.936, 0.893; Fig. 1A). We adopted these three eccentricities in order to roughly encompass the whole range of the illusory effects (Viviani and Stucchi 1992). The major axis had a length of 12.8 cm and was rotated  $45^\circ$  counterclockwise. The dot moved in a clockwise direction and took 3.85 s to complete an individual cycle, whatever the eccentricity employed. In the fixation condition (see below), a red pattern consisting of a circle with two crossed lines (diameter 4 mm) was also present in the central position.

Experiment 2 was designed to assess the influence of the stimulus velocity. To this purpose, only the more eccentric elliptical trajectory was employed but three different average velocities of the moving dot were used, namely 6.24, 8.58 and 13.73 cm/s. Given that the perimeter of the ellipse was 27.45 cm, these average velocities corresponded to periods of 4.4, 3.2 and 2.0 s. Moreover, an alternative fixation position was added, the red fixation pattern being presented either in the central position or in the upper left quadrant of the screen (Fig. 1B). Such a peripheral position was used to assess possible effects of retinal eccentricity on velocity perception. In fact, on fixating the central position, the range of retinal eccentricity of the moving dot was fairly large (from  $1.4^\circ$ , when the dot passed near the central position, to  $6.4^\circ$ , when the dot was in proximity of the point of maximal curvature of the ellipse). With the peripheral fixation position, the retinal eccentricity of the moving dot ranged from  $7.9^\circ$  to  $11.5^\circ$ .

A computer program calculated the kinematics of the dot in conformity with Equation 1 (the details of the procedure are described in Viviani and Stucchi 1992); the value of  $\beta$  could be controlled by the subjects by means of two keys, the effect of which was either to increase or to decrease the value of  $\beta$  in steps of 0.083. For positive values of  $\beta$ , the dot decelerated at higher curvatures and accelerated at lower curvatures of the ellipse. For negative values of  $\beta$ , the opposite occurred. For  $\beta = 0$ , the tangential velocity was independent of the curvature, i.e. it was constant. It should be noted that the time required by the dot to complete an individual cycle was not modified by changing  $\beta$ . The only effect of varying this parameter was to get a new distribution of velocity values on the trajectory.

**Fig. 1** **A** Stimulus configurations used in experiment 1, showing both the three eccentricities employed and the position of the fixation pattern. **B** Experiment 2. Only the most eccentric elliptical trajectory has been employed, with the dot moving with one of the three different velocities. Note the alternative fixation pattern in the upper left quadrant of the figure. The *filled dots* represent the moving dot (the *arrows* represent the direction of motion), but with enlarged dimension for graphical purposes. The fixation patterns (*open dots with cross*) have been slightly enlarged as well



## Procedure

In experiment 1, the subjects were seated at a distance of approximately 50 cm in front of the computer monitor in a moderately darkened room. They were told to adjust the velocity of the moving dot by means of two keys until it appeared constant. They could try as long as they wished and with an unlimited number of adjustments. The experimental design consisted of two groups (with or without eye movement recording, see below)  $\times$  two conditions (fixation or pursuit)  $\times$  three eccentricities  $\times$  six repetitions, for a total of 36 individual trials, randomly administered. The initial value of  $\beta$  was randomized as well. Subjects were told that, when only the moving dot was present (pursuit condition), they had to follow it with their eyes, while when also the central pattern appeared (fixation condition), they had to fixate the pattern instead. A preliminary session of about ten trials was allowed for training purposes.

