



UNIVERSITÉ  
DE GENÈVE

FACULTÉ DE PSYCHOLOGIE  
ET DES SCIENCES DE L'ÉDUCATION

Section de Psychologie

Sous la direction de Dirk Kerzel

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## ATTENTION FOR MOVING THE EYE

THESE

Présentée à la  
Faculté de psychologie et des sciences de l'éducation  
de l'Université de Genève  
pour obtenir le grade de Docteur en Psychologie

par

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Thèse No 427

GENEVE

Juin 2009



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## Remerciements

Je tiens tout d'abord à remercier le Professeur Dirk Kerzel. Ces années de thèse n'auraient pas été aussi agréables et productives s'il n'avait pas été un excellent mentor. Je dois également remercier Guillaume Masson et Karl Gegenfurtner pour m'avoir accueilli dans leurs laboratoires respectifs à bras ouvert, ainsi que leurs étudiants et post-docs, spécialement Anna Montagnini et Alexander Schütz.

Je remercie spécialement Sandrine Amstutz et Sofia Ferreira de m'avoir épaulé dans diverses tâches administratives avec tant d'efficacité et de bienveillance.

Je suis extrêmement redévable envers mes parents, David et Encarnita Souto, ainsi qu'envers Florence Vandenbeusch, pour leur soutien inconditionnel. *Last but not least*, je remercie ma *compagne* Marie Vandenbeusch d'avoir partagé avec moi ces dix dernières années, en me donnant l'énergie nécessaire à cette longue entreprise, ainsi que pour m'avoir soutenu sur le plan logistique et moral pendant la période de rédaction.

A miña abuelita Celsa

## Abstract

As a consequence of primate's inability to process detail outside the foveal region of the visual field, we have to move our eyes continuously. We can also overcome those structural limitations by moving attention while keeping our eyes still. A prominent theory, the premotor theory of attention, links our ability to covertly shift attention to the preparation of eye movements. This relation has been extensively studied in the context of programming of voluntary saccades. Much less is known about how attention is related to the programming of smooth pursuit eye movements, which role is to reduce objects' retinal speed and is needed in combination with saccades for a sharp perception of objects for scrutiny.

Contrary to the initiation of saccades, it was shown that initiation of smooth pursuit is not disrupted by attending to the periphery during movement programming. The results are consistent with the idea that pursuit can be engaged pre-attentively when there is no competing moving distractor. When we have to select the target in presence of a distractor moving in an opposite direction, pursuit can be initiated with little delay if attention is allocated in advance to the target location. In this condition, the pursuit choice reflects the perceptual priority given to the target over the distractor.

In another study, it was shown that exogenous effects of attention were maintained in retinotopic coordinates during smooth pursuit, which is consistent with recent research proposing that the coordinates of attention effects are retinotopic at first, and then are remapped in world-centered coordinates. The size of the cuing effects during pursuit and fixation indicates also that pursuit does not reduce the possibility to orient to task-irrelevant peripheral events, at least with a low demanding task.

Finally, an experiment was conducted in which motor and attentional components of inhibition of return were tested. Inhibition of return is the slowing of reaction times towards pre-cued locations after a long SOA, which affects saccadic as well and non directional responses, like key-presses. An attentional but no clear motor component was found to influence saccadic and manual reaction times, contrary to a previous report.

## Publications

Some of the studies reproduced in the experimental part are the author manuscripts of papers published in peer reviewed journals. Part of the data was also presented at international congresses. The status of the four studies is detailed below:

**Study 1:** Souto, D., & Kerzel, D. (2008). Dynamics of attention during the initiation of smooth pursuit eye movements. *Journal of Vision*, 8(14), 1-16.

**Study 2:** Souto, D., Zarian, L., & Kerzel D. (in preparation). Attentional constraints on target selection for smooth pursuit eye movements

**Study 3:** Souto, D., & Kerzel, D. (2009). Involuntary cueing effects during smooth pursuit: facilitation and inhibition of return in oculocentric coordinates. *Exp Brain Res*, 192(1), 25-31.

**Study 4:** Souto, D., & Kerzel, D. (in press). Evidence for an attentional component in saccadic IOR. *Exp Brain Res*

Presented at a congress:

Souto, D. & Kerzel, D. (2008, July at Morat, Switzerland). Do manual and ocular inhibition of return depend on different processing stages? Poster presented at the *International Symposium on Visual Search and Selective Attention*.

Souto, D. & Kerzel, D. (2007, May at Sarasota, Florida). Endogenous shifts of attention during smooth pursuit initiation. Poster presented at the *Vision Sciences Society*.

Souto, D. & Kerzel, D. (2007, 19-23 August at Potsdam, Germany). Is selective attention at the target location necessary for smooth pursuit initiation? Talk at the *European Conference on Eye Movements*.

Souto, D. & Kerzel, D. (2006, 20-25 August at St Petersburg, Russia). Attention and programming of smooth pursuit eye movements. Poster presented at the *European Conference on Visual Perception*.



# 1 Theoretical Introduction

This introduction was designed to complement the studies presented in the experimental section of this manuscript, but also to serve as a stand-alone review of the role of attention in eye movements. The studies presented here concern the relationships between the control structures responsible for overt and covert orienting. I will also try to present more deeply some themes that were only outlined in those studies and will sometimes expand upon the interpretations of the results. The issue that has prompted most of the research efforts on this topic, the validity of the premotor theory of attention, will be discussed at length. Finally, the smooth pursuit eye movement system will be introduced.

## 1.1 What is the purpose of eye movements?

Because sharp acuity is limited to the area around the fovea, object details cannot be resolved without directing one's gaze directly over them, such as when identifying someone, or reading a word in small print. Uneven spatial acuity across eccentricities can be approximated by blurring the image, as can be appreciated in Figure 1.

Not only are receptors of the retina unevenly distributed, but the foveal region of the retina is overrepresented on the visual cortex. Half of the surface of the V1 region of visual cortex represents only 2% of the visual field that falls on or near the fovea (Wandell 1995). Thus, we are built to process details in the foveal region, which is a simple way to drastically reduce the amount of incoming information (Anstis 1998). An obvious purpose of eye movements is therefore to align the fovea with the objects being visually scrutinized; this goal is achieved by the saccadic system. Further, retinal motion also contributes to reduced acuity and threatens clear vision because of the resulting motion blur. When we walk and fixate on a static object, or when an object (such as the tool we are handling) is moving in space, we typically use smooth pursuit eye movements to match the movement of our eyes with the speed of movement of the object of interest. Smooth pursuit is part of the so-called slow eye movement system (Ilg 1997), which also includes the slow phase movement of the optokinetic nystagmus (OKN) and the vestibular-ocular reflex (VOR) that stabilize gaze

during head motion. These movements are in contrast to the very fast peak speeds of 400-800°/sec reached during saccades (Sparks 2002). I will focus here on the two systems that are voluntarily engaged, the saccadic and smooth pursuit systems.



**Figure 1** Acuity diminishes as a function of distance from the fovea. The upper image shows the full resolution version of the lower image that has been blurred by applying a spatial filter that mimics an increasing loss of spatial resolution with eccentricity. However, if we fixate on the center of the two images, they should appear equally blurred at some given optimal distance (reproduced from Anstis 1998).

## 1.2 Attention

In addition to the structural limitations to acuity, attention represents the next bottleneck in the visual system. However, the role of attention is not only to narrow our focus to a subset of the incoming information, relieving the brain from processing all the visual information available from very early stages on (McAlonan et al. 2008), but also to serve an organizational process. Visual information is first processed in a modular fashion (Wandell 1995), with some processing units sensitive to single features of an object such as color, orientation, motion, or depth. However, the outcome is a unified percept of a “car” or “tree”—an object with its defining features bounded together, with “attention” providing part of the solution for the so-called binding problem (Treisman and Gelade 1980; Robertson 1998).

### 1.2.1 Definitions

As we are reminded by Cavanagh (2004), the main properties of attention, selection, binding and limited capacity that we take as recent achievements of cognitive scientists were already proposed several centuries ago. Accordingly, Anne Treisman should have credited the 18<sup>th</sup> century French philosopher Christian Wolff for having first proposed a feature-integration theory of attention in his “*Traité sur l’âme*” (Cavanagh 2004).

In this context, the famous definition of attention put forth by William James does not seem outdated:

*“Every one knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others and is a condition which has a real opposite in the confused, dazed, scatterbrained state which in French is called *distraction*, and *Zerstreutheit* in German”* (William James, 1890, p. 404).

Slightly rephrased, attention prioritizes the processing of one object (not two or three) out of many. Selection of one object implies that attention is withdrawn from the other objects. Also implied is the notion that attention selects objects for conscious

perception. Reportability is a defining feature of attention (Cavanagh 2004) and may be the reason why William James considers that humans know what attention is<sup>1</sup>.

Limited capacity and selectivity may be the two most agreed upon characteristics of attention (Desimone and Duncan 1995). Attention limited capacity is manifest in the fact that we can only track, perceive, or compare, for instance, a limited set of objects. It can therefore be seen like a limited resource that can appear very rapidly depleted on some tasks. The selectivity of attention is manifest in the ability to focus on an object, location or feature that is particularly relevant.

Before *focusing* on a more narrow area of attention, orienting in visual space, it may be good to remind ourselves that our ability to attend to something encompasses a lot more than just highlighting a particular location in space, we can also focus on a very specific stream of speech, as shown by our ability to keep track of one conversation in a cocktail party, or a particular action. We can also focus on specific internal representations, like the semantics of some spoken words, for instance. All of these instances may involve enhancement of the representation of selected items, the suppression of unselected items, or both.

### **1.2.2 Attention in visual space**

Most relevant for studies of selective attention for eye movements is the way in which attention is allocated among the objects in space, shifted, and utilized to select a particular object. In behavioral experiments, but also when physiological measures are recorded, allocation of attention in space is typically measured by the cueing paradigm, as set forth by Posner's seminal studies. Another technique involves the use of visual search tasks, but this paradigm is used less frequently in the studies I will discuss. In cuing paradigms, an endogenous (typically an arrow at fixation) or exogenous (typically a flashed disk in the periphery) cue draws attention (or at least, creates a response bias) towards the periphery. This response is believed to reflect voluntary and involuntary components. We

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<sup>1</sup> Even though proposals have been made suggesting that the processes involved in consciousness and attention are independent, those theories are highly speculative and controversial (Koch and Tsuchiya 2007; Evans and Treisman 2005).

can then measure the effects of the attention bias by comparing reaction times to cued compared to uncued locations or neutral cues (only a temporal cue) performance. More directly we can analyze the perceptual performance in discriminating two or more target identities, which is more directly related to the definition of attention mentioned above.

Several metaphors have been used to describe the phenomenon of spatial attention, to name but a few: the attentional “spotlight”, “zoom lens”, selection “gradient” (e.g. Pashler 1998), “blinking spotlight” (VanRullen et al. 2007), and a “Mexican hat” (Cutzu and Tsotsos 2003; Muller et al. 2005b) in reference to a selection area (the central part of the hat) with an inhibitory surround. Most metaphors are handy in describing a subset of results. For example, I will often describe how attention “shifts” toward some particular place. However, some metaphors may have been pushed beyond their utility, implying that the attention “spotlight” moves through space and has some inertia, as do moving objects in physical space (e.g. Spalek and Hammad 2004). Unlike real motion, attention shifts are actually isochronous over different distances (Remington and Pierce 1984; Sagi and Julesz 1985), and selection of a peripheral target is possible without selecting other objects in its “path” (Sperling 2001). There may even be multiple “spotlights” of attention (Cavanagh and Alvarez 2005). At a minimum, all authors would endorse the idea that spatial attention enhances the processing of objects at the attended region of space, but many other features can be debated.

### 1.3 Attention and saccade programming

The main contention surrounding the relationship between eye movements and attention has been whether or not we can independently dissociate the decision to execute a saccade towards the left, for instance, from the decision to focus attention in any place. The premotor theory suggests that we not only move the eyes by shifting attention to the target, but also that any shift of attention entails the first steps in the preparation for an eye movement. As usual, Helmholtz had his own ideas on this question, which he expressed in the *Handbuch der Physiologischen Optik*:

“[...] when the eyes are being used in the normal way, the two lines of fixation will be converged on the point which happens to attract the attention at the time, and the

*eyes will be accommodated for this point. But instead of ever letting them stay still for any length of time, they are being continually shifted (in obedience likewise to the incentive to move that is characteristic of the attention), being required especially to go over the contours of the observed objects. This is the explanation of the habitual connection between the movements of the two eyes and between these movements and the accommodation. [...] It also explains why the attention is so strongly attracted by prominent outlines, which have so much influence on the movements of the eyes, and why we have so much difficulty in concentrating our attention on a careful analysis of the phenomena connected with indirect vision, the blind spot, double images, etc. For we have formed the regular habit of looking directly at the places that occupy our attention.” (Helmholtz, 1925/1910, Treatise on Physiological Optics Vol. III, p. 534-535).*

The question regarding the relationship between the control of attention shifts and eye movements was first addressed empirically in the 1980's (Klein 1980; Posner 1980; Remington 1980). Posner (1980) described several possible relationships between eye movements and attention, ranging from complete independence to being an unique system, with two possible intermediary levels. There could be a functional relationship in which attention and eye movements are usually oriented together, as during responses to transient visual events, but it would be possible to dissociate them if required. This view may also represent the view of Helmholtz that we have quoted. Under the “theory of the efference”, Posner refers to an idea that he attributed to Wurtz and Mohler (1976): attention shifts at the same time oculomotor programs”. Finally, eye movement programming and covert attention could be regarded as parts of a common system, an idea that later promoters of the premotor theory seem to endorse.

Already in the 1980's, neurophysiologists found in the brain stem correlates of spatial orienting, based on observations of enhancement of activity of visual neurons in the superficial layers of the superior colliculus (SC) that are contingent on eye movements. Those cells show a visual response when a stimulus enters their receptive field. This response is enhanced when a saccade is made toward the cell receptive field, but not when the saccade is made to another location. This finding is indicative of the fact that the sensory enhancement is mediated by attention being shifted to the target during preparation of the

eye movement (Goldberg and Wurtz 1972; Mohler and Wurtz 1976; Wurtz and Mohler 1976). Furthermore, a similar task requiring a hand movement revealed much less sensory enhancement (Wurtz and Mohler 1976). Interestingly, the enhancement that was observed could occur earlier in time if the fixation point is removed before the target onset. Noteworthy, visuomotor cells, which respond to the onset of a visual probe and the onset of eye movement, also show the enhancement effect (an increased response to a visual stimulus when a saccade is directed within the receptive field). The difference is that the enhancement effect tends to be locked to the onset of the saccade. These authors therefore proposed that attention and motor readiness were two undifferentiated processes in the brain (Wurtz and Mohler 1976).

The work of Posner (1980) indicated that some degree of independence between attention and oculomotor readiness could be achieved. He tested the manual reaction times for detecting a probe, which location was pre-cued, presented either at the fixation point (80% of the time) or within a peripheral target box (20% of the time). In a dual-task paradigm the subjects had to move their eyes to the periphery. Odds provided a strong incentive to attend the central box, thus encouraging the dissociation of the locus of attention from the programming of the saccade. The reaction times did not decrease if the probe was presented at the saccade target shortly before the onset of the saccade, which would be predicted if attention had to be obligatorily allocated to the saccade target location. This finding led Posner to conclude that eye movements could be decoupled from attention, if necessary, by forcing a break from "habit". However, many methodological problems were revealed in subsequent years. Among them, reaction time measures were found to be poor indicators of attentional allocation because there is a component of expectation that can be independent from attention bias and can influence the reaction times. This can explain why foveal presentation was advantageous during acuity tasks but not during choice reaction time tasks (Posner, 1980). Furthermore, the reaction times in the dual-task paradigm were >50 ms longer than the reaction times in the single-task paradigm, which may indicate that the manual response may have been postponed after the saccade. Finally, saccadic suppression was not taken into account (see Section 1.5).

The results of other behavioral studies at the time suggested a loose link between oculomotor readiness and attention. However, these findings could also be due to

difficulties in interpreting the sources of interference in dual-task paradigms (see Section 1.5). The results of more sophisticated studies have subsequently led to the conclusion that attention and saccades are not only facilitated by exogenous cues, but also that a shift of attention precedes the initiation of voluntary saccades in a mandatory way (Shepherd et al. 1986; Crawford and Muller 1992; Reuter-Lorenz and Fendrich 1992; Hoffman and Subramaniam 1995; Deubel and Schneider 1996). Some amount of attentional resources cannot be diverted from the target location (Kowler et al. 1995; Deubel and Schneider 1996; Castet et al. 2006; Montagnini and Castet 2007).

One influential theory, the premotor theory of attention, proposed by Rizzolatti et al. (1994)<sup>2</sup>, stands against the notion that attention is controlled by a supramodal system and suggests that attention is controlled by “pragmatic circuits”. In the case of spatial attention, the pragmatic circuits are those circuits that are in control of eye movements. This theory does more than just equate spatial attention with eye movement programming. Any kind of action activates the corresponding circuitry that is used to process the stimuli that are relevant for the action. For instance, when preparing to grasp an object, attention to the graspable objects is engaged, facilitating the processing of objects compatible with the grasping movement that is being initiated (Craighero et al. 1999).

Evidence for strong coupling between attention and eye movements is derived from a variety of experimental results. One argument for the premotor theory stemmed from the observations of Rizzolatti et al. (1987) that the effects of cuing (based on a comparison of the key-press reaction times to a valid-cue location and an invalid-cue location) were bigger when the cue and the target laid on different meridians (a vertical or horizontal line perpendicular to the line of sight) than when they laid within the same quadrant. The differential effects of presenting the cue and the target on opposite sides of the vertical meridian could be due to an extra delay when attention has to cross the hemispheres. However, at the time, it was difficult to explain the extra delay in reaction times when the cue and the target were presented on opposite sides of the horizontal meridian. As a result, an explanation based on oculomotor programming was proposed. As shown in Figure 2, the eye is moved by the action of three pairs of muscles that enable movements along three

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<sup>2</sup> This idea is not new; one can find a similar formulation in Wurtz and Mohler (1976), which they in turn attribute to Roger Sperry.

degrees of freedom. The lateral and medial rectus muscles enable eye movements in the horizontal dimension. Rizzolatti et al. (1987) reasoned that the supplementary delay in reorienting attention across the meridians was due to the supplementary time necessary to re-engage the muscles because attention must activate another covert motor program when the target is presented on the other side. For instance, a leftward cue would generate a covert motor program that has to be recomputed if the target appears on the other side of the vertical meridian. Central to this interpretation is the idea that for cues and targets presented on the same side of the meridian only an increase or decrease in the command sent to the muscle is necessary, whereas, when cues and targets lie on different sides of a meridian, the adducens muscle instead of the abducens muscle will have to be activated, which may require more time than merely boosting the signal to one particular nerve. Therefore, oculomotor constraints may translate into the difficulties in reorienting attention. These results were extended when similar meridian effects were found with centrally presented cues but not with peripherally presented cues, with both saccadic and manual reaction times measures (Reuter-Lorenz and Fendrich 1992).

Another interesting interaction has been found between attention locus and saccade trajectories. When subjects had to shift their attention voluntarily to perceive a peripheral go-signal in order to execute an upward or downward saccade, the saccades were deviated in the direction that was opposite to the previous locus of attention. The reason given was that the previous attentional bias generated a tendency to saccade toward the location of the go-signal and that this response was inhibited, resulting in an overcompensated response to the right (Sheliga et al. 1994; Sheliga et al. 1995; Sheliga et al. 1997). Tipper et al. (2001) proposed a neural mechanism explaining this phenomenon of overcompensation. If the direction of the saccade or hand movement is based on the pooling of vectors representing every direction, and supposing that each vector is broadly tuned, then inhibition of a given direction (resulting in activity levels that are below resting levels) will cause deviation of movements toward the opposite direction.

Perhaps the most spectacular interactions between attention and eye movement were found with neuropsychological studies in which patients with oculomotor disorders

had difficulties in orienting attention. In eight patients with peripheral oculomotor palsy<sup>3</sup> (Craighero et al. 2001), latency of simple manual reaction times to the presentation of a peripheral probe was not affected by the location of the cue when patients were looking with their paretic eye whereas they showed a normal cuing effect when they look with their non-paretic eye. One shortcoming of the study was that all measures were expressed in terms of normalized reaction times, with no information on the actual reaction times, which were probably much longer than usual because a cutoff of 1500 ms was used for these patients compared to the usual cutoff of 600 ms. Another way to test the hypothesis that attention and eye movements are independent was to assess whether or not the constraints that impede our eyes from moving further within the orbit also reduce the cuing effects. In another study, (Craighero et al. 2004) used again a classical Posner cuing paradigm to test the reaction times of subjects while they viewed a screen with their eyes either positioned normally or rotated 40° in their orbits. Equivalence of their visual acuity under both conditions was assessed. There was no significant cuing effect when the eyes were rotated, by which those authors rejected the hypothesis of independence. Unfortunately, normalized reaction times were used, and only the significant results of the ANOVA tests were shown. It would also be important to use a perceptual measure of the cuing effects. Furthermore, it is difficult to exclude general resources (such as effort) other than attention as important factors limiting the cuing effects because, in my experience, effort is required to maintain the eye in a very eccentric location.

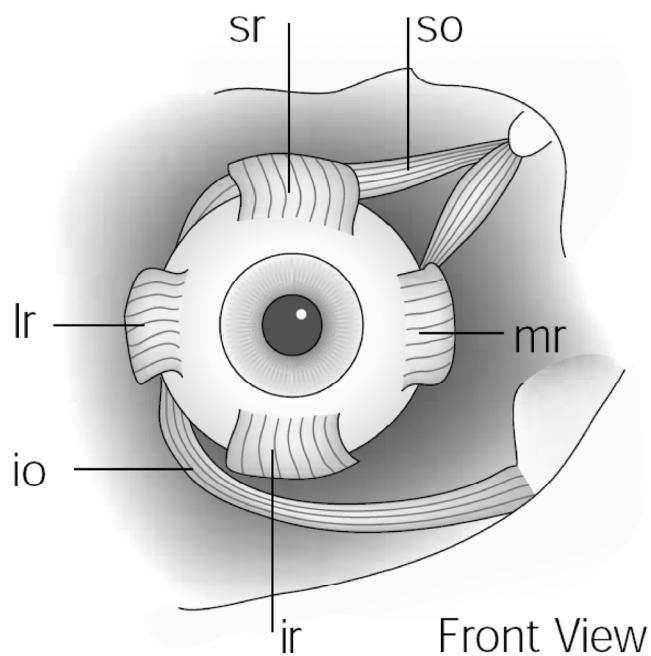
Similarly, the attention shifts of patients with progressive supranuclear palsy<sup>4</sup>, which affects the SC and other brain stem premotor structures implicated in the control of vertical saccades, were impaired for the abnormal side but not for the unimpaired horizontal dimension (Posner et al. 1982). The fact that the more severe symptoms delayed rather than prevented cuing effects after cue onset, compared to normal subjects, suggested that the oculomotor structures are not alone in controlling covert attention but that there is also a supramodal control of attention. Other tests were made with a patient with congenital

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<sup>3</sup> Peripheral palsy of the abducens nerve which is responsible for the conjugate horizontal eye movements (Leigh and Zee 2006).

<sup>4</sup> Progressive supranuclear nerve palsy is a degenerative disorder associated with slowing of vertical eye movements, which can also affect high-level cognitive functions (Leigh and Zee 2006).

ophthalmoplegia, known as A.I. (a detailed description is to be found in Gilchrist et al. 1998). This patient was unable to make saccades and had no other associated neurological symptom. It was shown that his exogenous cuing effects (tested with 50% valid cues, providing no incentive to voluntarily attend to either side) were abolished even though voluntary cuing effects were similar to the group of normal controls (Smith et al. 2004). This finding also supports a dual mechanism for controlling spatial attention, by supramodal and premotor structures. This study also provides a strong argument for the implication of the superior colliculus in shifting attention and preparing eye movements in response to exogenous cues.



**Figure 2** Front view of the eye and its three pairs of muscles: the lateral and medial recti, the superior and inferior recti, and the superior and inferior obliques. Abbreviated lr, mr, sr, ir, so, and io, respectively (reproduced from Sparks 2002).

### 1.3.1 Spatial specificity

How precisely does attention have to be focused on the saccade target in order to generate the eye movement? To answer this question, we can measure attention at the upcoming target location compared to neighboring locations. However, this question is difficult to answer in an absolute way. Supposing a model of saccade initiation in which attentional resources have to reach some fixed level at the saccade target before it can be

executed. The presence of distracting information can influence the need of attention to select the target and then the attention needed to select the target can hardly be separated from the attention needed to voluntarily initiate the action, when we consider that the two are not stringly part of the same process. Furthermore, the answer to the question will strongly depend on the task used to probe attention, such as the amount of time given to process the identity of the probe. Deubel and Schneider (1996) suggested that attention is narrowly allocated to the location of the upcoming saccade. Perceptual performance is strongly reduced when probes were shown as little as 1° from the target of the saccade. This finding also occurred when the probe stayed in the same location within a block of trials and different saccade goals surrounding the probe location were required, which provided a strong incentive to spread the attentional resources across locations.

To address whether or not attention could be distributed during the programming of saccades, McPeek et al. (1999) used a visual search task in order to identify the effect of a serial search (focused attention) on reaction time, as a function of the number of distractors, when a broad distribution of attention would be more efficient. Observers had to saccade to an odd-colored target that was located among several distractors. The results also indicated that focused attention is mandatory to execute saccades.

On the other hand, there is evidence that we can plan the sequences of saccades in advance. How is attention deployed when many saccades are planned? It seems that attention is not only allocated to the subsequent target locations in parallel but also that the perceptual enhancement observed at saccade goals decreases from the first to the last location (Godijn and Theeuwes 2003a; Baldauf and Deubel 2008). Interestingly, this finding does not correspond to a broadening of attention because when the locations in the path of a saccadic sequence are probed, the perceptual performance is much lower (almost like any other non-target location) compared to the performance compared at saccade goals (Baldauf and Deubel 2008).

### **1.3.2 Trade-offs**

What happens when attention is insufficient for the goal of the voluntary saccade? Two outcomes are expected. One is that the saccade is delayed because attention is necessary for initiation of the movement; the other is that the saccade is less precise because the activations for the target and the distractors are averaged. Each situation may

occur in a different context. In tasks when there is competition to move in different directions (i.e., if the targets are 180° apart) saccade will be delayed (e.g. Kowler et al. 1995). In paradigms when the target is presented in close proximity with the distractors, the saccade sometimes lands in-between them (Findlay 1982). The latter situation happens more often with short latency saccades (Ottes et al. 1985). This form of spatial averaging can be taken to reflect the fact that attention is too coarse to select a single target at first resulting in a speed-accuracy trade-off. A similar mechanism has been observed for pursuit initiation (see Section 1.6.1). Alternatively, averaging may be due to constraints other than the “resolution of attention” (Findlay and Blythe 2008). It could be that some perceptual constraint forces target and distractor signals to be averaged independently of attention, as proposed by Findlay and Blythe (2008). For instance, in the “crowding effect” we are unable to identify a peripheral target if it is surrounded by distractors, while it is easily recognizable in isolation. It has been proposed this effect is independent from attention (Freeman and Pelli 2007). However, in this domain too, it is an unresolved issue whether crowding reflects the resolution of attention (Intriligator and Cavanagh 2001) or another constraint of the visual system.

A trade-off analysis of saccadic latencies as a function of the attention allocated to locations that were opposite to the target of the saccade showed that, although some attention was necessary at the saccadic target location, some portion of the available attentional resources could be freed to attend elsewhere (Kowler et al. 1995) without incurring important costs in latency (see also Montagnini and Castet 2007). This finding was deemed as fortunate because the same pool of spatial attentional resources may be necessary for other tasks, such as holding objects in memory. However, the results of spatial averaging studies suggest that the attentional needs are high enough that they may only be met with after a minimum period of time, if we adopt the attentional explanation.

### 1.3.3 Time course

Until now, little has been said about the time at which attention attained the saccadic goal. Recent evidence indicates that the shift of attention that precedes voluntary saccadic eye movements can occur short before the saccade. Enhancement of perception at the saccade target location occurs mainly 150-200 ms after the go-signal when there is some

incentive to attend to adjacent locations (Castet et al. 2006) and occurs 50-150 ms after the go-signal when the saccade is made in order to discriminate target identity (Deubel 2008).

Interestingly, estimations of the time it takes to voluntarily shift attention are usually too long (typically > 200-400, Carlson et al. 2006) to expect that attention is systematically shifted before the saccade (Montagnini and Castet 2007; Deubel 2008). As noted by Deubel (2008), studies that tested the speed of attention shifts, did so during fixation. If eye movements and covert attention are coupled, a component of the inhibition on the saccade program may slow down voluntary orienting during fixation.

### **1.3.4 Intention versus actual movement**

There has been an interesting debate regarding the idea that the attention shift that precedes a saccade is directed to the intended saccade endpoint (supposedly the target location) and whether or not this shift follows the metrics of saccades, which typically undershoot the target. We may expect the latter if we think that the shift of attention is closely related to the motor command. However, some lines of evidence indicate that the SC (the typical structure related to attentional shifts and saccade programming) does not have access to the motor parameters that are set downstream. For instance, short-term saccadic adaptation does not shift the saccade endpoint represented in the SC (Frens and Van Opstal 1997).

Deubel and Schneider (1996) showed convincingly that the enhancement of perception was more closely related to the intended saccade endpoint than to its actual landing position. In contrast, other studies have shown that attention shifts in the direction of the adapted saccade amplitudes, supporting that attention has some access to the saccade metrics (Dore-Mazars and Collins 2005; Collins and Dore-Mazars 2006).

A similar debate concerns the locus of attention during smooth pursuit eye movements. Some authors have shown that attention preceded the target in space, as measured by detection reaction times for peripheral probes moving with the pursuit target but at different eccentric locations (Van Donkelaar and Drew 2002). This view was recently opposed when measurements of perceptual performance revealed that the attention locus is on the target (Lovejoy et al. in press).

### 1.3.5 Involuntary eye movements

Is the strong link of attention with eye movements specific to the situations when the action is initiated voluntarily? It could be that the results reviewed so far are reduced to the realm of the laboratory setting, as it is probably the sole occasion when we are supposed to voluntarily take control of our eyes. Some lines of research indicate this might not be the case.

In the oculomotor capture paradigm, a distractor is presented shortly after the target of the voluntary saccade is presented (a color singleton). Because the distractor onset is a salient localized event, the saccade is sometimes made to the location of the distractor (it is “captured”). Oculomotor capture is thought to be driven, in an exogenous manner, by the drawing of attention to the sudden onset of a distractor (Godijn and Theeuwes 2003b).

Presenting a discrimination target in different locations, including locations within the distractor, showed that when attention is first shifted to the distractor and then to the target, the eyes first move to the sudden onset (distractor) and then to the target. This pattern was considered to result from a competition between the effects of an exogenous signal that draws attention at its onset and an endogenous signal that drives attention to a particular target, with the exogenous signal reaching the movement threshold on some occasions(Peterson et al. 2004).

We will see in the first study that a special kind of involuntary saccades, the saccades that are made during the initiation of smooth pursuit eye movements in order to “catch-up” with the target, are also delayed when they compete for attention with a peripheral discrimination task. These findings indicate that these involuntary saccades are not executed unless attention is at the target, supporting previous results, but in a very different setting.

In summary, as also shown when discussing the speed-accuracy trade-offs, attention has a central role in the generation of saccades, whether its distribution is driven by top-down signals, like those induced by experimental instructions to select a given target, or by exogenous signals.

## 1.4 Neural correlates

Neural correlates of attention, inferred from the activity of visual cells of the SC, were already discussed. Several studies conducted in the last decade have provided a more complete picture of the neural networks and the single-cell mechanisms that participate in the orienting of spatial attention. Most recently, the perceptual consequences of activity in the SC and the frontal eye fields (FEF) have been tested and suggest that those areas can trigger spatial attention and saccades at the same time.

I will first report on the cortical areas involved in covert and overt spatial attention, as revealed by functional magnetic resonance imaging (fMRI). In a pioneering study, Corbetta et al. (1998) required subjects to shift attention to a peripheral location or to execute a saccade. Activity during saccades and during shifts of attention was contrasted to activity levels during fixation. As shown in Figure 3, the most surprising outcome of this comparison is that the brain areas that were more active during saccade programming were also more active during covert shifts in attention. Figure 3 shows that activation was most prominent in a region that included the FEF<sup>5</sup> (PrCeS = precentral sulcus), supplementary eye fields (SEF; MeFG = medial frontal gyrus), and the parietal brain regions (TOS = transverse occipital sulcus; IPS = intraparietal sulcus, which may be homologous with the lateral intraparietal (LIP) area of monkey brain)(see also Nobre et al. 1997; Nobre et al. 2000). Those findings are well in line with the evidence reviewed in previous sections, indicating that covert and overt orienting of attention activates a widely overlapping neural network composed of areas associated with oculomotor functions (SEF and FEF) and with areas with potential roles in the supramodal orienting of attention (PPC = posterior parietal cortex). Activation of the PPC is, however, ubiquitous in many tasks and therefore may be difficult to relate to activities that are uniquely associated with saccadic programming, intention to move, remapping of targets in space, or the orienting of attention (Snyder et al. 2000).

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<sup>5</sup> Although it might seem unorthodox to refer to the labeled areas according to the macaque anatomy instead of their human homologues, it reflects the fact that we have more information about the former, at least when it comes to eye movements.

However, the PPC is commonly activated in spatial and non-spatial orienting tasks (Nobre 2001)<sup>6</sup>.

Furthermore, recent inactivation studies permit a refinement of the simple hypothesis of a single system by showing that inactivation of the monkey LIP area impedes the covert orientation of attention without impairing the ability to execute eye movements (Wardak et al. 2004; Khan et al. 2009); the dual role of the FEF in covert attention and eye movements was confirmed in the same way (Wardak et al. 2006).

