Vision Research xxx (2010) xxx–xxx

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Biological motion influences the visuomotor transformation for smooth pursuit eye movements

Sébastien Coppe [a], Jean-Jacques Orban de Xivry [a,b], Marcus Missal [a], Philippe Lefèvre [a,*]

[a] CESAME and IoNS, Université catholique de Louvain, Belgium
[b] Biomedical Engineering Department, Johns Hopkins University, Baltimore, MD, USA

ARTICLE INFO

Article history:
Received 11 June 2010
Received in revised form 27 July 2010
Available online xxxx

Keywords:
Smooth pursuit
Biological motion
Action perception
Motion perception
Point-light animation

ABSTRACT

Humans are very sensitive to the presence of other living persons or animals in their surrounding. Human actions can readily be perceived, even in a noisy environment. We recently demonstrated that biological motion, which schematically represents human motion, influences smooth pursuit eye movements during the initiation period (Orban de Xivry, Coppe, Lefèvre, & Missal, 2010). This smooth pursuit response is driven both by a visuomotor pathway, which transforms retinal inputs into motor commands, and by a memory pathway, which is directly related to the predictive properties of smooth pursuit. To date, it is unknown which of these pathways is influenced by biological motion. In the present study, we first use a theoretical model to demonstrate that an influence of biological motion on the visuomotor and memory pathways might both explain its influence on smooth pursuit initiation. In light of this model, we made theoretical predictions of the possible influence of biological motion on smooth pursuit during and after the transient blanking of the stimulus. These qualitative predictions were then compared with recordings of eye movements acquired before, during and after the transient blanking of the stimulus. The absence of difference in smooth pursuit eye movements during blanking of the stimuli and the stronger visually guided smooth pursuit reacceleration after reappearance of the biological motion stimuli in comparison with control stimuli suggests that biological motion influences the visuomotor pathway but not the memory pathway.

1. Introduction

Perception and action have been hypothesized to be subserved by the independent ventral and dorsal streams (Goodale & Milner, 1992). However, data on smooth pursuit eye movements demonstrated that those two streams are not completely independent as perception can influence smooth pursuit eye movements (i.e. action). For instance, a sinusoidally-moving line-figure diamond perceived through two vertical apertures evokes different eye movements depending on whether the apertures are visible or not (Krauzlis & Stone, 1999; Stone, Beutter, & Lorenceau, 2000) even though the physical motion is completely identical in both cases. Similarly, a tilted line moving horizontally will first evoke oblique eye movements before the vertical component disappears within 200 ms (Masson & Stone, 2002; Pack & Born, 2001). This temporal dynamics reflects neuronal dynamics at the level of the middle temporal area (MT) (Born & Bradley, 2005; Pack & Born, 2001), which is the primary input to the smooth pursuit system (Lisberger, 2010; Orban de Xivry & Lefèvre, 2007; Thier & Ilg, 2005).

In the framework of modeling the smooth pursuit system, this interaction between perception and action occurs at the level of the visuomotor transformation stage, which consists in the transformation of retinal signals into motor commands (Blohm & Crawford, 2007; Blohm, Keith, & Crawford, 2009; Buneo, Jarvis, Batista, & Andersen, 2002). To account for pursuit maintenance during blanking periods or occlusions (Mitrani & Dimitrov, 1978; Pola & Wyatt, 1997), smooth pursuit models also incorporate a predictive component, which consists in a memory that stores a dynamic representation of target motion (Bennett & Barnes, 2003; Orban de Xivry, Missal, & Lefèvre, 2008). This predictive pathway allows maintaining non-zero eye velocity when the moving stimulus disappears from the screen for several hundreds of milliseconds, although the gain of the response is reduced (Becker & Fuchs, 1985; Bennett & Barnes, 2003; Bennett, Orban de Xivry, Lefèvre, & Barnes, 2010; Mitrani & Dimitrov, 1978; Orban de Xivry, Bennett, Lefèvre, & Barnes, 2006; Orban de Xivry et al., 2008).

We recently showed evidence for a specific interaction between perception and action by demonstrating that a point-light walker stimulus (Johansson, 1973) evoked a stronger smooth pursuit response than a control stimulus devoid of biological relevance (Orban de Xivry, Coppe, Lefèvre, & Missal, 2010). However, it is unclear which part of the smooth pursuit system is influenced by

* Corresponding author.
E-mail address: Philippe.Lefevre@UCLouvain.be (P. Lefèvre).

0042-6989/$ - see front matter © 2010 Published by Elsevier Ltd.
doi:10.1016/j.visres.2010.08.009

the percept of biological motion. Indeed, biological motion could influence either the visuomotor transformation stage or the output of the memory pathway.

The influence of biological motion on the visuomotor transformation would parallel the studies on the aperture problem where misleading retinal signals result in a bias during the initiation of the smooth pursuit response (Beutter & Stone, 2000; Masson & Stone, 2002; Pack & Born, 2001; Stone et al., 2000). The changes in smooth pursuit initiation observed in the aperture problem framework and with the biological motion stimulus could result from a similar influence on the visuomotor transformation stage. In contrast, an influence of biological motion on the predictive component of the smooth pursuit system would be compatible with different situations in which a trajectory with natural kinematics leads to better prediction of a moving object than a trajectory with non-natural kinematics. For instance, human subjects predict more accurately the endpoint of a given trajectory if this trajectory follows the natural dynamics of a human arm movement than if the trajectory is not natural (Pozzo, Papaxanthis, Petit, Schweighofer, & Stucchi, 2006; Saunier, Papaxanthis, Vargas, & Pozzo, 2008). Similarly, the kinematics of the hand and racket appear to be of particular importance to predict the ball trajectory from the opponent in tennis (Huys, Smeeton, Hodges, Beek, & Williams, 2008; Huys et al., 2009; Mark Williams, Huys, Cañal-Bruland, & Hagemann, 2009). Note that point-light displays are sufficient to make such accurate predictions (Munzert, Hohmann, & Hossner, 2010). Thus biological motion appears to enhance the ability to predict.