Experiment 2 was similar to experiment 1, but the independent variables were the average velocity of the moving dot and the position of the fixation pattern. The experimental design thus consisted of three velocities (6.24, 8.58 and 13.73 cm/s)  $\times$  three conditions (pursuit, fixation in the central position and fixation in the eccentric position)  $\times$  five repetitions. Each subject performed 45 trials without any measurement of eye movements. The averages of the final estimates of  $\beta$  were computed over five repetitions for each of the three stimulus velocities by each of the three conditions. These nine average values of  $\beta$  were subsequently employed in an additional session during which each subject was presented with stimuli, the  $\beta$  value of which was selected by himself, while the eye movements were recorded. To this aim, subjects were secured to a bite-board to eliminate major head movements, at the same distance of 57 cm from the screen. They had simply to either follow the moving dot in the pursuit conditions or fixate the central or peripheral pattern in the fixation conditions. No additional adjustments of  $\beta$  were required.

## Recording of eye movements

In experiment 1, recording of eye movements served mainly as a qualitative control that subjects were indeed following the given instructions. Out of the 22 subjects, seven performed the task while eye movements were currently assessed. The eye movements were recorded by means of an Ober 2 system (Permobil Meditech), based on infrared oculography. With the head fixed to a particular fixation unit, subjects wore special goggles mounting the sources and the detectors of infrared light. The goggles allowed a viewing field of  $\pm 20^\circ$  and  $\pm 15^\circ$  in the horizontal and the vertical plane, respectively. Monocular horizontal and vertical eye positions were sampled at a frequency of 50 Hz. Before starting the task, the subjects were presented on the computer screen with 20 dots, placed in a  $5 \times 4$  matrix, which they had to fixate. Such known gaze positions served to calibrate the subsequent eye position signal off line.

In order to perform quantitative eye movement analysis, in experiment 2 a sampling frequency of 200 Hz was used and a  $3 \times 3$  dots calibration matrix was presented just before the moving dot appeared. The eight external dots of the  $3 \times 3$  calibration matrix formed the perimeter of the square in which the ellipse described by the moving dot was inscribed. Ten cycles of rotation for each of the nine trials were used. The first cycle of pursuit was discarded from the data analysis. A computer program was written to calibrate and analyse eye movement signals. Eye velocity was obtained by passing the position signal through a 7-point digital filter.

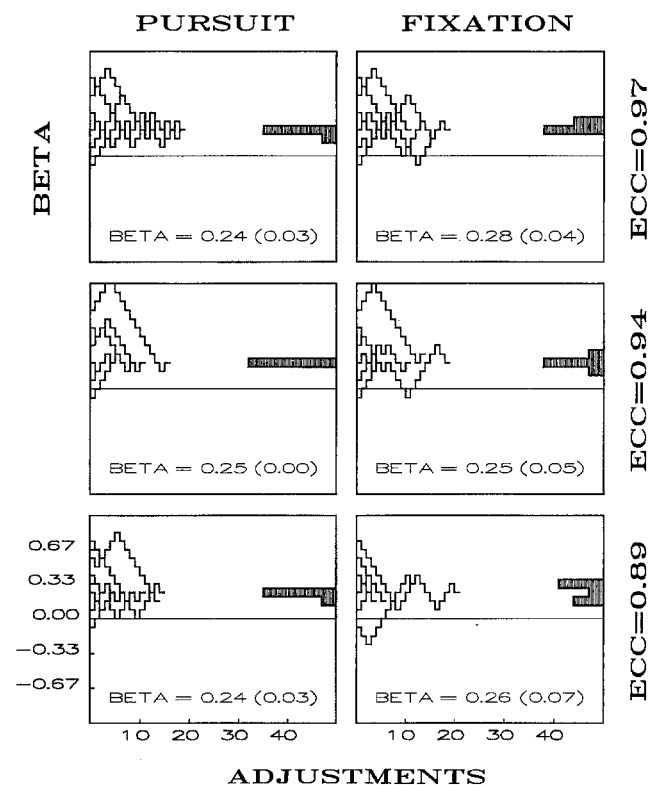
## Results

### Experiment 1

Figure 2 illustrates an experimental session of a single subject. The ladder-like lines on the left side of the panels show the progressive adjustments of  $\beta$  up to a final value that corresponds to the subjective perception of constant velocity. It should be noted that, whatever the initial value of  $\beta$ , the kinematics imposed by this subject to the moving dot converge approximately toward  $\beta = 0.25$ . The histograms on the right side of the panels are the distributions of the final values of  $\beta$  over the six repetitions.