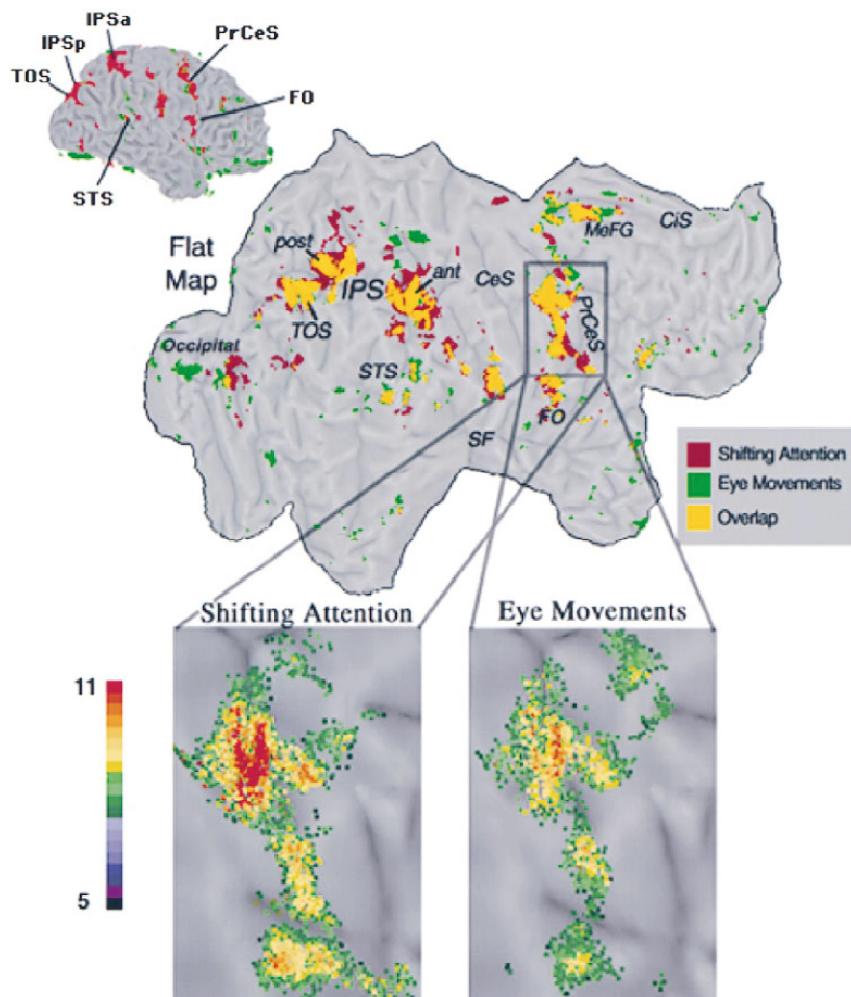
However tempting it may be, the fMRI activations observed by Corbetta et al. (1998) and others are not to be confounded with the neural circuits important for the orientation of attention. As pointed out by Nobre (2001), the neural circuits discovered are not a type of “attentional homunculus” because attention to finger movements, for instance, does not activate the FEF area. However, the orientation of spatial attention in a wide variety of tasks involves oculomotor areas, which is supported by many fMRI studies.

Recent neurophysiological studies are revealing causalities among the areas that are highlighted in fMRI. Guided by the fact that there are fast and strong connections between the FEF and the PPC, Moore and Fallah (2001; 2004) examined the attentional effects of the microstimulation of sites in the FEF. Saccades were artificially generated by microstimulation of some sites within the FEF, and the movement field (MF) was defined as the region of space where those saccades were directed. In their study, monkeys were rewarded when they detected a change in the luminance of a given target in the presence of distractors that were flashed at different random locations. Subthreshold stimulation (< 50% of the current necessary to trigger a saccade) improved the perceptual performance (smaller changes in luminance could be detected) in a spatially specific manner. That is, when the target was within the MF. Noteworthy, the investigators observed benefits for the detection of a dimming target when it occurred within the MF, but there were no significant costs in detection when the target appeared outside of the MF. Although no cuing task was

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<sup>6</sup>The predictions of the premotor theory may be very similar to the predictions of the ideomotor theory, at least when it comes to fMRI activations, with their low temporal resolution. The ideomotor theory postulates that we initiate voluntary movements by representing their learned sensory consequences. In this way, the representation of the required movement may guide attention rather than attention engagement itself initiating the action (Melcher, Weidema, Eenshuistra, Hommel and Gruber 2007).

performed for comparison, the magnitude of the effect was commensurable with effects of attention on perceptual performance that are typically obtained (approximately 10% benefits for microstimulation compared to control). Whether the effects are mediated by connections between FEF and SC, through direct connections from FEF to V4, or from FEF to LIP area is not clear. The main message is that artificially preparing for saccades is enough to enhance perception at the target goal even when the currents used to simulate FEF sites are not strong enough to trigger a saccade, providing a strong argument for a mechanical link between movement preparation and the orientation of attention.



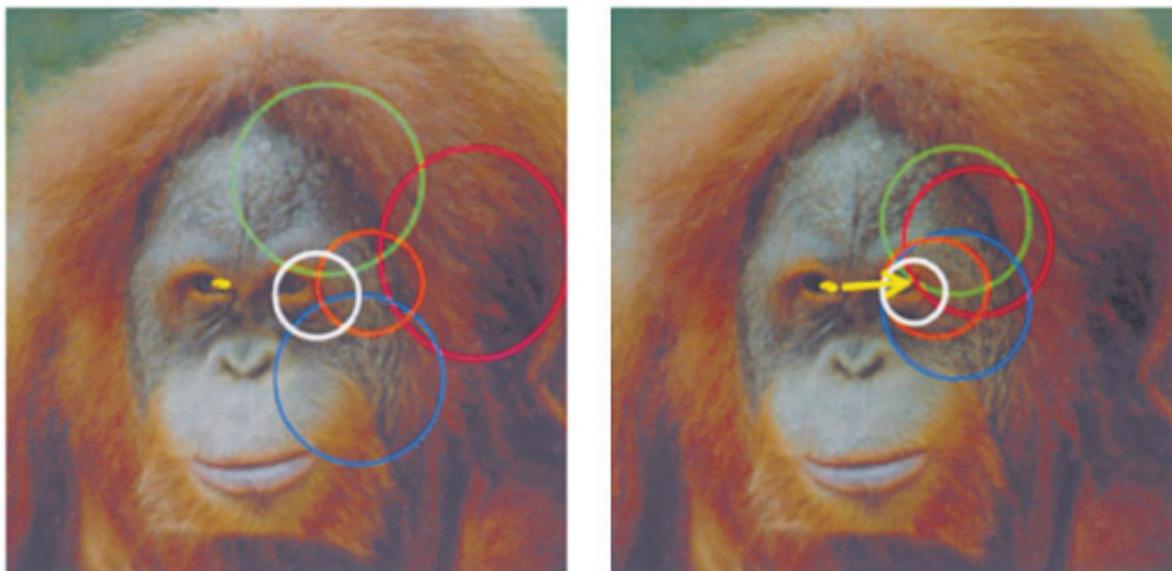
**Figure 3** Differential activations of one subject from the study of Corbetta et al. (1998) are displayed on a flattened cortical map; reproduced from their Figure 3. Red indicates greater activity during shifts in attention contrasted to fixation; green indicates greater activity during eye movement contrasted to fixation; yellow indicates the regions of overlap between those two types of activation.

The results of other studies have supported these conclusions; however, subthreshold microstimulation of SC sites was used, along with very different perceptual tasks (Cavanaugh and Wurtz 2004; Muller et al. 2005a). It was also shown that attention, as indexed by perceptual performance, selectively influenced the activity of a majority of the visuomotor neurons of the SC; visuomotor neurons show premotor activity, but are also responsive to the visual stimulus onset, which confirms the findings of older studies (Ignashchenkova et al. 2004). Furthermore, an important drawback of the microstimulation paradigms has been addressed: the possibility that phosphenes generated by microstimulation may mediate the changes in attention (Cavanaugh et al. 2006). These investigators compared the effects of microstimulation to the effects of presenting a cue at different times during a change detection task. The data show that if visual cues replaced microstimulation, mimicking the effects of a phosphene, change detection did not improve, in contrast to sub-threshold microstimulation. They also stimulated visual neurons of the superficial layers of the SC in which the visual field location was similar to the cue location or MF of the motor neurons. Improvements in stimulus change detection were much larger during microstimulation than when the visual cells were stimulated or when the stimulus was replaced with a visual cue.

How does FEF microstimulation mediate discrimination performance? This question was explored by analyzing the interactions between FEF and the visual area 4 (V4) (Armstrong and Moore 2007; Moore and Chang 2008). V4 is a good candidate for mediating the perceptual enhancement at the saccade goal because its location is “early” in the ventral branch of the visual cortex, specialized in object recognition, showing high-level spatial-invariant responses to complex forms (Cadieu et al. 2007), but also having strong interactions with the dorsal stream, more specialized in action control and containing more precise location information (see next Section). It was also shown that the response of V4 neurons to a stimulus is strongly enhanced when a saccade is made toward its receptive field (Moore et al. 1998), which was interpreted to counter-act the waning of the neural representation of the target that takes place during the saccade (due to saccadic suppression). Confirming a possible role for V4 in the mediation of perceptual effects, it was shown that subthreshold microstimulation of FEF sites improved the ability of V4 neurons to

discriminate stimuli within their receptive field (when the MF of a FEF neuron corresponds to the receptive field of a V4 neuron).

Not only is there an effect of eye movements on the enhancement of activity within the receptive field of V4 neurons, but also the shape of the receptive field may change considerably (Tolias et al. 2001). Attention may mediate the apparent shrinking and shifting of the V4 receptive fields toward the saccade target location, which is illustrated in Figure 4. The time-course of the enhancement, occurred within 100-200 ms before the saccade, is consistent with this interpretation (see Section 1.3.3). How this finding relates to perception and target selection is an open question. What we know for sure is that eye movements cause massive transformations in visual brain areas, some of which may be related to attention in the preparation of the next saccade.



**Figure 4 Illustration of the changes in the V4 receptive fields in the preparation of a saccade, in a natural scene (adapted from Tolias et al. 2001). The yellow mark in the left-hand image represents the point that is fixated in the image. Circles represent some of the V4 receptive fields. The right-hand image shows the same receptive fields just before a saccade, with the vector shown in yellow.**

Kustov and Robinson (1996) were the first to directly test a specific prediction of the premotor theory: that spatial orientation of attention is made by preparing a saccade. If attention and saccade preparation are two sides of the same coin, this should be as true as the proposition that a shift of attention must accompany a saccade. Thus, if attention

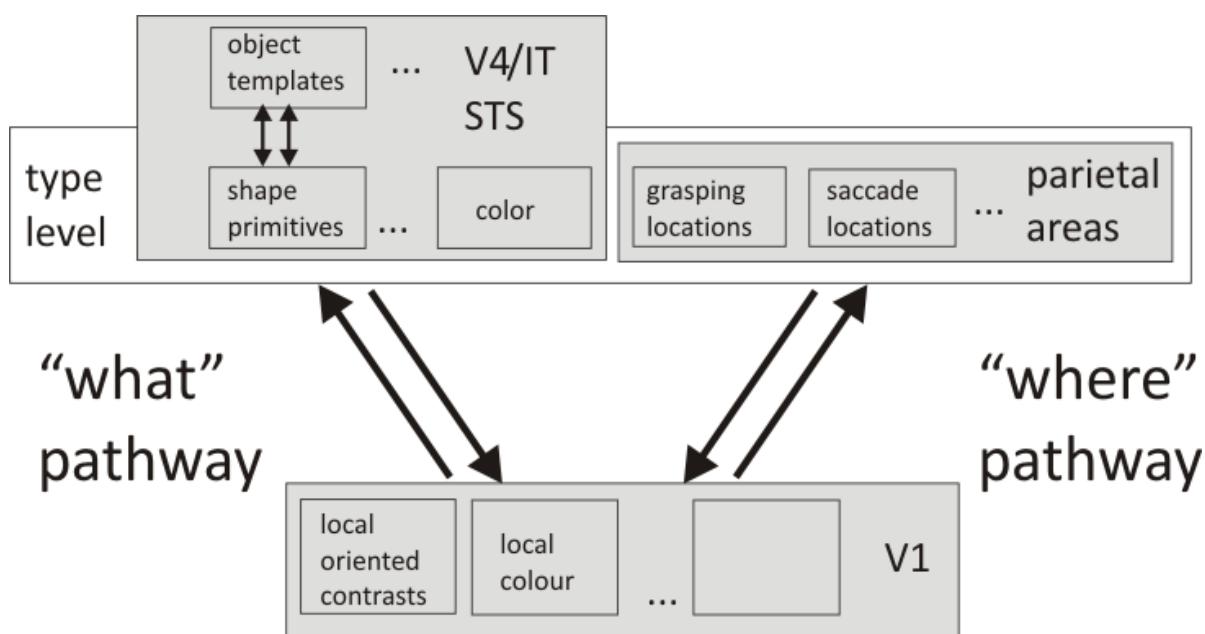
activates an oculomotor program this program should compete with another program that we can artificially generate by micro-stimulating a site on the SC. These investigators revealed a deviation of the artificial saccade vector toward an exogenously cued location (compared to microstimulation of the same site with no exogenous cue). The results provide a strong argument for attention being able to activate an oculomotor program. Further, endogenous cues (i.e. voluntary attention) were just as effective for deviating the artificial vector.

This finding has been challenged in a few studies, using an anti-saccade task, in which subjects have to program an eye movement toward or away from the location of a color singleton. Thus, the very nature of the anti-saccade task opposes voluntary and reflexive control of eye movements. It is known that attention first automatically selects the singleton (it is task-relevant and salient) and then a voluntary motor program overrides the tendency to orient to this stimulus. Following the same logic as Kustov and Robinson (1996), we expect that the initial selection of the cue results in the preparation of a saccade towards the cue. If we now micro-stimulate the FEF such that an orthogonal saccade is generated, we should expect that this saccade will be deviated towards the color singleton (because it was attended to). Although the activity of the FEF neurons indicates selective attention to the singleton, the saccade vector is not deviated accordingly. The saccade vector is, however, deviated toward the direction of the instructed eye movement (Juan et al. 2004). Thus, the idea that spatial orienting is equivalent to saccade programming is compromised (see also Murthy et al. 2001; Smith and Schenk 2007; Juan et al. 2008).

#### **1.4.1 Hypothetical mechanisms**

Several models for the interplay between eye movements and perception have been proposed. One model is the Visual Attention Model or VAM (Schneider 1995), endorsed by Deubel and Schneider (1996). This model proposes that there is a common selection mechanism for object recognition and for saccadic target selection, resulting from cross-talk between the dorsal and ventral branches of the visual system (e.g. Webster and Ungerleider 1998). This model also emphasizes that not only are locations enhanced or selected, but that the relevant unity is the object that is selected for perception and action. The model proposes that spatial parameters and the identity of an object are made available by the

same process of selection process. The possible brain mechanisms involved in shared selection are shown in Figure 5. This theory can be distanced from the premotor theory because it supposes that saccadic programming is made possible by allocating attention, but that attention is not preceded by the activation of a motor program (Deubel and Schneider 1996)<sup>7</sup>. Within this framework, selection propagates from the ventral to the dorsal branch, or the other way round depending of what is the initial basis for selection. For instance, when a location in space is selected for being the next saccade target, which is supposedly a dorsal stream function, objects at this location will be enhanced through connections between parietal and primary visual areas, which will enhance the “type level” representations of the object (its basic features), activating in a later stage the object representation in the ventral stream.



**Figure 5** The flow of information in selection for eye movement and selection for perception in the VAM model (redrawn from Schneider 1995).

<sup>7</sup> A computational model proposed recently by (Hamker 2003; 2005) shares some similarities.

## 1.5 Evidence for independence

*“Der Teufel steckt im Detail”* (Popular saying)

It might appear that the studies presented in the experimental section of this manuscript represent a one-sided view of the literature. Therefore, in this section, I will present a more detailed, critical review of the main evidence that has been overlooked thus far. For an exhaustive and balanced review, Hoffman (1998) can be consulted.

The strongest arguments for independence of eye movements and attention have been expressed by Raymond Klein (Klein 1980; Klein and Pontefract 1994; Klein and Shore 2000; Klein 2004). Those arguments will be detailed below.

First, Klein challenges the view that covert orienting is controlled by oculomotor structures. He argues that there is a fatal flaw in the Kustov and Robinson (1996) experiment (see above), reporting that covert attention is able to deviate an artificial saccadic vector. The monkey always had to saccade toward a target at the cue or at the uncued location, therefore, the activity induced by the cue may well represent the motor preparation in advance of the presentation of the target rather than the effect of shifting attention (Klein 2004). The studies of Juan et al. (2004; 2008) suggest that his point may be valid because there was no deviation in the vector of a saccade that was artificially triggered toward the focus of attention.

Second, fMRI evidence for overlapping structures is taken to mean a very different thing from the usual interpretation. Subjects have to move attention without moving their eyes; this is something that should require the cancellation of an eye movement. Therefore, activity in the FEF, for instance, may not reflect motor preparation but represents a more active fixation (see also Corbetta et al. 1998). This component has long been held as a plausible candidate in generating inhibition of return (IOR) (Rafal et al. 1989; Taylor and Klein 1998; Taylor and Klein 2000). Therefore, the activation patterns common to several structures may only be due to the inhibition of saccades and not to the preparation of saccades by attention. In Study 4, we will see that this attention may not be independent

from inhibition of return. However, evidence that transcranial magnetic stimulation (TMS) of the FEF disrupts IOR lends some support to this idea (Ro et al. 2003).

Third, Klein and Pontefract (1994) questioned the effects of the meridian on the control of attention, which formed the basis of the premotor theory (Rizzolatti et al. 1987), by pointing out that those effects are replicated when attention is allocated endogenously, but not when it is driven exogenously (Crawford and Muller 1992; Reuter-Lorenz and Fendrich 1992).

Fourth, Klein (2004) cites the study of Hunt and Kingstone (2003a), with older studies, as a direct argument for the independence of eye movements and attention, because they found in one condition a negative correlation between perceptual cuing effects and saccade latencies. I will detail this study below. As it was shown before, evidence seems stronger to support that attention can be moved in space without necessarily generating a movement program. I will concentrate on studies claiming that the eyes can be independently moved from the focus of attention.

The main argument supporting the independence of eye movements and attention comes first from the studies of Klein (1980) and Remington (1980). These studies represent the first attempts to address this question and, as such, should be regarded with caution. However, these studies are often cited as valid evidence supporting the point of view of independent process (e.g. Stelmach et al. 1997; Juan et al. 2004). Therefore, I will spend some time evaluating their claims.

Remington (1980) used a non-speeded task to measure the allocation of attention while avoiding one of the confound of the Posner experiments. In one of the experiments, which was designed to test the independence of attention and eye movements, a central arrow was used to indicate the direction of a saccade while perception was probed by increasing brightness of a box outline (for 3 ms) above the fixation point, the target, or the opposite location, with equal numbers of probe and no-probe trials. The argument for the independence of attention and eye movement programming was based on the finding that target perception was superior at the saccade target location only at the time of average saccade latency (after the target has been fixated). This result was contrasted to another experiment in which a peripheral cue summoned the saccade (and attention), and revealed that target perception was superior at the target location approximately 50 ms after cue

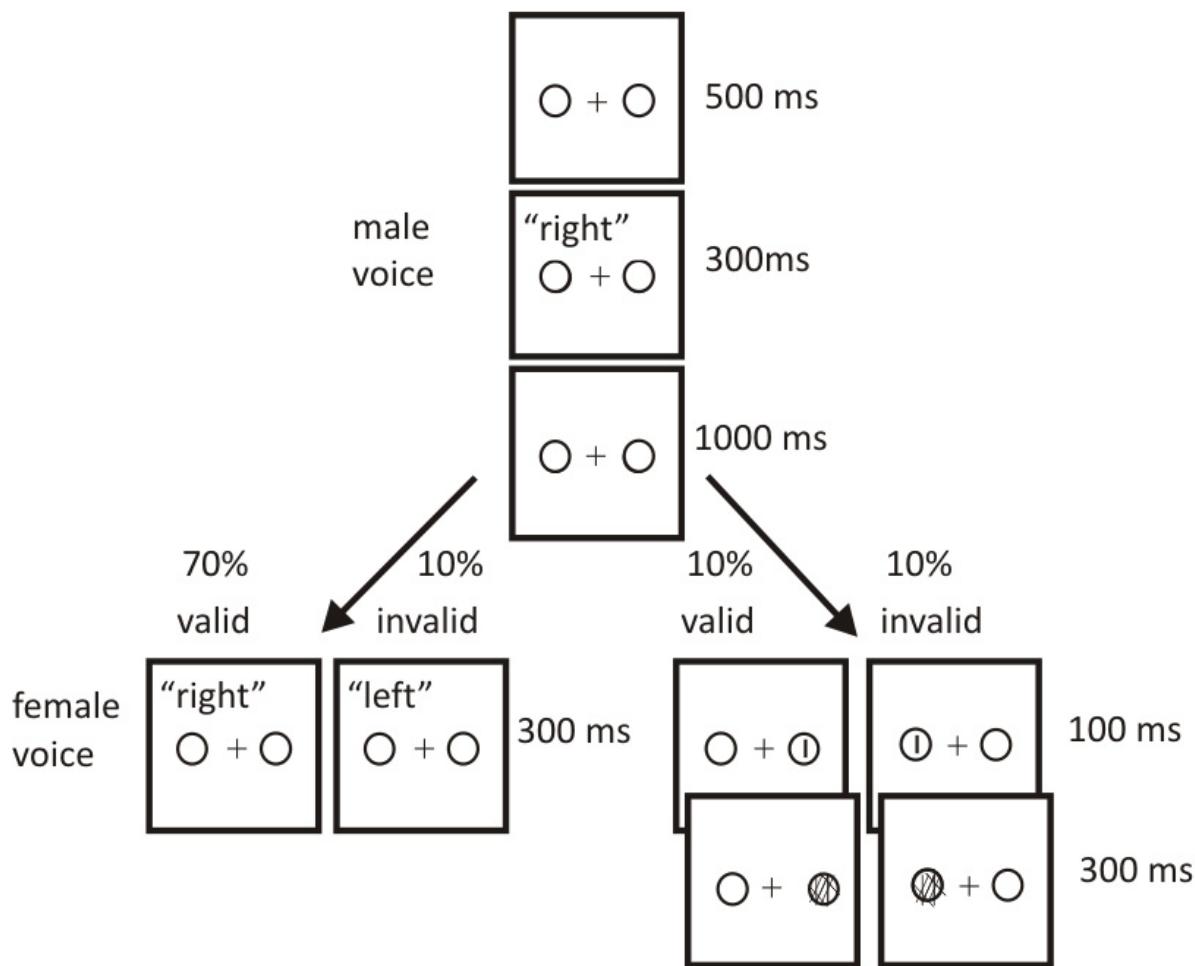
onset. However, the distance between possible probe locations in that experiment was twice the distance in the first experiment, which makes the cuing effects difficult to compare. Because measurement of perceptual performance was time-locked to the onset of the go-signal, there cannot be a single interpretation of the results. Averaged in this way, the data are comprised of trials in which the probe was detected before, during, or after the saccade. Thus, all the results were contaminated by saccadic suppression in a large portion of trials (the typical duration of a 10° saccade is approximately 50 ms; Carpenter 1988). Saccadic suppression reduces the difference between perceptual performance at the target and at other locations, as was found for the lack of attention at the target location. Furthermore, as will be discussed below, the attention shift that precedes a saccade is time-locked to the onset of the saccade (Deubel 2008).

Klein (1980) utilized a detection task with a speeded manual reaction time and required saccades to a peripheral target designated by a peripheral go-signal. Because manual responses were not facilitated when the saccade was made to the same side as the detection target, he concluded that an attention shift was not involved in the saccadic eye movements. A principal concern in this experiments is due to the “psychological refractory period” (PRP) effect (Pashler 1994). When there are two speeded tasks requiring different responses, even when the two tasks are very simple, one of the responses (the slowest) is delayed because there is a bottleneck at the response level. Therefore, when using two speeded tasks (eye movement and target detection) the delays observed in these tasks are difficult to interpret. Saccades latencies in Klein (1980) of approximately 450 ms in the dual-task condition compared to the 350-ms saccades in a single-task paradigm, thus indicate that the two tasks are incompatible at the response level. Other critics stated that subjects may be better off by not preparing an eye movement until they see the detection target, because it would be counterproductive to prepare a movement and potentially reduce the chances of seeing incremental changes in the light in another direction (Rizzolatti et al. 1987).. Furthermore, because reaction time measurements were used, it was acknowledged (Klein 1980) that the reaction time performance may represent a preparation to respond according to the cue probabilities rather than the allocation of attention, a point that was emphasized later (Shaw 1984). The same criticism can be made of the experiments reported by Klein and Pontefract (1994).

More recently, Hunt and Kingstone (2003a) tried to replicate Klein's results using only a single speeded task, avoiding the problem that the performance of one task may interfere with performance of the other. These investigators compared two groups. The so-called "eye movement" group had to saccade to one side for 70% of the time (there was an auditory go-signal, e.g., "left"), to the other side approximately 10% of the time, or they had to report if a vertical or horizontal line was presented in one of two locations (20% of the time)(Figure 7). The "key-press" group had the opposite task contingency: they performed the perceptual task (line orientation) 80% of the time. The eye movement group had faster saccadic reaction times when the go signal confirmed that they had to execute the saccade to the expected side. Noteworthy, the difference in latency between valid and invalid cue trials (the voice does not confirm the previous message) is of 137 ms, above 200 ms for two of the subjects (Klein 2004), that is as long as the average time it takes to execute a saccade. Such a large difference in the SRT indicates that the subjects had to cancel the expected eye movement most of the time in order to saccade to a target presented on the other side. On the other hand, perceptual performance is worse when the probe appears on the side of the saccade side (which occurred 20% of the time). In the key-press group, the manual reaction times did not differ in valid or invalid cue trials, but a significantly larger proportion of correct responses occurred in the valid condition, suggesting that attention was shifted to the cued location. A very unusual feature of the experiment was that after the first auditory cue to saccade left or right, the subjects had to wait a fixed period of 1 s before they were shown the go-signal for the execution of the saccade, which usually occurred to the same side (70% of the time). Then, the subjects had to either cancel the saccade or execute it. The strong expectation for executing the saccade to a particular side should provoke a large number of anticipatory saccadic responses toward the cued side. There is no mention of the number of anticipations or if the authors rejected saccades that occurred below a particular cutoff latency. Therefore, we are not able to disregard this interpretation of the data. This experimental design is somewhat similar to the one used by Deubel and Schneider (1996). In that experiment, subjects also had to withhold a saccadic response for a duration that randomly varied between 500 ms and 1 s, which reduced the number of anticipatory saccades, and then a probe was shown in the first 80 ms at the same time as the go-signal for the saccade was shown (the disappearance of the arrow cue), and the identity of the perceptual target had to be reported at the end of the trial. The incentives to attend

elsewhere were large because the target could appear in one of three locations that were near the target. Thus, we can argue that Deubel and Schneider (1996) utilized a similar method unless the saccades did not have to be cancelled on 20% of the trials. The results, however, were the opposite of the results reported by Hunt and Kingstone because they showed that attention was locked to the saccadic target location.

Therefore, it seems very likely that subjects can hardly refrain from anticipating a response to the pre-cued side, because the saccadic task is much more likely than the perceptual task, but not when manual key-press responses are required (as indicated by the reaction times), because it is much easier to withhold them. Second, in order to optimize performance, subjects would need to cancel a saccade and return attention to the central fixation point as soon as they perceive that there will be no saccade required (no voice, but a visual transient appears). The perceptual task can thus measure the consequences associated with canceling or inhibiting a saccade (Sheliga et al. 1994). The lack of any information besides the group averages makes additional interpretations of the data difficult.



**Figure 6** Shown is the experimental design from Hunt and Kingstone (2003a), redrawn from their Figure 1. One of the groups has to saccade to the cue side 70% of the time, saccade to the opposite side 10% of the time, and report if a vertical or horizontal bar appeared in 20% of the trials. Another group of subjects (the key-press group) has to do the same task but press a designated key instead of generating a saccade.

In a similar vein, there is no guarantee that subjects are not just waiting for the confirmation to prepare for an eye movement, thus optimizing their performance in the perceptual task, as we do not know if the saccades were delayed compared to the similar task without 20% perception trials.

Finally, in a clever series of experiments, Belopolsky and Theeuwes (in press) support the point that voluntary attention facilitates saccades, but only when they are frequently

needed. These authors utilized a paradigm similar to the one used to show deviations in the saccadic trajectories away from the voluntarily attended side (Sheliga et al. 1994; Sheliga et al. 1995). Subjects had to attend to a left or right location that was centrally cued. A go-signal (a number 1 or 2) eventually appeared, indicating the direction of the saccade. On a minority of trials (20%), the go-signal appeared on the uncued side. A critical point is that there was no incentive to program a saccade because the subjects were just as likely to saccade to the same side or the opposite side. Therefore, differences in the saccadic latencies in validly and invalidly cued trials should reflect the facilitation of saccade programming by attention. Indeed, saccades latencies were longer to the invalidly cued location (the subjects presumably had to reorient their attention) than to the validly cued location.

However, in their second experiment, Belopolsky and Theeuwes (in press) showed evidence that eye movements are independent from attention when the execution of the eye movement was less likely. In their second experiment, the probability of having to saccade to the location of the go-signal was reduced to 25% by having four possible locations, providing a strong incentive to cancel any saccadic program that could be initiated firsthand towards the attended location. These authors show that when the cue indicated the go-signal location, the saccades directed towards the cued side had longer latencies than the saccades directed towards the opposite side. The opposite finding occurred in the trials in which the go-signal was in the invalid location: the saccades were faster towards the location of the go-signal. This finding was taken as evidence that when it was necessary to decouple perception from saccadic preparation, the influence of the attended location could be suppressed. An alternative explanation, that the resulting pattern may simply represent the automated reorienting of attention to the center fixation point after processing of the go-signal in order to optimize performance. The slowed saccadic latencies toward the attended side could result from IOR. First, a saccade is prepared (supposing that the attention shift generates a motor program) and then it is cancelled in order to better prepare a saccade to the opposite location, which could generate IOR (Rafal et al. 1994)—the slowing of reaction times when the target is presented more than 300 ms after the cue. The authors reported that “three participants were replaced due to excessive saccade direction errors (>40%)”. The cutoff level established in the first experiment was 25%. This

discrepancy suggests that the task of maintaining attention without executing a saccade in this second experiment was very difficult; however, we do not know if the saccades in the wrong direction represent failures to refrain from looking to the cued side or wrong guesses.

I also feel the need to discuss the report of Stelmach et al. (1997) because they used a paradigm that differed from the previous ones, but also found that eye movements were independent from attentional shifts. In order to probe attention, subjects were asked to make temporal-order-judgments (TOJ) at different times before the saccade was executed. That is, two dots were presented together on both sides of the fixation point or presented asynchronously. The critical cue-target onset asynchronies were 250 ms and 300 ms. TOJ tasks were taken as an index attention allocation: objects appearing at attended locations tend to appear to lead objects appearing at unattended locations when they are actually synchronous instance (Stelmach and Herdman 1991). Therefore, this phenomenon has been termed “prior entry”. Because in their first experiment they do not show any bias in the TOJ for the saccade target location, the authors concluded that attention is not involved in the preparation of saccades. An important point is that they did not provide the saccadic latencies for their first set of experiments, because they only considered saccades that were made after presentation of the TOJ stimuli and thus comparisons of the latencies between the SOA cannot be made. However, we can examine the percentage of saccades that were longer than the 500-ms timed-out limit for saccadic responses. Those values were of 0%, 4.6%, and 25.2% for a SOA of 0, 250, and 300 ms, respectively. Those values indicate that the distribution of saccade latencies was displaced. Subjects seemed to keep their attention at the center, waiting for the TOJ targets, and then prepared to saccade. Their third and fourth experiments were also designed to test how well attention is dissociated from the saccadic goal. We had the same problem: approximately 20% more saccades exceeded the 500-ms cut-off duration with the 300-ms SOA compared to the 0-ms SOA. Furthermore, according to some studies, the prior entry effect can be attributed to decisional factors rather than to an acceleration of perception at the attended side (Schneider and Bavelier 2003). Therefore, the same problem as with the reaction time measures seems to apply: they do not necessarily indicate an allocation of attention.

Finally, we will also propose a different interpretation for the claims of Hunt and Kinstone (2003b) in our Study 4, which proposed that IOR measured with saccadic reaction

times is not related to attention, whereas IOR measured with manual key-press reaction times was related to attention.

We have shown that studies claiming that no attention is needed to execute a saccade are problematic, due to the following issues: the incompatibility of two speeded responses (Klein 1980; Klein and Pontefract 1994); the fact that the perceptual tasks required cancellation of an anticipated saccadic response (Hunt and Kingstone 2003a); the task did not permit one to differentiate post-saccade processing from pre-saccade processing (Posner 1980; Remington 1980); or reaction times or other measures that are strongly sensitive to decisional factors (and therefore are not good indexes of attention) were used (Posner 1980; Stelmach et al. 1997). Further, the study of Belopolsky and Theeuwes (in press) may measure inhibition of return rather than the suppression of perception simultaneous with saccade programming.

Some studies seem to disconfirm the proposition of Rizzolatti et al. (1987) that attention shifts generate oculomotor programs (e.g. Juan et al. 2004; Juan et al. 2008; Belopolsky and Theeuwes in press). Nonetheless, these are difficult to reconcile with the studies mostly stemming from neuropsychological research that show strong interactions between oculomotor function and the ability to covertly shift attention (Posner et al. 1982; Craighero et al. 2001; Smith et al. 2004), but also stemming from behavioral manipulations (Rizzolatti et al. 1987; Reuter-Lorenz and Fendrich 1992; Sheliga et al. 1994; Sheliga et al. 1995).

### 1.5.1 On economy

As an epilogue to the previous section, before going into further detail, I would like to add the argument that economical reasons can also be advanced to justify a strong coupling with attention and eye movement, as well as situations when this coupling does not have to be strict.

What is the most expensive for an organism when it comes to eye movements? Less important is the mechanical act of performing an eye movement *per se*, as eye muscles are among the muscles that are the least sensitive to fatigue, compared to the visual consequences of performing an eye movement (Harris 1995; Harris and Wolpert 2006). An otherwise puzzling feature of saccades is that they systematically tend to undershoot the

target, which may be a way to minimize the saccadic flight time (Harris 1995), during which visual perception is strongly impaired (maybe due to the very high retinal velocities during the saccade). The costs of falling slightly outside of the fovea are balanced by the ability to keep seeing the target for a longer duration. With this simple idea (plus some reasonable assumptions), we can explain the relationships, termed the “main sequence”, between saccade size and its duration, and between saccade size and its peak velocity (Harris and Wolpert 2006). This point may also explain why systematic saccadic overshoots are corrected in just a few trials but that we correct undershoots much more slowly (Panouilleres et al. 2009).