Given that the percept of biological motion could potentially influence either the visuomotor transformation or the memory pathway, the goal of the present study is to investigate which part of the smooth pursuit system is actually influenced by biological motion. Using a simplified model of the smooth pursuit system, we will first demonstrate that an influence of the biological motion percept on the visuomotor transformation or on the memory pathway could theoretically reproduce the results of our previous study (Orban de Xivry et al., 2010). Namely biological motion stimuli evoke a faster smooth eye velocity during pursuit initiation than control stimuli. We will then compare the predictions made by those two hypotheses during and after the transient blanking of the moving stimuli. These predictions will be confronted with the results of a behavioral study during which the stimulus (biological motion or control stimulus) was blanked temporarily for 800 ms.

2. Methods

2.1. Participants

Thirteen human subjects (four females) participated in the experiments after informed consent. They were between 22 and 42 years old (mean age of 26.2 years). Eight of them were completely naïve of oculomotor experiments. Eight subjects participated in the first experiment. Seven subjects (including two subjects from the first group) participated in the second one. All procedures were approved by the Université catholique de Louvain Ethics Committee and were in agreement with the Declaration of Helsinki.

2.2. Stimuli

All trials started with an initial fixation during which a green dot was visible. Then, we presented either a moving point-light walker or one of its scrambled versions. The stimulus appeared and immediately started to move in a randomized heading direction for 800 ms, before gradually disappearing behind an invisible occluder for 800 ms. After the blanking period, the stimulus gradually reappeared and moved for an additional 800 ms period. The temporary blanking mimicked the disappearance of a human walker behind a large object, i.e. it would not disappear and reappear at once. The type of stimulus (biological motion BM or control), its direction (leftward or rightward), and its velocity (5, 10 or 15 deg/s) were selected at random for each trial. Typically, subjects performed three sessions of this experiment and each session contained 13 blocks of 30 trials. In the first experiment, the control stimulus consisted of a scrambled walker (SCR) that was chosen randomly from a set of nine stimuli for each block. In the second experiment, the control stimulus was the inverted walker (INV), which is known for being devoid of biological relevance.

The point-light walker was created using Cutting's algorithm (1977) and consisted of a green hip dot and 10 red dots representing other body joints. Subjects were asked to pursue the green hip dot. The scrambled control stimulus was obtained by shuffling the mean vertical position of the 10 red dots (all dots except the hip dot) to disrupt the global form while keeping the same local motion for the 10 red dots. Subjects were asked to pursue the hip dot that was highlighted in green and had identical motion whatever the stimulus type.

2.3. Apparatus and data analysis

Subjects were seated in a dark room with their head restrained by a chin-rest and faced a 1.5 m distant tangent screen that spanned 40° of their visual field. Stimuli were projected onto the screen with a cine8 Barco projector (Refresh rate: 100 Hz; Barco NV, Belgium). Eye movements were recorded at 200 Hz using a Chronos Eye Tracker (Skalar Medical BV, The Netherlands) and with an Eyelink 1000 (SR Research Ltd., Ottawa, Ontario, Canada) at 1000 Hz for the three last subjects.

Eye movements were low-pass filtered at 45 Hz and velocity and acceleration signals were derived from position signals using a central difference algorithm on a ±10 ms interval. Saccades were detected using a 500 deg/s^2 acceleration threshold. Those saccades were removed from the smooth eye velocity trace (see details in de Brouwer et al. (2002)). Given that the vertical component of eye velocity was very small (below 3 deg/s), the analyses focus on the horizontal component of eye velocity. The analyses were aligned on stimulus onset. An experimenter unaware of the stimulus type, selected the trials manually (no blink during the trial, no come back of the eye to the fixation point during the trial). All experimental data shown in the different figures are averaged across subjects. These traces are for a target velocity of 15 deg/s.

2.4. Model

Our model incorporated two main elements: a visuomotor transformation process and a memory pathway (Fig. 1A). In our model, the retinal slip is computed from the subtraction of the eye velocity from the target velocity. This signal is delayed by 100 ms and sent to the visuomotor transformation box as in Krauzlis and Miles (1996). This box is composed of two parallel pathways. In the image acceleration pathway, the retinal slip signal is first differentiated (i.e. acceleration error) and then transformed into motor commands by the following equation:

$$y = a\,\mathrm{sgn}(x)\,e^{-\frac{(|x|-b)^2}{2c^2}}$$

where y is the resulting motor command and x the acceleration error signal. The constants a, b and c are set to 90, 200 and 62, respectively (same values as in Krauzlis & Miles, 1996). The image velocity pathway transforms the retinal slip signal into motor commands

Please cite this article in press as: Coppe, S., et al. Biological motion influences the visuomotor transformation for smooth pursuit eye movements. *Vision Research* (2010), doi:10.1016/j.visres.2010.08.009