The subjects were quite precise in their subjective estimates, the intra-individual standard deviations of the final values of  $\beta$  being very small. Table 1 shows means and standard errors of  $\beta$  estimates that corresponded to a perceived constant velocity. Each mean value is the average over the 22 subjects, in turn result-

**Fig. 2** Performance of an individual subject. Each panel refers to one of the two conditions (pursuit and fixation) and to one of the three tested eccentricities (experiment 1). The *ladder-like curves* on the left side of the panels represent the progressive adjustments of  $\beta$  ( $y$ -axis) made by the subject up to the final value. This corresponds to the subjective perception of constant velocity of the moving dot. The *horizontal thin lines* represent a  $\beta$  value of 0.0, i.e. the objective constant velocity. The *histograms* on the right side of the panels are the distributions of the final values of  $\beta$  selected by this subject. The *numbers* in the lower part of the panels are the averages of the final values of  $\beta$  (in parentheses the standard deviations) over the six repetitions



**Table 1** Experiment 1: mean and standard error of  $\beta$  for each of the three eccentricities ( $E1$ ,  $E2$ ,  $E3$ ; respectively 0.968, 0.936, 0.893) and in both pursuit and fixation conditions over 22 subjects

	E1	E2	E3
Central fixation	0.210 $\pm$ 0.013	0.186 $\pm$ 0.014	0.175 $\pm$ 0.013
Pursuit	0.220 $\pm$ 0.010	0.203 $\pm$ 0.010	0.187 $\pm$ 0.007

ing from the average of six individual trials for each of the two conditions and for each of the three eccentricities ( $E1$ ,  $E2$ ,  $E3$ ). The values of  $\beta$  which we found, are very similar to those previously reported with the same experimental protocol (Viviani and Stucchi 1992), and thus confirm the magnitude of such a dynamic illusion.

The main aim of this research was to find out possible differences in the strength of the illusion when eye movements were prevented. However, the ANOVA revealed no statistically significant difference in the values of  $\beta$  between fixation and pursuit conditions ( $F(1, 21) = 0.511$ ,  $P = 0.483$ ). We also checked for a possible interaction between the factor condition and the factor eccentricity of the ellipse, but these data also failed to reach statistical significance ( $F(5, 105) = 1.167$ ,  $P = 0.282$ ).

It could be argued that the lack of difference between the two experimental conditions is because, in the fixation condition, the subjects did not fixate the central pattern, in spite of the verbal instructions to keep their gaze on it, or that, vice versa, in the pursuit condition they did not visually follow the moving dot. Actually, the subjects reported that it was usually more difficult for them to perform the fixation task than the pursuit one. However, the number of adjustments employed to obtain the final estimate of  $\beta$  was not statistically different in the fixation trials and the pursuit trials [ $13 \pm 3$  SE and  $12 \pm 3$  SE, respectively, over all the trials;  $F(1, 21) = 0.230$ ,  $P = 0.636$ ].

In order to assess ocular behaviour, eye movements were constantly monitored during the perceptual task in seven subjects. From a qualitative visual inspection of the eye position records, it could be seen that the subjects performed very well, keeping their gaze still in the fixation condition and following the moving dot in the pursuit condition. The values of  $\beta$  were very similar both in subjects who performed the task without concomitant eye movement check and in subjects with the simultaneous control of eye movements. The ANOVA showed no statistical difference between them ( $F(1, 20) = 0.029$ ,  $P = 0.866$ ). Therefore, in spite of the differences in oculomotor behaviour, the illusion is clearly present in both conditions.

