

Gaze-orientation during transient occlusion

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Abstract

Fast moving objects are often transiently occluded in our normal surrounds as they pass behind other surfaces and objects. The consequent loss of drive from visual feedback can be compensated by extra-retinal input. Evidence from behavioural studies indicates that gaze orientation during transient occlusion is not simply a reflexive response but can also be predictive of the upcoming motion. Indeed, while smooth pursuit eye velocity often falls below target velocity during a transient occlusion, it increases prior to object reappearance in order to reduce retinal slip. Moreover, the smooth response is combined with saccadic eye movements that match eye displacement to object displacement and thus minimize position error at object reappearance. Comparisons of conditions that require fixation or pursuit suggest that the maintenance of gaze orientation during transient occlusion is the habitual response and can facilitate both spatial and temporal estimation. Interconnected areas of the frontal and parietal cortex have been shown to be active during pursuit of occluded object motion and are thus thought to be involved in the control of gaze-orientation as well as representing object motion. Future work should determine whether expertise in sport mediates oculomotor control and thereby perception of relevant information to support expert performance.

Key words: ocular movement, movement perception, extrapolation, prediction

Orientation du regard pendant les occlusions transitoires

Résumé

Il arrive fréquemment que des objets en mouvement dans notre environnement soient occultés. La perte de l'accès aux informations visuelles qui en résulte peut être compensée par l'utilisation d'informations extra-rétiniennes correspondant aux mouvements d'extrapolation des yeux pendant l'occultation. Les études comportementales sur le sujet montrent que l'orientation du regard pendant l'occultation n'est pas un simple réflexe mais permet de prédire le mouvement en cours. En effet, bien que la vitesse de poursuite chute après l'occultation, elle augmente à proximité de la réapparition attendue de l'objet pour diminuer le glissement de l'image rétinienne. De plus, la poursuite pendant l'occultation est combinée avec des saccades oculaires qui permettent un déplacement de l'œil en phase avec le déplacement de l'objet occulté et ainsi de minimiser les erreurs de position au moment de la réapparition de l'objet. La comparaison de conditions de fixation ou de poursuite pendant l'occultation montre que cette dernière est la réponse la plus habituelle et qu'elle permet des estimations spatiales et temporelles du déplacement plus précises. Il a été montré par ailleurs que les régions interconnectées du cortex frontal et pariétal sont actives pendant la poursuite d'objets occultés et sont impliquées dans le contrôle de l'orientation du regard ainsi que de la représentation du déplacement de l'objet. De futures recherches devraient permettre de déterminer si l'expertise en sport est susceptible de permettre un meilleur contrôle oculaire de la poursuite et l'extraction d'informations plus précises sur le mouvement.

Mots clés : mouvements oculaires, perception du mouvement, extrapolation, prédiction

Introduction

Playing sport and doing exercise often involves specialised motor skills performed under prescribed rules and regulations, whereby it is required to intercept and/or avoid various objects. Failure to perceive particular characteristics on the dynamic relationship between the performer and a moving object or opponent could result in a mistimed action or unintended collision. However, experience of spectating or competing in various sport and exercise settings tells us such errors are quite rare. This is no doubt partly due to the highly specific motion processing mechanisms of the human visual system, which can extract very precise information about an object's position, direction and speed as it moves across the retina (Anderson & Burr 1985; McKee 1981). Importantly, though, retinal input alone does not always provide sufficient information for accurate perception, and particularly if the object of interest is not maintained in foveal vision with appropriate eye movements. For instance, static acuity decreases with an increase in retinal eccentricity (Johnson, Keltner, & Balestrery, 1978), object velocity is generally underestimated in the periphery compared to the fovea (Yo & Wilson, 1993), and sensitivity in the periphery is lower for slow than fast moving objects (McKee & Nakayama, 1984).

To help avoid the complex relationship that exists between retinal eccentricity and motion perception (McKee & Nakayama, 1984; Tynan & Sekuler, 1982), the normal response when an object of interest moves relative to the retina, either because of self and/or object motion, is to move the eyes and/or head. Such eye movements can be classified as gaze-stabilizing, which provide the basis for a stable perception as we move in our surrounds (i.e., image stabilisation via vestibular ocular reflex and optokinetic reflex), or gaze-orienting eye (i.e., saccades, smooth pursuit and/or vergence), which bring and then hold an object image on the fovea. In this way, gaze-orienting eye movements ensure the object image is located in the region of high acuity to facilitate the discrimination of object characteristics, and also provide extra-retinal input in the form of outgoing motor signals that is critically important in interpreting retinal stimulation. This is clearly demonstrated in the case of smooth pursuit eye movements, where the object's image is maintained in the region of the fovea but with small amplitude oscillations (Goldreich, Krauzlis, & Lisberger, 1992). In this situation, retinal slip is decorrelated from object velocity, thus leaving extra-retinal input (i.e., efference copy) from smooth pursuit to make the major contribution to object velocity perception. Another benefit of extra-retinal input is that it can provide advance information (i.e. predictive) related to the upcoming object motion. Indeed, during smooth pursuit, extra-retinal input helps overcome delays in processing retinal feedback that would otherwise limit the ability to pursue a fast moving object. In addition, extra-retinal input allows the observer to initiate and/or perpetuate gaze-orientation eye movements when tracking an object in the absence of visual feedback. This ability is particularly important in situations where an object undergoes

transient occlusion such as when from a free-kick in soccer, the goalkeeper's view of the ball trajectory is occluded by the "wall" of defending players. Without extra-retinal input, smooth pursuit eye movements could quickly be replaced by saccades that would bring the eyes to the reappearance location (if it were known in advance). However, the eyes would then be stationary when the object reappeared, which could result in considerable retinal slip (see below for more detail) and potentially impaired perception (de'Sperati & Deubel, 2006).

Although gaze-orienting eye movements can, but not always, influence human perception (Stone, Miles and Banks, 2003; Schütz, Braun, & Gegenfurtner, 2011) until recently little was known about how the eyes are moved when visual feedback of a pursued moving object is suddenly occluded and, therefore, about the underlying control mechanisms. Similarly, little was known about how extra-retinal input from smooth pursuit eye movements influences perception of spatial and temporal characteristics towards the end of a transient occlusion, where an object would either reappear or reach its final destination. In this paper, a review of current research and understanding on this issue is provided. The focus will be on gaze-orienting eye movements exhibited in tracking smooth object motion as opposed to step changes in object position that elicit saccadic eye movements alone or changes of object position in depth that require vergence eye movements. To better understand reflexive and predictive contributions to such eye movements, research reviewed will be limited to experiments that have examined the ocular response in the absence of head movement during short-to-medium duration occlusion (i.e., 600-1200ms) of constant velocity and/or accelerating objects. A model of oculomotor control will then be described and consideration will be given to the role of extra-retinal input to perceptual estimation. To finish, a brief review will be provided on the neural pathways suggested to be involved in extrapolating occluded object motion. Therefore, the focus of this paper will be on fundamental control mechanisms in neurotypical participants, and is thereby intended to provide background from which to consider gaze-orientation in more natural settings such as those experienced when playing sports.

Prediction in Gaze Orientation

If an object moves relative to the retina with frequency of direction change in excess of 0.5 Hz (Westheimer & McKee, 1975), control of smooth pursuit based on visual feedback alone would not permit the maintenance of the object image on the fovea due to processing delays. One solution would be to make reflexive catch-up saccades to correct for the developing position error. However, due to the latency of saccades, which has been measured at approximately 150ms when elicited during smooth pursuit (de Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002), the eye would continually lag behind the moving object.