During fixation, misalignment of attention from the foveal region of the retina may be more beneficial than moving the eyes, for the reasons outlined above. However, the reduction in the costs associated with saccadic flight time or with saccadic suppression time would require a mechanism to impede misalignment of attention with the fovea right before, and maybe after, the saccade lands. Interestingly, the literature reports that a dissociation exists between the strict location of attention and the saccadic endpoint (one that has never been taken as evidence against the premotor theory, to my knowledge), that is, between the *intended* saccadic endpoint and the *actual* saccadic endpoint (see Section 1.3.3). Evidence seems to favor the idea that attention is shifted toward the location of the target. Indeed, the optimal strategy is to make shorter saccades, but because attention shifts do not have the same constraints, they need to reach the target for optimal processing.

We know of another situation in which it is advantageous not to align the fovea with the target location. Under conditions of very low background illumination, only rod photoreceptors respond to luminance contrasts. Because there are no rods at the center of the fovea, the eye should optimally fixate slightly off the target in such lighting conditions. This is indeed what happens for target-directed horizontal saccades that are made in the dark—they deviate upwards (e.g. Goffart et al. 2006). The optimal behavior in this situation would also be that attention is shifted to the target location rather than aligned with gaze in conditions of low background illumination (scotopic conditions).

There were other propositions, grounded in utility principles, regarding the shift of attention to the target prior to the eye movement. For instance, it was reasoned that the enhancement of target representation in V4 before a saccade may be necessary to boost the

neural representation of the target during the saccade, ensuring that this representation does not vanish during saccadic suppression (Moore et al. 1998). Economy could also explain why the criteria for initiating smooth pursuit eye movements may be less stringent than for saccades, because either there is no eye movement suppression during smooth pursuit movements or they are suppressed to a much lesser extent than during saccades (Westheimer and McKee 1975; Schutz et al. 2007a).

The speed-accuracy trade-offs discussed in Section 1.3.2 represent a form of optimization in that fast responses may be beneficial in some contexts even though the processing time does not allow them to be accurate.

## 1.6 Smooth pursuit eye movements

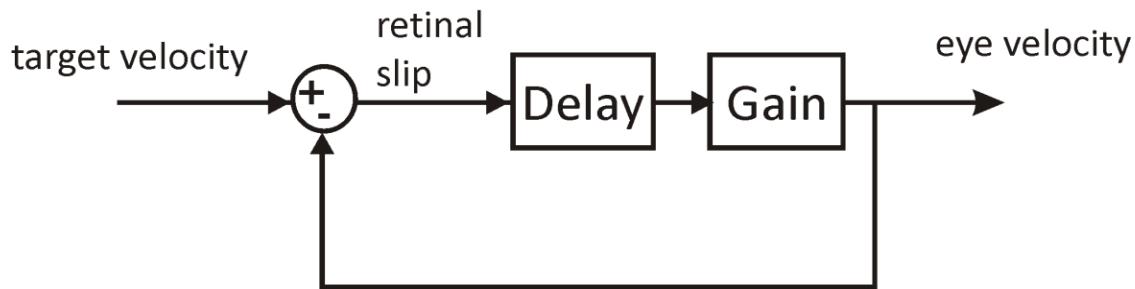
Smooth pursuit eye movements have been instrumental components of many studies on sensorimotor transformations, motor plasticity, the relationship between perception and action, etc. A great number of studies have also been conducted to understand how the brain controls pursuit and how these movements relate to other eye movements (for a review Leigh and Zee 2006).

Models of smooth pursuit control have been growing increasingly complicated. I have sketched only the basic building blocks of a model of smooth pursuit movements in Figure 7, without taking into account other important features such as the predictive capabilities of the system or saturation (e.g. Barnes 2008). At a basic level, pursuit can be said to be controlled by a negative-feedback loop that minimizes retinal slip (i.e., retinal motion) with a fixed delay of approximately 100 ms (Lisberger and Westbrook 1985; Carpenter 1988). As a consequence, the first 100 ms of pursuit are open-loop: pursuit is not sensitive to changes in the background or target motion in the first 100 ms after the eye starts to move. During the open-loop period, the eye accelerates steadily until the target speed is reached, as shown in Figure 7. After the open-loop period, we describe the eye movements as maintained pursuit or steady-state pursuit.

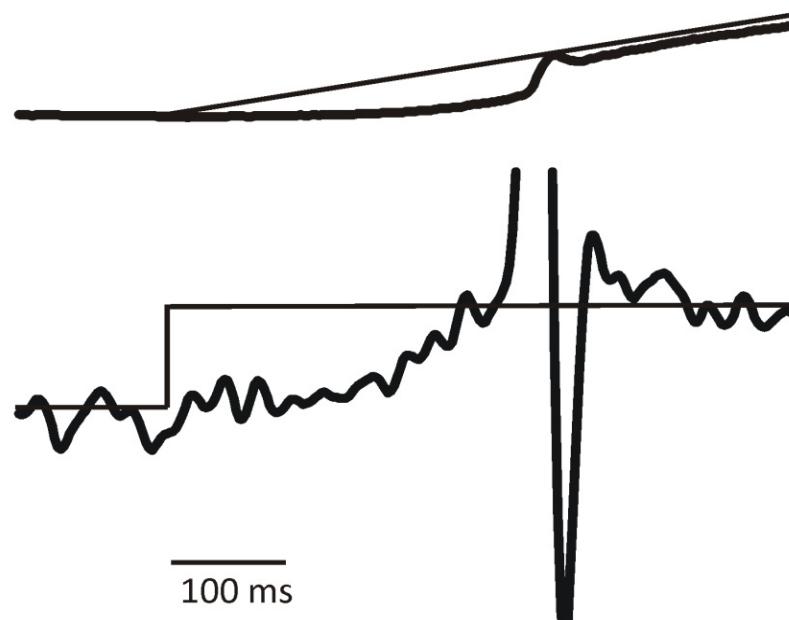
The difference between OKN and smooth pursuit eye movements is not always clear. Researchers differentiate two kinds of OKN with regard to the instructions given to each subject. The optimal stimulus for OKN is a large-field structured stimulus. Instructions to

“stare” at the stimulus produce smooth movements over large amplitudes, whereas instructions to “look” at the stimulus produce a periodic pattern with a small-amplitude smooth phase. When instructed to “look”, the observers track some detail of the moving image, which may represent a form of automatic engagement of the smooth pursuit system (Ilg 1997). Thus, stimulus size is not enough to differentiate OKN from smooth pursuit movements because global motion stimuli (Heinen and Watamaniuk 1998), and even targets defined only by peripheral cues, can serve as stimuli for smooth pursuit (Ilg and Thier 1999). It was proposed that the ability of the system to track a target over a stationary structured background might be a better criterion to differentiate smooth pursuit from OKN because it implies a suppression of the OKN automatically generated by self-induced retinal motion of the background (Krauzlis 2004). However, the distinction between OKN and smooth pursuit vanishes for the open-loop part of pursuit, which, by definition, is only driven by the motion signals sampled before the eye starts to move and, therefore, the self-generated background motion does not yet need to be suppressed.

A



B



**Figure 7** Panel A shows the basic building blocks of a model of the control of smooth pursuit eye movements (for a complete model see Barnes 2008). This model implements a negative-feedback loop, a delay (of 100 ms), and a constant factor for the visuomotor gain function (how much the eye velocity is increased by the retinal velocity of the target), with the purpose of minimizing retinal slip. Panel B shows a sample horizontal position and velocity trace (below) of the eye when a rightward target moving at 8.1°/sec has to be tracked, as measured with the IRIS infra-red eye-tracker (see Study 2).

We will see in the first study that attention does not seem to be necessary for pursuit initiation under conditions where there is not another motion competing for selection, i.e., when the pursuit target is the only motion signal. This may be a reason to classify the first pursuit response as driven from similar reflexive mechanisms as OKN.

### 1.6.1 Attention and pursuit initiation

I did not mention the work of Wyatt and Pola (1987) in Study 1, for which it is quite relevant. They showed that a pursuit response could be generated passively,<sup>8</sup> but with a low gain (the ratio of eye velocity to target velocity) for a brief period, even if the target was small. They consequently proposed that pursuit could subsume two different mechanisms: one that is independent of attention, and therefore can be engaged passively, and one that depends on attention, and hence is able to generate responses with higher gain. This proposition, however, does not take into account the fact that the passive responses may be generated through exogenous attention that is grabbed by the onset of the target. In any case, their study also shows that similar initial responses are obtained with extended stimuli suited for optokinetic responses, suggesting the existence of common mechanisms for optokinetic eye movements and pursuit eye movements.

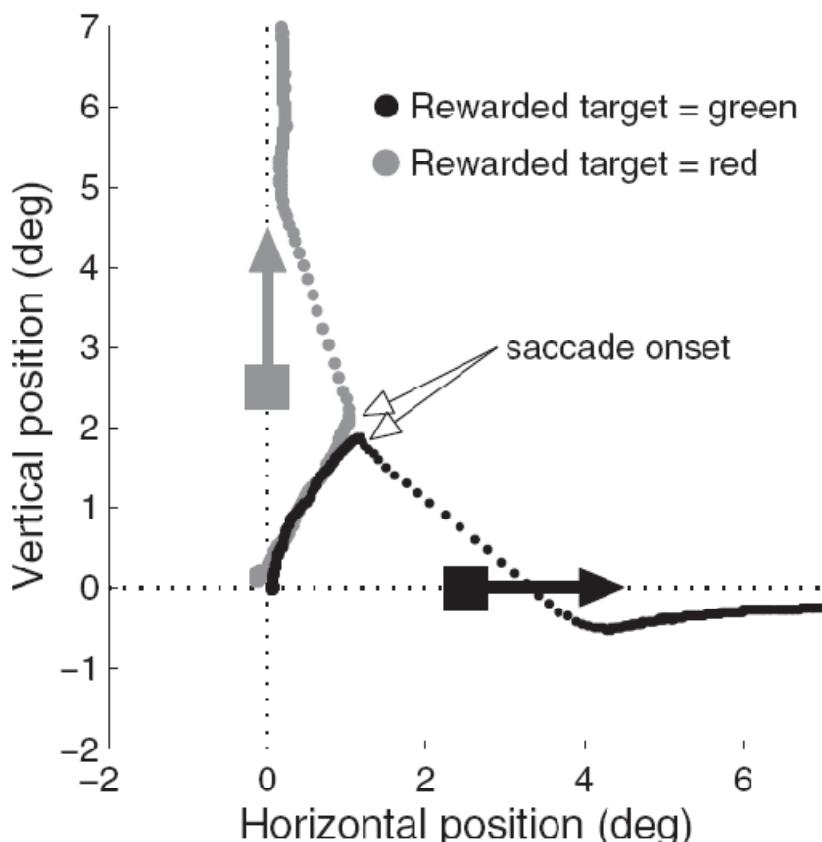
In contrast, it has been suggested that attention also precedes smooth pursuit eye movements (Schutz et al. 2007a), as indicated by a reduction in the contrast sensitivity for peripheral targets at the onset of the target and the onset of the eye movement. This finding implied at the very least a narrowing of attention to the target of the upcoming eye movement because the discrimination probes were horizontal bars above or below the target trajectory. However, as we will see in Studies 1 and 2, subjects may not be slower when keeping some attentional resources in the periphery, nor are they faster when paying more attention to the pursuit target.

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<sup>8</sup> The instructions may have been somewhat ambiguous in the passive condition: “Specifically, the subjects were told to be aware of the moving target, but to avoid attempts at foveal fixation. In not looking at the target, the subjects were not to choose some imaginary fixation point in space, and were not to attempt to hold their eyes still” (Wyatt and Pola 1987, p. 1566).

### 1.6.2 Vector averaging

Vector averaging is often the first pursuit response when a pursuit is initiated in the presence of a moving distractor. This averaging behavior indicates poor selectivity of pursuit initiation and, thus, can support the view of Wyatt and Pola (1987) that pursuit initiation can be a pre-attentive process.



**Figure 8** Sample trajectories of the eye for an upward moving rewarded target and a rightward moving rewarded target. The two squares start moving at the same time, and monkeys are rewarded if they follow the pre-designated target within some tolerance window. The monkeys have 400 ms after they cross the fixation point to be within the tolerance window to be rewarded. Typically, pursuit follows the vector average direction, and then the target direction is selected in a winner-take-all manner (adapted from Case and Ferrera 2007).

When the pre-designated target for pursuit starts to move at the same time as a distractor, pursuit is first directed to the vector average direction. Then, after approximately 80 ms, typically simultaneously with the execution of a saccade, the pursuit movement becomes selectively associated with the target direction (Ferrera and Lisberger 1997). By the

term vector average, we mean that the direction and velocity of the eye approaches the vector average of the distractor and the target vectors (and not the vector sum, in which the vector components are added). Figure 8 shows a typical trial in such a situation. Initially, the influence of the distractor on pursuit initiation was studied in a situation in which the target and distractor moved in opposite directions, and the pursuit latencies were compared to the pursuit latencies when the target was presented alone (Ferrera and Lisberger 1995). Pursuit was delayed in the opposite-motion signal condition compared to the single-motion signal condition. I will consider those effects under the same banner of vector averaging, even though we do not have an overt expression for this process.

Furthermore, although pursuit averaging is in contrast with the winner-take-all saccadic responses, averaging has also been observed for saccades. Some studies show that precision is traded for speed when a distractor is close to the target; short latency saccades tend to land in-between the target and the distractor (Ottes et al. 1985; Chou et al. 1999).

Initial pursuit averaging can be related to what we have already said about the speed of the attention shifts. It was found that saccade execution was preceded, by at least 50 ms, by attention at the target. Averaging may indicate that attention takes longer to select the target than the typical pursuit latency.

When studying the influence of distractor motion, the target is typically cued approximately 500-1000 ms before the target and the distractor start to move. The cue specifies the target by its color, location, or shape. The main difference in using different cue types is that location cues do not require a search for the target; otherwise, all cues require subjects to *voluntarily* shift attention to the target because exogenous effects are too short-lived to affect target selection (e.g. Cheal and Lyon 1991). Macaques show a very robust initial averaging response to a target (Lisberger and Ferrera 1997) or a delay when the distractor motion is in opposition to the expected (Ferrera and Lisberger 1995). When the target direction is blocked, monkeys show delays of similar size (approximately 20-25 ms) in the presence of a moving distractor as well as a strong averaging response (Lisberger and Ferrera 1997). Studies with humans also show similar delays (Krauzlis et al. 1999; Adler et al. 2002), as shown in Study 2.

However, humans could suppress the influence of the distractor when they were informed about the target direction prior to motion onset (Spering et al. 2006a). They did in

fact show a small effect to the opposite side; pursuit was deviated opposite to the distractor. This effect is similar to what Shelia et al. (1995) found on the curvature of saccades and was thought to arise from inhibition of the distractor. Either humans are better able to selectively attend to the target by using information provided by the cues, or pursuit initiation in monkeys is initially driven by a reflexive pooling of all the motion signals.

### 1.6.3 Attention and pursuit maintenance

If direct evidence has been lacking for the role of attention in pursuit initiation, attention certainly plays a role during pursuit maintenance. Khurana and Kowler (1987) tested the idea that pursuit and perception share the same selection filters, by examining maintained phases of smooth pursuit. This test is particularly difficult to conduct because it implies that the untracked targets must move at different speeds or in different directions. Therefore, subjects had to track targets that were presented foveally at very slow speeds ( $<0.5^\circ/\text{sec}$ ). The untracked perceptual targets moved slightly faster or slower. Despite the confounds of varying acuity and retinal slip in untracked and tracked stimuli, these authors showed quite convincingly that perception was closely dependent on which target was selected for smooth pursuit. Perceptual performance on untracked targets was strongly impaired, as well as fixation was impaired when attempts were made to attend to moving targets. They also noted, however, that when asking subjects to attend to the untracked target, decrements of pursuit performance were not as strong. The authors' conclusions were fairly similar to previous studies describing how diverting attention from the saccadic target offsets saccade latency (Kowler et al. 1995; see also our Study 2). They noted that pursuit, unlike the perceptual performance, is not a monotonic function of the amount of attention, as beyond some amount of resources, pursuit velocity is impaired very little by distracting resources from its target. As they put it "This is a fortunate state of affairs. It allows us to maintain the line of sight on selected objects while preserving enough attention left over to make decisions, solve problems, or think" (Khurana and Kowler, 1987, p. 1617). Following up on this question, it was shown that the effects of cuing peripheral locations could be found while pursuing a target, in speeded and in perceptual non-speeded tasks. It was possible to quantify the costs and their time course as a reduction in the gain of pursuit. One important finding was that there were little costs when the cued objects (placeholders) moved with the pursuit target, suggesting that attentional resources are limited to what is

necessary to filter-out the competing signals, such that a narrow focus of attention on the target does not appear to be a precondition for pursuit maintenance (Kerzel et al. 2008). Consistently, it was also shown that during maintained pursuit the perception of motion signals in the same direction were enhanced, which may indicate feature attention in the direction of motion of the pursuit target (Schutz et al. 2007b).

However, the latter results, that attention can be spread to the periphery without impairing pursuit, do not mean that the size of the attention window does not matter in pursuit control. Madelain et al. (2005) showed that the spatial scale of attention influences the pursuit responses to perturbations of target velocity in a paradigm in which pursuit target perturbations are injected while a wide-ring or a small-ring (within the wide ring) is attended.

#### **1.6.4 Physiology of pursuit and saccadic eye movements**

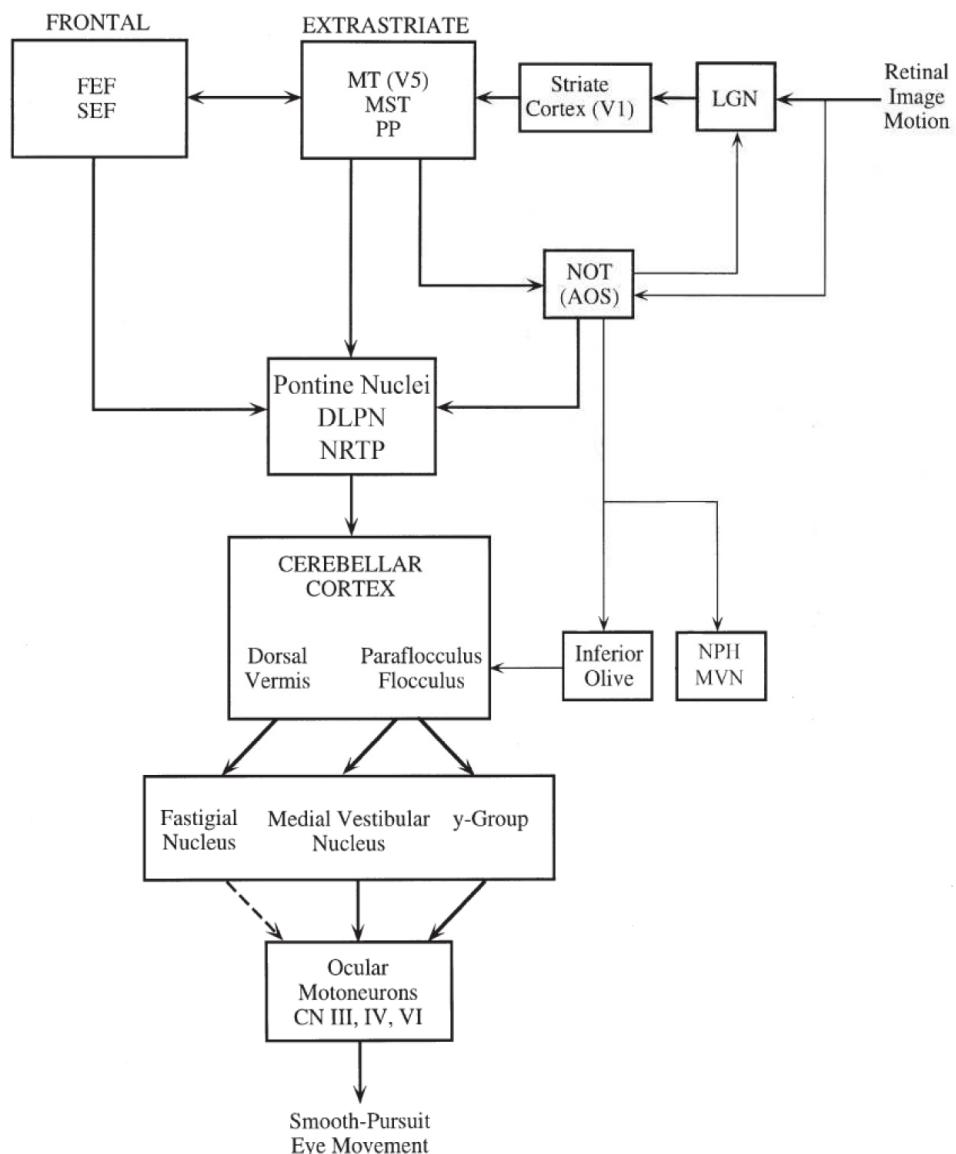
Our knowledge of the neural substrates of saccadic and pursuit eye movements is heavily based on monkey physiology. My emphasis will be on the pursuit system, and then on the areas that were classically associated with saccades and which were more recently shown to interact with pursuit movements (Krauzlis 2004; Thier and Ilg 2005; Leigh and Zee 2006).

Pursuit is mainly controlled by a pathway running from the cortex to the pontine nucleus to cerebellar areas, which in turn project to brain stem premotor nuclei (mainly the vestibular and fastigial nuclei) and then project to the oculomotor nuclei, as shown in Figure 8. The main input for pursuit movements is the retinal velocity of the object, which is mainly provided by the medial temporal (MT) and the medial superior temporal (MST) extrastriate areas. Some MST neurons (the lateral MST) selectively respond to motion in space (“world-centered” coordinates) as well as retinal motion (Newsome et al. 1988; Thier and Ilg 2005). That is, some neurons discharge even when no retinal motion is present, which may provide a common frame of reference for the important task of guiding hand and eye movements (Ilg and Schumann 2007), whereby the MT (feeding MST) can provide the retinal motion signal that principally drives pursuit (Thier and Ilg 2005). Although the MT and MST show a strong enhancement when attention is directed toward the receptive field of a neuron (Treue and Maunsell 1999), almost all neurons respond after the pursuit onset (Newsome et al. 1988), precluding a role for those areas in pursuit initiation (Thier and Ilg 2005). Other

parietal areas (such as the monkey homologues, VIP and LIP, not shown in Figure 9) may also have a role in smooth pursuit movements, presumably through their role in orienting spatial attention (Berman et al. 1999).

Another neural route passes from the parietal to the frontal areas: FEF and SEF. As might be expected from the higher-level areas, FEF and SEF have been shown to be involved in predictive behavior. For instance, Drew and van Donkelaar (2007) showed that the application of TMS to the FEF (for effects TMS over SEF see also Nyffeler et al. 2008) caused a longer delay in pursuit initiation when the target direction was predictable than when it was randomized (it is well known that pursuit can be initiated even well before target onset when direction is predictable, e.g. Barnes 2008).

Recently some brain areas have been shown to carry signals that are shared for the control of pursuit eye movements and saccades (Krauzlis 2004). Such is the case for the SC, an important area associated with saccade target selection. In contrast to the voluntary control in the FEF, the intermediate layers of the SC are believed to be involved in reflexive ocular and attentional orientation to salient targets. The intermediate layers of the SC form a retinotopic map covering the visual field. The rostral pole of the SC represents the foveal region of the retina, and the caudal SC represents the more eccentric regions of the visual field. The activity of build-up neurons (those neurons that increase their rate of action potentials in preparation for saccades) is increased when a stimulus within the receptive field of the neuron is either selected for pursuit or for a saccade (Krauzlis and Dill 2002). In the same vein, microstimulation of the SC could bias selection of the target or the distractor for either pursuit or saccades, depending on whether or not the target was moving (Carello and Krauzlis 2004)



**Figure 9** Shown are the main pathways implicated in the control of smooth pursuit eye movements. Several cortical sites are involved: signals for retinal motion are converted into inputs for the MT/MST and prediction involves the FEF and SEF. The motor parameters are set in the pontine nuclei (DLPN=dorsolateral pontine nuclei, NRTP=nucleus reticularis tegmenti pontis) and then passed to the cerebellum, which may modulate them by comparing the efference copy with the predicted output, and finally a command is sent to the ocular motoneurons of the brain stem (reproduced from Leigh and Zee (2004, p. 203). PP = posterior parietal cortex; NOT = nucleus of the optic tract; AOC = accessory optic system; MVN = medial vestibular nucleus; NPH = nucleus propositus hypoglossi; CN = cranial nerve.

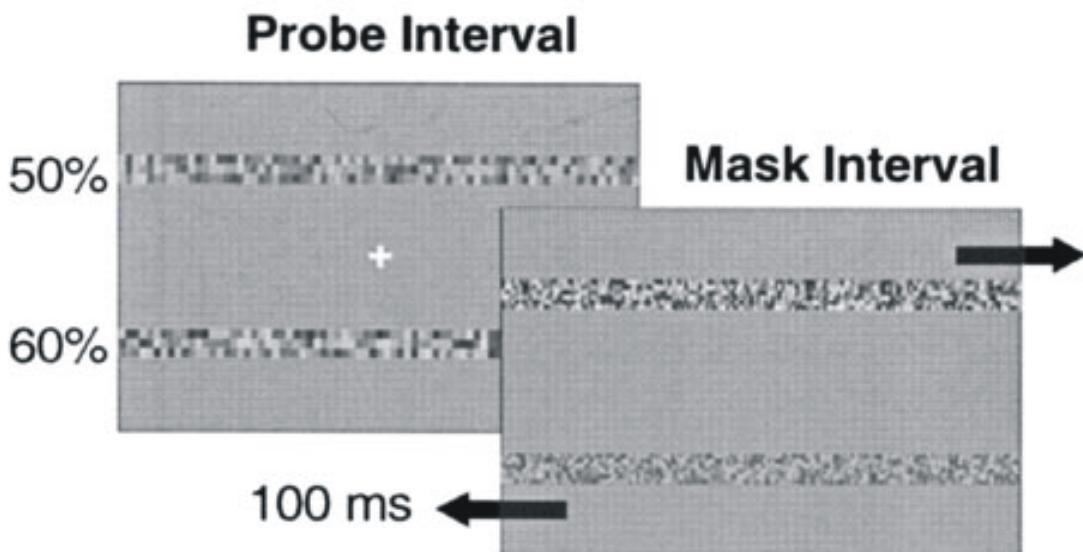
Similarly, the activity of omnipause neurons (OPN) has been related to the release of fixation for pursuit movements and saccades. OPN are located in the pontine nucleus raphe interpositus and are classically associated with the release of fixation for saccades (Leigh and Zee 2006). OPN discharge as long as the fixation is held and have inhibitory connections with neurons that innervate the motor neurons. Saccade generation may involve a signal from the SC that inhibits the OPN, in turn releasing the gate that permits the signal to be passed to the motor neurons (Sparks 2002). Missal and Keller (2002) showed that microstimulation of OPN reduced the pursuit gain during maintained pursuit. Conversely, activity of OPN was reduced during smooth pursuit movements (however, their activity was not silenced as during saccades). The role of the OPN can be viewed as that of a synchronizer of horizontal and vertical motor signals, which are separated in the brain stem nuclei (Sparks 2002). As shown by Missal and Keller (2002) experiments OPN neurons may also participate in synchronizing the gating of pursuit initiation and saccadic responses, a possibility that might explain the post-saccadic enhancement of pursuit velocity as suggested by Ogawa and Fujita (1998).

### 1.6.5 Shared target selection signals

Interactions between the saccadic and pursuit signals are not solely seen at the physiological level. The same manipulations that affect saccadic latencies can also affect pursuit latencies. For instance, a similar distractor effect, the lengthening of saccadic latencies when a distractor appears on the fovea or in the periphery (if it is far from the target), is revealed in pursuit latencies (Knox and Bekkour 2004). There is also a similar remote distractor effect (RDE) in pursuit initiation. The RDE involves the lengthening of saccadic latencies when a stimulus is presented at the same time or shortly after the target. Pursuit latencies show a similar dependence on where the distractor is presented in the visual field (Knox and Bekkour 2004). Also, anticipatory behavior and dependence on preparation time was similar for saccades and pursuit latencies (Burke and Barnes 2006; Joiner and Shelhamer 2006). When trying to reproduce the gap effect on pursuit movements, which is the facilitation of saccades when the fixation point is removed before the target onset, the evidence was less clear because the latency to pursuit initiation was reduced, but the bimodality in latencies that sometimes characterize saccadic latency distributions was not found for pursuit initiation (Knox 1998; Kimmig et al. 2002; Knox 2009).

Finally, it was shown that spatial cues are better at reducing latencies in the pursuit of the upcoming target than local motion cues, and the spatial cues similarly reduce the latencies for saccades and pursuit eye movements even though motion may be a better “prime” for pursuit movements (Adler et al. 2002).

Other psychophysical experiments have permitted us to derive precise models for the coordination of pursuit and saccadic eye movements based on the same target selection signals in the SC (see Krauzlis and Dill 2002). Liston and Krauzlis (2003) devised a task in which independent (vertical) saccadic and (horizontal) pursuit choices could be made. The stimuli of this experiment are shown in Figure 10. Observers were required to pursue and saccade to the stripe with the highest contrast shown within the first temporal interval before another set of stripes started to move in opposite, horizontal directions. Because the differences in contrast between the stimuli were small, there were many errors, which provided them the opportunity to compare the pursuit and saccadic choices, and whether or not the two types of movements were independent. For instance, pursuit could be initiated to the lower stripe motion direction, while a saccade is initiated to the upper stripe location, indicating independent choices. The whole point was to how likely was this independent choice, and interestingly how did the probability of an independent choice evolve in time. . The results show that the proportion of choices in the same direction was much greater than would be predicted if the two processes were independent. The difference between the two is sensible when information about the target approaches guessing level; in this situation, approximately 50% of the choices should be in the same direction. However, the percentage for choices in the same direction was about 90%. Another interesting analysis involved the percentage of same choices as a function of the proximity of the pursuit choice from the saccadic choice. There was a monotonic increase in the percentage of choices in the same direction, indicating that pursuit progressively conformed to the same choice. Finally, if there was a motion bias towards the upper or lower target in the pursuit choice, it ended up reflecting a bias in the saccade choices. The latter results are thus in agreement with the electrophysiological data that counter-intuitively indicated that pursuit eye movements are controlled by spatial signals (Krauzlis and Dill 2002; Liston and Krauzlis 2003).



**Figure 10** Shown are stimuli in one trial of the experiment by Liston and Krauzlis (2003). The task of the observers was to pursue and saccade to the location of the probe stripe with the higher contrast. The contrast of the two masks was varied but was task-irrelevant.

More recent elaborations on this theory stem from the analysis of speed-accuracy trade-offs of pursuit eye movements and saccades during a similar task. The findings indicate that the different systems share similar signals that accumulate across time, but that the pursuit choice has a lower decision threshold leading to a lower sensitivity in the detection of a target across a wide range of latencies (Liston and Krauzlis 2005). In reminder of our digression on economy, shorter pursuit latencies compared to saccadic latencies can be thought to reflect supplementary costs associated with saccades—costs due to saccadic suppression, for instance. Therefore, more evidence is required before a response is generated (see also Krauzlis and Dill 2002).

### 1.6.6 Attention as the oculomotor glue?

In the previous section, we encountered a situation in which the saccade choice could be at odds with the pursuit choice. Although artificial, it may represent a very common situation that can happen every time two possible targets are moving at the same time with different directions, or one target is static and the other is moving. If the two systems were controlled by completely independent processes, a situation could arise in which the moving object is selected for pursuit while another object is selected for a saccade, ruining the acuity for both objects. Therefore, just as it is better to align attention with the saccadic goal

in order to reduce the costs of acuity, it may also be necessary to align the pursuit and saccadic responses to the same target.

Several lines of evidence suggest that attention may play a part in coordinating the pursuit and saccadic responses. One line of evidence is the existence of vector-averaging and the winner-take-all choice during pursuit initiation (Gardner and Lisberger 2001; Gardner and Lisberger 2002; Case and Ferrera 2007). The second line of evidence comes from correlations between choices when pursuit starts toward a *new* target (Erkelens 2006). The third line of evidence comes from studies showing that there is a post-saccadic enhancement of pursuit speed, which may be related to the first point (Lisberger 1998; Schoppik and Lisberger 2006).

As stated before, when two moving targets are presented, we first start pursuing in the direction of the vector average (Lisberger and Ferrera 1997). Typically, pursuit then passes from the vector average to a winner-take-all choice after a saccade is executed (see Figure 8). Gardner and Lisberger (2001; 2002) proposed a “linked selection” model for the coordination of pursuit and saccadic choices based on the findings that a winner-take-all choice seems to occur *after* the saccade on a trial-by-trial basis (Gardner and Lisberger 2001). Furthermore, they show that microstimulation of the FEF and SC can artificially bias the pursuit choice towards the target. The results of other studies suggest that there is parallel access to the same signal, as suggested in the previous section (Liston and Krauzlis 2003; Liston and Krauzlis 2005; Case and Ferrera 2007).

It is noteworthy that the winner-take-all selection in pursuit movements that is caused by microstimulation of the FEF or SC can support either the hypothesis that the pursuit target selection is linked to saccade selection signal or the hypothesis that microstimulation causes spatial attention to simultaneously select the target for saccades and pursuit eye movements (see Section 1.4).

Erkelens (2006) compared the saccadic and pursuit latencies in two different paradigms. The task was unusual in that a sequence of moving targets appeared on the screen at random locations and moved in random directions (constrained by the limits of the screen). In one condition, the new target appeared at the same time that the old target disappeared. In another condition, presentation of the old and new targets overlapped in time. Saccadic and pursuit latencies at the onset of the new target were recorded. The first

situation more closely exemplifies a classic ramp paradigm, which leads to pursuit latencies that are much shorter for pursuit than for saccades and to no correlation between the two choices ( $R^2=0.01$ ). The second situation revealed a striking difference: the pursuit choice latencies were in the same order as the saccadic latencies (changes in direction of the pursuit movements were locked to the onset of the saccade), and the latencies of the pursuit and saccadic choices were highly correlated ( $R^2=0.91$ ). The interpretation was that, in a typical ramp paradigm in which the fixation target starts moving, engagement of the oculomotor system precedes attentional selection of the target (a similar view to that of Wyatt and Pola 1987); however, when the old target is still being pursued, the choice is made at the same time as for the saccades. The conclusions are not very different from what is implied by the results with vector averaging. What is new is that these findings indicate that not only is some time necessary to select a new target, resulting in averaging, but also that some time is necessary to disengage from the old target and that both processes can imply time-consuming attentive selection of the target that might not have ended by the time of the short-latency pursuit.