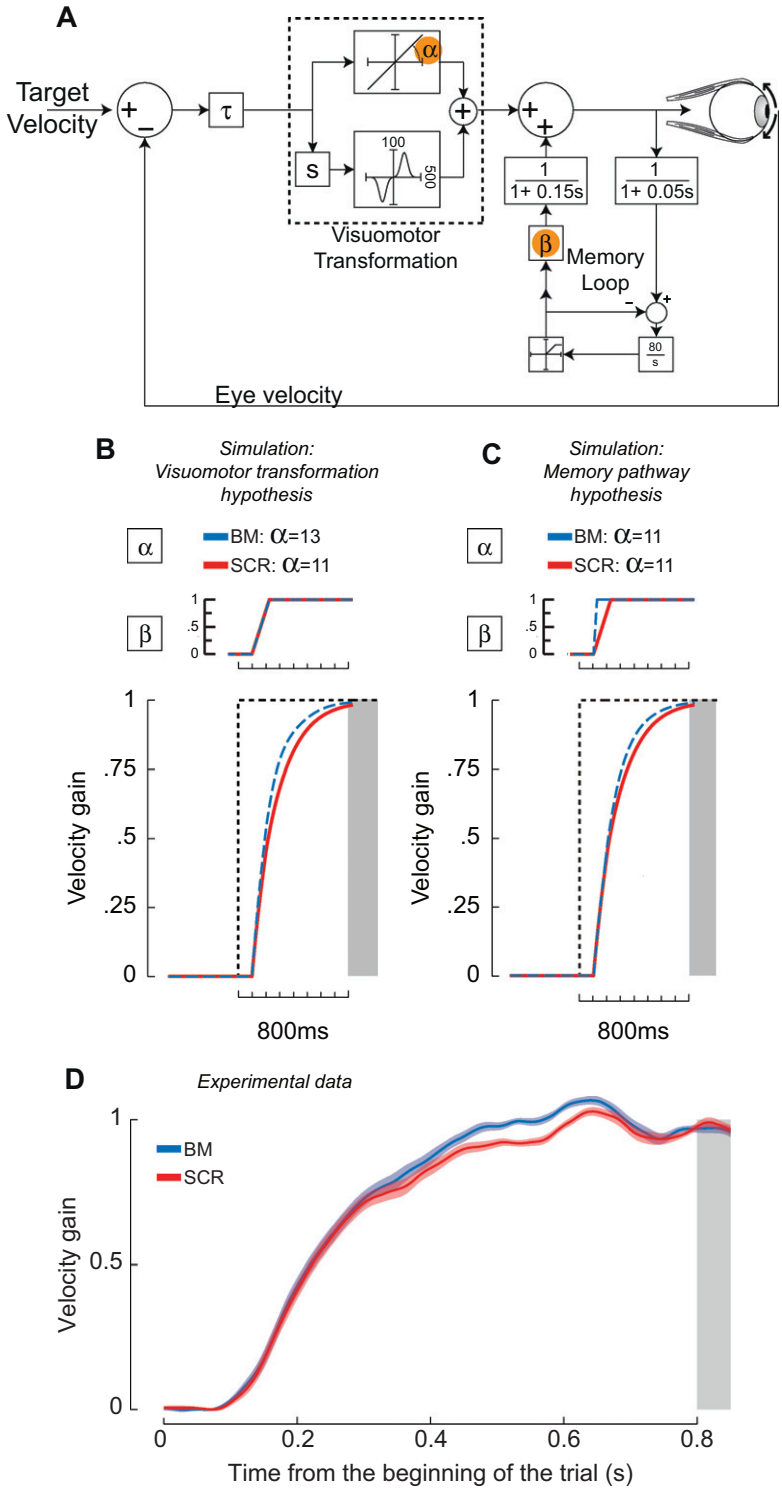

Fig. 1. (A) Smooth pursuit model of the ocular pursuit. The visuomotor transformation is adapted from Krauzlis and Miles (1996). The memory pathway is adapted from Bennett and Barnes (2003). The parameter α represents the gain of the visuomotor pathway and plays an important role in the transformation of the retinal slip into motor command. The parameter β is in the memory pathway, and represents the expectation to perceive an upcoming target. s corresponds to Laplace operator for derivative. Visual feedback delay $\tau = 0.1$ s. (B and C) Simulations of the pursuit gains for pursuit initiation by two different models corresponding to the two hypotheses. (B) Prediction when the visuomotor pathway gain is modulated by BM ($\alpha = 13$ for biological motion stimuli (BM, blue) and $\alpha = 11$ for control scrambled stimuli (SCR, red)). (C) Prediction when the gain of the memory pathway is modulated by BM. Top insets: gains of the memory pathway (β) evoked either by the BM (in blue) or by the SCR (in red). Bottom graphs: velocity smooth pursuit gains. Blue traces are BM-related and red are SCR-related. Black corresponds to a unitary velocity gain. Grey area represents the blanking of the stimuli. *X*-axis is time whereas *Y*-axis is the gain of the pursuit. (D) Average gain of the smooth pursuit from experimental data, evoked either by BM or by SCR during pursuit initiation. Areas surrounding the traces represent confidence intervals.

through a linear scaling with gain α. The outputs of the two pathways are then summed together. The motor command resulting from the visuomotor transformation is then summed up with the output of the memory pathway before being sent to the eye plant (modeled as a low-pass filter with a time constant of 150 ms). To simulate the effect of biological motion on the visuomotor

Please cite this article in press as: Coppe, S., et al. Biological motion influences the visuomotor transformation for smooth pursuit eye movements. *Vision Research* (2010), doi:10.1016/j.visres.2010.08.009

transformation, we set the gain α to 11 for control stimuli and 13 for the biological motion stimuli. Krauzlis and Miles (1996) set α to 12. The memory pathway works as a short-term memory. It contains an integrator that sums the motor commands within the local feedback loop until the output of the memory pathway matches the current motor commands (Bennett & Barnes, 2003). This output of the memory pathway is then multiplied by a memory gain β before being summed with the signal coming from the visuomotor transformation. The memory gain β is modulated by the blanking of the target and reinstated to its initial value to account for predictive velocity recovery before the end of the blanking period (Bennett & Barnes, 2003). To simulate the effect of biological motion on the memory pathway, we made beta reach its maximum value faster (for biological motion pursuit initiation and pursuit recovery after blanking). The value of the different parameters was not fit to our data but was inferred from existing models. Our model is only a tool to make qualitative predictions for both hypotheses.

3. Results

3.1. Pursuit initiation

In our model, increasing either the gain of the visuomotor transformation (α) or the gain of the memory pathway (β) could qualitatively reproduce the increase in smooth eye velocity observed in our previous experiment during pursuit initiation. Namely, biological motion stimuli evoke a transiently larger smooth eye velocity than control stimuli. In the case of the visuomotor transformation hypothesis, we increased the gain of the transformation of retinal slip into motor command (α, see Fig. 1A) by 20% when the stimulus was biologically relevant, which produced a larger eye velocity during pursuit initiation (Fig. 1B). In the case of the memory pathway hypothesis, the memory gain (β, see Fig. 1A) more rapidly reached its maximum (Fig. 1C, top insets). Therefore, this faster increase of the memory gain also produced a larger smooth eye velocity during pursuit initiation (Fig. 1C). In our dataset (see Section 2), we did observe a significant advantage to pursue biological motion (BM) instead of a scrambled stimulus from 150 ms to 500 ms after pursuit onset (Fig. 1D). For instance, a repeated measure ANOVA, with stimulus type (BM or SCR) and stimulus velocity as within subject factors indicated a main effect of stimulus type on smooth pursuit velocity 300 ms after stimulus onset ($F(1, 7) = 22.3$, $p = 0.002$) but no interaction between stimulus type and stimulus velocity ($F(2, 14) = 0.26$, $p = 0.77$).

Although both hypotheses might explain the difference in the smooth pursuit initiation observed in experimental data, these two hypotheses made very different predictions during and around the time of target blanking. These differences will be explained in the following paragraphs and tested against experimental results recorded during and after the temporary blanking of the moving stimuli.