Observation of eye movement records when tracking sinusoidal object motion of 1Hz and 5deg amplitude (Meyer, Lasker, & Robinson, 1985) shows that participants are quickly able to match well both the stimulus gain and phase. Evidence of similar behaviour can also be seen when pursuing more complex mixed sinusoid trajectories (Barnes, Donnelly, & Eason, 1987) and can be accompanied by phase lead when the mixed sinusoid trajectories have low frequencies (Yasui & Young, 1984).

To account for the ability of smooth ocular pursuit to match object motion, it has been suggested that input from efference copy provides a basic prediction of future object motion (Krauzlis & Lisberger, 1994a; Krauzlis & Miles, 1996; Robinson, Gordon, & Gordon, 1986; Yasui & Young, 1975). Importantly, though, the low-level prediction in these accounts is still thought to be part of the underlying reflexive kernel (see Churchland, Chou, & Lisberger, 2003). Specifically, the efference copy loop (referred to as *eye-velocity memory*) is modelled as an integral part of the reflexive mechanism and is believed to accumulate during the early stages of object pursuit as the eyes are moved in an attempt to nullify a velocity and acceleration error signal from visual feedback (Krauzlis & Lisberger, 1994a; Lisberger, Morris, & Tychsen, 1981). Although efference copy models can explain well the smooth pursuit eye movements in response to sudden onset and offset of constant velocity object motion, it is now well accepted that they do not provide a satisfactory account of the more complex prediction that is required to pursue the type of object motion that is experienced in our normal surrounds (for a review see Barnes, 2008). For instance, despite the efference copy loop quickly attaining a level close to the object velocity, which enables it to perpetuate the ongoing response and overcome visual feedback delay, it is unable to account for the onset of anticipatory smooth pursuit eye movements (up to 30deg/s) that precede regularly time object motion onset (Barnes & Asselman, 1991; Kao & Morrow, 1994). Similarly, without a mechanism to retain the contents of the efference copy loop, it would be unable to generate anticipatory smooth pursuit eye movements that are observed after a period of fixation up to 14.4 s (Chakraborti, Barnes, & Collins, 2002).

Anticipatory Smooth Pursuit during Transient Occlusion

Experiments on pursuit initiation and pursuit of sinusoidal trajectories have revealed much about the role of predictive and reflexive mechanisms in oculomotor control. However, as described in the opening paragraphs of this paper it is common in our normal surrounds for objects to move behind other surfaces and/or objects, which creates a trajectory involving intervals of transient occlusion. When an occlusion is longer than approximately 200ms, the human perceptual system provides constancy of characteristics such as object shape, colour and trajectory. Also, we understand that an object has not simply vanished when occluded (or extinguished in a laboratory setting), and hence that there is a benefit to move the eyes in an

attempt bring the object image near the fovea at object reappearance. If information from the occluder edges is available, it is possible to plan and execute a saccade that brings the eye to the reappearance position to coincide with reappearance time. Such a strategy develops by 21 weeks in human infants and brings the eye to within 2 degrees of the reappearance location with a lag of less than 200ms (Rosander & von Hofsten, 2004). Although a potentially useful way of compensating for the loss of retinal input, failure to maintain smooth pursuit of a moving object during a transient occlusion will result in significant retinal velocity error at reappearance, which may cause difficulties for discriminating object characteristics.

The best strategy during the transient occlusion would be to maintain pursuit gain near unity (i.e., the ratio of eye velocity to object velocity), thereby eliminating the need to predict reappearance time as well as minimizing image blur. However, adult human participants are not able maintain smooth pursuit with gain near unity without contribution from visual feedback (Barnes, 1993). When a moving object simply disappears and is not expected to reappear, eye velocity decays exponentially towards zero (Mitrani & Dimitrov, 1978). Expectation that the moving object will reappear later in its trajectory has been shown to modify smooth pursuit, with eye velocity decaying rapidly (within approximately 190ms) following object disappearance and then reaching a plateau (at approximately 450ms) before being maintained (up to 4000ms) at a reduced gain (Becker & Fuchs, 1985). Similar smooth ocular pursuit has been observed when attention is directed towards “pushing” the unseen object after disappearance (Pola & Wyatt, 1997). These findings, and in particular the relatively stereotypical decay in smooth pursuit, have been modelled as a decrease in the gain applied to the extra-retinal input that contributes to the visuomotor drive (Becker & Fuchs, 1985). More specifically, it has been suggested that the decay in eye velocity results from a reduction in gain applied to the efference copy loop when visual feedback is removed, which by virtue of being arranged as a leaky integrator causes it to decrease toward zero (Krauzlis & Lisberger, 1994; Krauzlis & Miles, 1996; Churchland *et al.*, 2003).

Although this arrangement can explain well the gradual decay in smooth pursuit in the absence of visual feedback, and the enhancement (adaptation) of pursuit gain following learning with auditory stimuli (Madelain & Krauzlis, 2003), it has limited ability to account for an anticipatory increase in eye velocity during transient occlusion back to existing levels. This can be partly overcome by increasing the value of the gain signal acting within the efference copy loop to well above unity but this could create undesirable instability in smooth pursuit following object reappearance (Dallos & Jones, 1963). The problems with this arrangement, therefore, are most evident when trials comprising visible object motion interspersed by a transient occlusion are received in blocked order such that the time, location and velocity of object reappearance are predictable. Under such conditions, Bennett and Barnes (2003) demonstrated that smooth pursuit initially

matches well the moving object when it is visible, then decays following object disappearance, and finally recovers prior to object reappearance (see Figure 1); for qualitative evidence see also (Becker & Fuchs, 1985; Churchland *et al.* 2003). No such decay was observed when the object remained visible throughout the trajectory, whereas no recovery was evident when participants knew the object would not reappear after occlusion. Interestingly, it was reported that the recovery in eye velocity occurred around a similar time for different duration (420, 660 and 900ms) of transient occlusion. This resulted in eye velocity that reached a peak and then decelerated up to and beyond the moment of object reappearance, until visual feedback became available.

Insert figure 1 here

The finding of an “early” anticipatory recovery in smooth pursuit following object disappearance was confirmed in a later study using a longer and wider range (660, 1140, 1620ms) of occlusion (Bennett & Barnes, 2005). Importantly, though, this study also manipulated the duration for which the moving object was visible before it disappeared (240, 480, 720ms). Under these conditions, it was found that the recovery in eye velocity occurred later when the moving object was initially visible for only 240ms. Therefore, the recovery in eye velocity did not occur at the same time after object disappearance, such as if a fixed amount of time was required to register and respond to the loss of visual feedback (i.e., to elicit a decrease and then increase in gain acting on the extra-retinal input). Rather, the recovery occurred when eye velocity approached a minimum threshold, which took longer to reach when pursuing the most briefly presented object (240ms) because eye velocity had not reached its peak before object disappearance. Still, it was again found that the recovery occurred well in advance of object reappearance, and thus although anticipatory, the timing of the recovery did not seem to be well suited to the duration of object occlusion.

Initially, it was suggested that an early recovery in eye velocity was inappropriate because it resulted in retinal slip and blur as the object reappeared (Bennett & Barnes, 2003). However, it was later realised that there are at least two advantages to such a response compared to maintaining low gain smooth pursuit until close to object reappearance. First, because both position and velocity error will accumulate following the decay in eye velocity, it may be advantageous to start reducing these errors as soon as possible rather than allowing them to reach levels that would require a large change in eye position and velocity just prior to object reappearance. Over a long occlusion, this could be achieved with an initial recovery followed by decay and then a further recovery that would thus occur closer to the object reappearance (see Bennett & Barnes, 2005). Second, by releasing a recovery when eye velocity approaches a threshold level, it removes the need

for a timing mechanism that represents the duration of the transient occlusion. This could free processing resources to extract and represent information about object speed and direction, and would be particularly valuable when participants do not have sufficient experience to construct a reliable estimate of occlusion duration. For instance, by maintaining eye velocity closer to object velocity for a greater proportion of the occlusion, it would be more appropriately scaled in the event of a mistimed reappearance.