## Experiment 2

The difference of the strength of the illusion between fixation and pursuit conditions was clearly not statis-

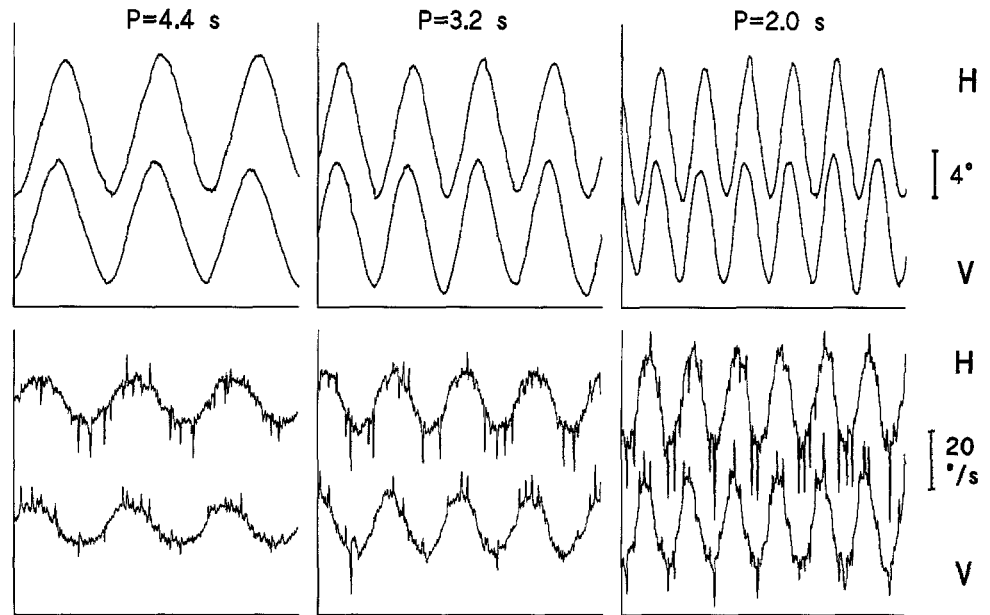
**Table 2** Experiment 2: mean and standard error of  $\beta$  for each of the three stimulus velocities ( $V1$ ,  $V2$ ,  $V3$ ; respectively 6.24, 8.58, 13.73 cm/s) and in pursuit, central fixation and peripheral fixation conditions over 14 subjects

	V1	V2	V3
Central fixation	0.183 $\pm$ 0.014	0.219 $\pm$ 0.009	0.227 $\pm$ 0.012
Peripheral fixation	0.192 $\pm$ 0.014	0.233 $\pm$ 0.014	0.243 $\pm$ 0.012
Pursuit	0.200 $\pm$ 0.016	0.224 $\pm$ 0.012	0.256 $\pm$ 0.010

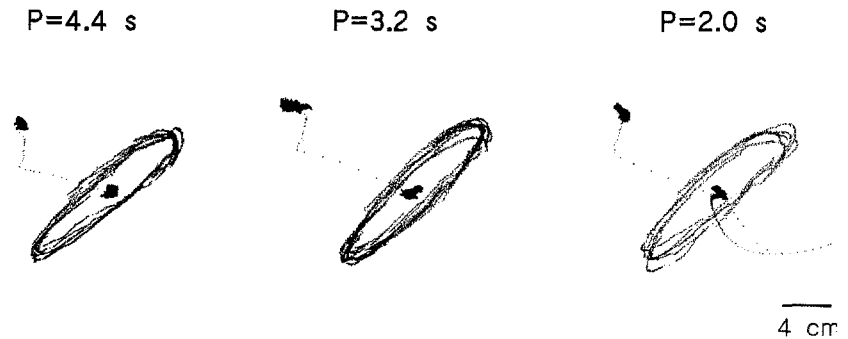
tically significant as assessed over the 22 subjects. However, it might be argued that the moderate increase of  $\beta$  (6% on average) observed in Table 1 between pursuit and fixation conditions is indicative of a tendency which might become more evident under different experimental conditions. Therefore, in experiment 2 we both extended the range of stimulus velocities and tested the effect of peripheral fixation. Table 2 shows the means and standard errors of  $\beta$  for stimulus periods of 4.4, 3.2 and 2.0 s ( $V1$ ,  $V2$ ,  $V3$ ) while tracking the dot or while fixating the central or the peripheral pattern. Again, no statistically significant effect was found for the condition factor (pursuit vs fixation) at any stimulus velocity ( $F(2, 26) = 1.655$ ,  $P = 0.211$ ). The interaction between the factor condition and the factor stimulus velocity was not statistically significant ( $F(4, 52) = 0.516$ ,  $P = 0.724$ ). The absence of relevant effects of pursuit was also confirmed by the average values of  $\beta$  over all three stimulus velocities, which were very similar in the peripheral fixation (0.223) and the pursuit (0.227) conditions. In addition, by contrasting peripheral and central fixation condition, it became apparent that retinal eccentricity did not affect constant velocity perception ( $F(1, 13) = 1.892$ ,  $P = 0.192$ ).