Also suggestive that attention mediates saccades and pursuit coordination are the results on the post-saccadic enhancement of pursuit velocity. When initiating the pursuit of a single object, the pursuit velocity is higher after the first catch-up saccade (Lisberger 1998). Unlike other reflex-like responses to wide-field motion (Takemura and Kawano 2006), this post-saccadic enhancement of pursuit velocity is not induced by retinal motion during the saccade. Further, it was shown that this enhancement depended on how far the endpoint of the saccade was from the moving target, which is compatible with the idea that it is a function of the amount of attention at the target (Schoppik and Lisberger 2006).

In summary, by analogy to the feature integration theory, it can be said that attention may be the glue that binds the oculomotor decisions of the pursuit and saccadic systems to the same target. Although more direct evidence is needed, the results of Study 1 together with the aforementioned studies indicate that this is the case.

## 2 Study 1: Dynamics of attention during the initiation of smooth pursuit eye movements

### 2.1 Abstract

Many studies indicate that saccades are preceded by a shift of attention to the target location. There is no direct evidence for the same coupling during smooth pursuit. If smooth pursuit and attention were coupled, pursuit onset should be delayed whenever attention is focused on a stationary, non-target location. To test this hypothesis, observers were instructed to shift their attention to a peripheral location according to a location cue (Exp. 1-2) or a symbolic cue (Exp. 3) around the time of smooth pursuit initiation. Attention was probed by discrimination performance at locations orthogonal to the pursuit trajectory. Observers had to indicate the direction of an 'E' (Exp. 1-2) or the orientation of a Gabor patch (Exp. 3). Attending to static targets had only negligible effects on smooth pursuit latencies and the early open-loop response, but lowered pursuit velocity substantially about the onset of closed-loop pursuit. Around this time, eye velocity reflected the competition between the to-be-tracked and to-be-attended object motion, entailing a reduction of eye velocity by 50% compared to the single task condition. The precise time-course of attentional modulation of smooth pursuit initiation was at odds with the idea that an attention shift must precede any voluntary eye movement. Finally, the initial catch-up saccades were strongly delayed with attention diverted from the pursuit target, even when we controlled for low level trigger signals. Implications for models of target selection for pursuit and saccades are discussed.

### 2.2 Introduction

Foveation and tracking of moving targets for full acuity perception is achieved by a coordination of smooth pursuit and saccadic eye movements. Pursuit serves the purpose of reducing retinal motion of objects we look at. Initiation of smooth pursuit differs from saccadic initiation in many ways. Among other things, pursuit is initiated with shorter latencies, and is mainly driven by a velocity signal (Rashbass 1961). Smooth pursuit is initiated by an open-loop phase that precedes the onset of functional pursuit by about 100ms, which is mainly controlled by a negative-feedback loop to ensure that the eye

velocity closely matches the target velocity (Tychsen and Lisberger 1986). Only recently researchers have unveiled that saccades and smooth pursuit share many common neural substrates and similar mechanisms of target selection and initiation (for a review see Krauzlis 2004). However, it is not well understood if attention plays the same role in the initiation of smooth pursuit and saccades.

Visual selective attention is believed to play a mandatory role in the initiation of voluntary saccades (e.g. Deubel and Schneider 1996; Deubel and Schneider 2003). This relation led some authors to suppose a pre-motor origin to covert shifts of attention (Rizzolatti et al. 1987; Kustov and Robinson 1996; Smith et al. 2004; Muller et al. 2005a). The extent of the overlap between covert attention and saccade programming is still under debate (e.g. Thompson et al. 2005). Nonetheless covert attention allocated to the saccade goal seems necessary for the initiation of voluntary saccades (Posner 1980; Shepherd et al. 1986; Crawford and Muller 1992; Reuter-Lorenz and Fendrich 1992; Hoffman and Subramaniam 1995; Kowler et al. 1995; Deubel and Schneider 1996).

Various lines of research suggest that a similar coupling exists for smooth pursuit. Evidence for this coupling is solid for steady-state pursuit and sparse for open-loop initiation. During the steady-state phase, selective attention is tightly coupled to the pursuit target, as shown by very poor perceptual performance for untracked targets moving in the same direction (Khurana and Kowler 1987), and the sensibility of pursuit gain to the size of the attentional window used to track the target (Madelain et al. 2005). Furthermore, spatial attention during smooth pursuit seems necessary to override OKN, which could theoretically be triggered by self-induced background motion during smooth pursuit (Lindner et al. 2001; Lindner and Ilg 2006). The role of locking attention to the pursuit target may therefore be to filter out disrupting motion signals from the background with some success (Sperling & Gegenfurtner, 2007).

The relationship between spatial attention and open-loop pursuit is less clear. Recent studies suggest that pursuit and saccades share mechanisms of target selection (Krauzlis et al. 1999; Liston and Krauzlis 2003; Liston and Krauzlis 2005; Krauzlis and Dill 2002). For example, spatial cuing (endogenous or exogenous) shortens pursuit as well as saccadic latency considerably (~30 and ~50ms respectively) in the presence of a distractor. In addition, cues indicating the location of the upcoming pursuit target were more effective in

reducing pursuit latencies than cues indicating motion direction, which should *a priori* directly prime the pursuit system (Adler et al. 2002). Those latter findings lend support to the idea of a common attentional selection mechanism.

Other lines of research suggest that spatial attention plays a privileged role well after movement initiation, corresponding to the beginning of the closed-loop phase. A number of studies suggest that attention for smooth pursuit is locked to the endpoint of the first catch-up saccade. This may explain why pursuit velocity is enhanced synchronous to saccade execution (Lisberger 1998; Ogawa and Fujita 1998; Schoppik and Lisberger 2006) as well as when the pursuit target is spatially close to the saccade endpoint (Schoppik and Lisberger 2006). Conversely, these findings may be taken to indicate that focused attention is not involved in pre-saccadic pursuit. Erkelens (2006) proposed that pursuit latencies in the classic step-ramp paradigm (Rashbass 1961) are shorter than saccadic latencies because pursuit can be initiated before the target is selected. The signal to select the target is made available at the same time for pursuit and saccades. Before that time, pursuit follows the available motion signals, not the voluntarily planned movement.

Ferrera and Lisberger (1995) showed that smooth pursuit latency was strongly delayed (~60ms) when monkeys were instructed to pursue a target indicated by a color cue in the presence of a distractor moving in the opposite direction (Ferrera and Lisberger 1995; Ferrera and Lisberger 1997). However, the dynamics of pursuit were unaffected. Importantly, the delay was reduced but still present if a location cue preceded target and distractor onset by up to 800 ms (Ferrera and Lisberger 1995), showing that advance target selection by selectively attending to the target is imperfect for smooth pursuit, in striking contrast to target selection for regular saccades.

Our brief summary shows that previous studies are not conclusive about the *effective* involvement of attention in smooth pursuit initiation and do not answer the question whether pursuit and saccades exhibit the same coupling of selection for perception and selection for eye movements (Deubel and Schneider 1996). This question is of particular interest to understand how attention contributes to the necessary coordination of saccadic and pursuit target choice. Single pursuit target conditions can reveal whether allocation of attention to the pursuit target is mandatory, quite similar to classic studies requiring saccades to non-attended locations. Therefore, we assessed the dynamics and strength of

the coupling of spatial attention and pursuit movement programming in a series of three experiments. To shift the focus of attention from the pursuit target location we used a dual-task paradigm in which spatial attention was summoned at a distant ( $7^\circ$ ) location, orthogonal to the upcoming motion direction of the pursuit target. The onset asynchrony between the cue (a location or symbolic cue, also referred to as an *exo-* or *endogenous* cue respectively) and the pursuit target motion (SOA) was varied from 0 to 500ms (50 to 550ms in the third experiment). Similar manipulations have shown that shifting attention in a direction opposite to the saccade goal caused saccadic latency to be delayed by some 20-50ms (Shepherd et al. 1986; Shepherd and Müller 1989; Crawford and Muller 1992; Reuter-Lorenz and Fendrich 1992).

When summoned by a cue flashed in the periphery, attention takes some 150ms to be maximally allocated at the cued location, and about 300ms to return to the fixated location as indicated by perceptual performance (e.g. Müller and Rabbitt 1989; Nakayama and Mackeben 1989b; Cheal and Lyon 1991). The same displacements of attention take a little longer with endogenous cues. Therefore, spatial attention should be maximally diverted from the pursuit target with SOAs of 0-200ms. In contrast, with a SOA of 500 ms attention should have time to return to the pursuit target location. As a control, we ran a single task condition in which observers were instructed to perform pursuit while ignoring the peripheral events. If attention was coupled to the location of the pursuit target at specific points in time, we should expect an interaction with task load (dual task vs. single task) and SOA, indicating that pursuit parameters (latency or/and speed) change as a function of SOA in the dual task condition, but not in the single task condition. While this approach does not tell us how spatially specific the coupling must be, it will tell us whether spatial attention at the target location is necessary for the initiation of the eye movement. Allocation of attention to the peripheral location was assessed by a perceptual discrimination task (e.g. Deubel & Schneider, 1996).

We contrasted a condition in which to-be-attended perceptual targets remained static with a condition in which they moved along with the pursuit target. The condition with static peripheral targets produced potentially conflicting relative motion whereas the moving peripheral targets condition did not. Only the former condition required attentional

filtering, but both conditions imposed similar dual task demands (pursuit + perceptual discrimination).

## 2.3 Method

### 2.3.1 Observers

There were 8 participants (age:  $M=23$ ,  $SD= 2.7$ ) in the first experiment: five experienced psychophysical observers, and three naïve observers. In Exp. 2 there were 7 participants (age:  $M=22$ ,  $SD=3.0$ ) and 6 were naïve. In Exp. 3 there were 8 participants (age:  $M=22$   $SD=2.8$ ), 7 were naïve, and 2 had participated in one of the previous experiments. The first author participated in the three experiments. Naïve observers were undergraduate students from the University of Geneva and were paid or received credit for an undergraduate class. All participants had normal or corrected-to-normal vision.

### 2.3.2 Apparatus

Eye movements were recorded with a head mounted Eyelink II eyetracker (EyeLink II, SR Research Ltd., Osgoode, Ontario, Canada). The signal was sampled at 250Hz and eye position was estimated from pupil centroid and corneal reflection, but on many occasions, only the pupil centroid was used, with a small loss of spatial resolution. The CRT monitor had a refresh rate of 100Hz and a resolution of 1280 x 1024pixels. To display the stimuli, we used a custom C program using SDL (<http://www.libsdl.org/>).

### 2.3.3 Experiment 1: ramp target, exogenous cue

In the first experiment, we contrasted conditions in which the to-be-attended discrimination stimuli presented in the periphery remained stationary and conditions in which the discrimination stimuli started to move at the same time and in the same direction as the pursuit target (see Figure 2.1A). The same manipulation was run during fixation to tease apart decrements in perceptual performance due to motion blur from those due to reorientation of attention to the pursuit target location. The comparison of static and moving peripheral targets further assessed how attention adjusts the weight given to the input of conflicting (relative motion) or synergistic peripheral motion (no relative motion) signals during pursuit initiation.

### 2.3.4 Stimuli

Stimuli were displayed on a uniform gray background (average luminance: 29cd/m<sup>2</sup>). The viewing distance was 46cm and the visible screen area 29.7 x 37°. The time-course is schematized in Figure 2.1A. A red cross (0.4 x 0.4°) had to be fixated or pursued after a random period of fixation, ranging from 0.3 to 1.3sec, when it started to move at 7.2°/sec. Placeholders 7° above or below fixation were present throughout the trial, that is during 2 seconds. To cue one of the two possible target locations, the placeholder was dimmed to 0cd/m<sup>2</sup> for 50ms. The cue indicated the correct position (valid cue) of the upcoming discrimination target (an “E” or its mirror-image) in 80% of the trials. On invalid cue trials (20%), the location of the distractor (an “S” or its mirror image) was cued. In dual task conditions, observers had to report whether an “E” or a mirror “E” had been displayed at the end of the trial, without any time pressure. The cue appeared 180ms before the onset of the discrimination target and distractor (e.g. Cheal and Lyon 1991; Cameron et al. 2002). The asynchrony between the location cue onset and pursuit target onset (SOA) was varied from 0 to 500. An effective allocation of attention should improve discrimination performance of validly over invalidly cued trials.

### 2.3.5 Procedure

The calibration of eye position preceded each trial block and was achieved by fixation of a dot appearing in 9 pseudo-random locations. The within-subjects design for the single and dual task conditions was: eye movement (fixation or smooth pursuit) x cue (valid or invalid) x relative motion (retinal or no relative motion) x SOA (500, 200, 100, 0ms or catch) x direction (left or right). There were 64 repetitions for valid and 16 for invalid cues by condition. In catch trials neither target nor cue was present. No catch trials were presented during fixation. Each combination of relative motion and eye movement was blocked. The other factors were randomized within a block. There were four dual task and two single task sessions. Each session was made up of four blocks, each comprising 100 pursuit trials and 80 fixation trials. Block order was balanced across subjects according to a Latin square design. The six sessions were run on different days. A threshold procedure following the UDTR rule (Macmillan and Creelman 1991) determined the presentation time of the discrimination target at the beginning of each session. The threshold value obtained was the presentation time that yielded 71% of correct discrimination responses (Exp. 1:  $M=94\text{ms}$ ,  $SD=25\text{ms}$ ; Exp.

2:  $M=82\text{ms}$ ,  $SD=28\text{ms}$ ). Participants triggered each trial by pressing a designated button on a gamepad. A drift correction was performed after the button press. Discrimination responses were made by left or right mouse clicks. At the end of each trial, acoustic feedback was given if the discrimination response was wrong. Visual feedback was displayed on the screen when blinks or saccades (amplitude  $> 1^\circ$ ) occurred. Participants were told to perform equally well the perceptual and the pursuit task in the dual task sessions, and that they had to maintain gaze on the red cross during the entire trial.

### **2.3.6 Experiment 2: step-ramp target, exogenous cue**

In the second experiment a step-ramp paradigm was used (Rashbass 1961). Step-ramp target motion allows for pursuit initiation without corrective saccades on a relative large number of trials. We will therefore be in a position to get pursuit trials initiated without a saccade, thus being able to test effects of attention on pursuit gain. Further, we added intermediate SOAs (300 and 400ms) to better trace the time course of attention shift effects.

The method was the same as for the Exp. 1 except for the following modifications. The within-subjects design was: relative motion (no relative motion or relative motion) x cue (valid or invalid) x SOA (500, 400, 300, 200, 100, 0ms or catch) x direction (left or right). There were 32 invalid and 128 valid cue trials per condition. The pursuit target followed a step-ramp trajectory (Rashbass 1961). The step, i.e. the time it took the target to reach its initial position, was set to the approximate mean latency of pursuit initiation in Exp. 1 of 120ms. The peripheral stimuli could not follow a step-ramp trajectory without perceptual performance being strongly disrupted, therefore the peripheral stimuli started to move when the pursuit target reached its initial position.

An additional feedback error message was displayed on the screen if the eye traveled less than 2 degrees during target motion. The purpose of this feedback was to provide a supplementary incentive to perform well on the two tasks at the same time.

### **2.3.7 Experiment 3: step-ramp target, endogenous cue**

Some concerns may be raised against our interpretations because we used a location (exogenous) cue. First, most of the studies that have tested the allocation of attention to the saccade goal used symbolic cues (e.g Kowler et al. 1995; Deubel and Schneider 1996).

Second, in one study (Reuter-Lorenz and Fendrich 1992), endogenous cuing was found to be more strongly coupled to eye movements than exogenous cuing (but see Kustov and Robinson 1996). Third, one could argue that the small differences between dual and single task conditions for pursuit onset could be attributable to a purely exogenous orienting of attention in the single task condition. Attention may have been automatically summoned by the abrupt peripheral onset of the cue even when it was task irrelevant. Some studies support this idea by finding cuing effects on discrimination tasks with non-informative exogenous cues (e.g. Liu et al. 2005). However, with our paradigm the cue could probably be ignored in the single task condition by adjusting the size of the attention spotlight (see Eriksen and St James 1986). Even onsets and singletons, thought to shorten RTs by capturing attention in some automatic manner, do not affect RTs when attention is focused on another location (Theeuwes 1991). This may have been the case in the single task condition.

To address the latter concerns we ran a similar experiment in which attention was summoned by a symbolic cue. This time, we presented low-contrast, unmasked Gabor patches and asked observers to report the orientation of the tilted grating (following Liu et al. 2005).

These stimuli were expected to reduce effects of the mere onset of the stimuli used in the perceptual discrimination task, as they are much less salient and unmasked. Furthermore, we added a control condition in which only the pursuit target was shown. Only the condition with relative motion was tested, as it was the condition in which attentional modulations of pursuit were largest.

Figure 2.1B shows the time-course of a trial and the stimuli used. In valid cue trials, the upper or lower part of the fixation cross disappeared for 50ms. The direction of disappearance of the branch always indicated the position of the upcoming discrimination target. The neutral cue was the disappearance of the upper and lower branches of the cross. The discrimination stimuli remained static on the screen (cf. relative motion condition of Exp. 1-2). We used five SOAs: 550, 350, 250, 150, 50ms intermingled with catch trials, with neither cue nor discrimination target. Half of the trials containing a cue were valid and the other half neutral. In single task blocks only neutral cues were presented. Because of the step-ramp dynamics of the pursuit target, there was no SOA of 0ms. A pre-test showed that perception of the central cue was degraded if it was presented at the same time as the

pursuit target step onset. The cue-target asynchrony was increased from 180 to 200ms, as maximum cuing benefits are reached later with central than with peripheral cues (Cheal and Lyon 1991). The threshold procedure estimated the orientation of the Gabor patches that yielded 71% of correct responses during fixation ( $M=3.2^\circ$ ,  $SD=0.8^\circ$ ). Sine-wave gratings of 2 and 4cpd were randomly alternated to avoid visual adaptation. The standard deviation of the Gaussian was  $0.9^\circ$ , and the placeholders had a diameter of  $1.7^\circ$ .

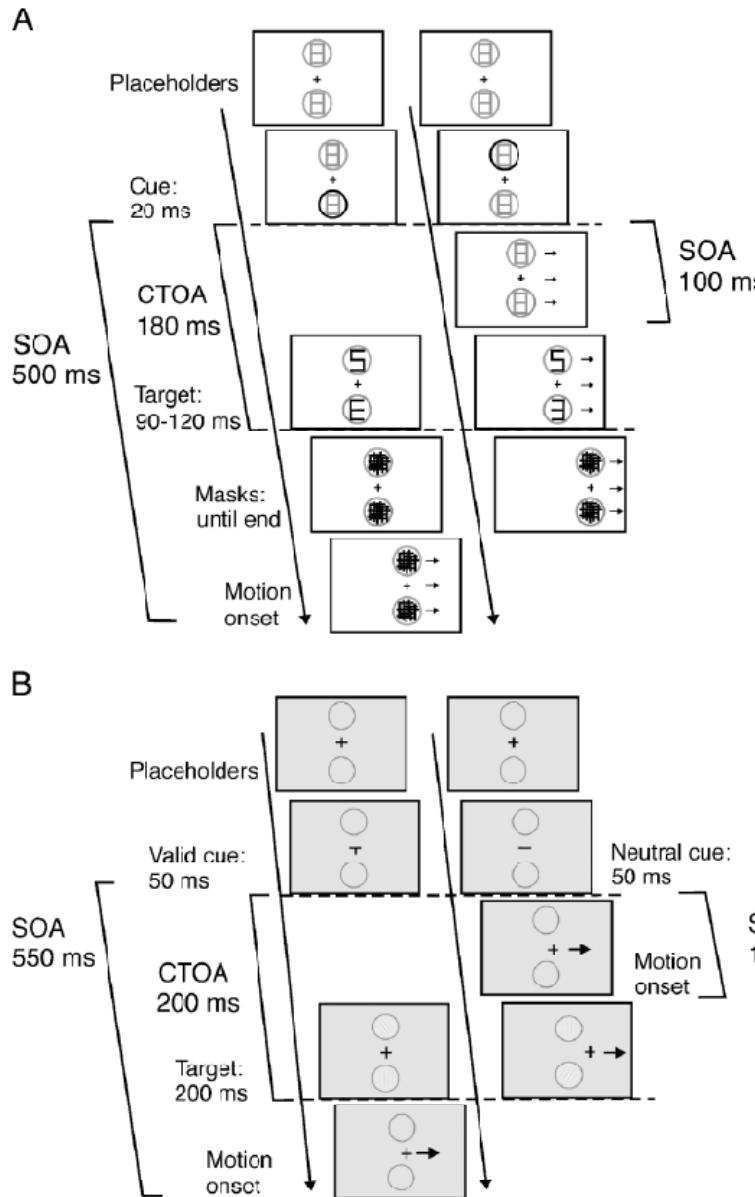
There were 4 sessions comprising four blocks, each lasting 45-60 minutes. The block order was balanced across subjects. The within-subjects design was: task load (dual or single)  $\times$  SOA (550, 350, 250, 150, 50ms or catch)  $\times$  cue validity (neutral or valid)  $\times$  direction (left or right). There were 40 trials for each condition. Single and dual task conditions were blocked. Additionally, a single task condition was run in a separate block (abbreviated single/no distractor), in which neither cue nor discrimination target was displayed.

### 2.3.8 Data analysis

Saccades were detected online by the Eyelink II parser with an acceleration threshold set at  $\pm 9'500^\circ/\text{sec}^2$ . Offline, a period of 12ms (3 samples) before and after a saccade was removed from the eye traces before averaging. Traces contaminated by eye-blanks, or with vertical saccades (amplitude  $>1^\circ$ ) were excluded from analysis. With a ramp target, closed-loop smooth pursuit is systematically preceded by a catch-up saccade, but open-loop pursuit did not always occur before the catch-up saccade. Thus, the first corrective saccade (henceforth CS1) latency was used as an exclusion criterion to ensure that the target was pursued. We excluded trials in which no CS1 with amplitude greater than  $1/3^\circ$  was detected from 100 to 400ms after motion onset. Effects were tested by running repeated measures analysis of variance (rmANOVA). When running multiple post-hoc comparisons we applied the Benjamini-Hochberg correction (Benjamini and Hochberg 1995)<sup>9</sup>.

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<sup>9</sup> Controls for the false discovery rate (FDR), offering the advantage over Bonferroni's correction of a higher statistical power with a large number of comparisons.



**Figure 2.1 Panel A:** Time course in Experiments 1-2. Placeholders appeared on the screen, and then a luminance increment cued the location of the subsequent discrimination target in 80% of trials (valid trials). The SOA between cue onset and motion onset was varied from 0 to 500ms. The cue-target onset asynchrony (CTOA) was fixed at 180ms. The left side of the graph shows a valid cue, and an SOA of 500ms, with the consequence that the discrimination target is presented before pursuit target motion. Subjects had to discriminate the "E" from its mirror-image. The duration of the presentation of the discrimination target was set to threshold. The right side shows an invalid trial, in which the cue indicates the distractor location, and an SOA of 100ms, implying that the discrimination target was displayed 80ms (CTOA - SOA) after motion onset. Panel B shows the time course of a trial in Exp. 3. The valid symbolic cue (i.e., endogenous cue), always indicated the position of the upcoming target. Disappearance of the upper or lower branch of fixation cross indicated that the target was located above or below, respectively. Peripheral discrimination targets remained static on the screen (relative motion condition).

To determine the pursuit onset, two regression lines separated by 75 samples were moved by a sample increment along the filtered velocity trace from target onset until the CS1 onset; the first regression line was a baseline that encompassed 60 samples (240ms); the second one comprised 15 samples (60ms). If the difference of the two slopes, that is acceleration, was above a threshold set to  $5'000^{\circ}/sec*sec$  the intersection of the two regression lines was taken as an estimation of the pursuit onset. To avoid false detections, 80% of velocity samples of the second regression line had to be above/below baseline. False onsets were removed manually after visual inspection. Velocity traces were smoothed by the application of a second order Butterworth filter with a 60Hz cutoff frequency. Pursuit onset latencies shorter than 52ms or longer than 400ms were excluded as anticipations and timed-out responses, respectively.

## 2.4 Results

### 2.4.1 Error analysis

Table 2.1 shows the proportion of trials removed from further analysis for Exp. 1-3. Overall, CS1 and pursuit latencies overlap to some extent such that CS1 can start before smooth pursuit. With pursuit of a ramp target at  $6-20^{\circ}/sec$ , Kimmig et al. (2002) reported 27% of movement initiation with a catch-up saccade. This is very close to the overall 33% of no pre-saccadic pursuit onset found in the ramp experiment. In Experiments 2-3, the pursuit onset was not detected before a saccade in about 10% of the trials, far less frequent than in the ramp experiment.

### 2.4.2 Perceptual performance

Cuing effects, indexed by higher discrimination for valid than invalid/neutral trials, remained high at every SOA, with the exception of short SOAs when peripheral stimuli where moving on the screen.

*Ramp, exogenous cue (Exp. 1).* Percent correct discrimination responses showed impaired performance for the shortest SOA when the discrimination target moved on the screen (during fixation or pursuit) but not when it remained stationary on the screen. A four-way rmANOVA (eye movement x cue validity x relative motion x SOA) confirmed a significant interaction between eye movement, relative motion and cue validity,  $F(3,21)=5.56$ ,  $p<.01$ , and a marginally significant four-way interaction,  $F(3,21)=2.85$ ,  $p<.06$ . Importantly, valid cues

produced 17% better discrimination performance than invalid cues (80 vs 63%),  $F(1,7)=42.4$ ,  $p<.001$ , confirming that subjects allocated attention to the peripheral target.

*Step-ramp, exogenous cue (Exp. 2).* A three-way rmANOVA (cue validity x relative motion x SOA) showed that performance was 23% better with valid than with invalid cues (82 vs. 59%),  $F(1,6)=42.25$ ,  $p<.001$ . Overall discrimination performance decreased somewhat with smaller SOAs,  $F(5,6)=3.49$ ,  $p<.02$ . However there was no indication that the cuing effects (valid vs. invalid) were modulated by SOA,  $F < 0.04$ .

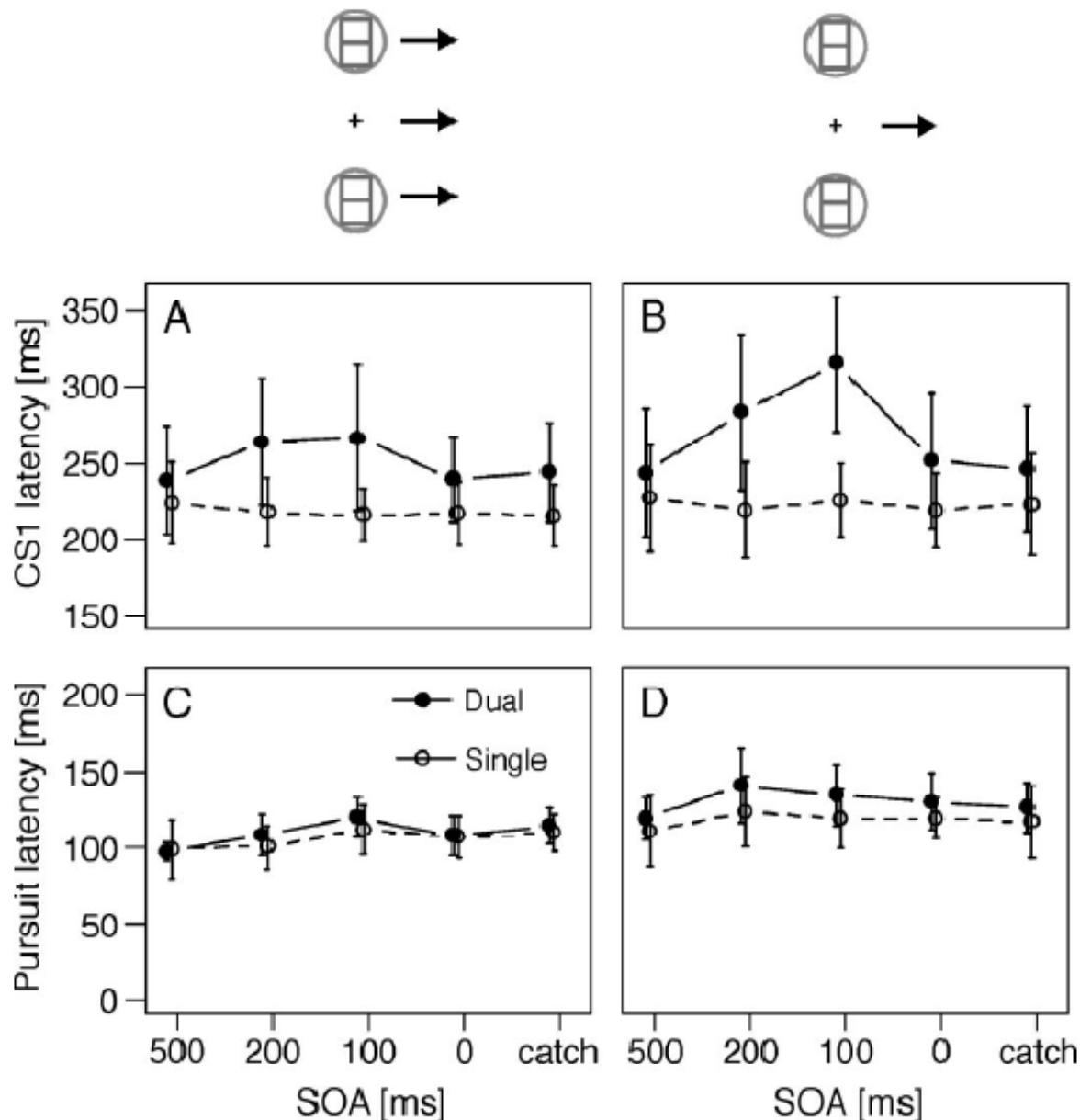
*Step-ramp, endogenous cue (Exp. 3).* A two-way rmANOVA (cue validity x SOA) confirmed 9.8% higher performance with a valid than with a neutral cue (79 vs. 70%),  $F(1,7)=21.61$ ,  $p<.002$ . Cue validity and SOA did not interact,  $F(4, 28)= .53$ ,  $p=.74$ .

**Table 2.1 Percentage of eliminated trials in the Experiments 1-3.**

	Exp. 1	Exp. 2	Exp. 3
Blinks	0.80%	0.30%	0.60%
Vertical saccades	1.35%	0.30%	0.90%
Visual inspection	0.82%	1.10%	1.30%
Pursuit anticipations or timed-outs (<52ms or > 400ms)	2.10%	0.60%	0.80%
CS1 anticipations or timed-outs (< 100 or >500ms)	18.9	-	-
Pursuit on-line criterion	-	2.60%	2.60%

#### 2.4.3 Pursuit and catch-up saccade latency

If perceptual performance is maintained at a high level, as shown in the previous section, then some differences in latency should be found as a result of attention shifts away from the target in the dual task condition. We expect the effect of task to interact with SOA, as attention has time to return to the pursuit target with long SOAs.



**Figure 2.2 Latency of the first catch-up saccade (CS1, A-B) and pursuit onset (C-D) in Exp. 1, as a function of relative motion, task load and SOA. Error bars represent inter-subject SD.**

*Ramp, exogenous cue (Exp. 1).* Figure 2.2 graphs the mean latency (of median individual latencies) of CS1 (A-B) and of pursuit (C-D), as a function of relative motion and SOA. Trials with valid and invalid cues were pooled in this and subsequent analysis. As described above, with a step-ramp target, smooth pursuit starts often after a catch-up saccade. Even when pre-saccadic smooth pursuit is detected, the first corrective saccade usually marks the beginning of the closed-loop phase of smooth pursuit with a ramp target trajectory. Pursuit latency and the first CS1 latency were analyzed separately in a three-way, rmANOVA (task load x relative motion x SOA).