Predictive Smooth Pursuit during Transient Occlusion

Although not entirely satisfactory, the finding of an anticipatory recovery in smooth pursuit during transient occlusion could be achieved by increasing the value of the gain signal acting within the efference copy loop to a value greater than unity. It is debatable, however, whether such an approach could generate a predictive increase in eye velocity during occlusion, such as required if there were a step change in object velocity due to contact with another moving object. To examine this issue, a study was conducted in which participants were instructed to pursue a moving object that underwent a predictable increase or decrease in velocity during the occlusion (Bennett & Barnes, 2004). Participants received 12 blocked presentations where the object moved at 12 or 24deg/s for 400ms, after which it was occluded for either 400 or 800ms, and then reappeared at either the same (12-12 or 24-24deg/s) or a changed velocity (12-24 or 24-12deg/s). By presenting trials in blocked order participants had implicit knowledge of the upcoming object motion and the opportunity to consolidate their response (i.e., a form of so-called long-term prediction; Deno, Crandall, Sherman, & Keller, 1995), which we expected to facilitate predictive smooth pursuit. Consistent with previous work, eye velocity decayed following object disappearance and then recovered back towards previous levels in advance of object reappearance. More importantly, though, in trials with a predictable increase in object velocity, eye velocity initially decayed from approximately 12deg/s following object occlusion but then increased to almost 20deg/s at object reappearance.

Insert figure 2 here

More subtle predictive scaling of eye velocity is required when tracking an object that undergoes acceleration. With visual feedback continuously available the human oculomotor system is able to pursue well sinusoidal object motion that comprises changing acceleration (Bahill & McDonald, 1983; Waterston, Barnes, & Grealy, 1992). Sensitivity to object acceleration has also been shown during the initial 100ms of smooth pursuit onset in discrete step-ramp stimuli (Krauzlis & Lisberger, 1994a, 1994b). Subsequent work indicated that participants in fact have high oculomotor discrimination thresholds for object acceleration and

thus pursue accelerating objects by matching the different levels of velocity (i.e., the effects of acceleration) (Watamaniuk & Heinen, 2003). This could be expected given that the visual system does not have acceleration sensitive cells and instead would have to rely on indirect determination of acceleration by population coding of a velocity signal in the medial temporal (MT) area (Lisberger & Movshon, 1999). Such a process would also be subject to processing delays and thus it would remain necessary that the internal drive (i.e., extra-retinal input) also represents the changing velocity characteristics of accelerative object motion. For sinusoidal object motion it has been suggested that the internal drive can adequately represent the previous half-cycle by storing samples of velocity taken at regular intervals (Barnes & Asselman, 1991). As well as simulating well the smooth ocular response by the second cycle of object motion, subsequent work indicated that the ocular response persisted in catch trials (e.g., no appearance of the object, sudden cessation of object motion, or sudden change of object motion), thus providing strong evidence for the storage and subsequent release of an internal drive (Barnes, Barnes, & Chakraborti, 2000).

Bennett and Barnes (2006) examined whether smooth ocular pursuit persists during transient occlusion (i.e., 800ms) and if so, whether it is representative of accelerative object motion. Objects moved with either constant velocity or accelerated throughout the trajectory (4 or 8deg/s^2), and were presented in random and blocked order. Also, objects were initially seen moving for 200 or 600ms, and had different velocity at occlusion. For random order trials, eye velocity when pursuing the constant velocity (0deg/s^2) object for a short duration (200ms) was too high at the moment of object disappearance and eventually resulted in eye velocity that was inappropriately high at the moment of reappearance. Conversely, eye velocity when pursuing the object accelerating at 8deg/s^2 for a short duration (200ms) was well matched to object velocity at the moment of object disappearance but did not quite reach the level of object velocity at the moment of reappearance, despite showing a significant recovery after the typical decay. Therefore, eye velocity in these trials was reflective of a predictive process that attempted to minimize retinal slip by generating a response that was biased toward the trajectory of the accelerating objects. A similar lack of scaling of eye velocity to object velocity at the moment of reappearance was evident in random presentations when the object had initially been pursued for a longer duration (600ms). For blocked order trials, there was evidence of better scaling during the initial period of object tracking, throughout the transient occlusion, and at reappearance. Eye velocity when pursuing the constant velocity object was well matched to object velocity at the moment of disappearance and reappearance. Also, for objects accelerating at 8deg/s^2 , eye velocity at reappearance undershot object velocity to a lesser extent than in random order trials. Notably, having pursued blocked, and hence predictable object motion (8deg/s^2) for both the shorter (200ms) and longer (600ms) duration ramp, the majority of participants exhibited an additional increase in eye velocity at the

moment of reappearance over and above the level achieved at the end of the initial visible ramp.

Insert figure 3 here

While the above study confirmed that participants are able to scale smooth eye velocity during transient occlusion when object motion is predictable, the design did not eliminate the possibility that smooth pursuit was based on an expected step-change in object velocity either side of the occlusion. Therefore, a follow-up experiment was performed in which object position and velocity just prior to occlusion, as well as mean object velocity during the initial visible ramp, were decorrelated from object acceleration (Bennett, de Xivry, Barnes, & Lefèvre, 2007). It was found that as long as the object was visible for 500ms, smooth eye velocity was appropriately scaled to object velocity (0 or 8deg/s) generated by the different levels of object acceleration (-4, -8, -12, -16 or -8, -4, 0, 4, 8deg/s²) before, during and after occlusion. However, there was significant retinal slip at object reappearance at the outermost levels of acceleration (-8 and 8deg/s²). Thus it was suggested that while information related to object acceleration can be extracted on-the-fly during the initial visible ramp, the process is not entirely sufficient to drive the predictive oculomotor response in the absence of visual input.

To examine the influence of so-called short-term and long-term prediction (Deno *et al.*, 1995) on the oculomotor response, Bennett, de Xivry, Lefèvre, and Barnes (2010) compared ocular pursuit to constant velocity and accelerating objects (-8, 0, 8deg/s²) presented in random or blocked order. Catch trials were also randomly interleaved in which object acceleration was unexpectedly modified (-4 or +4deg/s²). As expected, irrespective of trials order, smooth eye velocity decayed following object occlusion and then recovered towards the different levels of object velocity at reappearance. However, the recovery was better scaled in late blocked-order trials (i.e., last 6) than early blocked-order trials (i.e., first 3) or random-order trials (i.e., last 6). Still, even following adaptation in blocked-order trials there was significant undershoot when pursuing the positively accelerating object. It was found that participants exhibited evidence of a scaled response to an unexpected change in object acceleration (i.e., catch trials), although there were also transfer effects from the preceding blocked-order trials. These findings were suggested to show that on-the-fly prediction (short-term) is combined with memorized information from previous trials (long-term) to generate a persistent and veridical prediction of occluded object motion. Further evidence for this interpretation was found in the combined displacement produced by saccades and smooth pursuit during occlusion (i.e., total eye displacement), which was well matched to object displacement after only 3 repeats of blocked-order trials.