However, as in experiment 1, the values of  $\beta$  selected by our subjects in the pursuit condition were slightly higher than those selected in the central fixation condition. Therefore, despite the fact that ANOVA did not reveal any significant difference, we performed a bayesian analysis of comparisons to estimate the expected size of such a difference in the parent population (Rouanet and Lecoutre 1983) in order to quantitatively ascertain its relevance. Basically, bayesian analysis allows one to generalize descriptive results about the size of the observed effect, i.e. to infer the size of the parent effect  $\delta$  in the population with a given fiducial probability (or guarantee) from the observed value  $d$  in the sample. The magnitude of the effect can be assessed through fiducial limits obtained from a distribution over the parent effect  $\delta$ . This Bayes-fiducial distribution is a usual *Student* distribution centred on  $d$  and with a dispersion that reflects the potential of generalizability over  $\delta$  carried by experimental data ( $d^2/F$ ). In experiment 1, the observed average difference between the fixation and pursuit conditions was 0.013 (see Table 1). This means that we have only

**Fig. 3** Records of eye position (*upper traces*) and velocity (*lower traces*) during pursuit of the moving dot at different velocities. Some small saccades are discernible in the velocity traces in the form of peaks in the signal. Note the increase of smooth pursuit eye velocity at increasing stimulus velocities. Duration of each recording: 13 s. (*H, V*)



**Fig. 4** Plots of eye position during pursuit and both central and peripheral fixations at the three stimulus velocities in an individual subject. An eyeblink occurred during central fixation in the 2.0 s period condition



a guarantee of 0.76 that the parent effect is greater than zero, which does not satisfy the usual criterion of 0.95. In experiment 2, by contrasting the pursuit and the central fixation condition ( $d = 0.017$ , see Table 2) we obtain an effect that is close to usual significance criteria ( $F(1, 13) = 4.995$ ,  $P = 0.0537$ ). Bayes-fiducial methods allow us to infer that there is a guarantee of 0.99 to find an effect less than 0.031.

By means of bayesian methods we can also predict the proportion of subjects in the population showing an effect equal or greater than the observed effect of 0.017. Given the observed proportion of 0.5, i.e. seven subjects out of 14 satisfying the restriction, it can be inferred, with a guarantee of 0.95, that the expected frequency in the population is 0.26.

A factor significantly affecting the estimation of  $\beta$  was found to be the stimulus velocity ( $F(2, 26) = 18.282$ ,  $P < 0.001$ ). In fact, as can be seen from Table 2, the  $\beta$  values increase at increasing stimulus velocities, both while tracking the stimulus and while fixating peripherally or centrally, which is attested also by the already mentioned absence of interaction between the factor condition and the factor stimulus velocity.