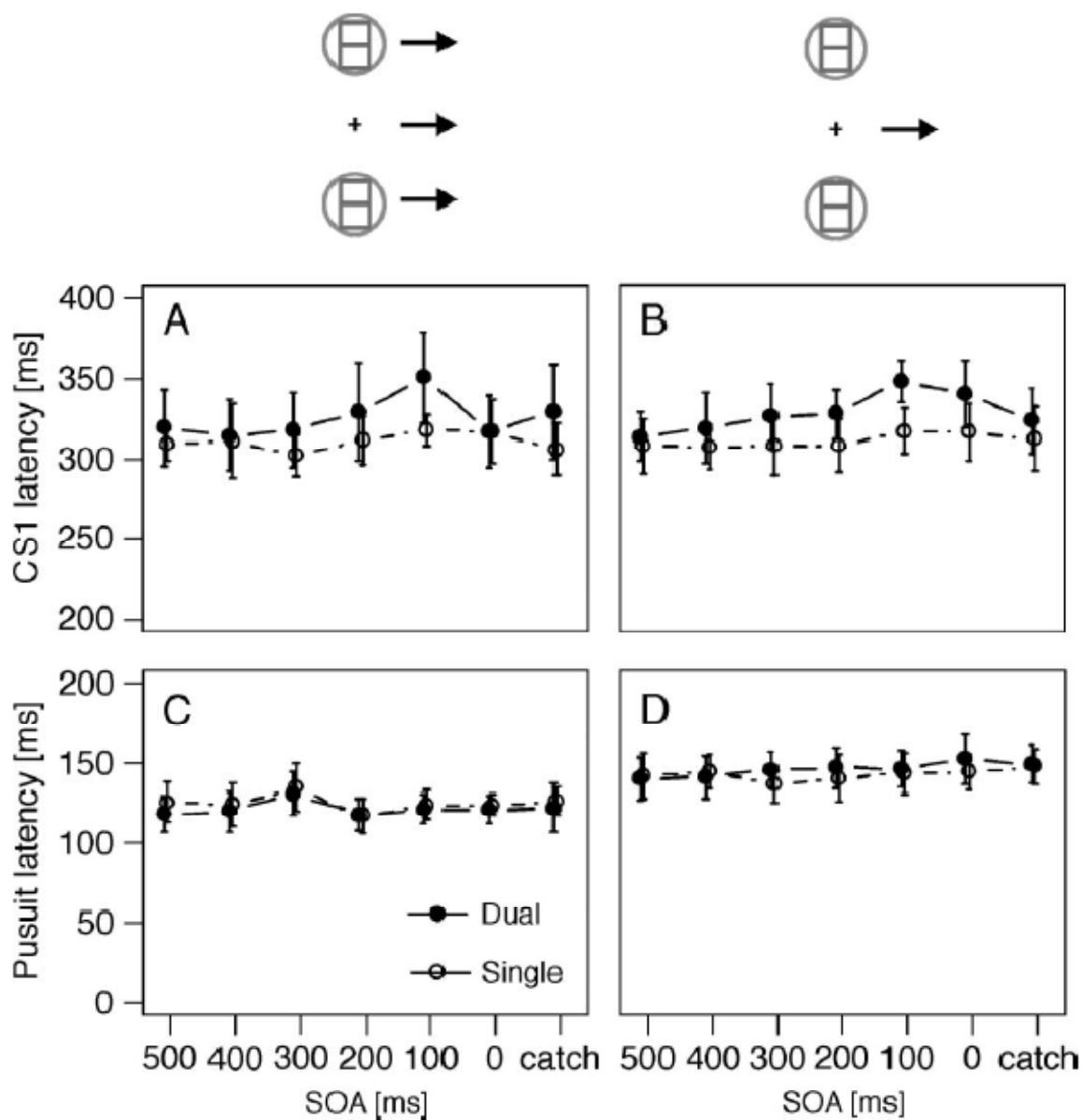
Inspection of Figure 2.2 (C-D) shows that latency of smooth pursuit in the dual task condition increased compared to the single task with SOAs of 100-200ms. This increase was smaller for the remaining SOAs, which supports our hypothesis. With SOAs of 100-200 ms, latencies increased by 16-19ms with relative motion, and by 10-13ms without relative motion. However, the interaction of SOA and task load was only marginally significant,  $F(4,28)=2.43, p=.07$ . Overall, latencies were longer in the dual than in the single task condition (123 vs. 114ms),  $F(1,7)=6.33, p<.04$ , and they were longer by 14ms with than without relative motion (112 vs. 125ms),  $F(1,7)=39.84, p<.001$ . There also was a main effect of SOA  $F(4,28)=12.89, p<.001$ . With SOAs of 100 and 200ms, latencies were longer than with the SOA of 500ms and catch trials (121 and 126ms vs. 110 and 112ms respectively; corrected  $p < .05$ ). Effects of SOA were modulated by relative motion,  $F(4,28)=4.17, p<.01$ , probably due to a slowing at short SOAs with relative motion that was not present without relative motion.

For latency of CS1 (Figure 2.2 A-B), an interaction between task load and SOA was confirmed,  $F(4,28)=13.42, p<.001$ , indicating a pronounced increase in latency for SOAs of 200 (+56ms) and 100ms (+64ms) in the dual compared to the single task condition. This increase was somewhat less pronounced for the SOA of 0ms (+27ms),  $t_{\text{S}}(7)>4$ , corrected  $p<.02$ . A main effect of SOA showed that latencies were longer for SOAs of 100 and 200ms,  $F(4,28)=10.29, p<.001$ . Further, latencies were 37ms longer in the dual than in the single task condition (211 vs. 248),  $F(1,7)=12.90, p<.01$ , and 8ms longer with than without relative motion (232 vs. 225ms),  $F(1,7)=8.03, p<.05$ .

*Step-Ramp, exogenous cue (Exp. 2).* Figure 2.3 graphs pursuit and CS1 latency as a function of relative motion and SOA. Pursuit latencies were 21ms longer with than without relative motion (144 and 123 ms),  $F(1,6)=178.47, p<.001$ . Effects of relative motion were modulated by task load,  $F(1,6)=8.54, p<.05$ . In the dual task condition, the effect of relative motion was 6 ms larger (146 vs. 122ms) than in the single task condition (143 vs. 125ms). There was a main effect of SOA,  $F(6,6)=2.65, p<.05$ , modulated by relative motion,  $F(6, 36)=7.13, p<.001$ . This is probably due to the increase of pursuit latencies with the SOA of 300 ms without relative motion. Post-hoc comparisons showed significantly longer latencies for the SOA of 300ms compared to the SOA of 200ms (difference of 15 ms),  $t(7)= 6.95$ ,

$p < .001$ . There was no interaction between SOA and task load,  $F(6, 6) = 1.46, p = .22$ , nor a main effect of task load,  $F(1, 6) = 0.01, p = .92$ .

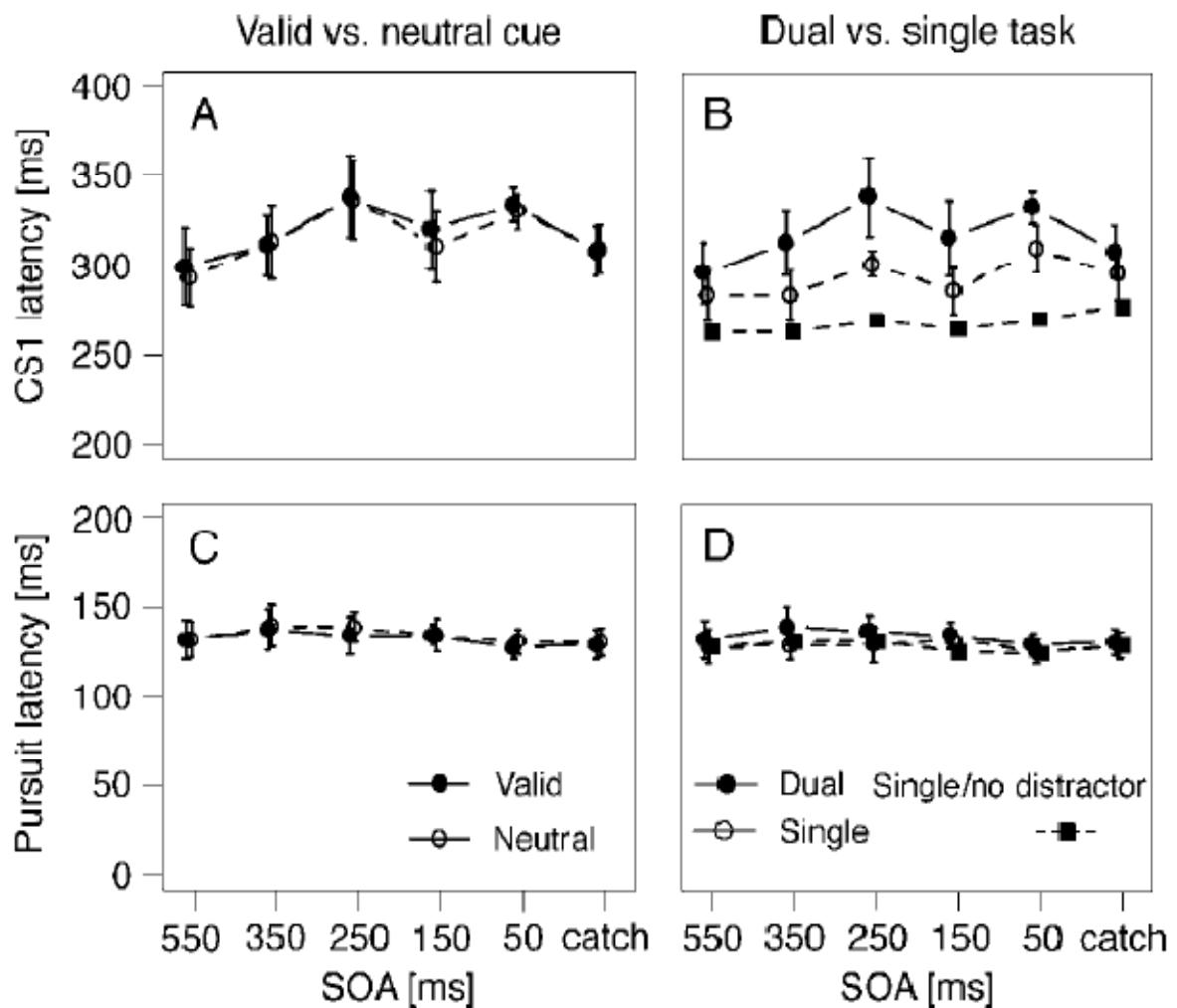
Similar to Experiment 1, pursuit latencies were overall little delayed in the dual compared to the single task condition. However, the dual task condition accentuated the detrimental effect of relative motion, indicating that attention to static peripheral stimuli delays smooth pursuit. This difference was not modulated by SOA, suggesting that task-relevance rather than the timing of the attention shift was important.



**Figure 2.3 Latency of the first catch-up saccade (CS1, A-B) and pursuit (C-D) in Exp. 2, as a function of relative motion, task load and SOA. Error bars represent inter-subject SD.**

As shown in Figure 2.3 (A-B), effects of attention shifts (dual task compared to single task) on saccadic latency were smaller than in Exp. 1. As a consequence of the step-ramp paradigm, catch-up saccades were triggered some 50ms later than in the first experiment. A trivial reason is that critical eye crossing time for saccade execution was not reached right after target onset as often as with a ramp target motion. Therefore, effects of attention are expected to be smaller. A three-way rmANOVA (task load x relative motion x SOA) showed longer latencies in the dual than in the single task condition (324 vs. 308ms),  $F(1,5)=8.72$ ,  $p<.05$ . The effect of task load was modulated by SOA,  $F(6,30)= 4.26$ ,  $p<.01$ . Post-hoc comparisons confirmed that latencies in the dual task were 31ms longer than in the single task condition with the SOA of 100ms (345 vs. 314ms),  $t(6)=4.8$ , corrected  $p<.02$ , and 16ms with the SOA of 0ms (328 vs. 312ms),  $t(6)=4.7$ , corrected  $p<.02$ . Additionally, there was a main effect of SOA,  $F(6,30)=5.10$ ,  $p<.001$ , indicating that latencies were longer with SOAs of 300 to 0ms than with SOAs of 500 to 400ms.

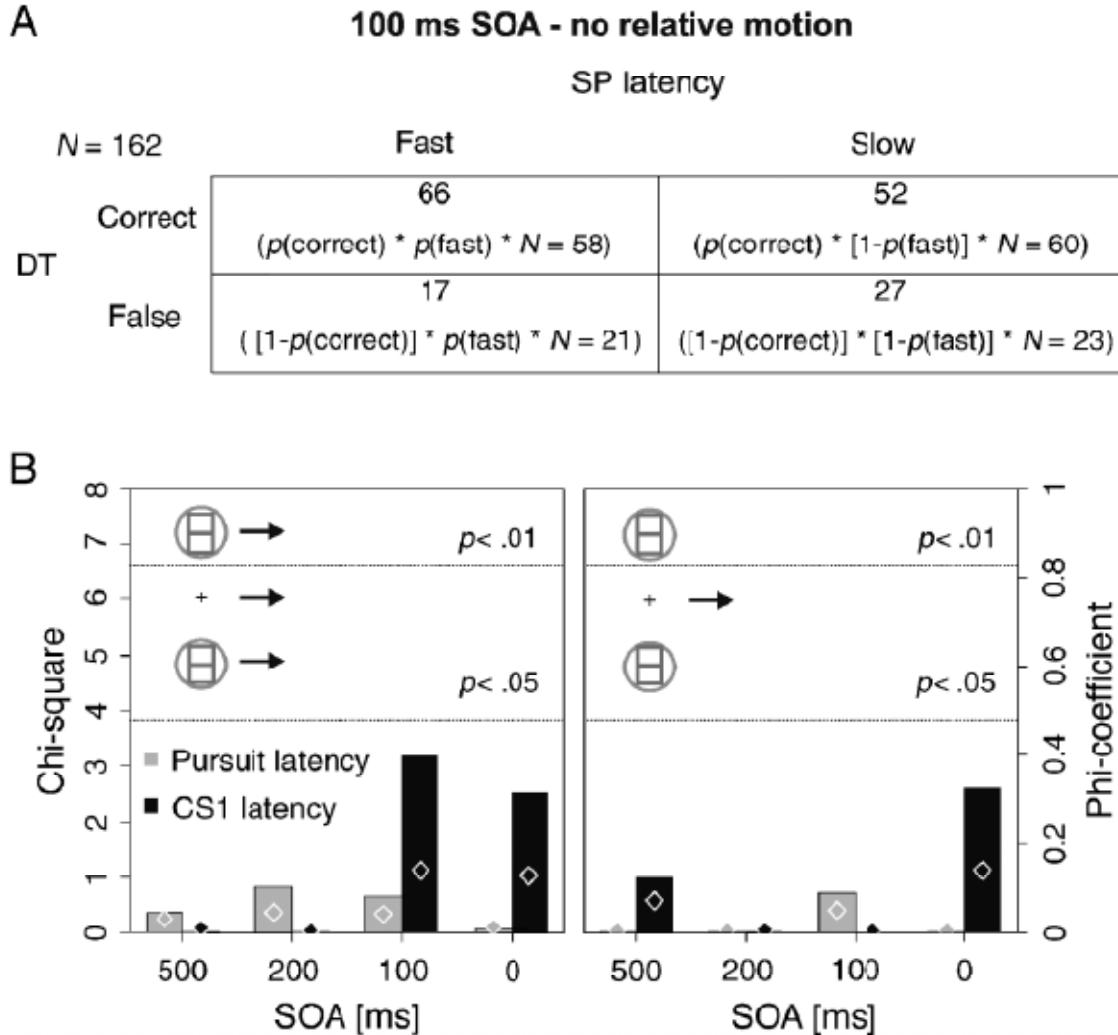
*Step-Ramp, endogenous cues (Exp. 3).* Pursuit and CS1 latency are graphed in Figure 2.4. In the previous experiments, we averaged across valid and invalid cues when we analyzed the eye movement data. The reason was that both valid and invalid cues imply shifts of attention to the peripheral location with the only difference that the target is either presented at the expected or unexpected location. With neutral cues, the situation is less clear. Attention may either stay focused on the pursuit target, or it may be equally spread between possible target locations. The latter interpretation was favored by previous research (de Gonzaga Gawryszewski et al. 1987). To evaluate effects of cue type (neutral or valid), we first ran separate rmANOVAs (cue validity x SOA) on pursuit and then on CS1 latencies in the dual task conditions. This analysis could not be run for the single task conditions as only the neutral cue was presented in these trials. Figure 2.4 (A, C) shows that latency, of pursuit or CS1, overlaps in valid and neutral cue trials. The main effect of cue validity (valid vs. neutral) was not significant for pursuit and CS1 latencies.



**Figure 2.4 Pursuit and saccadic (CS1) latency in Exp. 3.** The left panels (A, C) show latencies in valid compared to neutral endogenous cue trials. The right panels (B, D) show average pursuit latency in dual compared to single task trials. Additionally, data from the condition without peripheral stimuli are shown (single/no distractor). In all conditions, the discrimination target always remained static on the screen (cf. relative motion conditions of the Exp. 1-2). Error bars represent inter-subject SD.

Therefore, data were collapsed across valid and neutral trials. A two-way rmANOVA (task load x SOA) was run separately on pursuit and CS1 latency without single/no distractor trials to increase statistical power. The latency of pursuit onset in dual task conditions was 5ms longer than in the single task condition (134 vs. 129),  $F(1,7)=11.96$ ,  $p<.02$ . Furthermore, there was a significant interaction between task load and SOA,  $F(5,35)=2.59$ ,  $p<.05$ . Post-hoc comparisons showed a significant 11ms difference between dual and single task for the SOA of 350ms,  $t(7) =3.9$ , corrected  $p<.05$ . A main effect of SOA was found,  $F(5, 35)=3.28$ ,  $p<.02$ , indicating that latency increased with the SOA of 350-250ms (133-132 vs. 126-130).

Again, CS1 latency was more strongly affected by task load. Latencies were 30ms longer in the dual than in the single tasks (315 vs. 285ms),  $F(1,7)=32.97$ ,  $p<.001$ . However, interaction between SOA and task load was only marginally significant,  $F(5,35)=2.18$ ,  $p=.08$ . Latencies were modulated by SOA,  $F(5,35)=4.02$ ,  $p<.01$ , indicating longer latencies for the SOA of 250 and 50ms compared to the other SOAs, corrected  $p<.01$ .



**Figure 2.5 Analysis of trade-offs in Exp. 1. Panel A:** Example of a contingency table used to test the compatibility of the oculomotor and discrimination task. The expected number of observations, under the hypothesis of independence, is displayed in parenthesis. **Panel B:** The small values of the chi-square and phi-coefficient (i.e., a measure of effect-size) in all conditions for pursuit and catch-up saccades latencies support a shared resources strategy and not a switch between two different incompatible states. The bars represent the chi-square (left axis) and the diamonds represent the phi-coefficient (right axis). Horizontal lines indicate the p-values for the chi-square statistic. Data was pooled across subjects.

The lack of a significant interaction of SOA and task load can be explained by the fact that even the largest SOA of 550ms was modulated by task load. Similarly, some effects on closed-loop pursuit velocity were also found at this SOA (velocity analysis below). With the use of endogenous cues, facilitation takes usually longer to develop, but also lasts longer (e.g. Müller and Rabbitt 1989; Nakayama and Mackeben 1989b). It may be that an SOA of 550ms was too short to allow for attention to fully return to the target, thus explaining the only near-significant interaction of task load and SOA on CS1 latency.

#### 2.4.4 Effect size of the task load x SOA interaction

Effect-size ( $\eta_p^2$ ) of the interaction between SOA and task load for pursuit latency was similar across experiments: 0.25, 0.20 and 0.27 in Exp. 1 to 3 respectively. This interaction was only significant for the third experiment, presumably as a result of a greater statistical power. For CS1 latency effect-size was: 0.67, 0.46 and 0.24 in Exp. 1-3. A smaller effect in Exp. 2-3 could be accounted for by saccades with much longer latency in the single task as a consequence of the step-ramp and the use of endogenous cues (Exp. 3).

#### 2.4.5 ECT analysis

Next, we verified that low-level factors, such as position error and retinal slip resulting from pre-saccadic velocity, did not contribute to the observed increase in saccadic latencies in the dual task conditions. According to de Bouwer et al.'s (2002) model, the execution of catch-up saccades are mainly predicted by the *eye crossing time* (ECT). Defined as the time it would take the eye to cross the target's path with its actual velocity. ECT is determined by retinal velocity (or retinal slip, RS) and distance between the target from the fovea (or position error, PS):  $ECT = -PE/RS$  (de Brouwer et al. 2002). Negative values denote that the fovea is lagging behind the target. ECT measures were based on eye velocity and position 124ms before CS1. In the Exp. 1, a three-way rmANOVA (task load x relative motion x SOA) was run on ECT values. With relative motion, saccades were triggered at more negative ECTs than without (-122 vs. -111ms),  $F(1,7)=6.50$ ,  $p<.05$ . There were more negative ECTs in the dual task than in the single task condition (-135 vs. -98ms),  $F(1,7)=14.00$ ,  $p<.001$ . The interaction between SOA and relative motion,  $F(4,28)=5.89$ ,  $p<.001$ , indicated that the effect of relative motion was maximal at an SOA of 100ms (with vs. without relative motion: -150 vs. -115ms),  $t(7)= 4.21$ , corrected  $p<.02$ . The expected interaction between SOA and task load was also confirmed,  $F(4,28)=5.88$ ,  $p<.001$ . Post-hoc comparisons showed more

negative ECTs in the dual than in the single task conditions for the SOA of 200 and 100ms (difference of -63 and -52ms,  $t(7)=3.44$  and  $t(7)=3.79$ , respectively, corrected  $p < .05$ ). In sum, the analysis shows that the pattern of latency of catch-up saccades is matched by the pattern of differences of the ECT distributions. The same analysis was run on Exp. 2-3, and confirmed independence of pre-saccadic ECT values and the latency delay observed in the dual task.

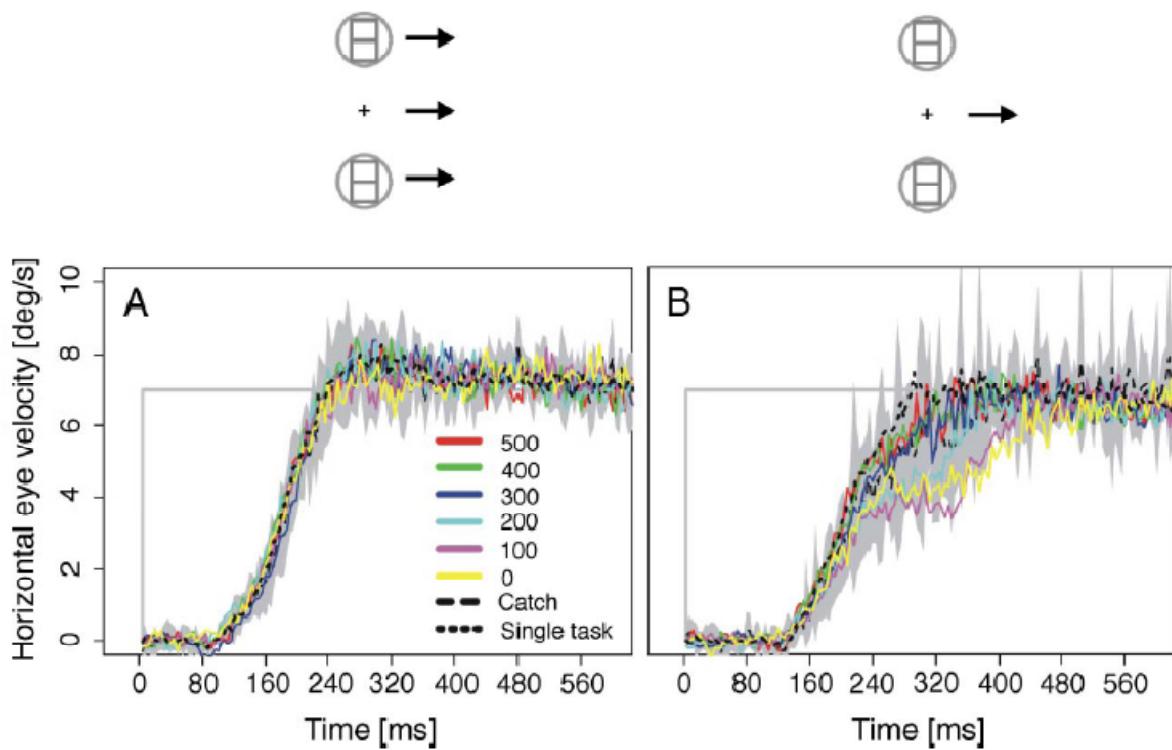
#### 2.4.6 Analysis of trade-offs

Perceptual performance and eye movement latency suggest that pursuit can be initiated with little selective attention at the pursuit target location. We further asked whether a tradeoff could unveil some incompatibility of the two tasks. Sperling and Melchner (1978) proposed a method to test the strategy used by participants to trade attentional resources between two simultaneously monitored tasks (see also Khurana and Kowler 1987). They contrasted “shared” or “switch” strategies of attention allocation. Their argument states that if attention is shared between tasks A and B, performance on tasks A and B should decrease by the same amount compared to the single task condition, but A and B may still be independent. On the other hand, if attention is switched between tasks from trial to trial, then performance on the two tasks is expected to depend on each other: good performance on task A should lead to bad performance on task B and vice-versa. A chi-test on the contingency table of *successes* and *misses* on the two tasks tests this dependence (see Figure 2.5A). As a measure of success in the oculomotor task, we used latencies of smooth pursuit and of the first catch-up saccade and divided them into *fast* or *slow* by a median split. Only the validly cued trials were considered, as the opposite relation between pursuit and perception may hold in invalidly cued trials. When the cue is invalid it may be better for discrimination performance to keep attention at the pursuit target rather than shifting attention to the more distant downwards or upwards locations.

Chi-tests on individual contingency tables or across subjects (Figure 2.5B) never indicated a significant negative relation between oculomotor and perceptual performance as measured by pursuit or CS1 latency in Exp. 1, supporting the use of a “shared” resources strategy (Sperling and Melchner 1978). Analysis of Experiments 2 and 3 yielded similar results (data not shown).

### 2.4.7 Velocity traces

Because the manipulations modified CS1 latency, only average velocity traces of pursuit initiation of trials in which no catch-up saccade was executed are shown. This was only possible in Exp. 2 and 3. Modulation of horizontal eye velocity during initiation is shown on Figure 2.6 (Exp. 2) and 7 (Exp. 3). With moving peripheral stimuli, the pursuit target and the attended discrimination target moved in the same direction (Exp. 2 only, see Figure 2.6A). Any modulation of eye velocity by shifting attention to the periphery therefore resulted from spreading attention across a larger region of space. It cannot be due to conflicting motion signals. Smooth pursuit gain was relatively unimpaired by attention shifts in this condition, suggesting that a small focus of attention around the pursuit target is not necessary for successful pursuit initiation.



**Figure 2.6 Average horizontal velocity in Exp. 2 ( $N = 7$ ) of trials in which pursuit was initiated without a catch-up saccade for no relative motion (A) and relative motion conditions (B). Gray lines represent pursuit target speed. Dotted lines represent single task performance averaged across SOAs. Gray area represents the inter-subject SD of catch trials.**

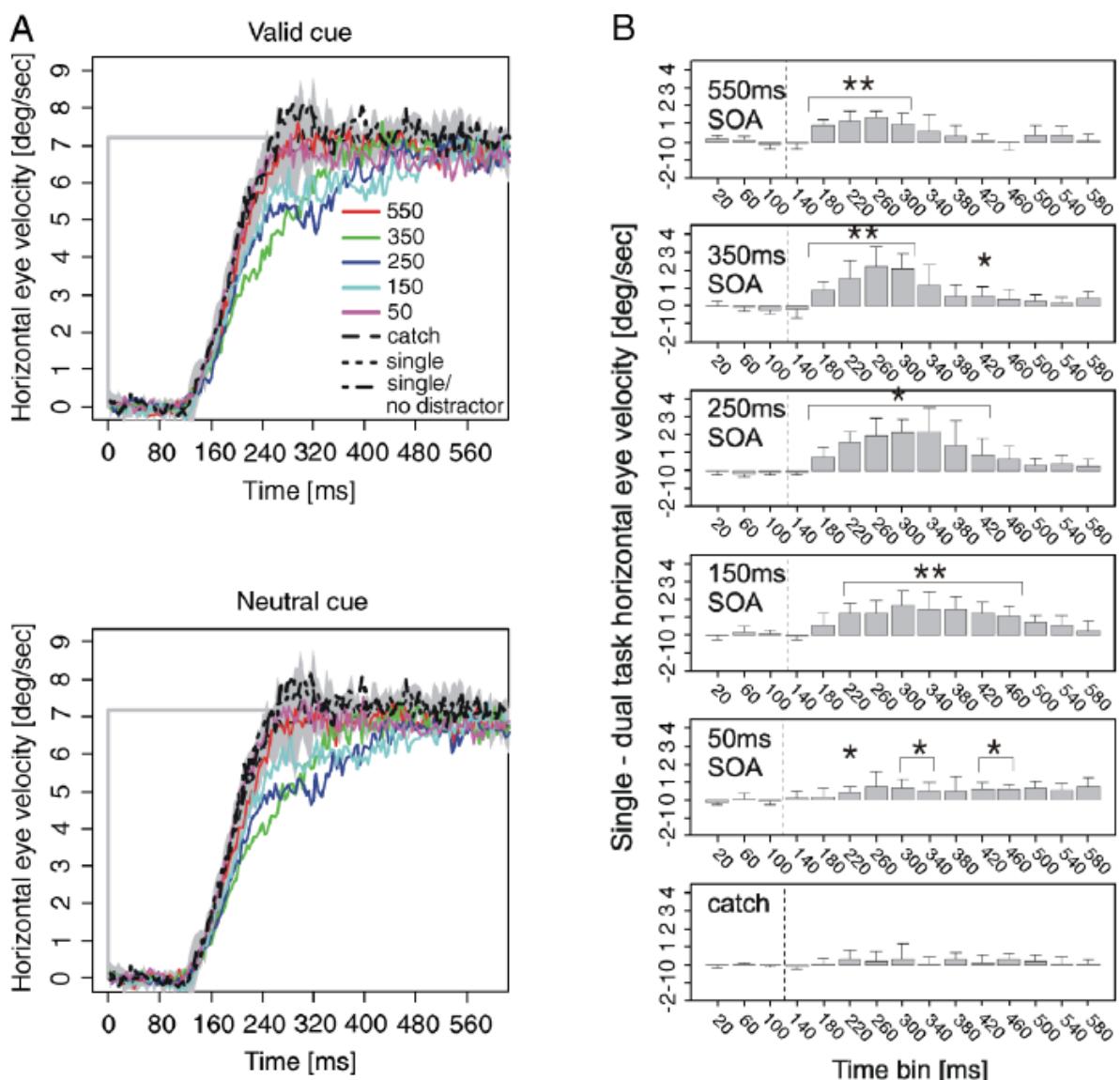
While attention shifts without relative motion attention shifts had little effect on pursuit velocity (a maximum of about 5%), eye velocity was strongly modulated about open-loop initiation with relative motion (about 40%, see Figure 2.6B). Exp. 3 (with more observers) confirmed the same pattern, as seen in Figure 2.7. Similar to pursuit latencies, velocity traces were very similar for valid and neutral cue trials (see Figure 2.7A), and were therefore pooled. For testing differences between dual and single task, horizontal velocity traces were divided into 40ms bins within a 0 to 600ms time range (see Figure 2.7B). Significant differences were found no earlier than the 160-200ms time bin, and lasted until the 400-440 time bins for the SOA of 150-350ms, and with a shorter time range for the SOA of 550ms. Maximal differences were found with the SOA of 250ms and 350ms. Effects are of comparable size and timing were confirmed in the condition with retinal motion of the Exp.2.

## 2.5 Discussion

Because spatial attention at the saccade goal is needed for saccade initiation, it cannot be shifted away from the target location without some costs on eye movement latency or accuracy (Posner 1980; Kowler et al. 1995; Deubel and Schneider 1996). Suggestive of a similar involvement of attention for pursuit initiation, previous studies showed shorter pursuit latencies when the target was cued by color, motion, direction, or position (e.g. Krauzlis et al. 1999; Adler et al. 2002), as well as when the target was more salient (Hashimoto et al. 2003; Hashimoto et al. 2004).

Our study assessed the costs associated with shifts of attention away from the pursuit target location and asked whether attention is strictly necessary for pursuit initiation. Attention shifts made to the periphery were indexed by discrimination performance between valid and invalid/neutral cue trials. Cueing effects on discrimination performance were not different from those obtained in a control condition during fixation. The only exception was for the shortest SOAs with physical motion of the peripheral targets, but the observed difference may be entirely due to motion smear. The substantial shifts of attention induced by our cueing procedure had (i) no reliable effect on pursuit latency when the peripheral discrimination targets moved along with the pursuit target (i.e., without relative motion condition). (ii) Small, but significant effects on pursuit latency were found only when

attention was shifted by means of an endogenous cue to static a target (Exp. 3). However, lack of statistical power, rather than cue type *per se*, were likely to account for the difference. Effects of similar size were observed in Experiments 1-2, but failed to reach significance.



**Figure 2.7** Panel A shows average horizontal velocity in Exp. 3 (N=9) of trials in which pursuit was initiated without a catch-up saccade. Peripheral stimuli were static (relative motion condition). Gray areas represent the inter-subject SD in catch trials. Single task trials are averaged across SOAs. Data from valid and neutral trials are shown in the upper and lower panels. Panel B: Increased horizontal velocity in dual compared to single task as a function of SOA. On the x-axis, the center values of 40ms time bins are displayed. Vertical, dashed lines indicate pursuit onset (around 120 ms). When contiguous time bins were significant, the least significant p-value is reported above the respective bracket. The Benjamini-Hochberg correction was applied to the p-values. \*\*\* =  $p < .001$ ; \*\* =  $p < .01$ ; \* =  $p < .05$ .

We found no evidence for trade-offs between pursuit and perception. Tradeoffs are considered a hallmark of incompatible tasks (Sperling & Melchner, 1978). There was little interference between attention shifts and smooth pursuit latency on a trial-by-trial basis. If a strong coupling existed, pursuit latency should have been traded for perceptual accuracy on the peripheral task. Similarly, no significant trial-by-trial trade-off was found with CS1 latencies. Incompatibility was manifest on average latency of the first corrective saccade and closed-loop gain.

Compared to the initial pursuit response, much larger differences between conditions without and with relative motion were obtained for post-onset pursuit velocity and catch-up saccades. Without relative motion (iii): moderate effects on pursuit gain were observed near the onset of steady-state pursuit phase with a ramp target. These effects were even smaller with a step ramp target presumably because retinal motion was further reduced (step-ramp experiments: ~5% difference between single and dual task conditions). With relative motion (iv), attention shifts at the time of pursuit onset strongly reduced (~40%) pursuit velocity in the late open-loop (some 100ms after movement onset), or near closed-loop pursuit phase, until ~400ms after movement onset. (iv) Catch-up saccades were strongly delayed (up to >50) in the dual task condition when attention was shifted to stationary objects in the periphery. Thus, catch-up saccades are similar to voluntary saccades in that both are delayed when attention is shifted away from the oculomotor target.

To sum up, the results show that pursuit onset does not depend strongly on the prior allocation of attention on the pursuit target. Some costs on latency are incurred when the attended object competes with the relevant motion signal. Significant attention-dependent latency increases on the order of 10ms were observed in one experiment. Thus, our results support the notion of a loose coupling of selective spatial attention and pursuit initiation. On the other hand, initial corrective saccades were as much delayed in both competing (relative motion) and synergistic (no relative motion) conditions. The delay was of similar magnitude as in studies that tested effects of shifts of attention in opposite direction to the saccade goal (Shepherd et al. 1986; Shepherd and Müller 1989; Crawford and Muller 1992; Reuter-Lorenz and Fendrich 1992). Similarly, Ferrera et al. (1995) neither found an interference of a

moving distractor on initial corrective saccade latency when comparing distractor and single target condition, nor when running a similar saccadic task.