Insert figure 4 here

Although it is uncertain how short-term and long-term prediction is realised within the neural regions known to be involved in oculomotor control (for a brief discussion for section below), it is clear that such effects need to be taken into account. Reflexive models that propose an accumulation of internal drive in the form of efference copy can explain well the onset and offset of smooth pursuit eye movements to unexpected object motion. However, an additional way of representing and storing more complex internal drive, which can be released under volitional control, is required to account for pursuit of the varied object motion experienced in our normal surrounds. In recognition of these demands, it is necessary that a model of oculomotor control should include a reflexive and predictive loop. Barnes and colleagues (Barnes & Asselman, 1991; Barnes & Wells, 1999) modelled the reflexive loop (i.e., direct pathway) as an ongoing efference copy, which perpetuates eye motion when there is only a weak expectation regarding the upcoming stimulus characteristics. The predictive loop (i.e., indirect pathway) was placed in parallel with the reflexive loop and thus receives the same input. However, the predictive loop is modelled as a form of working memory (MEM), with the key features being that the representation of object motion is adaptive to prior stimulation/experience (i.e., dynamic) and can be temporarily retained in the absence of eye movement (i.e., fixation) and/or visual feedback (i.e., occlusion). Another advantage of including a mechanism that retains a representation of object motion is that this could be used to control eye displacement via saccades in the event that eye velocity control is inadequate. This issue is considered in the following section.

Coordination between Smooth Pursuit and Saccades

Although once seen as distinct gaze-orienting eye movements with different dynamics and function, smooth pursuit and saccades play complimentary roles when tracking a moving object. This is particularly evident when attempting to foveate a fast moving object that follows an unpredictable trajectory (e.g., a rugby football bouncing unpredictably across the pitch). Under such circumstances, the delay in initiating smooth pursuit combined with the limited onset dynamics would make continuous foveation of the object unfeasible. Therefore, the pursuit system tracks the unpredictable moving object with a combination of smooth pursuit and saccades. This necessitates that the smooth and saccadic systems share information. For instance, with a saccade latency of approximately 150ms when exhibited during smooth pursuit, it follows that the saccade would always fall short of the moving object if programmed according to position error alone. To overcome this it is necessary for the saccadic system to also take account of the extrapolated object location, as well

as displacement from smooth eye movement that occurs during saccade programming (see de Brouwer *et al.*, 2002). There are also several observations indicating a contribution from position error to smooth pursuit. For example, the step of object position in the Rashbass paradigm (Rashbass, 1961), which was originally developed to eliminate saccades during smooth pursuit onset, generates some smooth eye movement (Wyatt & Pola, 1987). Furthermore, it has been shown that a sudden change of an object's position when in motion causes a change in smooth eye velocity in order to minimize the position error (Carl & Gellman, 1987; Segraves & Goldberg, 1994).

When a moving object undergoes transient occlusion, visual feedback regarding position and velocity error is no longer available. Consequently, the development of position and velocity error that occurs as a result of reduced eye velocity can only be corrected by reference to an internal representation that reflects the moving object's trajectory. Observation of eye position data indicates that reduced gain of smooth pursuit during occlusion is often combined with saccades that place the eye slightly ahead of the expected trajectory (for qualitative description see Becker & Fuchs, 1985; Madelain & Krauzlis, 2003). Therefore, a more detailed examination of saccadic and smooth pursuit eye movements object occlusion was achieved by asking participants to pursue a moving object that was subject to an independent but predictable step change of position (-6deg, 0deg, or 6deg) and/or velocity (-6deg/s, 0deg/s or 6deg/s) at reappearance (Orban de Xivry, Bennett, Lefèvre, & Barnes, 2006). Investigation of the interaction between the smooth and saccadic eye movements on a trial-by-trial basis indicated that both systems worked in synergy during object occlusion. That is, the saccadic system modified its contribution to the total eye displacement to compensate for changes in the smooth eye displacement resulting from smooth pursuit (see Figure 5). Thus, when smooth pursuit eye movements contributed less to the eye displacement during the occlusion, the saccadic system increased its contribution and vice versa. This synergy between smooth and saccadic eye movements was very effective in minimizing position error at the moment the object reappeared. For instance, when there was no position step, eye position error as the object reappeared was almost zero (mean=0.15deg), whereas for the negative and positive position steps, eye position error was equal to +1.5deg and -1.5deg, respectively. Such eye position control would have ensured the object was in foveal vision at the moment it reappeared, thereby providing the opportunity for improved perception of object characteristics. Moreover, the fact that this response occurred without any visual feedback, indicates that participants compare the ongoing trajectory of the eye to an internal representation of future object motion. Other work in which participants tracked curvilinear object motion has indicated discrepant findings regarding the control of position error by saccades during occlusion but nonetheless confirms that the internal

representation is not limited to a single axis of motion (Mrotek & Soechting, 2007; Orban de Xivry, Missal, & Lefèvre, 2009).

Insert figure 5 here

Gaze-Orientation for Temporal and Spatial Estimation

Up to this point, it has been shown that gaze-orientation can be maintained during transient occlusion such that eye displacement is well matched to object displacement for even quite complex motion trajectories (for a detailed consideration of the factors driving eye position control see Orban de Xivry *et al.*, 2009). Eye velocity is not as well controlled but still there is evidence of perpetuation and predictive scaling. Such volitional control over gaze-orientation could facilitate visual perception, and thereby a subsequent motor response made after an object reappears. Indeed, if a goalkeeper did not continue to pursue the ball during a transient occlusion, position and velocity error at reappearance could be so large that perception would be impaired. Experimental evidence supporting this supposition can be found in work that has compared temporal and spatial estimation after a period of occlusion in conditions of fixation and pursuit, and as shown below is somewhat dependent on the characteristics of object motion (i.e., velocity, duration of occlusion).

Peterken, Brown, & Bowman, (1991) reported that there were no differences in temporal estimation errors of time-to-contact (TTC) between fixation and pursuit conditions with medium and fast velocity objects (i.e., 5 and 10deg/s). There was, however, an increase in absolute error of TTC estimation with a slow moving object (i.e., 2.5deg/s), which was compounded when pursuit was not permitted. The authors concluded that while continued pursuit of the occluded object might be the preferred and most effective strategy, eye movements are not a prerequisite for accurate estimation of TTC; for a review of the potential processes involved in TTC estimation see Tresilian (1995); DeLucia and Lidell (1998). To overcome some of the limitations in the design of Peterken *et al.* (1991), a more recent study revisited the issue of temporal estimation during fixation or pursuit (Bennett, Baures, Hecht, & Benguigui, 2010). Using a design that included 15 temporal intervals ranging from 400 to 1500ms and three object velocities (2.5, 5 or 10deg/s), it was found that both constant error and variable error increased as a function of TTC. However, for the fixation group only there was a significant effect of object velocity with a relative overestimation of TTC for the slower velocity and underestimation for the faster velocity. The velocity effect exhibited by the fixation group was consistent with participants exhibiting a relatively constant misperception for each level of object velocity. Therefore, it was suggested that maintaining fixation at the arrival location introduces error in motion

perception associated with the processing of peripheral retinal input (i.e., moving object). Overall, these findings show that there is an advantage for temporal estimation to pursue the moving object with the eyes.