3.2. Blanking period and predictive recovery

During the transient blanking of the pursued target, the smooth pursuit response is solely driven by the memory pathway given that there are no visual inputs. Therefore, any difference in the visuomotor transformation will not produce differences in behavior during blanking periods. In contrast, differences in memory gain will result in differences in behavior during blanking. For instance, if the biological motion influenced the plateau value of the memory gain β, it would influence the minimum of speed velocity during the blanking.

To account for predictive recovery of smooth eye velocity during blanking of the target, several authors have hypothesized that the memory gain is reinstated to its maximal value before the end of the occlusion. Under the memory loop hypothesis, the reinstatement of beta would be faster during the blanking as it was during the initiation. Therefore, the memory loop hypothesis predicts a higher predictive velocity recovery for the biological motion stimuli than for the control ones (Fig. 2B). Again, no difference is expected from the visuomotor transformation hypothesis (Fig. 2A).

The analysis of smooth pursuit velocity of human subjects during the blanking period did not reveal any significant difference (no effect of stimulus type on velocity measured each 50 ms from the beginning to the end of the blanking; all $p > 0.3$) between the two types of stimuli (Fig. 2C). For instance, 200 ms before reappearance of the stimuli, a repeated measure ANOVA, with stimulus type (BM or SCR) and stimulus velocity as within subject factors indicated no main effect of stimulus type on smooth pursuit velocity ($F(1, 7) = 0.085$, $p = 0.78$), whereas there was a main effect for stimulus velocity ($F(2, 14) = 72.6$, $p < 0.001$).

The comparison of eye velocity evoked by BM and control stimuli around the time of target reappearance (before visual feedback can influence the smooth pursuit response) did not reveal any significant difference in predictive recovery. We measured the predictive recovery by subtracting eye velocity measured 200 ms before

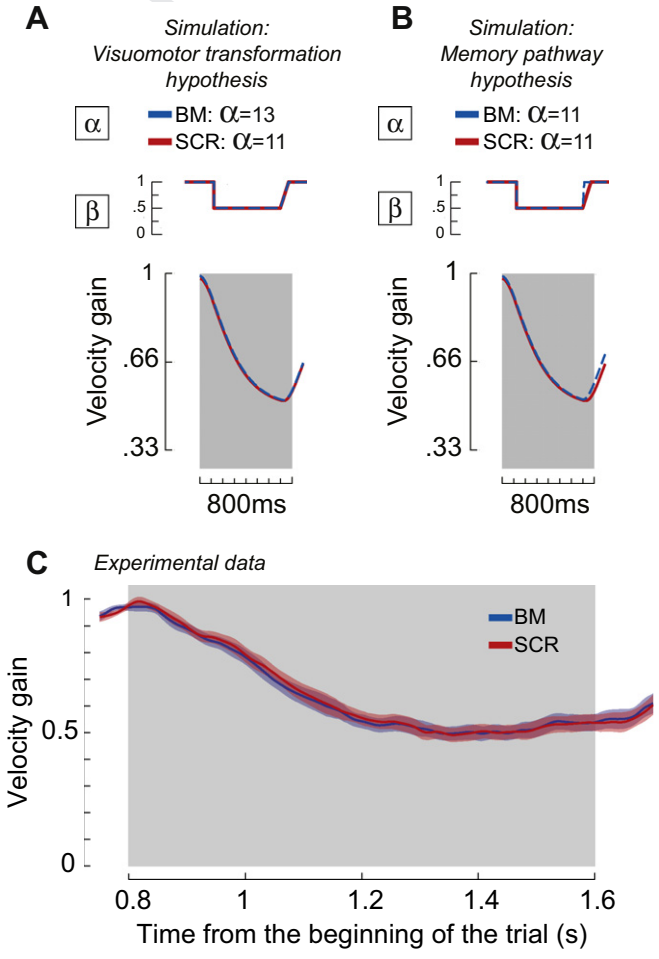

Fig. 2. Comparison between simulations and experimental data for the blanking period. Top insets (A and B): gains of the visuomotor pathway (α) and the memory pathway (β) for the biological motion stimuli (BM, blue) or the control stimuli (SCR, red). Bottom: prediction when the visuomotor pathway gain α is modulated by BM (A) or when the gain β of the memory pathway is modulated by BM (B). Blue traces are BM-related and red are SCR-related. Grey area represents the blanking of the stimuli. *X*-axis is time whereas *Y*-axis is the gain of the pursuit. (C) Average gain of the smooth pursuit from experimental data, evoked either by BM or by SCR. Areas surrounding the traces represent confidence intervals.

Please cite this article in press as: Coppe, S., et al. Biological motion influences the visuomotor transformation for smooth pursuit eye movements. *Vision Research* (2010), doi:10.1016/j.visres.2010.08.009

the end of blanking from eye velocity measured 50 ms after target reappearance (before any influence of visual feedback). The change in smooth pursuit gain during the predictive recovery ranged from 0.13 to 0.2 for the different conditions and was significantly larger than zero in all six conditions (two stimulus types and three stimulus velocities; paired t-test, all $p < 0.002$; Bonferroni correction requires all $p < 0.008$). A repeated measure ANOVA on smooth pursuit gain with time (200 ms before and 50 ms after target reappearance), stimulus type (BM or SCR) and stimulus velocity as within subject factors demonstrated the significance of the predictive recovery (main effect of time, $F(1, 7) = 22.9$, $p = 0.002$). This measure significantly varied with stimulus velocity (interaction between time and stimulus velocity, $F(1, 7) = 7.15$, $p = 0.007$) as it was larger for smaller stimulus velocities. However, this analysis did not reveal any significant effect of stimulus type on the predictive recovery (main effect, $F(1, 7) = 0.61$, $p = 0.46$; interaction between time and stimulus type, $F(1, 7) = 0.001$, $p = 0.97$; between velocity and stimulus type, $F(2, 14) = 0.006$, $p = 0.99$; three way interaction, $F(2, 14) = 0.05$, $p = 0.95$). In sum, our behavioral data appear to reject any influence of the percept of biological motion when this stimulus is not present on the screen. Thus biological motion does not influence the predictive component of the smooth pursuit response. This conclusion seems incompatible with the memory pathway hypothesis.

3.3. Visually-guided reacceleration

When motor commands are again partially driven by visual feedback (>100 ms after target reappearance), the visuomotor transformation hypothesis predicts some differences between the smooth eye velocity evoked by biological motion stimuli and by control stimuli. Indeed, given the residual retinal slip present after target reappearance, the visuomotor transformation hypothesis predicts a stronger reacceleration in the case of biological motion stimuli than in the case of control stimuli (Fig. 3A). In contrast, the differences observed following the memory hypothesis arise from the differences predicted during the occlusion (Fig. 3B).