Further, we observed that neutral trials have very similar effects on latencies and eye velocity as valid cues although it is clear from the discrimination performance that only valid cues resulted in allocation of attention to a specific location. Some studies indicate that with endogenous shifts of attention, cuing effects are more compatible with a “zoom lens” metaphor of attention (as proposed by Eriksen and St James 1986), with attention initially spread out and then focused on the cued location; whereas exogenous cuing may be more compatible with a “spotlight” metaphor (as proposed by Posner et al. 1980), with attention focused over a zone of constant size moving in space (Shepherd and Müller 1989). Accordingly, it has been shown that with an incentive to keep attention focused on the fixation point, RTs to peripheral stimuli are longer than in the neutral cue condition, suggesting that the distribution of attention is diffuse in the neutral condition (de Gonzaga Gawryszewski et al. 1987) and not, as often supposed, focused on the fixation cross. Thus, performance in neutral trials may reflect the same mechanisms of endogenous attention as performance in valid trials. In the neutral condition, both peripheral targets received some attention as a result of a broad attentional window. Consequently, less attention was devoted to the pursuit target. Spreading attentional resources over space is probably the best strategy as the discrimination target can appear in two different locations with equal probability.

Finally, the presence of static peripheral objects lengthened pursuit latency by some 20ms. This effect was poorly modulated by the timing of attention shifts, but rather by task-relevance of the peripheral targets. A large reduction of acceleration, of steady-state velocity, and less often a delay in latency is documented in studies in which the pursuit target moves over a stationary structured background (Sperling and Gegenfurtner 2007)

According to some estimations (Lisberger and Westbrook 1985; Tychsen and Lisberger 1986), the first 100ms after pursuit onset can be considered as an open-loop phase. In our experiments, the earliest significant attention-dependent effects were found within the 160-200ms time window (i.e., some 40-80ms after pursuit onset) and maximal changes of velocities were reached in bins centered on 200 to 320ms time (i.e., some 80 to 200ms after pursuit onset).

As proposed by Ferrera and Lisberger (1995), the role of attention in target selection for pursuit initiation may be to bias the strength of one over many competing motion signals. With monkeys, latencies were much longer in the presence of a distractor moving in the opposite direction than with a single target. However, the average velocity traces were very similar before and during loop closure (Ferrera and Lisberger 1995), suggesting a winner-take-all response. Subsequent results suggested that a vector-average is generally the first response but that under the latter circumstances winner-take-all response can be achieved via a delay in latency (Lisberger and Ferrera 1997). Our manipulations show that pursuit velocity can be modified by giving different weights to the signals of the to-be-attended target and the pursuit target. Our results are not incompatible with Ferrera et al.'s interpretation; they rather add that shifts of attention can modulate the late open-loop or beginning of closed-loop phase of smooth pursuit when there is a competition between the to-be-pursued and to-be-attended motion signals (i.e. between signals prompting fixation and pursuit). We can suppose that the delay found in their first study is due to the time it takes to select the appropriate target among incompatible bottom-up signals.

Our results lend support to the recent “two-stage” model of coordination of smooth pursuit and saccades proposed by Erkelens (2006). The model claims that preparation for saccades and pursuit by engagement of attention to the new target goal is synchronous. In conditions of temporal overlap between the old and new target, latencies of pursuit and saccades are indeed synchronized and highly correlated ( $R^2=0.91$ ; (Erkelens 2006)). In the classic conditions for comparison of pursuit and saccadic latencies (i.e. no temporal overlap between old and new target) saccades and pursuit show uncorrelated latencies (Merrison and Carpenter 1994; Erkelens 2006)). The difference between the two systems could then be that pursuit can be “prematurely” disengaged at the oculomotor level when the old target disappears at the time the new target appears (Erkelens 2006)). But in conditions of temporal overlap, the new target's speed and direction is only selected by the eye at the time when a saccade can be executed. Erkelens further speculated that attentional engagement to the new target is concomitant with movement programming, and that the outcome of this process is allowed to reach the execution level at the same time for pursuit and saccades. This point was suggested by directional changes occurring almost exclusively after saccades in overlap conditions. This interpretation is not too far from our conclusion that attention for

pursuit and saccades follow a similar time-course, with smooth pursuit starting in some cases without attention being focused on the target, as a result of pursuit shorter latency.

### 2.5.1 Shared gating and target selection for pursuit and saccades

The role of the rostral superior colliculus (SC) in the gating of pursuit, in addition to its well established role in release from fixation for saccades, has been recently pinpointed (for a review Krauzlis, 2004). There is also evidence for shared target selection from studies showing that subthreshold micro-stimulation of SC can manipulate the target choice for saccades and pursuit independently of the direction of the eye movement (Carello and Krauzlis 2004). Moreover, the region of omnipause neurons have excitatory connections with the rostral SC (Gandhi & Keller, 1999) which is classically implied in the gating of the impulse burst that trigger saccades (Munoz and Wurtz 1993b; Munoz and Wurtz 1993a), also strongly modulates steady-state pursuit (Missal and Keller 2002). This circuitry leads to the idea that the fixation system that gates saccades can also gate pursuit. Shared gating also offers an explanation for similar latency reductions with the gap paradigm (Merrison and Carpenter 1995; Krauzlis and Miles 1996c; Krauzlis and Miles 1996a; Krauzlis and Miles 1996b; Knox 1998; Kimmig et al. 2002). That is, smooth pursuit and saccadic latencies are reduced when the fixated stimulus disappears some time before target onset. Further, latencies of saccades and smooth pursuit are prolonged when a remote distractor appears at the same time as the target (Knox and Bekkour 2004). Ogawa et al. (1998) proposed the common gating system as a factor contributing to post-saccadic pursuit enhancement: Inactivation of the fixation system too low to trigger a saccade may be sufficient to release a weak pursuit response. Once the fixation system is fully inactivated, enhanced pursuit and saccades are released. Liston and Krauzlis (2003; 2005) proposed a model of shared selection that builds on race to threshold models of decision making (e.g. Carpenter and Williams 1995; Carpenter 1999). It supposes that initiation of pursuit and saccades share the same signals that accumulate across time but with a different threshold for triggering the movement, leading to different latencies.

Concerning the joint programming of eye movements and attention shifts, recent studies show that microstimulation of either FEF or SC neurons below saccade execution threshold can nonetheless cause an attention shift (Cavanaugh & Wurtz, 2004; Moore & Fallah, 2001, 2004; Muller et al., 2005). We speculate that the strength of the attention shift

will depend on the strength of the eye movement signal. As some authors have argued that the necessary signal strength to trigger pursuit is smaller than for saccades (Krauzlis & Dill, 2002), the attention shift preceding smooth pursuit will also be weaker. The present results confirm the flip side of this mechanism: pursuit is far less affected by attention shifts away from the eye movement goal than saccades.

### 2.5.2 Conclusion

Our study shows that pursuit may be started at little cost when attention is diverted from the pursuit target, unlike the first catch-up saccade. A strong coupling may not emerge until the first steps of steady-state pursuit. We demonstrated that attention can weigh conflicting motion signals (or fixation against movement signals) differently, resulting in a compromised pursuit response in the late open-loop or early closed-loop phase. Some features of the pursuit system are consistent with this view, like its susceptibility to bottom-up influences and enhanced gain after the first catch-up saccade. Further studies would be needed to clarify if a time-locked coupling is shared by pursuit and saccades, by evaluating its strength for responses with similar latency.

### **3 Study 2: Attentional constraints on target selection for smooth pursuit eye movements**

#### **3.1 Abstract**

During fixation we are able to voluntarily select objects for enhanced perceptual processing. Here, we examined whether this ability is reduced when pursuit of a moving object has to be initiated. Two stimuli appeared above and below fixation and moved in opposite directions after a central cue instructed observers to pursue one of the two stimuli (smooth pursuit task). For 80 ms after stimulus onset, a grating was displayed on the opposite stimulus. Observers had to report its orientation at the end of the trial (perceptual task). We varied the priority given to smooth pursuit and perception. The results showed that the selection of the target for pursuit and perception were not independent. When priority was equal or greater to the perceptual task target, observers frequently pursued the wrong target or pursuit latency was delayed, suggesting a strong coupling between eye movement and perceptual choices.

#### **3.2 Introduction**

Voluntary control over oculomotor programs allows the selection of a target object in the presence of distracting information. An important question is whether different objects may be selected for eye movements and perception, and how do concurrent attentional demands trade off with oculomotor performance.

In the absence of eye movements the voluntary allocation of attention results in enhanced perceptual performance at the attended location (e.g. Müller and Rabbitt 1989; Nakayama and Mackeben 1989a; Cheal and Lyon 1991). Perceptual performance at the saccade target location is selectively increased short before the saccade (Deubel and Schneider 1996; Castet et al. 2006; Montagnini and Castet 2007), suggesting what is selected for as saccade is also selected for perception. Most researchers agree that attentional selection and eye movement selection are closely coupled (for a review Godijn and Theeuwes 2003b; Kowler et al. 1995; Schneider 1995; Deubel and Schneider 1996; Madelain et al. 2005; Awh et al. 2006).

This coupling transpires in the saccade latencies are delayed by paying attention to non-target locations. Attentional resources necessary for saccade initiation were estimated (Kowler et al. 1995) from the attention operating characteristic (AOC, Sperling and Melchner 1978). In AOC paradigms, the simultaneous execution of a perceptual and a saccade task is compared to performance in single task conditions. If perception and eye movements relied on independent selection filters, there should be no difference between performance in the dual and single task conditions. Otherwise, performance on the eye movement task would have to be traded for performance on the perceptual task. Kowler et al. (1995) demonstrated that the latency of a saccadic eye movement was traded for the accuracy of perceptual judgments of an object opposite to the saccade target, which is clear evidence for shared attentional resources.

In the present study, we will measure AOC curves for perception and the initiation of smooth pursuit. While a number of studies have investigated the efficacy of target selection (and therefore attention) during the initiation of pursuit (e.g. Ferrera and Lisberger 1995; Ferrera and Lisberger 1997; Garbutt and Lisberger 2006; Sperling et al. 2006b), there are only few studies that have investigated the interaction of perception and smooth pursuit. In a study on sustained smooth pursuit, Khurana and Kowler (1987) showed that the perception of pursued objects was better than the perception of adjacent, but non-pursuit objects. To some degree, the perception of non-pursued objects could be improved by increasing the priority of the perceptual task. However, improvements in perceptual performance were not traded for decreases in pursuit gain which can be explained by a ceiling in the needs of spatial attention to the pursuit target (Khurana and Kowler 1987). Further, tradeoffs between perception and steady-state pursuit were not observed with flashed stimuli, suggesting that it is attention to competing motion signals that specifically impairs pursuit performance (Kerzel et al. in press).

Further, we have shown that attention can be shifted into the periphery without delaying the initiation of smooth pursuit when the to-be-attended peripheral object does not carry conflicting motion signals (Souto and Kerzel 2008a). In contrast, the latency of the first catch-up saccade during pursuit initiation is delayed, quite similar to the delay of saccadic eye movements when attending to non-target locations (Kowler et al. 1995; Shepherd et al. 1986; Reuter-Lorenz and Fendrich 1992). Unperturbed smooth pursuit

initiation despite diverting attentional resources to the periphery suggests that the coupling between perception and the initiation of smooth pursuit is weaker than for saccades.

Supporting this view several findings indicate that target selection during pursuit initiation is poor. For instance, when the target competes with an orthogonally moving distractor, pursuit is first initiated toward the vector-average direction and subsequently (often after a saccade) to the designated target in a winner-take-all manner (Ferrera and Lisberger 1997; Lisberger and Ferrera 1997). Also, studies that tested the ability to pursue a target in the presence of a distractor moving in the opposite direction showed a delay of some 15 ms in humans (Krauzlis et al. 1999; Adler et al. 2002) and at least some 30 ms in monkeys (Ferrera and Lisberger 1995). One can interpret the latter results either as the mandatory averaging of motion signals, as it was sometimes postulated for short-latency averaging saccades (Ottes et al. 1985), or as the result of imperfect attentional selection.

To evaluate the coupling between target selection for pursuit and target selection for perception, we examined observers' ability to select one object for pursuit, while trying to perceive the features of another object moving in the opposite direction. Some time before stimulus onset, a cue informed subjects about which object to pursue. The perceptual task was to discriminate the orientation of a sine-wave grating appearing on the stimulus opposite to the pursuit target. If pursuit initiation and perception were independent, performance in the dual task conditions should approach performance attained when the two tasks are performed in isolation. Graphically, dual task performance should be at the intersection between the single task performance in an AOC plot. If the tasks rely on the same set of attentional resources, as it was shown for saccades, execution of the two tasks necessitates a trade-off between smooth pursuit and perception, resulting in poorer performance on one or both tasks. The conclusion of dependence is corroborated if dual task performance follows the priorities assigned to the two tasks.

### 3.3 Methods

#### 3.3.1 Subjects

Five observers participated in this study: two of the authors (DK and DS, marked S1 and S2 respectively) and three students that were naïve to the purpose of the experiments.

All had normal or corrected to normal vision at the distances displayed. Our protocol was approved by the Ethics Commission of the University of Geneva.

### 3.3.2 Materials

We used an IRIS infrared head-mounted eye-tracker (Skalar, Delft) to record eye movements at 500Hz. A bite bar was used to minimize head movements. Observers' eyes were at a distance of 46 cm from a 75 Hz CRT screen, with 1280 x 1024 pixels resolution. The eye-tracker was calibrated every 1-3 blocks, which was done by fixation of three horizontal locations followed by fixation of three vertical locations.

### 3.3.3 Stimuli and Procedure

Stimuli and trial time course are shown on Figure 3.1. A black fixation square (0.3 x 0.3°) was shown for 200 ms before a cue made up of a vertical and horizontal bar appeared for 133 ms inside the square to indicate the position of the pursuit target. The position of the vertical line indicated which object was to be pursued. The position of the horizontal line indicated which object was to be attended for perceptual discrimination judgments. After a random interval of 200 to 505 ms, two rectangles appeared above and below fixation and started to move in opposite horizontal directions for 1 s, at the velocity of 8.1°/sec. For 80 ms, the target and distractor contained superimposed sine-wave gratings. In most cases, the sine-wave grating of the target was vertical, whereas the distractor<sup>10</sup> grating was tilted to the left or right. After 80 ms, the sine-wave gratings were replaced by luminance noise. At the end of each trial a blank screen was displayed until a 2AFC orientation response (left/right keyboard key). The stimulus orientation selected by the participant was briefly displayed on the screen. Auditory feedback about the perceptual judgment was given after each trial.

The rectangular stimuli were 2.9 x 0.7° (width x height) located 0.7° above or below the fixation square (center-to-center). Because it was difficult to find a discrimination task that would work in a step-ramp paradigm, we used wide parafoveal targets to minimize the tendency of executing vertical saccades and to maximize the number of trials in which

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<sup>10</sup> We sometimes refer to the stimuli opposite to the pursuit target as the distractor, however only the motion is a distractor for the pursuit task, the stimulus itself is the target for the discrimination task (unless the Dt=Pt condition, where the opposite stimulus is really entirely irrelevant for the task).

pursuit is initiated before a catch-up saccade. When the stimulus is wide, it is possible to follow the trailing edge without the need to make a catch-up saccade. The background was medium gray (29 cd/m<sup>2</sup>). The discrimination targets were 1.5 cpd gratings at 40% Michelson contrast added to the luminance noise that was made up of 2-pixel squares at a maximal contrast of 60%. The maximal contrast of the combined stimulus was thus 100%. Without the sine-wave, the luminance noise had a maximal contrast of 100% contrast. There was a jitter of the phase of the sine-wave grating, such that no visual detail could be the basis for direction discrimination.

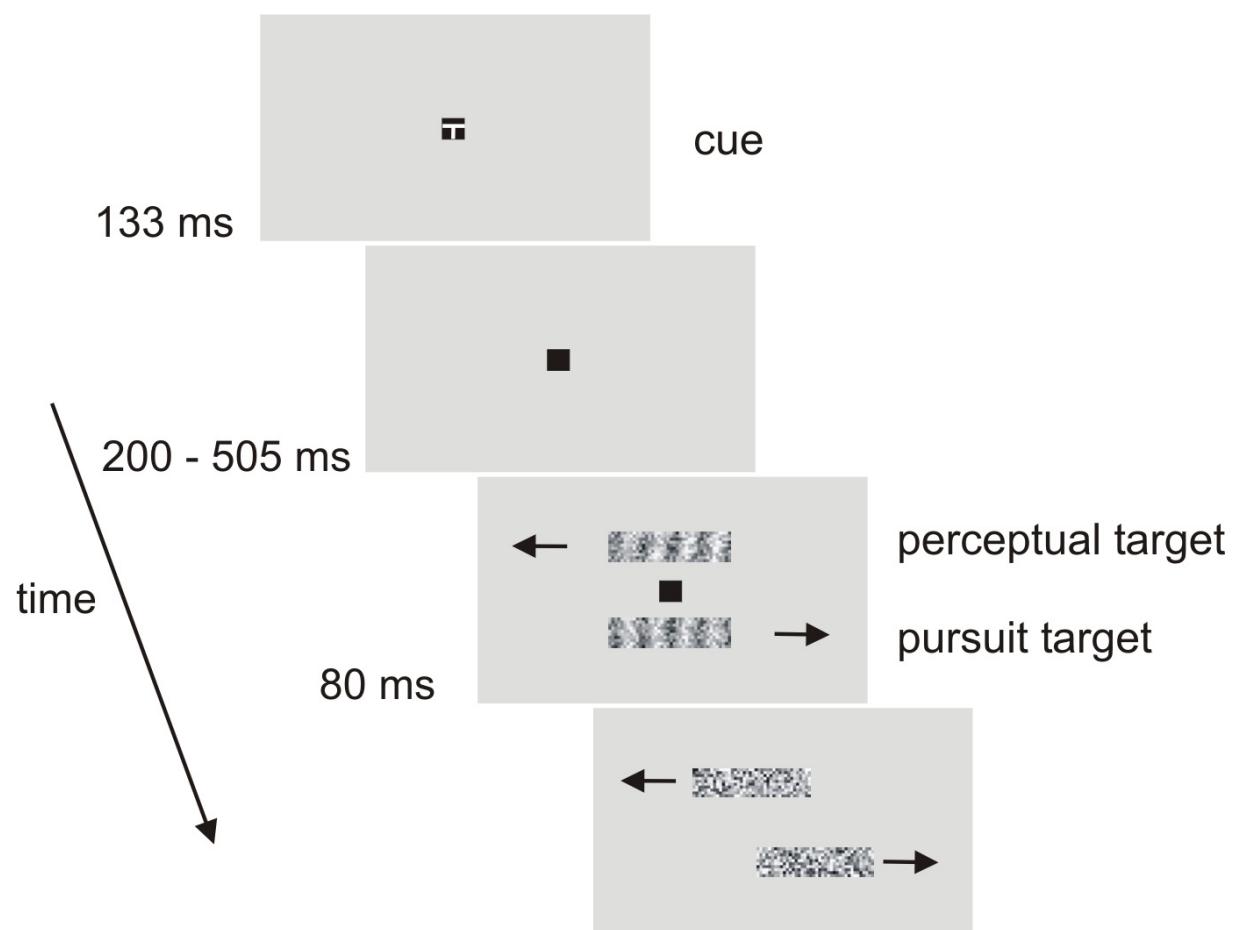
We manipulated the allocation of voluntary attention by different instructions that prioritized the perceptual (Dt) or the pursuit target (Pt). The precise instructions given to the participants (translated from French) are detailed in Table 3.1.

**Table 3.1 Instructions given in the first experiment.**

Label	Instruction
<b>50Pt/50Dt</b>	pay an equal amount of attention to the pursuit target and to the opposite target
<b>10Pt/90Dt</b>	pay attention to the discrimination target, but try nonetheless to follow the pursuit target
<b>90Pt/10Dt</b>	pay attention to the pursuit target only, but try nonetheless to report the discrimination target's identity
<b>100Pt</b>	pay only attention to the pursuit target
<b>100Dt</b>	pay only attention to the discrimination target
<b>Dt=Pt</b>	attend only to the discrimination target, which is the same as the pursuit target

We used an intra-subject factorial design: instruction (50Pt/50Dt, 10Pt/90Dt, 90Pt/10Dt, 100Pt, 100Dt, Dt=Pt, 100Dt) x target location (up or down) x target direction (leftward or rightward). Instruction was a blocked variable; location and direction were randomized variables within a block. Each combination of location and direction was repeated 12 times per block. There were four experimental sessions run on different days, amounting to 192 trials per instruction. Subjects received feedback if their eyes had moved in the wrong direction 500 ms after target motion onset. This was not done in the 90Pt/10Dt

condition to keep subjects motivated, because we observed in a pre-test that direction errors were very frequent in this condition. We balanced the order of instructions in single task and dual task blocks. There were additional single task blocks in which only the pursuit target moved on the screen ("100Pt no distr.", with the 100Pt instruction). Trials with vertical saccades, blinks or pursuit in the wrong direction were repeated at the end of each block. We used a very sensitive velocity criterion ( $12^{\circ}/s$ ) to detect vertical saccades. In pre-tests, we found that vertical saccades as small as  $0.3^{\circ}$  were reliably detected by this criterion.



**Figure 3.1** The time course of a sample trial. The cue (the vertical line) instructed observers to follow the stimulus below fixation. A rightward tilted grating ( $12^{\circ}$  tilt) is shown in the upper rectangle at motion onset. Observers have to indicate its orientation at motion offset. The figure is not drawn to scale.

We ran a threshold procedure at the beginning of each session to find the grating orientation that yielded 71% correct responses. Stimulus and task for the threshold

procedure was almost identical to the 100Dt condition, as subjects were supposed to attend only to the discrimination target. Orientation thresholds ranged between 6-11°, 9-11°, 9-17° and 7-12° for observers S1-S4, respectively. Observer S5 had an extreme but stable threshold of 45°. A critical point was that the subjects were able to do the task properly and showed little improvement in the discrimination task within a session, as shown by the similarity between threshold and 100Dt percent correct performance and evolution of thresholds across sessions. To achieve stability, naïve subjects were extensively trained on the same tasks as in the experiment (6 to 4 training sessions).

### 3.3.4 Data analysis

The algorithm that was used to detect pursuit onsets is based on low-pass filtered (de-saccaded) velocity traces (10Hz low-pass Butterworth filter) to reduce the effect of local variations caused by measurement error. First, the algorithm searched the first sample that was more than 6 standard deviations above the baseline velocity. The mean and SD of the velocity baseline were estimated from samples 100 before to 80 ms after target onset. Then, the algorithm went backwards to find the first sample that was below 20% of the maximum acceleration (obtained by differentiation of the filtered velocity trace). This sample was considered as the pursuit onset. The sign of the slope of the aforementioned regression line was used to evaluate whether the subject had pursued the correct target. The slope of a regression line fitting the velocity trace from the estimated onset to the next 80 ms was taken as the estimate of acceleration during the initial open-loop smooth pursuit (e.g. Braun et al. 2008).

We applied the “Attentional Operating Characteristic” (AOC) analysis introduced by Sperling and Melcher (1978) to our results. The standard procedure was adapted by Kowler et al. (1995) to examine tradeoffs between perceptual and saccadic performance. We normalized the perceptual performance to the Dt100 performance (following Reddy et al. 2004), with 0.5 still representing chance level. Given the percent correct proportion on a given block  $P_c$  and the proportion correct trials on block 100Dt, PDT100, the normalized perceptual performance  $P_n$  is:

$$P_n = 0.5 + 0.5 [(P_c - 0.5)/(P_{Dt100} - 0.5)]$$

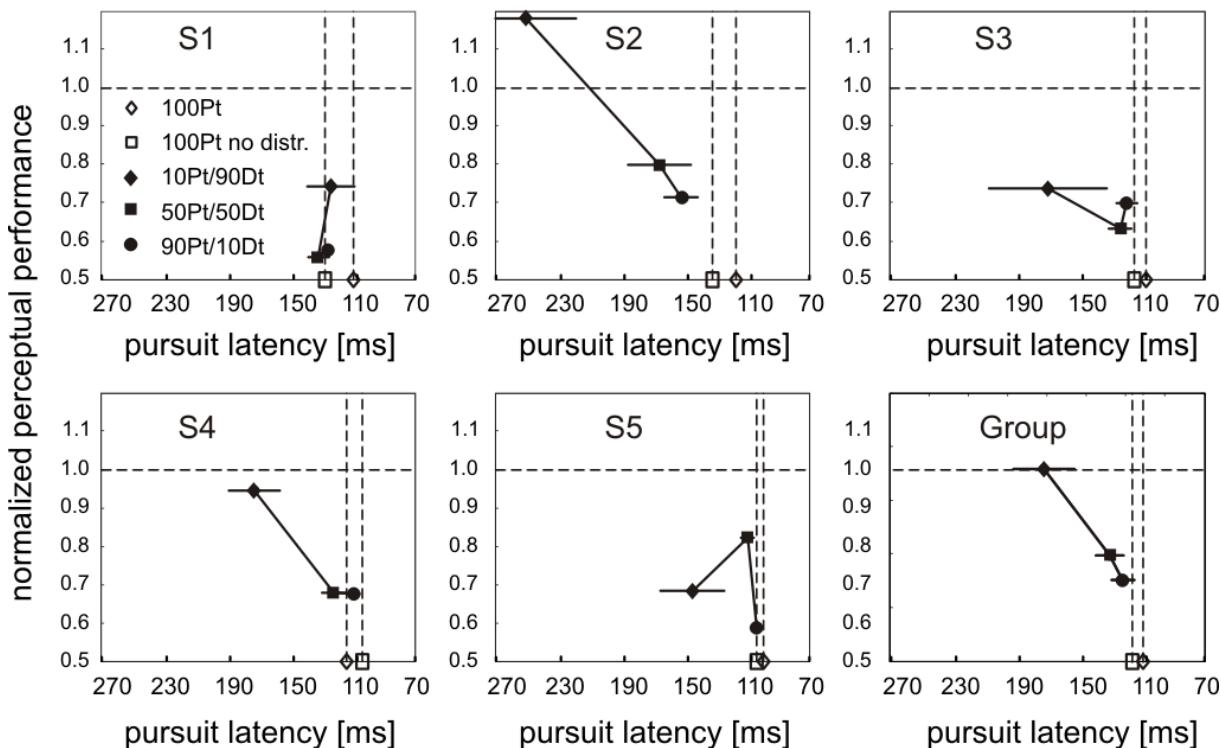
### 3.4 Results

We first looked at the way pursuit latency is traded for perceptual performance. AOC plots are shown in Figure 3.2 for each individual and for the group average. Most of the subjects (S1, S3 and S5) show perceptual performance much lower in dual task than in single task conditions, indicating the difficulty to follow the instructions to fully attend to the perceptual target. In particular, observers should show a perceptual performance close to 1 when the perceptual task had to be prioritized in the 10Pt/90Dt condition (like S2 and S4). It was also difficult to fully attend to the discrimination target without following it, as indicated by the large proportion of direction errors and very long latencies for observers S2 and S4 (Figure 3.3A). Probably for the same reason there is little difference in perceptual performance or latency between 50Pt/50Dt and 90Pt/10Dt, as only correctly executed trials were analyzed. Thus, tradeoffs between perception and pursuit may not be as evident in the averaged performance, but rather in the error rates. As shown in the Figure 3.3 the percent of direction errors indicates that participants tried to distribute attention differently between targets, thereby following the instructions. The group average panel of Figure 3.2 shows that the costs of prioritizing the perceptual target on pursuit latency were much larger than those of sharing resources, when compared to full priority to the pursuit target.

One-way analyses of variance (ANOVA) for repeated measures were run to test for effects of instruction. The arcsine transformation was applied to the normalized perceptual performance for statistical analysis, which revealed a significant effect of instruction (with the three competing dual-task instructions included),  $F(2,10)=87.1$ ,  $p<0.001$ . As shown in the Figure 3.2, most of the subjects (except S5) had a much larger increase in perceptual performance in 10Pt/90Dt compared to 50Pt/50Pt (.86 compared to .70),  $t(4)=2.49$ ,  $p=0.07$ , but there was little difference between 50Pt/50Dt and 90Pt/10Dt conditions (.70 and .65 respectively), as well as for their latencies. Perceptual performance was of 1.0 ( $SD=0.19$ ) in the Dt=Pt condition.

Further, we included all instructions for which a pursuit response was required in a one-way ANOVA. There was a significant effect of instruction on pursuit latencies (see Figure 3.4),  $F(4,20)=8.1$ ,  $p<0.001$ . We also wanted to know which instruction led to significantly longer latencies compared to “100Pt no distractor” condition. As shown in Figure 3.2, the group average smallest delay was of 6 ms in 100Pt condition and was not significant; the

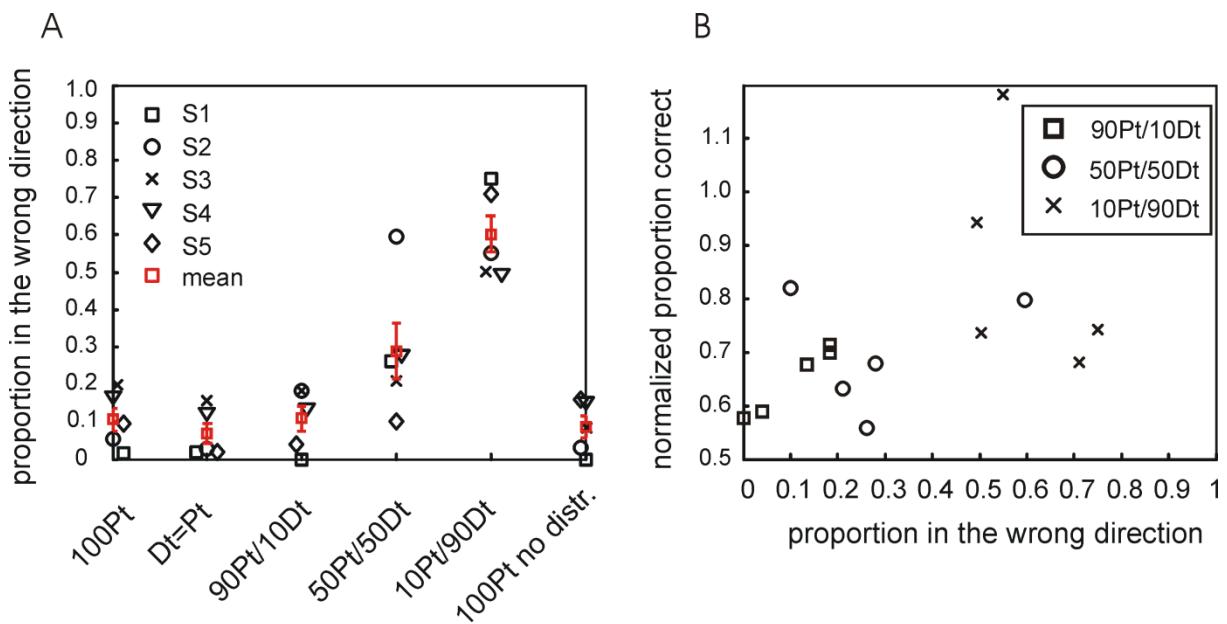
biggest was of 62 ms in the 10Pt/90Dt condition,  $t(4)=3.18$ ,  $p<0.05$ . The delay was of 13 ms in 90Pt/10Dt,  $t(4)=1.9$ ,  $p=0.13$ , of 21 ms in 50Pt/50Dt,  $t(4)=2.8$ ,  $p<0.05$ , and of 12 ms in Dt=Pt condition,  $t(4)=4.1$ ,  $p<0.02$ . Although small in absolute terms, those effects represent a substantial proportion of pursuit reaction time, and are within the range of previous studies with human participants (Adler et al. 2002).



**Figure 3.2 Plots of the Attention Operating Characteristic.** Normalized perceptual performance is plotted against median pursuit latency in three dual task conditions (10Pt/90Dt, 50Pt/50Dt, 90Pt/10Dt). Mean group values are plotted in the bottom right panel. Error-bars represent the standard error of the mean.

The effort to share resources according to the instructions also showed up on the tendency to follow the target of the perceptual task rather than the pursuit target. The effect of dual-task instruction was significant effect on the (arcsine transformed) proportion of direction errors,  $F(2,10)=13.22$ ,  $p<0.005$ . However, only the 10Pt/90Dt condition leaded to a significantly larger proportion of errors than the 90Pt/10Dt condition (65% compared to 11%),  $t(4)= 5.14$ ,  $p<0.01$ .

The results on pursuit acceleration are also of particular interest (Figure 3.4). According to Ferrera and Lisberger's (1995), the role of attention in pursuit target selection is to bias the competition between motion signals to drive pursuit. The response is then winner-take-all, as indicated by small effects of distractor motion after pursuit initiation. Accordingly we see no reduced acceleration in distractor compared to no distractor conditions, but rather the opposite tendency.

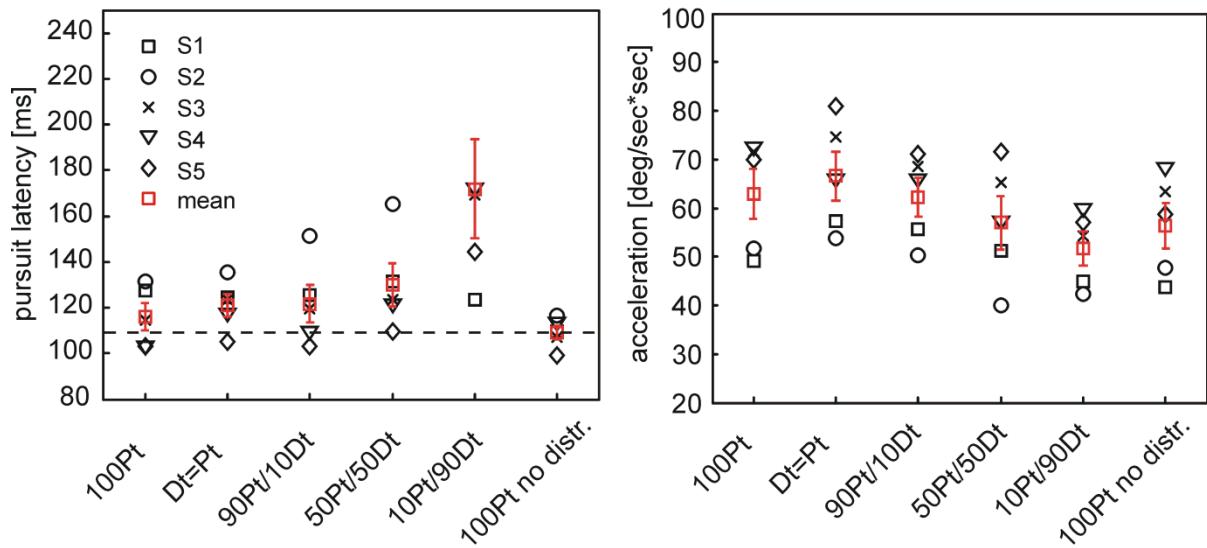


**Figure 3.3** Panel A shows the proportion of wrong direction errors as a function of instruction. Some horizontal jitter was added for clarity. Panel B shows the perceptual performance against the proportion of wrong direction errors ( $p=.47$ , n.s.). Symbols represent different dual task conditions.