Insert figure 6 here

In terms of how gaze is oriented in such tasks, anecdotal reports (Rosenbaum, 1975) suggest that participants initially track the visible object and then maintain smooth pursuit of the occluded object all the way up to point of contact. This would seem at odds with work described above on ocular pursuit during transient occlusion but admittedly there are differences in the stimulus conditions. Therefore, we conducted a detailed quantitative analysis of eye movements in a temporal estimation task with constant velocity and accelerating objects (Benguigui & Bennett, 2010). It was found that participants initially maintained pursuit during occlusion but then made a large amplitude saccade to the region of the arrival location. After arrival of the eye, participants gave their manual estimation of TTC, which was found not to be functionally related in the majority of participants. In the main, eye movements during occlusion did not predict well TTC estimation, even though both are best predicted by first-order information based on visual properties from the moving object and the point of contact. While not questioning these findings, there are two attributes of the stimulus used in the temporal estimation task that could influence gaze-orientation: i) the object does not reappear when it reaches the arrival location, and ii) a visual cue representing the arrival location remains present throughout the presentation. Together, these stimulus features reduce the ability and need to match eye position and velocity to that of the object during occlusion, and thereby the potential contribution of oculomotor information to estimation accuracy. Also, the presence of a visual cue at the arrival location could facilitate the use of cognitive strategies. For instance, participants might perceive information related to the properties of the moving object (e.g., velocity and occlusion distance), and then count down the time from object occlusion to arrival at the point of contact (Tresilian, 1995). This process would not be dependent on continued pursuit but it could be affected by a misperception of object motion during the initial visible part of the trajectory, and thus account for the temporal estimation error observed during fixation.

Using a task that required participants to estimate if the time at which an occluded object reappeared was correct, Makin and Poliakoff (2011) sought to determine the contribution of the oculomotor system by comparing conditions of fixation and pursuit. It was found that participants made more errors in their estimation of early reappearing objects (-300ms) in the fixation than pursuit condition. Also, there was some tentative evidence indicating that estimation errors for early reappearing objects (-150ms) were related to the correspondence between eye and object position during the initial 360ms of motion (i.e., 298ms visible +

72ms occlusion). Using a similar task, Bennett and Benguigui (2012) examined gaze-orientation when participants were required to make a spatial estimation in the absence of a fixed visual cue indicating reappearance position (i.e., did the object reappear behind or ahead of its correct location). Response accuracy with these stimulus conditions places greater demand on extrapolation of the occluded trajectory because the participant does not know in advance where and when the object will reappear. Results indicated that participants pursued the moving object up to the moment of occlusion in accord with the veridical motion properties. They then continued to pursue the occluded object with a combination of smooth and saccadic eye movements (see also Bennett & Barnes, 2006). However, ocular pursuit of the randomly-ordered accelerative object motion during occlusion was not ideal, and resulted in undershoot of eye position and velocity at the moment of object reappearance. As for spatial estimation, there was a bias such that participants were less likely to report object reappearance being behind than ahead of the actual position. Also, participants' spatial estimation did not take into account the effects of object acceleration. Finally, spatial estimation was found to be best predicted by the difference between object reappearance position (not eye position) and an extrapolation based on pre-occlusion velocity.

In combination, the above findings indicate that eye movements during occlusion contribute to, but do not uniquely specify information used for spatial and temporal estimation. It would seem that participants continue to move their eyes during occlusion in order to facilitate a visual discrimination between object reappearance position and the most recent and salient information for the goal of the task at hand. Indeed, not attempting to maintain pursuit would be a somewhat unnatural response that could also result in significant position and velocity error at reappearance, as well as a delayed reorienting of gaze (de'Sperati & Deubel, 2006). Moreover, not pursuing the object prior to occlusion could impair velocity perception, and thus contribute to differences between conditions of fixation and pursuit. In this respect, it is noteworthy that in a task that required participants to estimate accuracy of reappearance position for an object moving on a circular trajectory, we have recently confirmed that performance is improved in a condition of pursuit compared to fixation (Bennett & Benguigui, 2013). The key point here is that with an object moving on circular trajectory the distance from the fixation point is kept constant, thus minimizing effects of velocity misperception due to retinal eccentricity.

Neural Pathways for Ocular Pursuit

On the basis of electrophysiological recordings in non-human primates, and more recent functional imaging studies of humans, there is now good understanding about the neural pathways involved in evoking smooth pursuit and saccadic eye movements (for a review see Pierrot-Deseilligny, Milea, & Müri, 2004).

These findings have challenged the notion that smooth pursuit and saccades receive input through distinct neural pathways and some authors have identified areas of considerable overlap (see Krauzlis, 2004, 2005; Krauzlis & Stone, 1999; Their & Ilg, 2005; Bastin *et al.*, 2012). There have also been several studies that have sought to determine whether the same and/or other neural pathways contribute to pursuit of a moving object that undergoes transient occlusion compared to one that is constantly visible. Indeed, given that no retinal input is available during transient occlusion, it is clear that extra-retinal signals are required if smooth and saccadic eye movements are to be maintained. The following paragraphs provide a summary of evidence from relevant studies on this issue.

The medial superior temporal (MST) area of the visual association cortex (V5a in humans), which processes velocity error signals when an object is visible, is known to receive extra-retinal inputs (Komatsu & Wurtz, 1989; Newsome, Wurtz, & Komatsu, 1988; Ono & Mustari, 2006). MST is implicated in the maintenance of smooth pursuit (Dürsteler & Wurtz, 1988) and a subset of neurons continues to be active when an object undergoes transient occlusion (Ilg & Their, 2003; Newsome *et al.*, 1988). However, there is some evidence that MST activation does not differ when tracking an object that is continuously visible compared to one that is temporarily extinguished (Lencer, *et al.*, 2004). These same authors did, however, report differential activation in frontal eye fields (FEF), intraparietal sulcus (IPS) and dorsolateral prefrontal cortex (DLPFC) between conditions of continuous vision and transient occlusion. In terms of the behaviour, it was reported in later studies that saccade frequency increased during occlusion, and that saccade frequency was negatively correlated with activity in IPS (Nagel, *et al.*, 2006; Nagel, Sprenger, Hohagen, Binkofski, & Lencer, 2008). In a separate study that controlled for the presence of saccades by requiring participants to covertly pursue a moving object (i.e., eyes fixated on central location), increased IPS activity was still observed during transient occlusion (Olson, Gatenby, Leung, Skudlarski, & Gore, 2003). While such activity could in part be related to the suppression of saccades (Tzelepi, Lutz, & Kapoula, 2004), it would seem that a key role for the IPS is the representation of an occluded object for the purpose of later action (Bremmer, Distler, & Hoffmann, 1997; Duhamel, Colby, & Goldberg, 1992; Schlack, Hoffmann, & Bremmer, 2003).

FEF has been suggested to play a major role in the control of smooth pursuit onset (Gottlieb, Bruce, & MacAvoy, 1993; Tanaka & Lisberger, 2001) and prediction during pursuit of sinusoidal trajectories (MacAvoy, Gottlieb, & Bruce, 1991). FEF is also part of the main pathway to the oculomotor neurons for control of saccades, with direct projections to the superior colliculus (SC) and brainstem premotor nuclei (PMN), as well as through the Basal Ganglia (caudate nucleus and substantia nigra pars reticulata) and lateral intraparietal area (LIP) of the IPS. Activity in monkey FEF during transient occlusion with eyes stationary is related to object velocity and was suggested to provide a dynamic internal representation for subsequent

action (Barborica & Ferrera, 2003; 2004). While there has been some evidence that activity in FEF of humans does not differ between conditions of continuous vision and occlusion (Ding *et al.*, 2009; Nagel *et al.*, 2008), there are other reports that there is a difference and that this is also related to smooth eye velocity. For instance, Nagel *et al.* (2006) found a negative correlation between smooth eye velocity and activity in FEF, which was reversed when the object was continuously visible. It was suggested that the negative correlation reflected the fact that reduced smooth eye velocity during occlusion demanded increased contribution from extra-retinal input to predict the ongoing object trajectory.