Our analysis revealed that the behavior was consistent with the visuomotor transformation hypothesis. Indeed, ANOVA on smooth eye acceleration between 100 and 250 ms after stimuli reappearance exhibited a significant main effect of stimulus type ($F(1, 7) = 19.11$, $p = 0.003$) and of target speed ($F(1, 7) = 22.17$, $p < 0.001$). Independently of target speed ($F(2, 14) = 2.51$, $p = 0.11$), the visually guided acceleration evoked by biological motion between 100 and 250 ms after stimulus reappearance was significantly larger than the one evoked by the scrambled stimuli (Fig. 3C). This higher acceleration for BM than SCR resulted in a higher velocity from 150 ms to 350 ms after reappearance (main effect on stimulus type on pursuit velocity 150 ms after stimulus reappearance: $F(1, 7) = 3.2$, $p = 0.031$).

Our results are independent of the type of control stimuli as we reproduced the same results in a second experiment where the scrambled walker was replaced by the inverted walker (Fig. 4A). As summarized on Fig. 4A and B (green trace), the biological motion stimuli evoked a larger smooth eye velocity gain than the inverted walker both during pursuit initiation (main effect of stimulus type on eye velocity gain 300 ms after target onset: $F(1, 6) = 21.7$, $p = 0.009$) and during the reacceleration after the transient blanking of the target (main effect of stimulus type on eye acceleration computed between 100 and 250 ms after stimulus reappearance: $F(1, 6) = 48.4$, $p < 0.001$). The influence of the type of stimulus on the smooth pursuit response occurred earlier at reappearance (around 150 ms after target reappearance) than during pursuit initiation (around 260 ms after stimulus onset).

Independently of the control stimulus, there is an important difference in gain during smooth pursuit initiation (Orban de Xivry et al., 2010) and after reappearance of the target (Fig. 4B). This last result reflects a larger visually-guided pursuit reacceleration evoked by biological motion. The upper bar in Fig. 4C shows the significant difference between the pursuit response evoked by BM and SCR. We used a threshold (difference of velocity gains of 0.037) based on the average 99% confidence interval of these differences during the trial. The two lower bars show the qualitative difference between the theoretical predictions for BM and SCR, for both hypotheses. This schema summarizes our results and shows that the influence of biological motion on the smooth pursuit response observed in the experimental data is likely due to changes in the visuomotor transformation pathway.

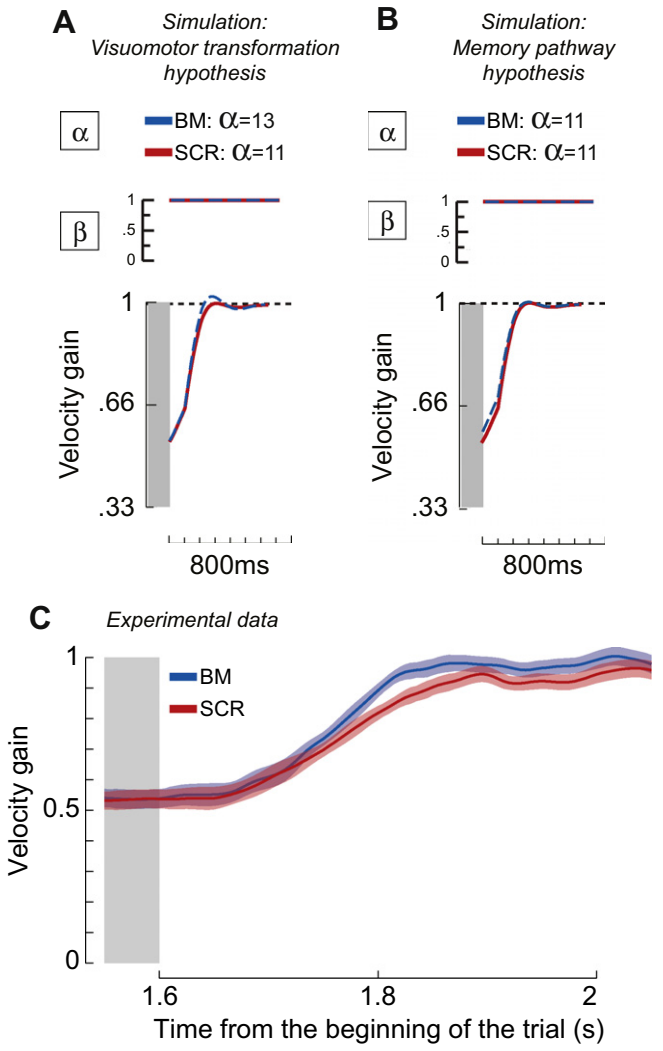

Fig. 3. Comparison between simulations and experimental data for the reappearance of the stimulus. Top insets (A and B): gains of the visuomotor pathway (α) and the memory pathway (β) for the biological motion stimuli (BM, blue) or the control stimuli (SCR, red). Bottom: prediction when the visual feedback gain α is modulated by BM (A) or when the gain β of the memory pathway is modulated by BM (B). Blue traces are BM-related and red are SCR-related. Black corresponds to a unitary velocity gain. Grey area represents the occlusion (blanking of the stimuli). X-axis is time whereas Y-axis shows the gain of the pursuit. (C) Average gain of the smooth pursuit from experimental data, evoked either by the BM or by SCR. Areas surrounding the traces represent confidence intervals.