There was a significant negative correlation ( $\rho=-.59$ ,  $p<0.05$ ) between latency and acceleration. The later the eye started to move, the weaker was pre-saccadic pursuit. This may be due to lower pursuit acceleration in response to more peripheral motion signals (e.g. Tychsen and Lisberger 1986). When the eye started later, the target had already moved away, resulting in a more peripheral location of the motion signal. However, we do not expect acceleration to be different in conditions that have similar latencies.

A one-way ANOVA showed that pursuit acceleration was significantly modulated by the instruction,  $F(4,20)=7.68$ ,  $p<0.001$ . The Dt=Pt condition led to significantly greater acceleration compared to 50Pt/50Dt, 10Pt/90Dt and 100Pt without distractor motion, as shown by multiple-comparisons t-tests with the Bonferroni correction applied,  $p<0.05$ . Acceleration strongly depends on the physical contrast of the target (Sperling et al. 2005).

Attention may have increased the effective contrast of the target motion signal (Treue and Maunsell 1996; Seidemann and Newsome 1999). The mere fact of combining pursuit and perceptual target in the Dt=Pt condition may help to focus attention (Shagass et al. 1976; Sweeney et al. 1994). Conversely, this interpretation would mean that attention is not completely focused on the target in the other conditions. If attention had been completely focused in conditions with priority of the pursuit task, we would expect the same acceleration in Dt=Pt and 100Pt without distractor conditions. However, the Dt=Pt condition produced higher acceleration, but not shorter latencies. Remember that the Dt=Pt condition was significantly delayed compared to the 100Pt no distractor condition.



**Figure 3.4** The left panel shows pursuit latency (average values are replotted from Figure 3.2) and acceleration as a function of instruction.

### 3.4.1 Dissociation experiment

Possibly, the frequent instruction changes between blocks in the same session made it difficult to dissociate perceptual from oculomotor decisions. To test this possibility, subjects S2 and S4 were tested in six additional sessions with the same instruction. Each session was initiated by a threshold procedure aiming at 71% correct responses and followed by 4 blocks of at least 48 trials. The instruction was to reach 70% correct perceptual performance, that is to perform as well as during the threshold single-task block; to approach the “100Pt no distractor” latency measured in the previous experiment, and to minimize the number of pursuit errors. In a way it was similar to the 50Pt/50Dt instruction of the previous experiment. To optimize performance, subjects received feedback about their

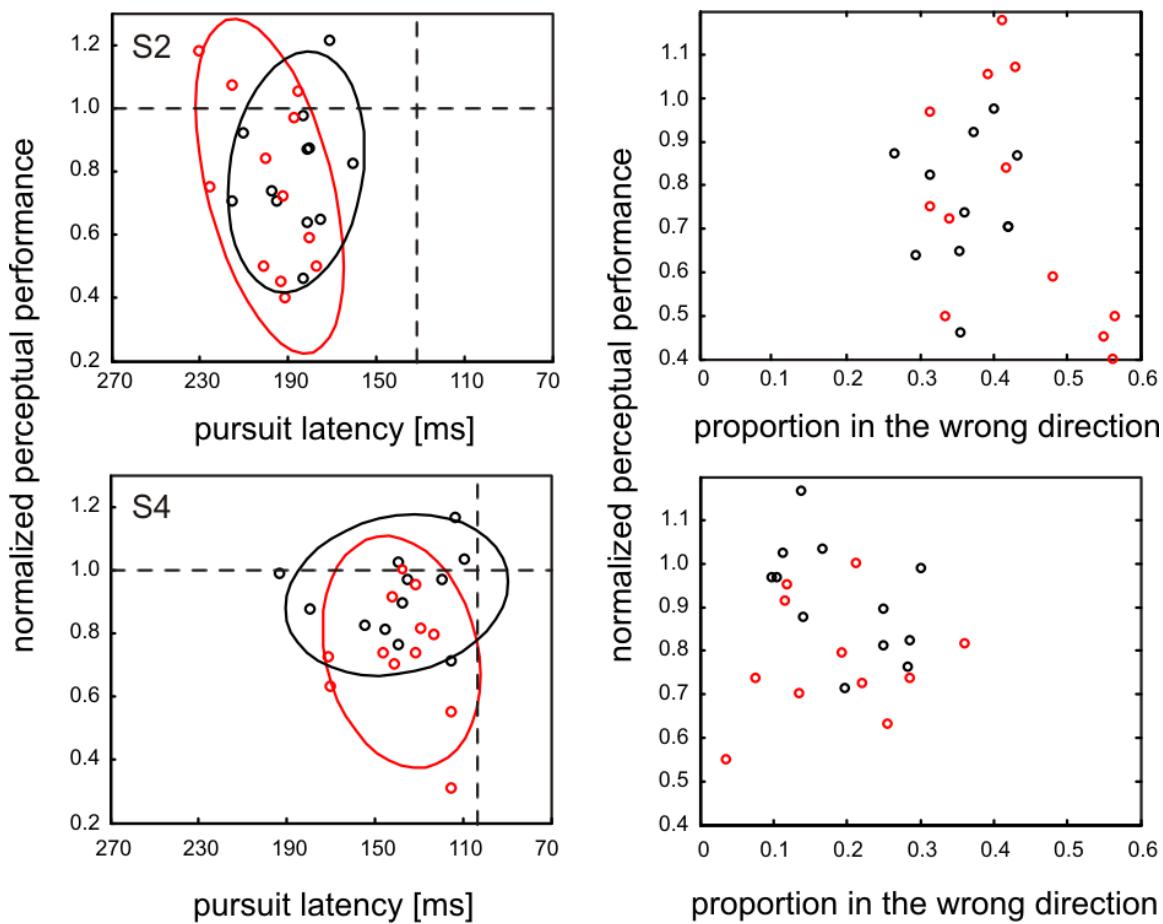
perceptual performance after each block (i.e., four times per session): their median pursuit latency, the histogram of latencies, and the number of errors due to pursuit in the wrong direction. Thresholds measured at the beginning of the session ranged from 8 to 9° for S2, and were constant at 8° for S4.

To explore improvements in performance we analyzed blockwise performance in the first and second half of the experimental sessions (3 sessions each). Figure 3.5 shows performance in each block in AOC plots for the two subjects. Improvements in dual-task performance would be indicated by displacement of the ellipses toward the independence point. The plot shows little evidence for improvements despite extensive training. Therefore, we believe that task-switching was not the limiting factor when trying to dissociate attentional from oculomotor selection. The other interesting outcome of this control experiment is that even when subjects receive feedback about pursuit errors, the proportion of trials in which they pursued the wrong target remained very high (10-30% for S4 and 30-50% for S2), reflecting the tendency to follow the perceptual target on a great proportion of trials when it received more attentional resources than the pursuit target. Nevertheless, despite the large variability, there was no significant correlation between perceptual performance and pursuit errors ( $p=-.35$  for S2;  $p=-.11$  for S4). Unexpectedly, the tendency was for a negative correlation. This may indicate that successful trials were those in which more effort was put into the two tasks; on shifting attention to the perceptual target and eventually head to the pursuit target. Put otherwise, a wrong direction could be chosen because no attention was paid to either target, and then a correct response in the orientation task will be less likely in such trial.

### 3.5 Discussion

We examined the AOC for pursuit initiation and perception. The results show that pursuit cannot be initiated independently from the perception of another moving object. In contrast, pursuit initiation is almost unaffected when attention is directed at stationary objects (Souto and Kerzel 2008a). Thus, the present study is the first to confirm that the "mind's eye" and pursuit initiation are strongly coupled when the target has to be selected among competing motion signals. Analysis of latencies showed that all dual task conditions led a delayed response compared to pursuit initiation without a distractor. The current

results complement studies on the link between attention and target selection for pursuit. For both saccades and smooth pursuit, selection for perception and action is shared, at least when there is competition among task-relevant signals. This conclusion is supported by ample evidence showing that pursuit and saccades share similar selection and gating signals (Krauzlis and Dill 2002; Krauzlis 2003; Liston and Krauzlis 2003; Carello and Krauzlis 2004; Liston and Krauzlis 2005; Case and Ferrera 2007). However, pursuit can appear to be poorly selective to the designated target until a saccade is made (Gardner and Lisberger 2001; Gardner and Lisberger 2002; Case and Ferrera 2007).



**Figure 3.5** Black symbols indicate the average performance for each block in the first three sessions. Red symbols indicate data from the last three sessions. Confidence ellipses are shown separately for each halve. Vertical lines represent 100Pt performance in the first main experiment. Horizontal lines represent perceptual performance normalized to .71 correct – the value targeted by the threshold procedure. Panel B shows direction errors as a function of normalized perceptual performance for each block of 48 trials.

Psychophysical studies show that attention precedes execution of saccades in a mandatory way (e.g. Deubel and Schneider 1996; Castet et al. 2006; Montagnini and Castet 2007). Assuming shared selection signals, poor selectivity of pursuit may be simply explained by the fact that attention takes longer than usual pursuit latencies to suppress the influence of the distractor (Castet et al. 2006; Deubel 2008), as it may be the case for fast saccades (Ottes et al. 1985; Chou et al. 1999). If this were the case we expect that selectivity will be modulated by instructions to increase attentional resources on the target location. Alternatively it might be the case that averaging is a default strategy favoring speed over precision. Our results favor the former interpretation, that it is the slow deployment of attention to the target that explains the influence of distractor motion during pursuit initiation , as indicated by our observers showing very little delay when the task required to attend uniquely to the pursuit target. Previous results showed a strong modulation of vector-averaging by prior knowledge of target direction (Sperling et al. 2006b). This contrasts with the robust delays that are found with macaques under the same conditions (Ferrera and Lisberger 1995).

Monkeys showed longer latencies when they had to pursue a target in the presence of a conflicting motion signal. Even when selection was facilitated by blocking the target direction; the delay remained unchanged (Ferrera and Lisberger 1995). Ferrera and Lisberger (1995) proposed that when there is a competition between moving stimulus, attention acts by biasing the competition in favor of one signal, resulting in a winner-take-all response. Our experiments add that when sufficient resources are allocated to the target spatial location we can also impede this competition from taking place, as indicated by a negligible delay in presence of a distractor (100Pt condition).

In a biased competition model of attention, benefits of attention are confined to conflicting situations. Otherwise bottom-up salience is sufficient to specify the target to the pursuit system. Instructions to attend the pursuit target and pursue led to significantly larger accelerations than when the task was pursuing without the presence of a distractor, while latencies where similar. This implicates that less attention is paid in the latter condition. Erkelens (2006) already proposed that unlike saccades, pursuit can be pre-attentively initiated. He showed that much longer pursuit latencies than with the classic ramp paradigm (the fixated stimulus starts to move) are obtained when an old pursuit target remains when

a new pursuit target appears. In this situation pursuit latencies approach saccade latencies and the two become strongly correlated.

Our previous studies showed that without distractor motion signals, smooth pursuit initiation contrasted with saccadic initiation by showing that attention could be endogenously or exogenously cued to the periphery with nearly no effect on pursuit latency. Other studies have shown decrements in perceptual performance in the periphery during pursuit initiation indicative of a shift of attention to the pursuit target (Schutz et al. 2007a; Schutz et al. 2008). Both results can be accommodated by supposing that a small amount of attentional resources is required, but much smaller than for saccades.

Kowler et al. (1995) analyzed how attention is traded for oculomotor performance in the context of saccades. It was shown that some fixed amount of resources was needed at the target goal location, but that some share of resources could be freed from the target location to be allocated to an opposite location. In a similar vein, we show that ocular performance depends on attention resources biased towards the designated target. We also showed that performance was not only limited by frequent task-switching, nor the absence of oculomotor feedback. However, we do not show strong evidence that attention could be paid to the distractor motion without incurring large costs in pursuit latency and in error rates.

Instructions to pay attention to the oculomotor task distractor led to a large number of direction errors which may signify a lack of awareness of very fast responses, as shown for fast involuntary saccades in the antisaccade (Mokler and Fischer 1999) or in the oculomotor capture (e.g. Godijn and Theeuwes 2003b) tasks. It seems that erroneous eye movements that take less than 100 ms to be corrected, as it can often be the case during pursuit initiation (Krauzlis et al. 1999), may go unnoticed. We may also lack a trustful estimate about the direction our eyes are heading for slow speeds over small periods of time.

As pointed out by Kowler et al. (1995; see also Khurana and Kowler 1987) it is desirable that eye movements follow perceptual decisions but do not depend too strongly on attentional resources, as it permits eye movements to be in line with perception and at the same time it permits relatively constant motor performance with continuous concurrent internal and external demands of attentional resources. In this regard pursuit initiation

seems to require a stronger attentional bias to overcome the competition of motion signals, and thus might be an even better indicator of perceptual choices.

## **4 Study 3: Involuntary cueing effects during smooth pursuit: facilitation and inhibition of return in oculocentric coordinates**

### **4.1 Abstract**

Peripheral cues induce facilitation with short cue-target intervals and inhibition of return (IOR) with long cue-target intervals. Modulations of facilitation and IOR by continuous displacements of the eye or the cued stimuli are poorly understood. Previously, the retinal coordinates of the cued location were changed by saccadic or smooth pursuit eye movements during the cue-target interval. In contrast, we probed the relevant coordinates for facilitation and IOR by orthogonally varying object motion (stationary, moving) and eye movement (fixation, smooth pursuit). In the pursuit conditions, cue and target were presented during the ongoing eye movement and observers made a saccade to the target. Importantly, we found facilitation and IOR of similar size during smooth pursuit and fixation. The results suggest that involuntary orienting is possible even when attention has to be allocated to the moving target during smooth pursuit. Comparison of conditions with stabilized and moving objects suggest an oculocentric basis for facilitation as well as inhibition: facilitation and IOR were reduced with objects that moved on the retina both with smooth pursuit and eye fixation.

### **4.2 Introduction**

When a peripheral location is cued by a transient event (i.e., a luminance change) and the cue-target interval is shorter than 200-300 ms, responses are faster to targets appearing at the cued location than to targets appearing at an uncued location. Facilitation of responses was attributed to involuntary shifts of attention to the cued location. With longer cue-target intervals, responses are slower to targets appearing at the cued location (Posner & Cohen, 1984), which is referred to as inhibition of return. IOR is often understood as an adaptive mechanism by which previously attended objects are less likely to be attended later on. In agreement with this interpretation, IOR has been proposed to operate as a visual foraging facilitator (Klein & MacInnes, 1999; Gilchrist & Harvey, 2000; but see Hooge, Over,

van Wezel, & Frens, 2005): IOR optimizes the distribution of saccades over the whole visual scene by avoiding repeated selection of a salient location.

One important question is how inhibition is updated after an eye movement. Is the retinal location, the object, or the location in the environment inhibited? To answer this question, Posner and Cohen (1984) asked their subjects to make a saccade in the interval between cue and target presentation, which changed the retinal (but not environmental) location of the cue. Unaffected IOR indicated it was coded in environmental coordinates. More recently, Abrams and Pratt (2000) confirmed a dissociation between manual and saccadic responses. While manual IOR was coded in environmental coordinates, saccadic IOR was coded in retinal<sup>11</sup> coordinates. Observers were asked to pursue a moving fixation mark during the cue-target interval and to foveate the peripheral target by making a saccade. Saccades were slower when the target appeared in the same retinal location as the cue, but not when it appeared in the same spatial location (see Exp. 2, Abrams & Pratt, 2000). Therefore, Abrams and Pratt concluded that saccadic IOR operates in retinal coordinates. They gave the following reason for using smooth pursuit rather than a saccade during the cue-target interval: “We used a smooth-pursuit movement to change the position of the participant’s gaze because the sudden onset of a saccade target, or possibly even the production of an endogenous saccade, might be expected to attract or otherwise activate the attention system and thus disrupt the inhibition that had been established by the initial cue” (p. 780). The rationale seems to suggest that using smooth pursuit does not implicate the attention system.

In light of research on the connection between smooth pursuit and attention, this conclusion seems quite wrong and warrants further research. First, previous studies have shown that attention is bound to the pursuit target during steady-state pursuit (Kerzel & Ziegler, 2005; Khurana & Kowler, 1987; Madelain, Krauzlis, & Wallman, 2005; Schutz, Delipetkos, Braun, Kerzel, & Gegenfurtner, 2007). For instance, observers were unable to shift attention to a distractor while correctly pursuing the target (Khurana & Kowler, 1987),

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<sup>11</sup> We use the term “retinal” synonymous to “oculocentric”. In keeping with general usage, we oppose this reference frame to “environmental” that is synonymous to “spatial”. We would like to point out that “environmental” is inexact because a head-centric (egocentric) reference frame cannot be ruled out, as the head was fixed. The term “non-retinotopic” would be more exact.

even when target and distractor moved in the same direction, but at slightly different speeds. The allocation of attention was measured by means of a secondary perceptual task. Without incentive to prioritize distractor or target, perceptual performance on the target was much better than perceptual performance on the distractor.

Given the attention-demanding nature of smooth pursuit, that was somewhat downplayed by Abrams and Pratt (2000), one may wonder whether the reduction of IOR when the retinal location of the cue changed was exclusively due to retinal displacement. Second, it seems important to investigate effects of eye movements because there is little consensus on the coordinate frame of IOR. When retinal- and environment-based coordinates were carefully separated, many experiments have confirmed inhibition that is attached to the object as it moves (S. P. Tipper, Driver, & Weaver, 1991; S. P. Tipper, Weaver, Jerreat, & Burak, 1994). Object-based IOR may even overrule space-based IOR (S. P. Tipper et al., 1991). However this effect was elusive with saccadic (Abrams & Dobkin, 1994; Ro & Rafal, 1999) as well as with manual responses, in a different setting (Muller & von Muhlenen, 1996). At least with manual responses, it appears that object- and environment-based IOR may vanish after extended training (Weaver, Lupianez, & Watson, 1998). However, effects of practice on environment-based IOR were not replicated in a series of three experiments (Pratt & McAuliffe, 1999).

The purpose of this study was to disentangle effects of coordinate frame and eye movements. In a previous study, we showed that effects of voluntary attention on manual RTs were similar during fixation and smooth pursuit (Kerzel, Souto, & Ziegler, 2008). Because the peripheral or central cues predicted the upcoming target location, subjects in Kerzel et al. were likely to voluntarily attend to the cued locations. Facilitation was observed with cue-target SOAs as long as 500 ms, and was coupled to a decrease of pursuit gain when the peripheral target did not move along with the pursuit target. In the present study, the cues did not predict the subsequent target location. As a consequence, the best strategy was to ignore them. Any cueing effects that are observed would therefore more likely be involuntary.

There is reason to believe that cueing effects will not occur during smooth pursuit. The strong coupling between attention and smooth pursuit may help observers to filter out irrelevant peripheral events. In some instances, onsets failed to capture attention when

attention was narrowly focused on a given location (Theeuwes, 1991). If the execution of smooth pursuit induced such a strong attentional focus on the pursuit target, facilitation and IOR may disappear during smooth pursuit. Alternatively, exogenous shifts of attention may still occur under the assumption that only endogenous attention is allocated to the pursuit target. Some authors have proposed that endogenous and exogenous attention are partially independent resources (e.g. Riggio & Kirsner, 1997).

To tease apart retinocentric from environmental coordinates, we compared conditions in which cued objects moved on the retina with conditions in which objects were stabilized on the retina. Because object or eye movements were continuous, our paradigm avoids transients between cue and target presentation that may have contaminated effects in previous studies. The comparison between fixation and smooth pursuit is expected to produce similar latencies, as the readiness to make a saccade has been shown to be very similar during pursuit and fixation (Boman, Braun, & Hotson, 1996; Krauzlis & Miles, 1996).

## 4.3 Methods

### 4.3.1 Subjects

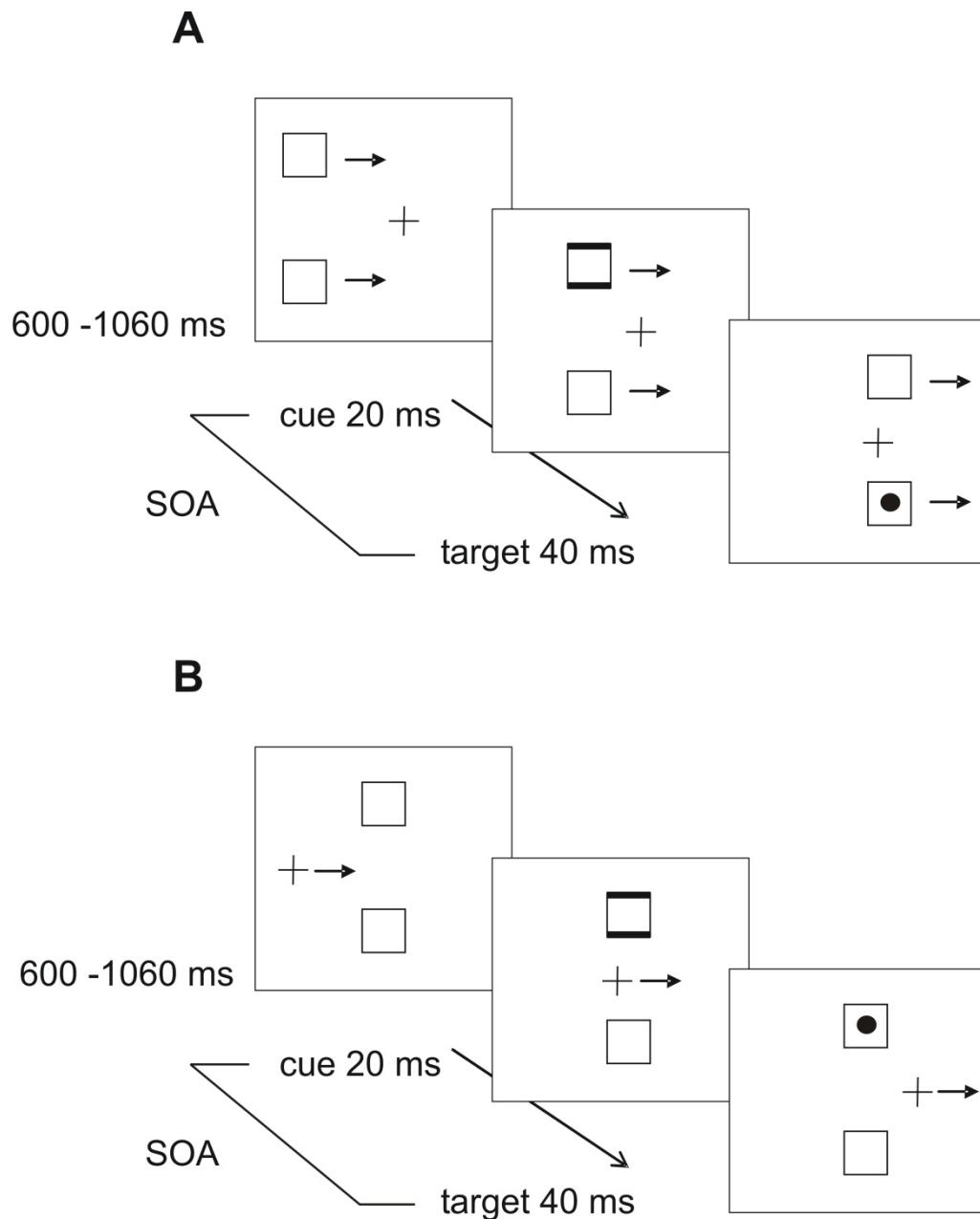
The first author (DS) and 11 students (10 females) of the University of Geneva participated for course credit ( $M=20.5$  years old,  $SD=2.8$ ). Students were naïve with respect to the purpose of the experiment and the first author's results followed the average pattern.

The experiment was conducted in compliance with the ethical regulations of the University of Geneva and with the Helsinki Declaration of 1964.

### 4.3.2 Materials and stimuli

Eye movements were recorded with an Eyelink II (Osgood, Ontario, Canada) eye-tracker, in pupil only mode. Sampling frequency was 250 Hz. A 9 point pseudo-random calibration procedure was run at the beginning of each session, and every two blocks if needed. Experiments took place in a dimly lit room. Head movements were minimized with a chinrest, at a distance of 46 cm from the screen. The luminance of the gray background was  $29 \text{ cd/m}^2$ . Dark gray placeholders ( $22 \text{ cd/m}^2$ ,  $1^\circ \times 1^\circ$ ), were shown at a vertical eccentricity of  $5^\circ$ . The size of the red fixation cross was  $0.2^\circ \times 0.2^\circ$ . The cue was a dimming (to  $0 \text{ cd/m}^2$ ) and

thickening (from  $0.04^\circ$  to  $0.21^\circ$ ) of the horizontal lines of the placeholders. The target was a black circle ( $0 \text{ cd/m}^2$ ) of  $0.4^\circ$  diameter.



**Figure 4.1 Time-course for relative motion conditions with eye fixation (A) and smooth pursuit (B).** The cue appeared at the same horizontal eccentricity in both conditions and could be invalid (A) or valid (B) with equal probability. In stabilized conditions, which are not shown, everything was static or moved together. The stimulus onset asynchrony (SOA) was either 130 or 600 ms. The response was a saccade to the target disk.

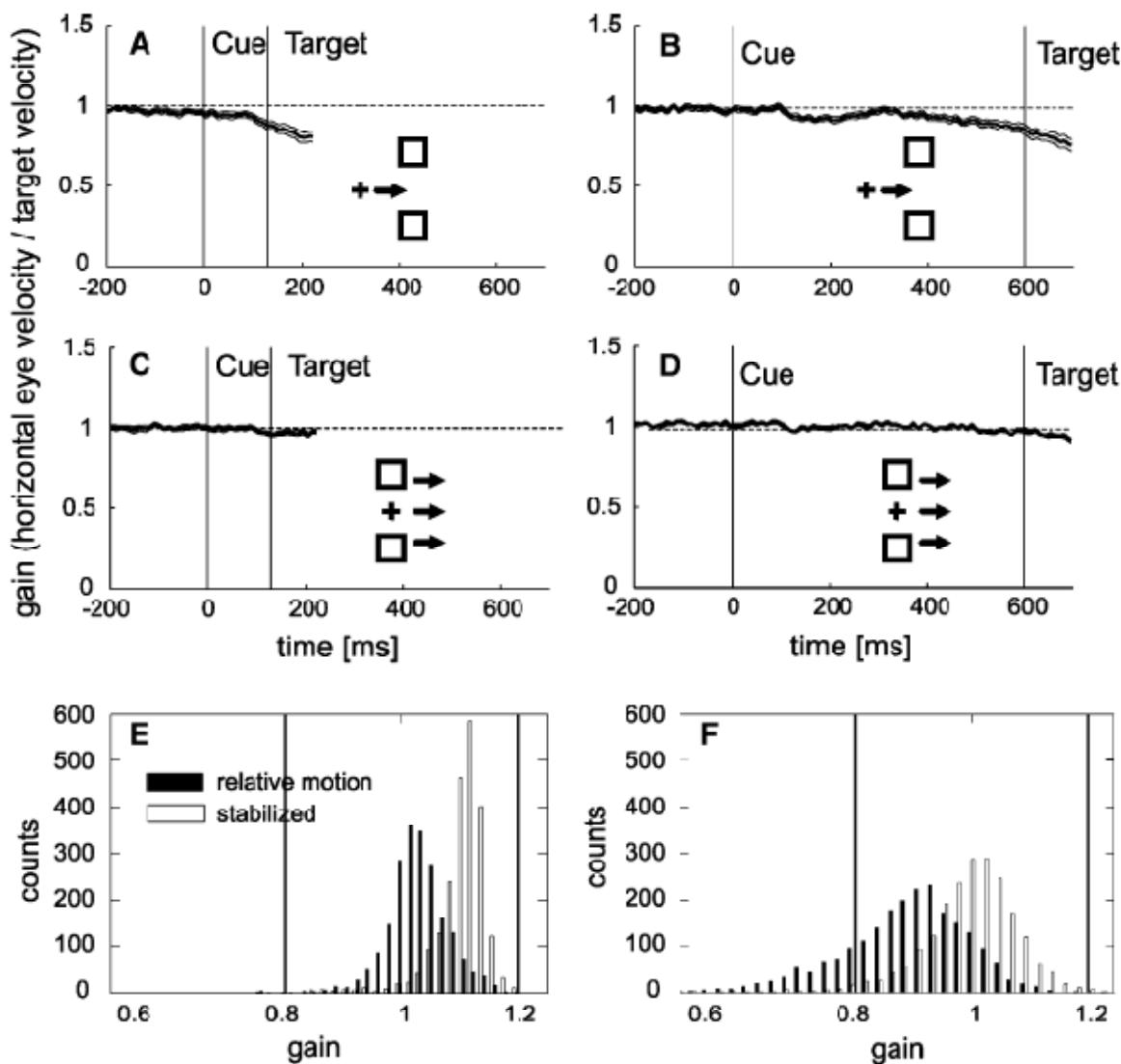
Figure 4.1 depicts the *relative motion* conditions, in which the pursuit target and peripheral boxes moved relative to each other at  $10.8^\circ/\text{s}$ . After a random time interval, from 600 to 1060 ms after start of the trial, the cue was displayed for 20 ms. After a variable time interval, the target appeared in the cued (valid condition) or opposite location (invalid condition) for 40 ms. The stimulus onset asynchrony (SOA) between cue and target was set to either 130 or 600 ms to maximize saccadic facilitation and IOR, respectively (Briand, Larrison, & Sereno, 2000). In two *stabilized conditions*, the fixation cross and peripheral boxes were static or moved together, and were therefore approximately stabilized on the retina by fixation or pursuit eye movements, respectively. Cue onset was as unpredictable in the relative motion as in the stabilized conditions. In stabilized conditions the placeholders were exactly above and below the fixation target. In relative motion conditions, horizontal eccentricity of the cue relative to the fixation target varied randomly around  $0^\circ$  of eccentricity ( $-2.5^\circ$  to  $2.5^\circ$ ).

A potentially important point about the cue is that it avoided perceptual interference with the target because only the upper and lower bars were highlighted (see Figures 4.1A and 1B). If the vertical lines had been dimmed, the flashed box could be perceived as overlapping the target due to the mislocalization of flashed objects during smooth pursuit (e.g., Kerzel, Aivar, Ziegler, & Brenner, 2006) or because of the flash-lag effect during fixation (e.g., Nijhawan, 2002).

### 4.3.3 Procedure

Subjects were asked to accurately track or fixate the red cross until they saw a black dot, which they had to fixate as fast as possible, while avoiding anticipatory responses. The experimental design was within-subjects with the factors relative motion (with or without relative motion), eye movement (fixation or pursuit), validity (valid or invalid) and SOA (130 or 600 ms). Relative motion, eye movement, and SOA were blocked. SOA was blocked to maximize IOR (C. Tipper & Kingstone, 2005) and help subjects maintain smooth pursuit after presentation of the exogenous cue. With uncertainty about the SOA, subjects tended to stop pursuit after the exogenous cue, because they were getting ready to make a saccade. This reduced pursuit gain considerably in the long SOA condition. The direction of eye or object motion was randomized. There were 48 repetitions for fixation trials, 96 for eye movement trials because we assumed that the dual task situation would increase variability. Each

subject completed at least 1152 trials in three sessions. Erroneous trials were repeated. An error message and a tone was displayed whenever any of the following events was detected: a blink between 100 ms before cue onset to 500 ms after target onset, an anticipatory saccade (latencies shorter than 100 ms), a late saccade (latencies longer than 500 ms which are more than ~3 standard deviations away from the median latency), a saccade in the wrong direction, or bad pursuit.



**Figure 4.2 Analyses of pursuit gain.** Panels A-D show pursuit gain (eye velocity / target velocity) averaged over the 12 subjects from 200 ms before cue presentation until 100 ms after target presentation. Relative motion (A-B) and stabilized (C-D) conditions are shown on different panels. The short cue-target stimulus onset asynchrony (SOA) is shown on the left (A,C) and the long SOA on the right (B,D). Thin lines represent the between-subjects standard error of the mean. Panels E-F: Histograms of pursuit gain in the cue-target interval for short (E) and long (F) SOAs. Vertical lines show the cut-off used for inclusion of trials in our analyses.

The online criterion for smooth pursuit was that the eye had to travel a distance corresponding to a pursuit gain of 0.8-1.2 during the cue-target interval. A small proportion of trials was repeated because of anticipations (4 %), timed-out responses (2 %), saccades in the wrong direction (2 %), or low pursuit gain (6 %).