The most obvious and consistent differences between pursuit of a continuously visible versus occluded object have been observed in DLPFC, which exhibits greater activation in the absence of visual feedback (Ding, Powell, & Jiang, 2009; Nagel *et al.*, 2006; 2008). There is evidence that the magnitude of smooth eye velocity and activity in DLPFC are correlated during occlusion (Nagel *et al.*, 2006; 2008), and that activation of DLPFC is correlated with FEF (Ding *et al.*, 2009). DLPFC has been associated for some time with working memory (Levy & Goldman-Rakic, 2000; Passingham & Sakai, 2004), as well as other executive functions such as decision making and object selection (Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000; Hagler & Sereno, 2006). Importantly, DLPFC has connections with FEF, which permit control of saccades (Pierrot-Deseilligny *et al.*, 2005), and could maintain activity in pursuit related areas of FEF during occlusion by providing a visual memory in the absence of retinal input (Ding *et al.*, 2009). In this respect, it is notable that increased activity in DLPFC during occlusion, and hence the reliance on working memory to guide smooth pursuit, is suggested to occur around 200ms after the loss of visual input (Makin, Poliakoff, Ackerley, & El-Deredy, 2012). This is somewhat earlier than the recovery in smooth eye velocity (Bennett & Barnes, 2003), but this could be expected given the time needed to initiate a new oculomotor response. Finally, it has been reported that DLPFC activation differs depending on the short-term and long-term predictability of object motion as conveyed by trial order (i.e., random vs. blocked) or cues to motion trajectory, which is again consistent with the demand placed on spatial working memory (Burke & Barnes, 2008; Nagel *et al.*, 2008).

Summary

Predictive smooth and saccadic eye movements are critical to maintain gaze-orientation in our normal surrounds where fast moving objects are frequently occluded by other surfaces and objects. Such behaviour requires extra-retinal input that can account for both reflexive and predictive control of the eyes required to track simple and complex object motion. Evidence from behavioural studies on gaze orientation during occlusion indicate that participants exhibit a synergy between smooth pursuit and saccades in order to

minimize position error and retinal slip at the moment the object reappears. Electrophysiological and imaging studies indicate that interconnected areas of the frontal and parietal cortex provide the means to represent occluded object motion and thereby control gaze-orientation. An intriguing next challenge will be to determine whether, and how, the interplay between reflexive and predictive mechanisms in fundamental gaze-orienting tasks differs as a function of expertise in sport where participants pursue moving objects within our natural surrounds.

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Figures and captions

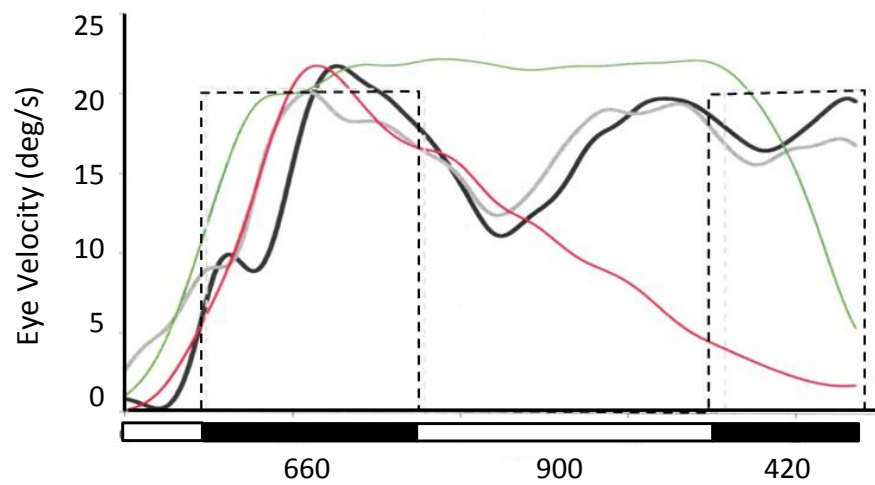


Figure 1. Smooth eye velocity averaged across trials for a single participant vs. time when pursuing a 20deg/s object presented in random order (solid grey lines) and blocked order (solid black lines). Broken line indicates when object was visible (high) and occluded (low). Bars beneath abscissa indicate time for which object was visible (black) and occluded (white). Smooth eye velocity from control trials presented in blocked order (red solid line= no reappearance; green solid line = no occlusion) are shown for comparison. Adapted from "Human ocular pursuit during the transient disappearance of a visual object" by S.J. Bennett and G.R. Barnes, G.R., 2003, *Journal of Neurophysiology*, 90, 2504-2520.