4. Discussion

In this paper, we investigated the influence of the biological motion percept on the smooth pursuit system. We hypothesized that

Please cite this article in press as: Coppe, S., et al. Biological motion influences the visuomotor transformation for smooth pursuit eye movements. *Vision Research* (2010), doi:10.1016/j.visres.2010.08.009

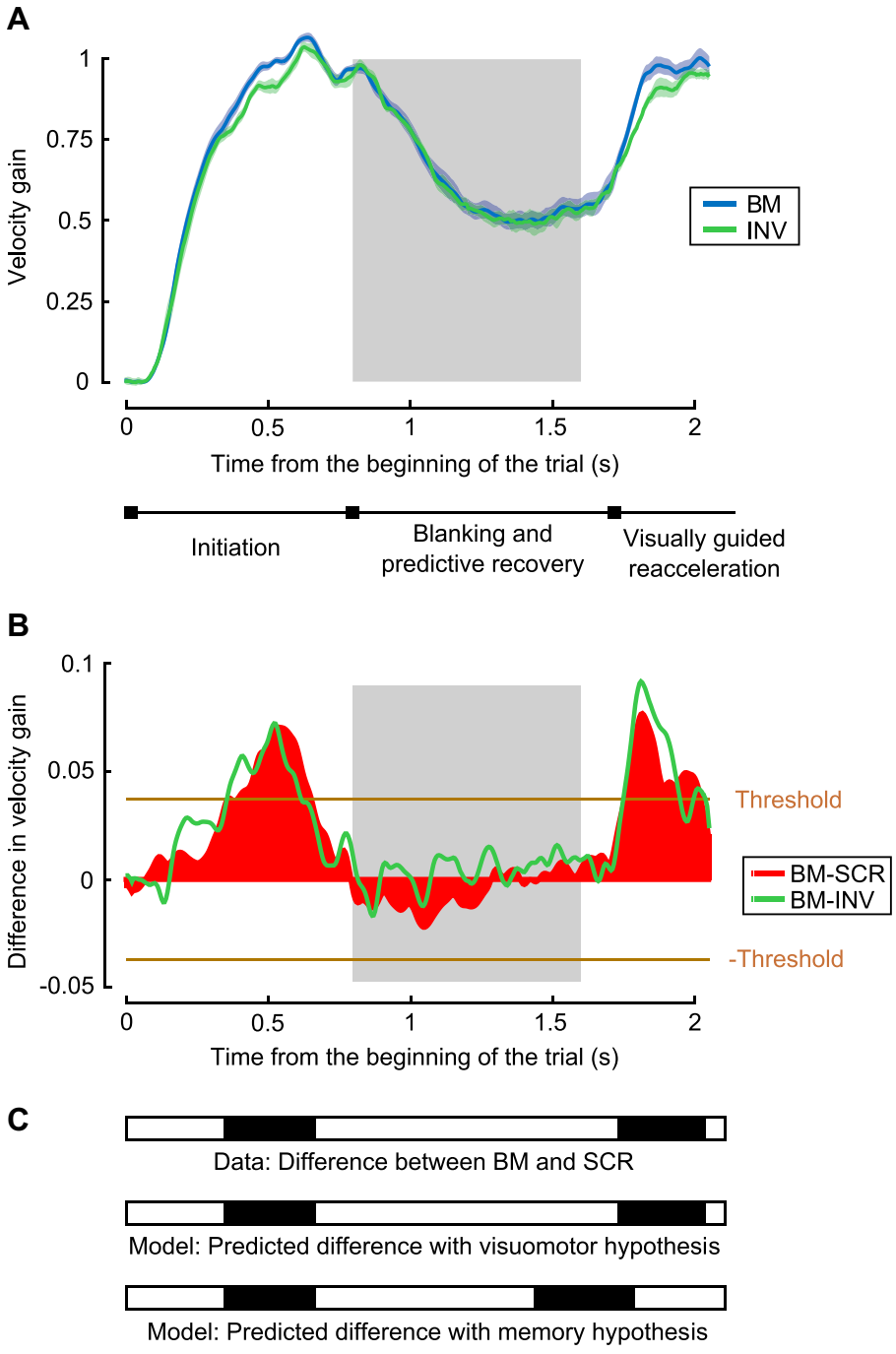

Fig. 4. (A) Average gain of the smooth pursuit from experimental data, evoked either by the BM (blue) or by the INV (green). Areas surrounding the traces represent confidence intervals. Grey area represents the occlusion (blanking of the stimuli). *X*-axis is time whereas *Y*-axis shows the gain of the pursuit. (B) Average difference between the pursuit gains evoked by BM and by SCR (red trace) and between the pursuit gains evoked by BM and by INV (green trace) versus time. (C) The upper horizontal bar shows the periods where the difference between the pursuit responses evoked by BM and SCR (red) is larger than a given threshold. This threshold corresponds to the average 99% confidence interval of the difference between pursuit gains evoked either by BM and SCR during all the trial. The two lower bars represent the periods during which there is a theoretical difference between pursuit induced by BM or a control stimulus (SCR).

biological motion could either influence the transformation of motion perception into motor commands or increase the reliance of the system on its predictive pathway. Although we found that both hypotheses could account for the observed difference during pursuit initiation, the absence of difference in predictive smooth pursuit during the transient blanking of the stimulus appeared to rule out the influence of the biological motion stimulus on the predictive pathway. In contrast, the observation that reacceleration after the blanking period was again facilitated by the biological motion stimuli with respect to control stimuli appeared to support an influence of biological motion on the visuomotor transformation process.

The influence of perception on smooth pursuit initiation has also been studied in the framework of the aperture problem (Pack & Born, 2001) where a tilted stimulus that is moving horizontally is initially perceived moving in an oblique direction (Marr & Ullman, 1981). Similarly to our study, this percept of an oblique moving direction influences smooth pursuit eye movements, i.e. this

Please cite this article in press as: Coppe, S., et al. Biological motion influences the visuomotor transformation for smooth pursuit eye movements. *Vision Research* (2010), doi:10.1016/j.visres.2010.08.009

percept initially biases smooth pursuit eye movements towards the oblique direction. The influence of the aperture problem and of biological motion on the visuomotor transformation clearly differs. Indeed, unlike our study, the reacceleration phase after a short blanking period of a tilted diamond stimulus that is moving horizontally does not exhibit the same vertical deviation as during pursuit initiation (Masson & Stone, 2002). Two possible explanations might account for this difference. On one hand, the blanking period used by Masson and Stone (2002) might have been too short (90 ms) to cause a sufficiently large reduction in eye velocity. A higher reduction in eye velocity during the blanking period would have required a higher involvement of the visuomotor transformation process during the reacceleration phase. Consequently, oblique eye movements might have been evoked again during the reacceleration phase. On the other hand, the biological motion perception and the tilted line perception are thought to be mediated by different neuronal substrates and might therefore impact different stages of the visuomotor transformation. Indeed, object motion is processed by MT (Born & Bradley, 2005; Pack & Born, 2001) whereas biological motion is processed by the posterior part of superior temporal sulcus (STS) and the anterior portion of the intraparietal sulcus (IPS) among others (Billino, Braun, Böhm, Bremmer, & Gegenfurtner, 2009; Decety & Grezes, 1999; Grezes et al., 2001; Oram & Perrett, 1994). In addition, MT lesion does not abolish biological motion perception (McLeod, Dittrich, Driver, Perrett, & Zihl, 1996; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990). Therefore, the difference in the reacceleration phase could also be due to differences in neural substrates.