The eye movement data confirmed that the tracking performance was accurate. Only data taken from five

subjects could be used for analysis, because, although we took care to minimize signal instability, some subjects showed clear, though little, head movements during the recording session. In these subjects, the eye position signal was not sufficiently reliable to perform a quantitative analysis.

Figure 3 shows horizontal and vertical components of eye position and velocity in an individual subject tracking the dot motion, the  $\beta$  values of which corresponded to his perception of constant velocity. Figure 4 shows the traces of the eye position for the three stimulus velocities and for the three conditions in the same subject. The movement of the eyes is mainly smooth, the saccades being of small amplitude and not very frequent. Over five subjects, the average tangential eye velocities in the three stimulus conditions were (mean  $\pm$  SD)  $6.5 \pm 0.4^\circ/\text{s}$ ,  $9.2 \pm 0.5^\circ/\text{s}$  and  $13.5 \pm 1.0^\circ/\text{s}$ , which confirmed that subjects tracked the moving dot also at higher stimulus velocities. During central fixation, the eyes remained within an area of  $0.46^\circ$  of radius (80% confidence interval), with an average tangential velocity below  $0.7^\circ/\text{s}$ . During peripheral fixation, the eyes remained within an area of  $0.53^\circ$ , with a velocity below  $0.8^\circ/\text{s}$ . This indicated that fixation was accurate as well.

## Discussion

The aim of the present research was to assess whether eye movements could explain the visual sensitivity to biological motion. By allowing or preventing visual tracking of the moving stimulus under several different experimental conditions, we showed that the dynamic illusion of constant velocity is present regardless of the concurrent oculomotor command. This finding clearly demonstrates that smooth pursuit signals (i.e. proprioception and/or efferent copy signals) are neither necessary nor sufficient for the visual system being constrained by the two-thirds power law.

However, a possible minor contribution of smooth pursuit eye movements in dynamically reinforcing the illusion could still be present. With regard to this, it should be noted that, first, the effect of pursuit was not statistically significant, and, next, the difference of the estimated  $\beta$  between pursuit and fixation conditions was less than 0.031, as assessed through bayesian methods. This difference is less than half of the JND (just noticeable difference), the latter being, for the eccentricities employed in our study, 0.064 (Viviani and Stucchi 1992). This means that the influence, if any, of eye motion on the estimation of  $\beta$  falls well below the perceptual threshold. Thus, our data cannot support a relevant on-line role for eye motion in increasing the illusory effect.

Our findings might therefore suggest, *prima facie*, that visual mechanisms are chiefly responsible for the illusion, and that, conversely, motor processes do not constrain perception. Indeed, since Purkinje and Bell's observations on the role of active and passive displacement of the eyes upon afterimage movement, the involvement of eye movements has often served as a support for those theories advocating a role of efference (or reafference) in visual perception. Correlations between the pattern of eye movements and the perceptual performance have been described in a number of experiments (Festinger et al. 1968; Coren et al. 1975; Bradley and Godiksen 1984). Although in some circumstances visual information appears to be dominant (Wallach 1990), explanations based on motor theories of perception have been used to interpret many empirical observations (see Coren 1986; Grüsser 1986).

Although we ruled out eye motion as a fundamental on-line source of motor knowledge, nonetheless the possibility that different forms of perceptuo-motor interactions modulate the sensitivity of the visual system to particular kinematic motor rules cannot be rejected. In fact, the presence of the illusion in the absence of motor execution does not exclude that the visual system has a direct internal access to implicit motor rules. In a more general approach to perception, internalized kinematic rules have been postulated to explain several perceptual facts (see Shepard 1984). In addition, oculomotor activity might gradually refine,

in the long-term, the visual sensitivity to such velocity-curvature relation. Indeed, eye movements have been suggested as taking part in adaptive processes of the oculomotor system (Ludvig 1952; Gauthier et al. 1995), as well as playing a slow calibrating role in the development of some visual capabilities (Washburn 1916, cited in Coren 1986; Steinbach 1987). Such a slow-acting role for eye movements remains to be tested in the case of the visual tuning to geometry-kinematics relationship.