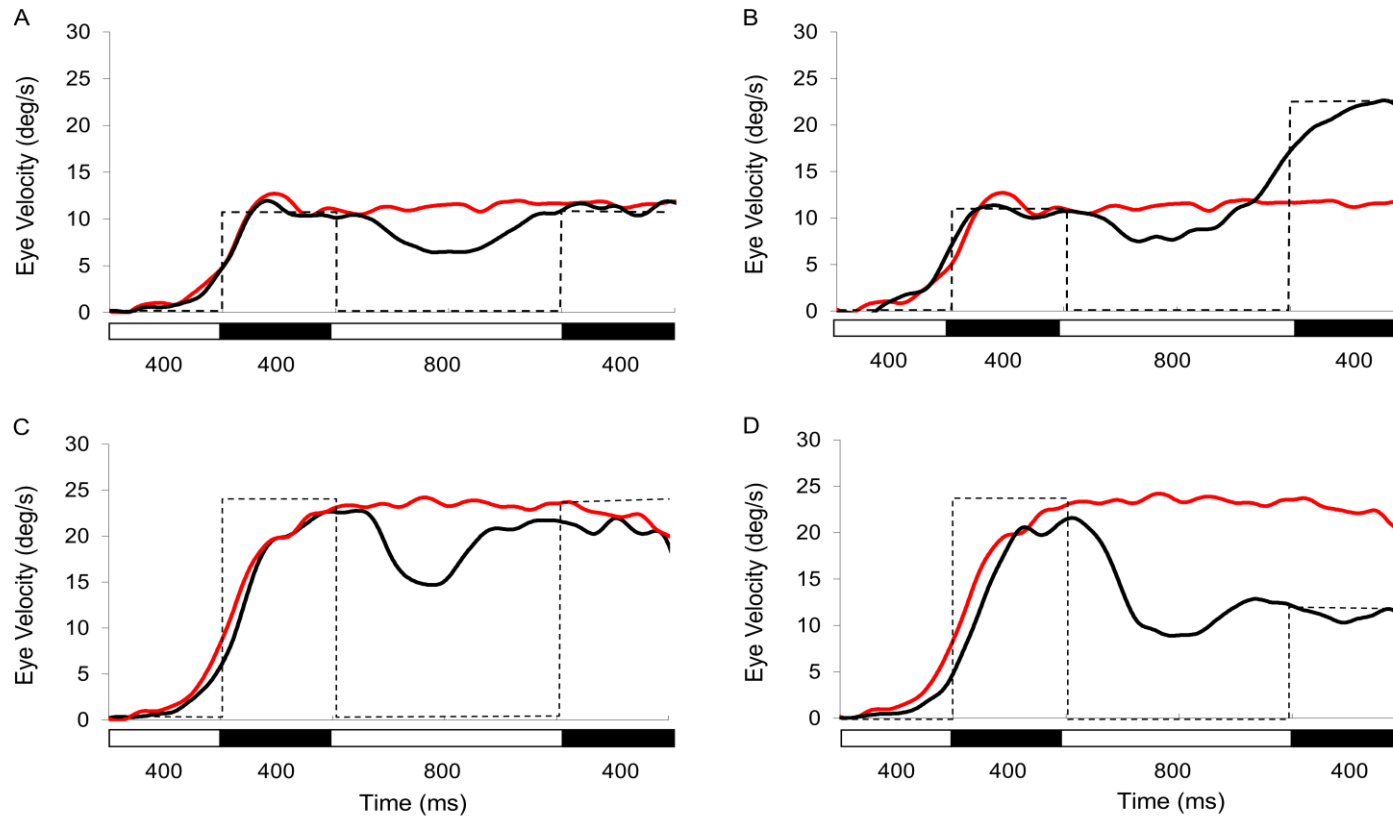


Figure 2. Smooth eye velocity averaged across trials for a single participant (thick black lines) and pursuit object (thin black lines) vs. time (ms). In A, object velocity was initially 12deg/s and reappeared at 12deg/s. In B, object velocity was initially 12deg/s and reappeared at 24deg/s. In C, object velocity was initially 24deg/s and reappeared at 24deg/s. In D, object velocity was initially 24deg/s and reappeared at 12deg/s. Broken line indicates when object was visible (high) and occluded (low). Bars beneath abscissa indicate time for which object was visible (black) and occluded (white). Smooth eye velocity (thick red lines) for control presentations (no occlusion) is included for comparison. Adapted from "Predictive smooth ocular pursuit during the transient disappearance of a visual object" by S.J. Bennett and G.R. Barnes, G.R., 2004, *Journal of Neurophysiology*, 92, 578-590.

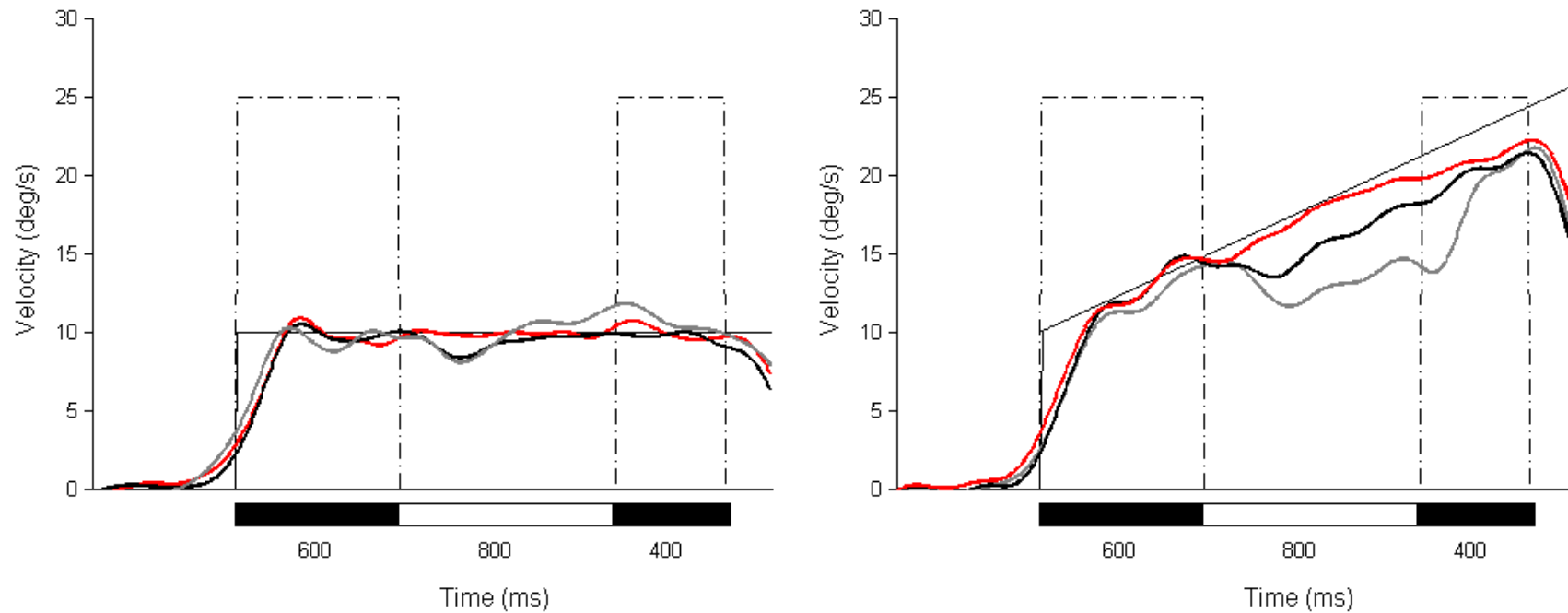


Figure 3. Smooth eye velocity averaged across trials for a single participant in random (solid grey lines) and blocked (solid black lines) presentations vs. time (ms). Pursuit object is represented by solid thin black lines. The object was initially visible for 600ms and then moved with acceleration of 0deg/s^2 (left panel) or 8deg/s^2 (right panel). Broken line indicates when object was visible (high) and occluded (low). Bars beneath abscissa indicate time for which object was visible (black) and occluded (white). Smooth eye velocity for control presentations (thin red line) is included for comparison. Adapted from "Smooth ocular pursuit during the transient disappearance of an accelerating visual target: The role of reflexive and voluntary control" by S.J. Bennett and G.R. Barnes, G.R., 2006, *Experimental Brain Research*, 175, 1-10

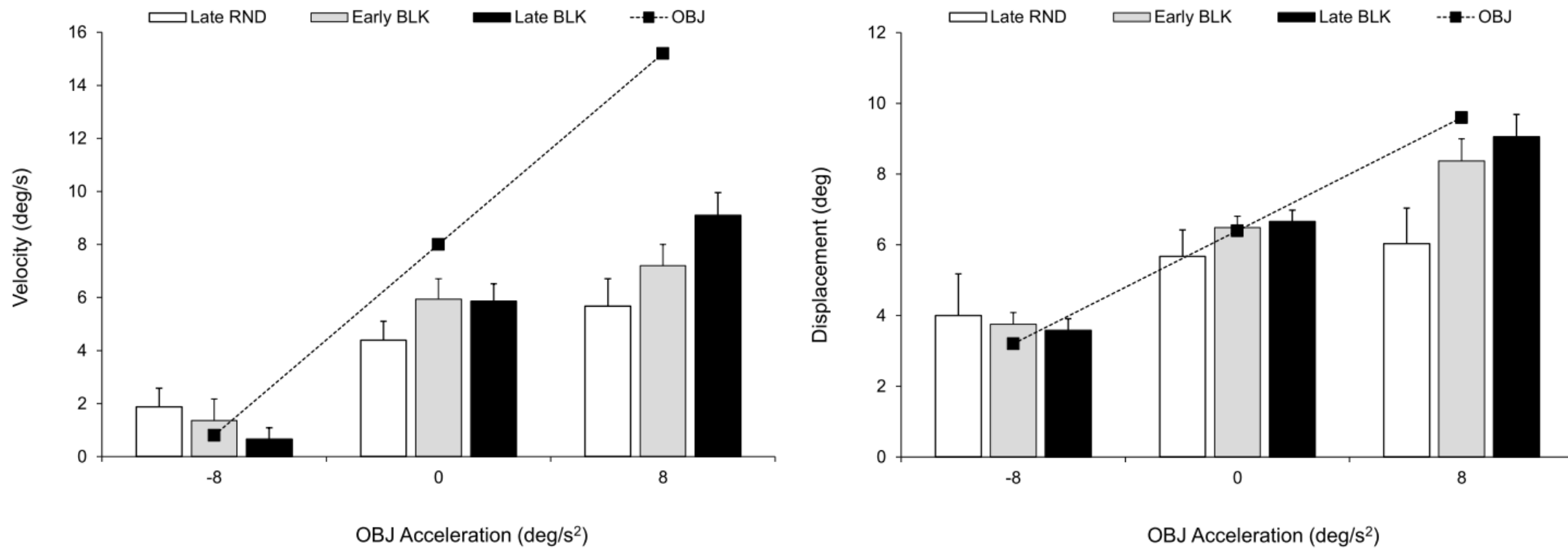


Figure 4. Group mean (+SE) eye velocity at the end of occlusion (left panel) and total eye displacement (TED- right panel) as a function of object (OBJ) acceleration. White bars (late random-order: Late RND), light grey bars (early blocked-order: Early BLK) and black bars (late blocked-order: Late BLK) represent experimental trials, respectively. Object velocity and displacement (diagonal dashed line) is included for comparison. Adapted from "Oculomotor prediction of accelerative target motion during occlusion: long-term and short-term effects" by S.J. Bennett, J.J.O. de Xivry, P. Lefèvre and G.R. Barnes, G.R., 2010, *Experimental Brain Research*, 204, 493-504.