It was possible for Lisberger and Movshon (1999) to reconstruct image velocity (input of the visuomotor transformation) with a distributed response recorded in MT in monkeys. MT is essential for both motion perception (Born & Bradley, 2005) and smooth pursuit eye movements (Newsome, Wurtz, Dursteler, & Mikami, 1985). The biological motion network could act directly (in parallel to MT) or indirectly (via MT/MST) on the visuomotor transformation process. Projections from STS to MT/MST have been demonstrated anatomically (Boussaoud, Ungerleider, & Desimone, 1990) and hypothesized to be responsible for the activation of these areas in the case of implied human motion (Jellema & Perrett, 2003a).

In other contexts, perception of human action has been shown to influence action production, hence the visuomotor transformation stage (see Blake and Shiffrar (2007) for review). Observing actions performed by a human actor, not a robot, can influence the production of other actions (Kilner, Paulignan, & Blakemore, 2003). In one study, visual presentation of a finger movement slows down the reaction time to initiate another finger movement (Brass, Bekkering, & Prinz, 2001) and this finding has been reproduced in another study with grasping movements (Craighero, Bello, Fadiga, & Rizzolatti, 2002). These results illustrate that perception of human action can influence the visuomotor transformation process (for arm or hand movements but also for pursuit eye movements).

In addition, action can also influence perception (Casile & Giese, 2005; Grezes et al., 2001; Hamilton, Wolpert, & Frith, 2004; Schütz-Bosbach & Prinz, 2007). For instance, Jacobs and Shiffrar (2005) showed that discriminating point-light walker speed is disrupted by concurrent walking of the observer. In sum, an observer's own activity influences his/her perception of the activity of other people. Therefore, the link between perception and action is then present in both ways (Blake & Shiffrar, 2007).

Finally, the absence of influence of the biological motion on the predictive pursuit response during the temporary blanking of the target was unexpected for several reasons. First, observation of biological motion leads to better prediction than when this component of motion is absent (Huys et al., 2008, 2009; Mark Williams et al., 2009). Second, some neurons in STS that are selectively responsive to biological motion (Oram & Perrett, 1994; Puce & Perrett, 2003) continue to respond when the initially visible moving walker disappears behind an occluder (Baker, Keysers, Jellema, Wicker, & Perrett, 2001; Jellema & Perrett, 2003b). These cells showed their highest levels of activity when the walker was totally hidden from view. Although it did not influence the predictive smooth pursuit response, the maintenance of BM-related activity during occlusion might result in a priming effect for biological motion and be responsible for the earlier effect observed at target reappearance. On the basis of those two observations, biological motion could have yielded a better prediction based on an improved internal representation of the biological relevant stimulus.

In conclusion, the present study shed some light on how biological motion acts on the smooth pursuit system. Although biological motion does not influence the response of the smooth pursuit system during blanking periods, it does during initiation phase of the response and during the reacceleration phase after the blanking period. Importantly, during those periods, the smooth pursuit response was primarily driven by retinal inputs. Therefore, we conclude that biological motion influences the visuomotor transformation for smooth pursuit eye movements.

Acknowledgments

This work was supported by the Fonds National de la Recherche Scientifique, the Fondation pour la Recherche Scientifique Médicale, the Belgian Program on Interuniversity Attraction Poles initiated by the Belgian Federal Science Policy Office, Actions de Recherche Concertées (French community, Belgium), an internal research grant (Fonds Spéciaux de Recherche) of the Universiteé catholique de Louvain, and the European Space Agency (ESA) of the European Union. J.J.O. is supported by the Belgian American Educational Foundation, by an internal research grant from the Université catholique de Louvain (Fonds spéciaux de recherche) and by the Fondation pour la Vocation (Belgium).

References

Baker, C. I., Keysers, C., Jellema, T., Wicker, B., & Perrett, D. I. (2001). Neuronal representation of disappearing and hidden objects in temporal cortex of the macaque. *Experimental Brain Research, 140*(3), 375–381.

Becker, W., & Fuchs, A. F. (1985). Prediction in the oculomotor system: Smooth pursuit during transient disappearance of a visual target. *Experimental Brain Research, 57*(3), 562–575.

Bennett, S. J., & Barnes, G. R. (2003). Human ocular pursuit during the transient disappearance of a visual target. *Journal of Neurophysiology, 90*(4), 2504–2520.

Bennett, S., Orban de Xivry, J., Lefèvre, P., & Barnes, G. (2010). Oculomotor prediction of accelerative target motion during occlusion: Long-term and short-term effects. *Experimental Brain Research, 204*(4), 493–504.

Beutter, B. R., & Stone, L. S. (2000). Motion coherence affects human perception and pursuit similarly. *Visual Neuroscience, 17*(1), 139–153.

Billino, J., Braun, D., Böhm, K., Bremmer, F., & Gegenfurtner, K. (2009). Cortical networks for motion processing: Effects of focal brain lesions on perception of different motion types. *Neuropsychologia, 47*(10), 2133–2144.

Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of Psychology, 58*, 47–73.

Blohm, G., & Crawford, J. (2007). Computations for geometrically accurate visually guided reaching in 3-D space. *Journal of Vision, 7*(5), 4.1–22.

Blohm, G., Keith, G., & Crawford, J. (2009). Decoding the cortical transformations for visually guided reaching in 3D space. *Cerebral Cortex, 19*(6), 1372–1393.

Born, R. T., & Bradley, D. C. (2005). Structure and function of visual area MT. *Annual Review of Neuroscience, 28*, 157–189.

Boussaoud, D., Ungerleider, L., & Desimone, R. (1990). Pathways for motion analysis: Cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque. *Journal of Comparative Neurology, 296*(3), 462–495.

Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica (Amst), 106*(1–2), 3–22.

Buneo, C. A., Jarvis, M. R., Batista, A. P., & Andersen, R. A. (2002). Direct visuomotor transformations for reaching. *Nature, 416*(6881), 632–636.