Therefore, our data should be taken as an indication that, whatever mechanisms of on-line visual processing are at play in producing such a dynamic illusion, they are not based upon eye motion-related signals. As a consequence, visual tuning to biological motion should be ascribed either to purely visual mechanisms, and/or, as proposed by Viviani and Stucchi (1992), to an internal interplay between visual and motor processes.

## References

- Beardworth T, Bukner T (1981) The ability to recognize oneself from a video recording of one's movement without one's body. *Bull Psychonom Soc* 18: 19–22
- Bertenthal BI, Proffitt DR, Kramer SJ (1987) Perception of biomechanical motion by infants: implementation of various processing constraints. *J Exp Psychol Hum Percept Perform* 13: 577–585
- Bradley DR, Godiksen EB (1984) The "shrinking circle illusion" is a shrinking ellipse. *Perception* 13: 207–212
- Coren S (1986) An efferent component in the visual perception of direction and extent. *Psychol Rev* 93: 391–410
- Coren S, Bradley DR, Hoenig P, Girgus JS (1975) The effect of smooth tracking and saccadic eye movements on the perception of size: the shrinking circle illusion. *Vision Res* 15: 49–52
- Cutting JE (1981) Coding theory adapted to gait perception. *J Exp Psychol Hum Percept Perform* 7: 71–87
- Festinger L, White CW, Allyn MR (1968) Eye movements and decrement in the Muller-Lyer illusion. *Percept Psychophys* 3: 376–382
- Gauthier GM, de'Sperati C, Tempia F, Marchetti E, Strata P (1995) Eye motion-coding information mediates adaptive modification of vestibulo-ocular reflex in rat. *Exp Brain Res* (in press)
- Grüsser OJ (1986) The effect of gaze motor signals and spatially directed attention on eye movements and visual perception. *Prog Brain Res* 64: 391–404
- Johansson G (1977) Studies on visual perception of locomotion. *Perception* 6: 365–376
- Ludvig E (1952) Possible role of proprioception in the extraocular muscles. *Arch Ophthalmol* 48: 436–441
- Massey JT, Lurito JT, Pellizzer G, Georgopoulos AP (1992) Three-dimensional drawings in isometric conditions: relation between geometry and kinematics. *Exp Brain Res* 88: 685–690
- Rouanet H, Lecoutre B (1983) Specific inference in ANOVA: from significance tests to Bayesian procedures. *B J Math Stat Psychol* 36: 252–268
- Shepard RN (1984) Ecological constraints on internal representation: resonant kinematics of perceiving, imaging, thinking, and dreaming. *Psychol Rev* 4: 417–447
- Shiffrar M, Freyd JJ (1990) Apparent motion of the human body. *Psychol Sci* 1: 257–264
- Steinbach MJ (1987) Proprioceptive knowledge of eye position. *Vision Res* 10: 1737–1744

- Viviani P, Mounoud P (1990) Perceptuo-motor compatibility in pursuit tracking of two-dimensional movements. *J Mot Behav* 22: 407–443
- Viviani P, Schneider R (1991) A developmental study of the relation between geometry and kinematics in drawing movements. *J Exp Psychol Hum Percept Perform* 17: 198–218
- Viviani P, Stucchi N (1989) The effect of movement velocity on form perception: geometric illusions in dynamic displays. *Percept Psychophys* 46: 266–274
- Viviani P, Stucchi N (1992) Biological movements look uniform: evidence of motor-perceptual interactions. *J Exp Psychol Hum Percept Perform* 18: 603–623
- Viviani P, Terzuolo CA (1982) Trajectory determines movement dynamics. *Neuroscience* 7: 431–437
- Wallach H (1990) The role of eye movements in the perception of motion and shape. In: Kowler E (ed) *Eye movements and their role in visual and cognitive processes*. Elsevier, Amsterdam, pp 289–305