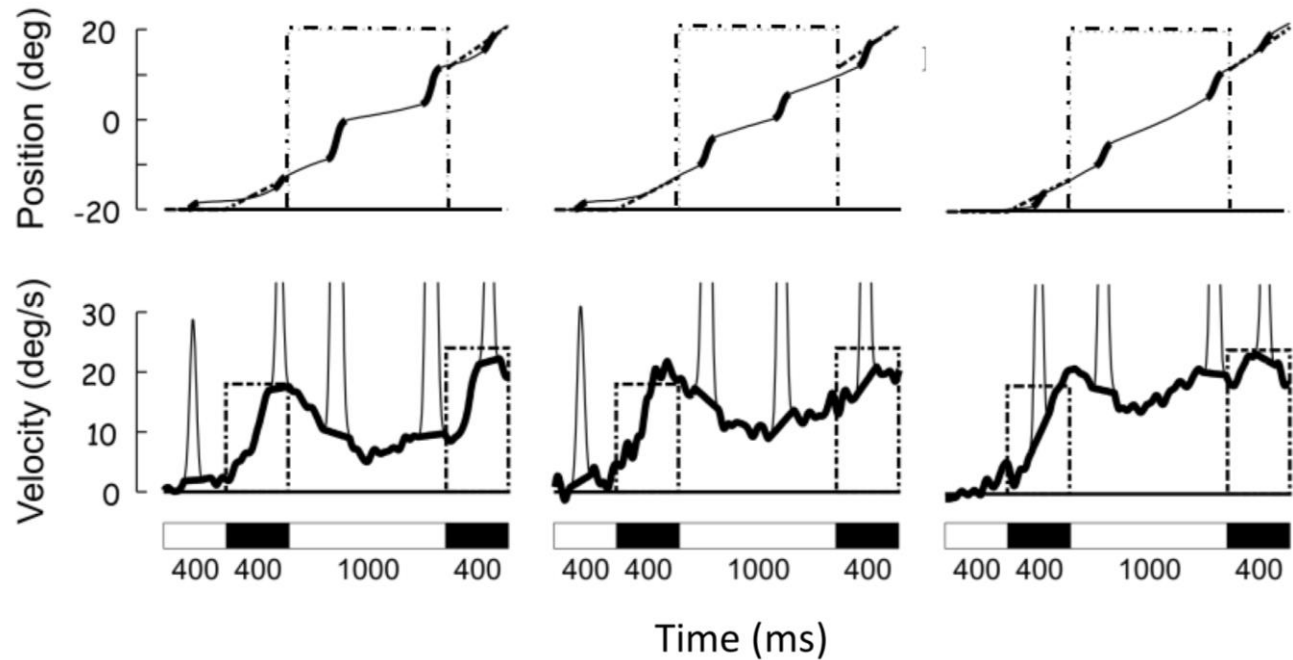


Figure 5. Representative examples of eye (solid lines) position (upper panels) and velocity (lower panels) vs. time (ms) for 3 presentations of an object (dashed traces) that underwent a +6deg position step and +6deg/s velocity step during occlusion. The object was visible when time bars (on the bottom of the graphs) are black. On the position panels, thin and thick solid lines correspond to smooth and saccadic eye movements respectively. On the velocity panels, thick solid lines represent desaccaded smooth eye velocity and thin solid lines correspond to saccades. Adapted from “Evidence for synergy between saccades and smooth pursuit during transient target disappearance” by J.J.O. de Xivry, S.J. Bennett, P. Lefèvre and G.R. Barnes, G.R., 2006, *Journal of Neurophysiology*, 95, 418-427.

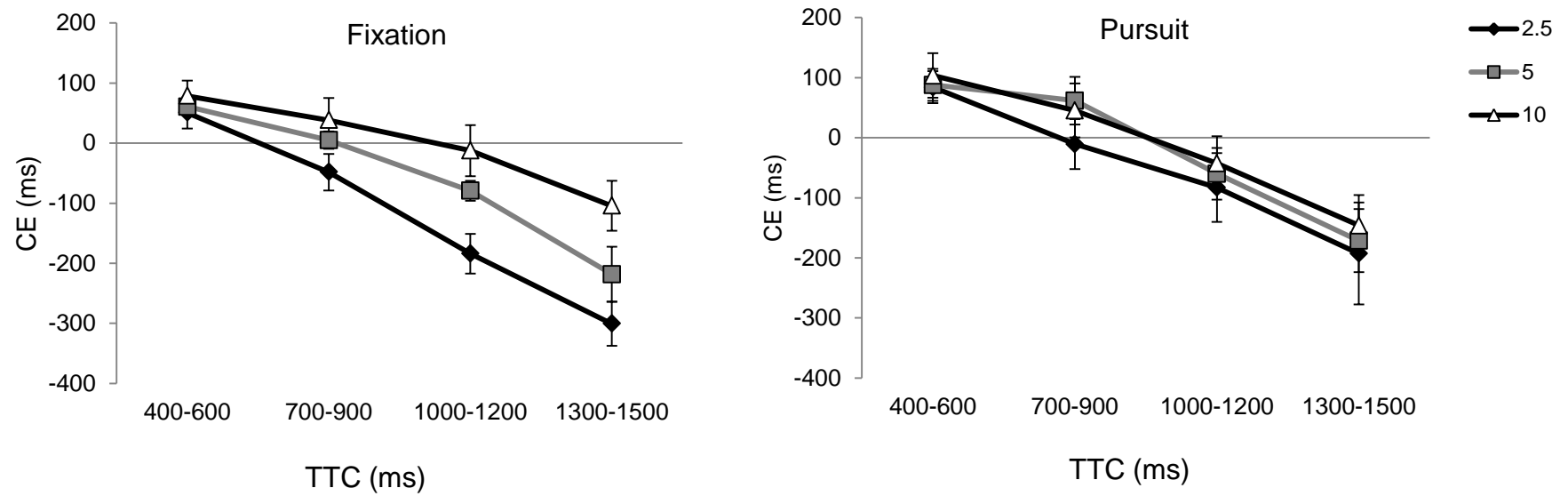


Figure 6. Constant error (CE) in estimated TTC as a function of viewing condition and object velocity for the fixation (left panel) and pursuit (right panel) groups. Error bars represent SE of mean. NB. Negative CE indicates underestimation of TTC. Adapted from "Eye movements influence estimation of time-to-contact in prediction motion" by S.J. Bennett, R. Baures, H. Hecht and N. Benguigui 2010, *Experimental Brain Research*, 206, 399-407.