Casile, A., & Giese, M. A. (2005). Critical features for the recognition of biological motion. *Journal of Vision, 5*(4), 348–360.

Craighero, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the responses to hand pictures. *Neuropsychologia, 40*(5), 492–502.
Decety, J., & Grezes, J. (1999). Neural mechanisms subserving the perception of human actions. *Trends in Cognitive Sciences, 3*(5), 172–178.
Goodale, M., & Milner, A. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15*(1), 20–25.
Grezes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., & Decety, J. (2001). Does perception of biological motion rely on specific brain regions? *Neuroimage, 13*(5), 775–785.
Hamilton, A., Wolpert, D., & Frith, U. (2004). Your own action influences how you perceive another person's action. *Current Biology, 14*(6), 493–498.
Huys, R., Cañal-Bruland, R., Hagemann, N., Beek, P., Smeeton, N., & Williams, A. (2009). Global information pickup underpins anticipation of tennis shot direction. *Journal of Motor Behavior, 41*(2), 158–171.
Huys, R., Smeeton, N., Hodges, N., Beek, P., & Williams, A. (2008). On the dynamic information underlying visual anticipation skill. *Perception & Psychophysics, 70*(7), 1217–1234.
Jacobs, A., & Shiffrar, M. (2005). Walking perception by walking observers. *Journal of Experimental Psychology: Human Perception and Performance, 31*(1), 157–169.
Jellema, T., & Perrett, D. (2003a). Cells in monkey STS responsive to articulated body motions and consequent static posture: A case of implied motion? *Neuropsychologia, 41*(13), 1728–1737.
Jellema, T., & Perrett, D. (2003b). Perceptual history influences neural responses to face and body postures. *Journal of Cognitive Neuroscience, 15*(7), 961–971.
Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics, 14*(2), 201–211.
Kilner, J., Paulignan, Y., & Blakemore, S. (2003). An interference effect of observed biological movement on action. *Current Biology, 13*(6), 522–525.
Krauzlis, R. J., & Miles, F. A. (1996). Transitions between pursuit eye movements and fixation in the monkey: Dependence on context. *Journal of Neurophysiology, 76*(3), 1622–1638.
Krauzlis, R. J., & Stone, L. S. (1999). Tracking with the mind's eye. *Trends in Neurosciences, 22*(12), 544–550.
Lisberger, S. (2010). Visual guidance of smooth-pursuit eye movements: Sensation, action, and what happens in between. *Neuron, 66*(4), 477–491.
Mark Williams, A., Huys, R., Cañal-Bruland, R., & Hagemann, N. (2009). The dynamical information underpinning anticipation skill. *Human Movement Science, 28*(3), 362–370.
Marr, D., & Ullman, S. (1981). Directional selectivity and its use in early visual processing. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 211*(1183), 151–180.
Masson, G. S., & Stone, L. S. (2002). From following edges to pursuing objects. *Journal of Neurophysiology, 88*(5), 2869–2873.
McLeod, P., Dittrich, W., Driver, J., Perrett, D., & Zihl, J. (1996). Preserved and impaired detection of structure from motion by a "motion-blind" patient. *Visual Cognition, 3*(4), 363–391.
Mitrani, L., & Dimitrov, G. (1978). Pursuit eye movements of a disappearing moving target. *Vision Research, 18*(5), 537–539.
Munzert, J., Hohmann, T., & Hossner, E.-J. (2010). Discriminating throwing distances from point-light displays with masked ball flight. *European Journal of Cognitive Psychology, 22*(2), 247–264.
Newsome, W. T., Wurtz, R. H., Dursteler, M. R., & Mikami, A. (1985). Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *Journal of Neuroscience, 5*(3), 825–840.
Oram, M. W., & Perrett, D. I. (1994). Responses of anterior superior temporal polysensory (STPa) neurones to "biological motion" stimuli. *Journal of Cognitive Neuroscience, 6*, 99–116.
Orban de Xivry, J. J., Bennett, S. J., Lefèvre, P., & Barnes, G. R. (2006). Evidence for synergy between saccades and smooth pursuit during transient target disappearance. *Journal of Neurophysiology, 95*(1), 418–427.
Orban de Xivry, J., Coppe, S., Lefèvre, P., & Missal, M. (2010). Biological motion drives perception and action. *Journal of Vision, 10*(2), 6.1–11.
Orban de Xivry, J. J., & Lefèvre, P. (2007). Saccades and pursuit: Two outcomes of a single sensorimotor process. *Journal of Physiology, 584*(Pt 1), 11–23.
Orban de Xivry, J., Missal, M., & Lefèvre, P. (2008). A dynamic representation of target motion drives predictive smooth pursuit during target blanking. *Journal of Vision, 8*(15), 6.1–13.
Pack, C. C., & Born, R. T. (2001). Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature, 409*(6823), 1040–1042.
Pola, J., & Wyatt, H. J. (1997). Offset dynamics of human smooth pursuit eye movements: Effects of target presence and subject attention. *Vision Research, 37*(18), 2579–2595.
Pozzo, T., Papaxanthis, C., Petit, J., Schweighofer, N., & Stucchi, N. (2006). Kinematic features of movement tunes perception and action coupling. *Behavioural Brain Research, 169*(1), 75–82.
Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 358*(1431), 435–445.
Saunier, G., Papaxanthis, C., Vargas, C., & Pozzo, T. (2008). Inference of complex human motion requires internal models of action: Behavioral evidence. *Experimental Brain Research, 185*(3), 399–409.
Schütz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: Action-induced modulation of perception. *Trends in Cognitive Sciences, 11*(8), 349–355.
Stone, L. S., Beutter, B. R., & Lorenceau, J. (2000). Visual motion integration for perception and pursuit. *Perception, 29*(7), 771–787.
Thier, P., & Ilg, U. J. (2005). The neural basis of smooth-pursuit eye movements. *Current Opinion in Neurobiology, 15*(6), 645–652.
Vaina, L., Lemay, M., Bienfang, D., Choi, A., & Nakayama, K. (1990). Intact "biological motion" and "structure from motion" perception in a patient with impaired motion mechanisms: A case study. *Visual Neuroscience, 5*(4), 353–369.

Please cite this article in press as: Coppe, S., et al. Biological motion influences the visuomotor transformation for smooth pursuit eye movements. *Vision Research* (2010), doi:10.1016/j.visres.2010.08.009