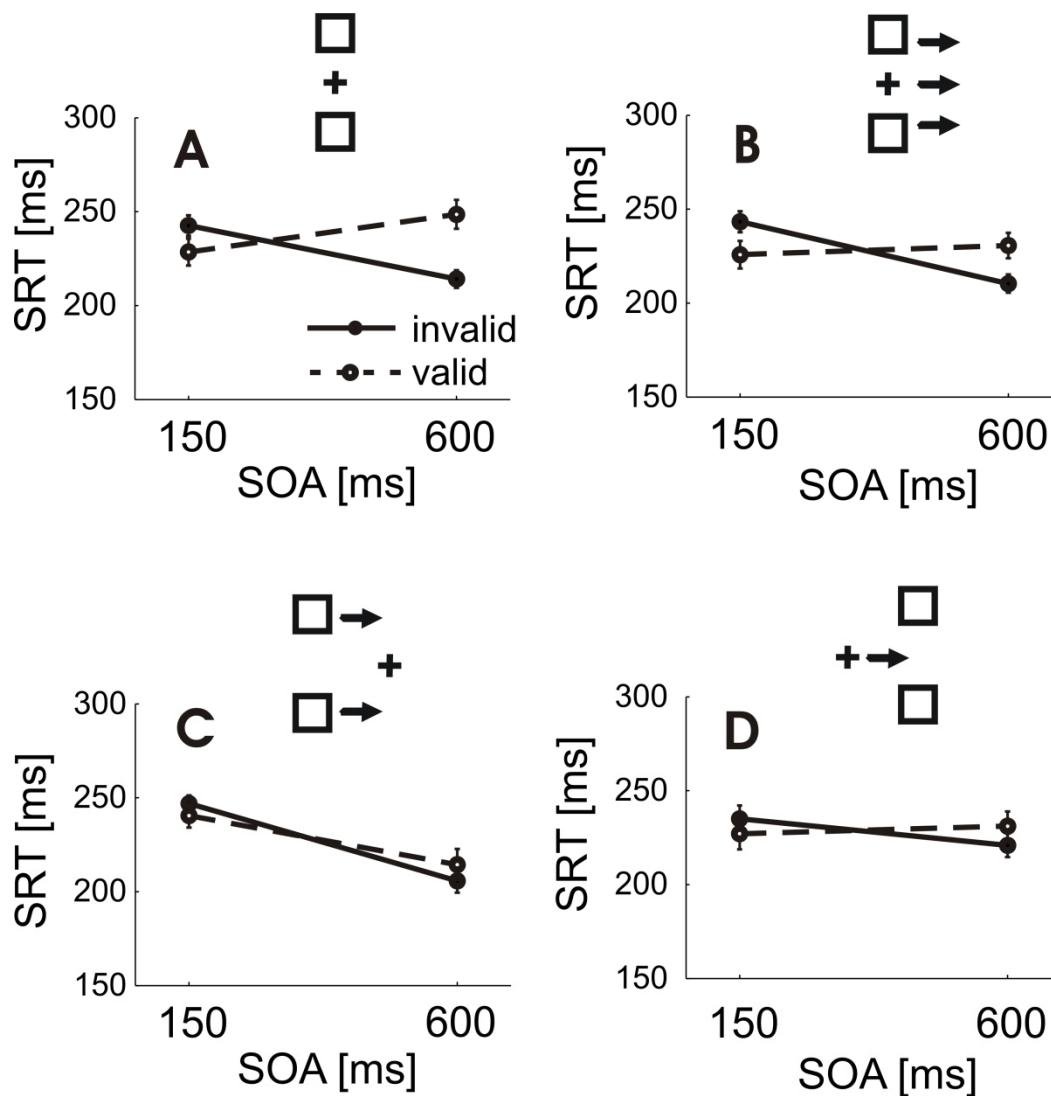
#### 4.4 Results

We calculated the gain (eye velocity/target velocity) of smooth pursuit after removing saccades from the eye movement traces. We then retained trials in which pursuit gain was between 0.8 and 1.2 in the cue-target interval. Figure 4.2A-D shows pursuit gain. Indeed, there was a tendency for most of the subjects to slow down in anticipation of target presentation when the target was stationary, notably for the long SOA (see Figure 4.2A-B). As shown in Figure 4.2E-F, the proportion of trials with gain below cut-off is only substantial in the relative motion conditions with the long SOA (11 %). Overall, 3 % of trials were removed in the offline analysis.

We calculated median saccadic reaction times for each condition and participant. Mean of median saccadic latencies for all conditions are graphed in Figure 4.3. A repeated-measures ANOVA (relative motion x eye movement x validity x SOA) was run on median saccadic reaction times. Most importantly, we found a three-way interaction between relative motion (stabilized vs. relative motion), SOA, and validity,  $F(1,11)=10.44$ ,  $p<0.01$ , but no effects including eye movement. This means that cueing effects were as strong during smooth pursuit as during fixation. The only factor that modulated cueing effects was relative motion. To follow up on the significant interaction, we calculated cueing effects (i.e., the difference between invalid and valid trials) for each relative motion condition and SOA. For short SOAs, cuing effects were not significantly different in relative motion and stabilized conditions (facilitation of 12 vs. 17 ms, respectively),  $p=0.14$ . For long SOAs, cueing effects were significantly smaller with relative motion than without (inhibition of -9 vs. -23 ms),  $t(11)= 4.28$ ,  $p<0.001$ . Further, we ran separate three-way ANOVAs (eye movement x validity x SOA) for each relative motion and stabilized condition.

#### 4.4.1 Stabilized conditions

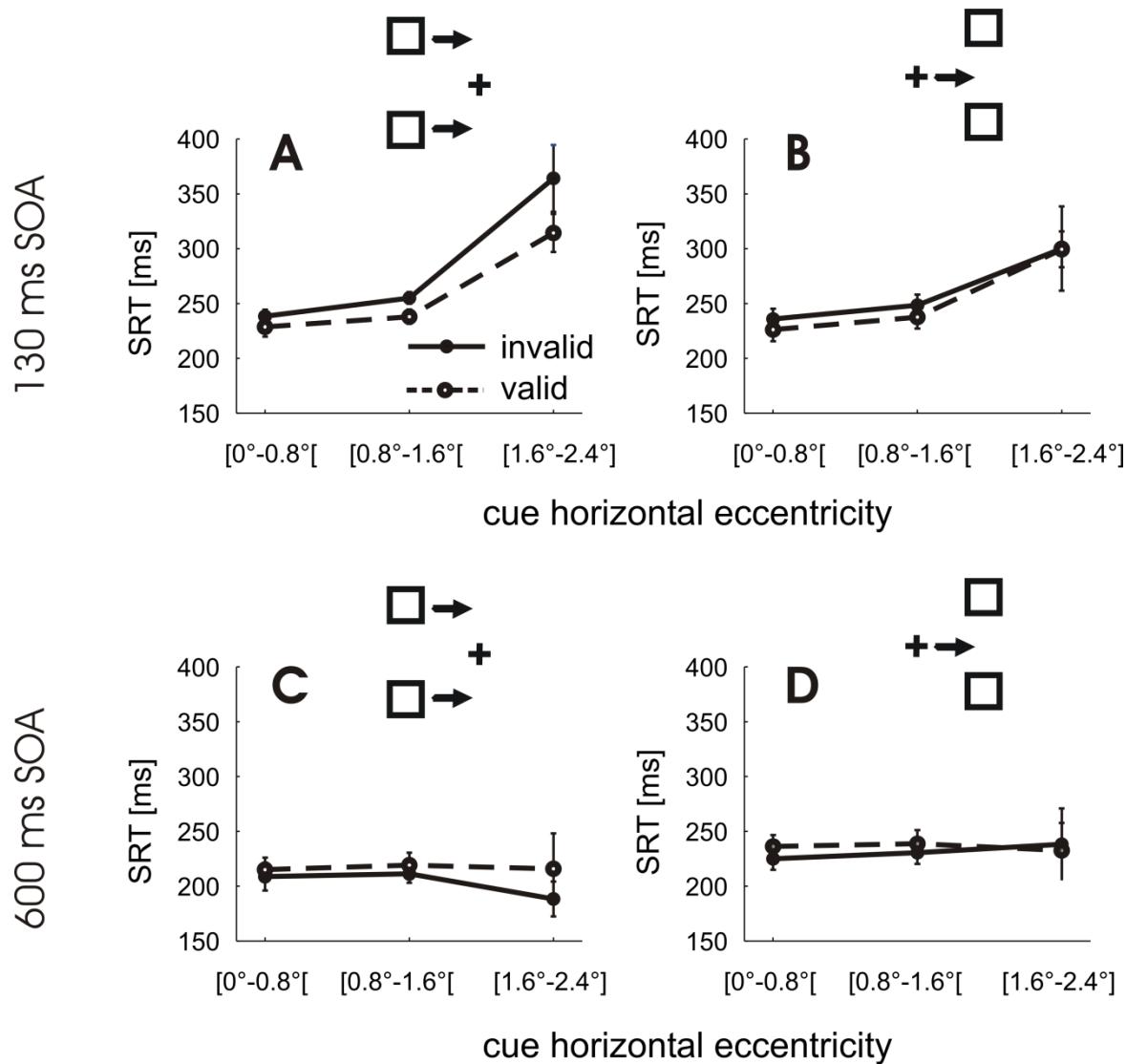
The similarity of fixation and pursuit is remarkable when the peripheral objects were stabilized (see Figure 4.3A-B). The classic facilitation and inhibitions effects were found in both conditions and no significant interaction with eye movement was observed. A repeated-measures ANOVA (eye movement x validity x SOA) showed a significant interaction of validity and SOA,  $F(1,11)=45.89$ ,  $p<0.001$ , not modulated by eye movement,  $F<0.4$ .



**Figure 4.3 Mean of median saccadic reaction times (SRT).** The upper panels show the conditions with stabilized peripheral objects during fixation (panel A) or smooth pursuit (panel B). The lower panels show the condition with relative motion during fixation (panel C) or smooth pursuit (panel D). Error bars represent between-subjects standard error of the mean.

Eye movement interacted with validity,  $F(1,11)=11.59$ ,  $p<0.01$ , indicating longer latencies (across SOAs) with valid cues during fixation than during pursuit (239 vs. 229),  $t(11)=5.9$ ,  $p<0.05$ .

For the short SOA, facilitation was of 14 ms for the static condition (valid vs. invalid: 231 vs. 245 ms),  $t(11)=6.07$ ,  $p<0.05$ , and of 20 ms for the pursuit condition (224 vs. 244 ms),  $t(11)=15.2$ ,  $p<0.01$ . For the long SOA, an IOR effect of -29 ms (248 vs. 219 ms) was found during fixation,  $t(11)=21.46$ ,  $p<0.001$ , and of -17 ms during pursuit (233 vs. 216 ms),  $t(11)=10.2$ ,  $p<0.01$ .



**Figure 4.4 Effects of eccentricity on median saccadic reaction time (SRT).** Facilitation was observed at short stimulus onset asynchronies (panels A and B) and inhibition of return at long stimulus onset asynchronies (panels C and D). The left and right columns show fixation and pursuit conditions as shown in the insets at the top. Error bars represent between-subjects standard error of the mean.

#### 4.4.2 Relative motion conditions

With relative motion between fixation cross and peripheral boxes, the cue could be presented with a slightly variable horizontal eccentricity (between -2.5° and 2.5°). To rule out that the reduction of the cueing effects with relative motion was due to target eccentricity, we calculated median saccadic reaction time in three eccentricity bins that were 0.8° wide (0° to 0.8°, 0.8° to 1.6°, and 1.6° to 2.4°). Figures 4.4 show that the differences between valid and invalid (short or long SOA) were stable over eccentricities ranging from 0 to 1.6°. It also indicates that the reduction of IOR and facilitation with relative motion was not due to decreasing cueing effects with increasing eccentricity. If anything, the opposite was the case. We then tested cueing effects for trials with eccentricities smaller than 1°. A repeated measures ANOVA (eye movement x validity x SOA) confirmed an interaction between SOA and validity,  $F(1,11)=20.35$ ,  $p<0.001$ , indicating that facilitation with the short SOA turned into inhibition with the long SOA. Again, the interaction of SOA and validity was not qualified by eye movement,  $F<0.02$ . Further, there was an interaction of eye movement and SOA,  $F(1,11)=7.3$ ,  $p<0.05$ , indicating shorter latencies during fixation compared to pursuit with the long SOA (209 vs. 227 ms),  $t(11)=2.17$ ,  $p=0.05$ , but longer latencies during fixation compared to pursuit with the short SOA (244 vs. 235 ms). We then tested the reliability of cueing effects for each combination of SOA and eye movement. T-tests showed tendencies in the predicted direction for facilitation effects ( $p > .19$ ), and statistically significant or nearly significant effects for inhibition. Facilitation with the short SOA was of 8 ms (240 vs. 248 ms) during fixation and of 3 ms (233 vs. 236 ms) during pursuit. Inhibition with the long SOA was of -8 ms during fixation (214 vs. 206 ms),  $t(11)=2.11$ ,  $p=0.06$ , and of -11 ms during pursuit (233 vs. 222 ms),  $t(11)=3.13$ ,  $p=0.01$ .

### 4.5 Discussion

We wanted to know how smooth pursuit affects involuntary cueing effects and in which reference frame these effects operate. We measured facilitation and IOR during pursuit and fixation, with peripheral objects that either moved on the retina or remained on the same retinal location. We found similar effects with a static display during fixation as with objects that moved at the same velocity as the pursuit target. The size of these effects is comparable to those previously reported in the literature, which confirms the existence of

automatic orienting and inhibition by peripheral cues during smooth pursuit. This finding complements our earlier study on voluntary attention during smooth pursuit (Kerzel et al., 2008). Involuntary cuing effects occur even if instructions required participants to focus on the pursuit task until the peripheral saccade target appeared. Pursuit with a high gain requires attention on the pursuit target, yet this is not a sufficient condition for filtering out the influence of irrelevant, peripheral transients (i.e., the cue).

With relative motion of fixation cross and peripheral objects, cuing effects were reduced to half of those in stabilized conditions. A decrease of pursuit gain was observed when a static target was cued, indicating anticipatory preparation of fixation in response to cue onset. Nonetheless, cuing effects were smaller than in the stabilized condition.

One might argue that perception of the cue was hampered because of motion smear in conditions with retinal motion. If this was true, saccadic latencies with relative motion should be increased relative to the stabilized conditions. However, responses were not delayed with relative motion.

The smaller effects when the cued object moved only 5° (long SOA) or 1.1° (short SOA) on the retina before target onset suggest a retinal basis of saccadic facilitation and IOR. Consistent with Abrams and Pratt (2000), these results confirm that facilitation and inhibition of saccades return are anchored in retinal coordinates. In contrast, IOR with manual responses was found to be environment- (Maylor & Hockey, 1985; Posner & Cohen, 1984) and object-based (e.g. S. P. Tipper et al., 1991). The idea of more than one mechanism underlying IOR may explain differences between manual and saccadic responses (e.g. Kingstone & Pratt, 1999). First, there is inhibition of saccadic responses to the cued location (i.e., a motor component), with a presumed neural substrate in the superior colliculus (Sapir, Soroker, Berger, & Henik, 1999; Sumner, Nachev, Vora, Husain, & Kennard, 2004). The superior colliculus is known to have a retinotopic organization (e.g., Cynader & Berman, 1972). Second, there is inhibition of attention shifts to the cued location, with a presumed cortical substrate (Sapir et al., 1999; Sumner et al., 2004). Cortical maps may either be space-based or retinotopic (e.g., Duhamel, Bremmer, BenHamed, & Graf, 1997). The two mechanisms do not necessarily share the same coordinate frame. For instance, patients with cortical lesions in the parietal lobe showed impaired environmental, but preserved retinotopic IOR (Sapir, Hayes, Henik, Danziger, & Rafal, 2004). Although IOR of similar size is

sometimes found with saccadic and key-press responses (Reuter-Lorenz, Jha, & Rosenquist, 1996), it appears that saccadic IOR depends more strongly on the motor component (Hunt & Kingstone, 2003; Kingstone & Pratt, 1999; Taylor & Klein, 2000). Thus, stronger IOR with stabilized stimuli in the present study may be a consequence of the prominence of the retinotopic motor component with saccadic responses.

How can retinotopic IOR with single saccades to cued locations be reconciled with studies indicating space-based IOR in “saccadic search” (Gilchrist & Harvey, 2000; Klein & MacInnes, 1999)? A possible reason is the need for space-based memory in saccadic search. In order to keep track of object locations and identities after multiple saccades, the retinotopic input has to be recoded in a space-invariant memory representation (see Pouget & Snyder, 2000). The need for such a map is much smaller in trials with single saccades that do not require any form of memory. Therefore, it may be that the discrepancy arises from different task demands.

Further, we found no significant facilitation effect when the cued object was moving during fixation. In contrast, previous studies in which object motion started simultaneous with cue presentation found significant facilitation (Abrams & Dobkin, 1994; Ro & Rafal, 1999). It may be that the simultaneous onsets induced attentional tracking of the cued object. In our study, object motion started well before cue presentation, and object motion was therefore seen as unrelated to cue presentation. Thus, the cue may have attracted attention to a particular location, and not to the moving object.

Our results point to the superior colliculus as the neural substrate of IOR with saccades (see also some early hypothesis by Posner & Cohen, 1984), but they are only suggestive. While it is true that the SC happens to code gaze shifts (eye + head) in retinal coordinates (Klier, Wang, & Crawford, 2001), retinotopic coding schemes are found at multiple levels in the visual pathways. For instance, structures upstream from the SC, like the FEF (e.g. Dassonville, Schlag, & Schlag-Rey, 1992; Schlag-Rey, Schlag, & Dassonville, 1992), code eye movements to a specific retinal location. Similarly, facilitation was found to be retinotopic and early visual cortical areas that encode space in a retinotopic reference frame (e.g., Gardner, Merriam, Movshon, & Heeger, 2008) were believed to underlie these effects (Posner & Cohen, 1984). Thus, retinotopy is very weak evidence for the involvement of the

superior colliculus. Clearly, more neurophysiologic data is needed to pinpoint the neural substrate of IOR.

## 5 Study 4: Evidence for an attentional component in saccadic IOR

### 5.1 Abstract

After presentation of a peripheral cue, facilitation at the cued location is followed by inhibition of return (IOR). It has been recently proposed that IOR may originate at different processing stages for manual and ocular responses, with manual IOR resulting from inhibited attentional orienting, and ocular IOR resulting from inhibited motor preparation. Contrary to this interpretation, we found an effect of target contrast on saccadic IOR. The effect of contrast decreased with increasing reaction times (RTs) for saccades, but not for manual key-press responses. This may have masked the effect of contrast on IOR with saccades in previous studies (Hunt and Kingstone, 2003b) because only mean RTs were considered. We also found that background luminance strongly influenced the effects of gap and target contrast on IOR.

### 5.2 Introduction

*Inhibition of return* (IOR) is the slowing of responses to targets appearing at a previously cued peripheral location. It occurs from 300 ms to several seconds after cue onset. Several alternative explanations of this effect have been proposed. They can be roughly parsed into attentional/perceptual and motor explanations (e.g. Posner and Cohen 1984). Among the possible mechanisms, the attentional momentum hypothesis states that attention overshoots the fixation point when it returns from the peripheral cue. As a result, there is attentional enhancement opposite to the cued location (e.g. Machado and Rafal 2004; Spalek and Hammad 2004). However, IOR cannot be unequivocally accounted for by an attention shift. For instance, it is difficult to find IOR with discrimination tasks (for a graphical meta-analysis see Figure 1 of Ivanoff and Klein 2006), and with perceptual measures of attention such as temporal order judgments (Maylor and Hockey 1985; but see Li and Lin 2002b) or illusory line motion (Schmidt 1996). IOR must therefore be more than the direct consequence of prior facilitation. It has also been shown to be more than the carry-over of an inhibitory set induced by the instruction to ignore the cue, as IOR is found even in target-target paradigms (see Welsh and Pratt 2006). In contrast, the mere

programming of a saccade (without a cue capturing attention) is enough to produce IOR (Rafal et al. 1989), which is the main behavioral evidence supporting the role of eye movement programming in the generation of IOR.

The motor bias account states that IOR arises from voluntary or reflexive programming of eye movements. Activation of a motor program, regardless of whether it is executed or cancelled, slows down subsequent motor actions directed towards the cued location (Taylor and Klein 1998; Taylor and Klein 2000). Accordingly, IOR is found with central as well as peripheral cues (Rafal et al. 1989; Taylor and Klein 2000). Additional support for a privileged role of the oculomotor system in the generation of IOR comes from the involvement of the superior colliculus in IOR (Sapir et al. 1999) and from the fact that IOR is stronger with saccades than with manual pointing responses (Fischer et al. 2003; Pratt and Neggers 2008). Further, some studies have employed the gap effect (i.e. the shortening of saccadic latencies when the fixation stimulus is removed some time before target onset) to test whether IOR affects the motor preparation stage. It is known that the gap effect has a motor component, and is independent of attentional facilitation (e.g. Reuter-Lorenz, Hughes & Fendrich, 1991). Following Sternberg's additive factors logic (Sternberg, 1969), interactive effects should be expected if both effects share a common stage. Indeed, IOR was found to interact with the gap effect (Abrams and Dobkin 1994; Hunt and Kingstone 2003b). However, there is no consensus on the nature of the interaction. Different studies reported contradictory results (Abrams and Dobkin 1994; Hunt and Kingstone 2003b).

On the other hand, many studies found evidence that attention contributes to IOR, indicating that it is the consequence of both motor and attentional biases (Kingstone and Pratt 1999; Taylor and Klein 2000; Sumner et al. 2004). For instance, reliable IOR was found in conditions that should not elicit a motor bias. When a symbolic and uninformative cue was presented and the response was a choice key-press to a peripheral target, IOR was observed (Taylor and Klein 2000), possibly because of the automatic attentional orienting by arrow cues (Tippl 2002). Another argument for an attentional component in IOR is provided by an effect of target luminance<sup>12</sup> on IOR (Reuter-Lorenz et al. 1996; Hunt and Kingstone 2003b). Because effects of attention on visual detection are larger with weak

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<sup>12</sup> To avoid ambiguities, we mostly refer to target luminance relative to background luminance (i.e., target contrast) instead of absolute luminance.

compared to strong signals (e.g. Hawkins et al. 1988), IOR should be stronger with low-contrast targets than with high-contrast targets, presumably because of a lack of attention on the cued side. A possible mechanism for effects of target contrast on IOR is depicted in Figure 5.1A. If the effect of attention was to increase the rate of accrual of evidence, benefits of attention on latency should be greater when the rate of accrual is low, as with low-contrast targets (Hawkins et al. 1988). Consistent with an attentional component, IOR was found to be larger with dim (low-contrast) than with bright (high-contrast) targets (Reuter-Lorenz et al. 1996; Hunt and Kingstone 2003b).

Further, the gap effect (on saccadic RT) is additive with the effect of luminance (Reuter-Lorenz et al. 1991; Kingstone and Klein 1993), suggesting that it does not result from attentional facilitation. Exploiting this property, Hunt and Kingstone (2003b) examined effects of gap and target contrast on IOR with saccadic and key-press responses. IOR was affected by the gap effect only when measured with saccadic responses, suggesting that the motor component of IOR affects movements specifically directed at the cued location. Because key-presses were executed on a keyboard and never directed at the cued location, the effect of gap on IOR was absent for key-presses. Importantly, IOR was affected by target contrast only with key-press responses, but not with saccades, suggesting that IOR in saccadic responses had no effect on the perceptual stage. This finding is surprising in light of the close relation between attention and saccade programming. It is well known that attention is needed at the target location for the generation of voluntary saccades (Deubel and Schneider 1996). Attention to non-target locations can curve saccadic trajectories (Sheliga et al. 1994; Sheliga et al. 1995), or delay saccadic latency (e.g. Shephard et al. 1986). Also, ample physiological evidence confirms the involvement of premotor structures in both attention shifts and eye movements (Ignashchenkova et al. 2004). Temporarily disrupting neuronal activity in one such interface between attention and eye movements, the frontal eye field (FEF), eliminated IOR with manual responses (Ro et al. 2003).

Our main concern was to reexamine the presence of perceptual and motor components in IOR with saccadic and key-press responses. We specifically looked at the effects of gap and target contrast on IOR, and the evolution of these effects across reaction time bins. To anticipate the results, the effect of luminance on IOR confirms an attentional component with saccadic responses, which is in line with a premotor conception of covert

attention. Our results show also a dependence of IOR on background luminance, an unexpected finding that may support differential contributions of the parvo- and magnocellular system in the generation of IOR.

## **Experiment 1: perceptual and motor components with saccadic and key-press responses**

### **5.3 Method**

#### **5.3.1 Subjects**

There were 22 participants in this study ( $M = 22$  years,  $SD = 4$  years). Eighteen students participated in partial fulfillment of class requirements. Four were experienced observers in psychophysical studies and all were naïve with respect to the purpose of the experiment. Experiments were done in compliance with the Helsinki Declaration of 1964 and the ethical regulations of the University of Geneva.

#### **5.3.2 Materials and Stimuli**

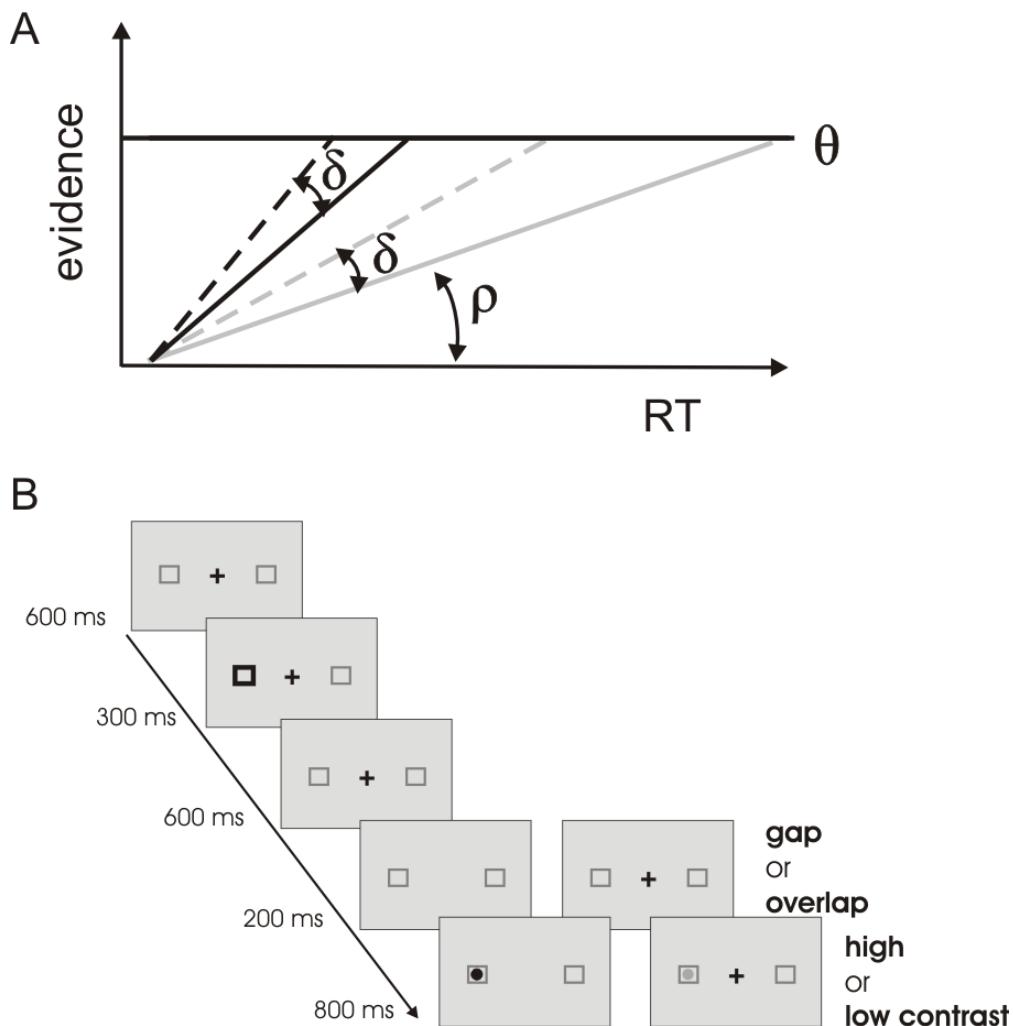
Head movements were constrained by a chinrest at a distance of 46 cm from a 100 Hz CRT monitor. Eye movements were monitored with a head-mounted eyetracker (Eyelink II, Ontario, Osgoode) set in pupil centroid mode, with a sampling frequency of 250 Hz. Calibration was achieved by fixation of three locations presented along a horizontal line. Only the horizontal eye position was sampled. The mean spatial error when retesting the same locations was less than half a degree.

Stimuli and trial time course are depicted in Figure 5.1B. In the first screen, two square placeholders ( $0.9 \times 0.9^\circ$ ,  $23.3 \text{ cd/m}^2$ ) were presented at  $6^\circ$  (center-to-center) from a fixation cross ( $0.2 \times 0.2^\circ$ ,  $0 \text{ cd/m}^2$ ) for 600 ms. The cue was a thickening (from  $0.04^\circ$  to  $0.3^\circ$ ) and dimming (from  $23.3 \text{ cd/m}^2$  to  $0 \text{ cd/m}^2$ ) of the box outline and was presented for 300 ms. After 600 ms, the fixation cross was removed for 200 ms in the *gap* condition, whereas it remained on the screen in the *overlap* condition. After this period the target was presented inside one of the two placeholders for 800 ms. The target ( $0.4^\circ \times 0.4^\circ$ ) was of *low-contrast* ( $27.4 \text{ cd/m}^2$ , Weber contrast of 7.1 %) or *high-contrast* ( $0 \text{ cd/m}^2$ , Weber contrast of 100%). The background luminance was light gray,  $29.5 \text{ cd/m}^2$ . Weber contrast is the difference between the stimulus and the background luminance divided by the background luminance.

The contrast of the dim and bright targets in Hunt and Kingstone (2003b) were 55% and 1453%, respectively. Their luminance values were 6.7, 10.4, and 104.1 cd/m<sup>2</sup> for background, dim, and bright targets, respectively. The decrease of reaction times with increasing stimulus contrast is much steeper for contrasts below 10% than it is for larger contrasts (e.g. Murray and Plainis, 2003). Therefore, we expect larger benefits of attention in our experiment, because we used a contrast of 7.1% for our low-contrast target.

### 5.3.3 Procedure

The two response modes were tested in two sessions on different days. The order of sessions was balanced across subjects. Gap, target contrast, cue side (left or right), and cue validity were randomized within a block. There were 40 repetitions for each combination of response mode, gap, target contrast, and validity, amounting to at least 320 trials per session. Error trials were repeated at a random position in the remainder of the block. Participants were instructed to foveate the target or to press a left or right key of a game pad as fast as they could without making anticipation errors. They were told that the cue did not predict the location of the target, and therefore should be ignored. Participants triggered the next trial by pressing the two lateral keys of the game pad simultaneously. Saccades had to be larger than 1° and to occur no sooner than 50 ms after target onset, and no later than 600 ms (that is, more than 3 SD above median latency). Manual responses had to occur within 100 to 700 ms after target onset ( $> M + 3 \text{ SD}$ ). A low percentage of saccadic responses was anticipatory (5 %), timed-out (0.5 %) or in the wrong direction (1 %); for manual responses, these proportions were 0.3 %, 1.2 % and 1.3 %, respectively.



**Figure 5.1 Experimental predictions and paradigm.** Panel A explains why the contrast manipulation is an indicator for the involvement of attention (see Reuter-Lorenz et al. 1991; Hawkins et al. 1988). This conceptualization is based upon a rise-to-threshold model of reaction times (akin to the LATER model, e.g. Carpenter and Williams 1995). Diagonal lines represent the accrual of information (“evidence”) after target onset. Once evidence has reached some threshold level  $\theta$ , the decision to move is made. This model can explain the way target contrast affects attentional benefits. The gray line with slope  $p$  represents the accrual of evidence for a low contrast target in the absence of any cue (baseline condition, solid gray line), and  $\delta$  represents the increase of this rate due to attention (attention condition, dotted gray line). Black lines represent the accrual of evidence with high-contrast targets. The threshold is reached faster in the baseline condition with high-contrast targets because of faster accrual with high- than with low-contrast targets (compare solid gray and solid black lines). Despite an identical increase of the accrual rate  $\delta$ , attention has a larger effect on reaction times with low-contrast targets than with high-contrast targets (compare the difference between solid and dotted lines for black and gray lines). Thus additive effects on slopes result in multiplicative effects on latencies. Panel B shows stimuli and time-course in Experiment 1. The fixation cross either disappeared 200 ms before target onset (gap) or remained visible throughout (overlap). The target was either black (high contrast) or gray (low contrast). A valid trial is depicted in which the target appears at the cued location 1.1 seconds after cue onset.

## 5.4 Results

We calculated median response times for each subject and combination of response mode, gap, target contrast, and validity. Absolute latencies and IOR (valid minus invalid) are shown in Table 4.1 and Figure 5.2, respectively. Inspection of Figure 5.2A shows that the most prominent effects are stronger IOR with saccadic compared to manual responses, and stronger IOR with low- compared to high-contrast targets. A four-way, repeated-measures ANOVA (response mode x gap x target contrast x validity) was run on median RTs. Note that IOR should result in faster RTs in invalid than valid trials. Unsurprisingly, saccadic responses were 120 ms faster than manual responses (212 vs. 334 ms),  $F(1,21)=149.7$ ,  $p<0.001$ . A 30 ms gap effect was found,  $F(1,21)=90.7$ ,  $p<0.001$ , that was greater with saccadic than manual reaction times (51 vs. 9 ms),  $F(1, 21) =53.6$ ,  $p<0.001$ . IOR was of 26 ms,  $F(1,21)=87.7$ ,  $p<0.001$ , and was also modulated by responses mode,  $F(1,21)=4.76$ ,  $p<0.05$ , indicating slightly stronger IOR with saccadic than with key-press responses (29 vs. 22 ms).

**Table 4.1 Mean reaction time (RT) and between-subject standard error of the mean in Experiments 1 and 2 in the format  $M \pm SE$ . Inhibition of return (IOR) is the difference between valid and invalid conditions.**

<b>Experiment 1 (N = 22)</b>						
	saccadic RT (ms)			manual RT (ms)		
	valid	invalid	IOR	valid	invalid	IOR
gap						
high contrast	178 $\pm$ 6	155 $\pm$ 6	23	319 $\pm$ 9	298 $\pm$ 8	21
low contrast	228 $\pm$ 10	187 $\pm$ 7	41	365 $\pm$ 10	336 $\pm$ 9	29
overlap						
high contrast	231 $\pm$ 8	207 $\pm$ 6	24	325 $\pm$ 10	312 $\pm$ 8	13
low contrast	274 $\pm$ 9	241 $\pm$ 8	33	372 $\pm$ 10	349 $\pm$ 9	23
<b>Experiment 2 (N = 18, saccadic responses)</b>						
	light background			dark background		
	valid	invalid	IOR	valid	invalid	IOR
step						
high contrast	212 $\pm$ 9	189 $\pm$ 8	23	203 $\pm$ 8	181 $\pm$ 5	22
low contrast	258 $\pm$ 10	211 $\pm$ 8	47	211 $\pm$ 8	192 $\pm$ 6	19
overlap						
high contrast	246 $\pm$ 12	204 $\pm$ 8	42	237 $\pm$ 12	206 $\pm$ 9	31
low contrast	305 $\pm$ 15	262 $\pm$ 11	43	276 $\pm$ 14	219 $\pm$ 9	57

There was no significant interaction between gap and validity,  $F<2.15$ ,  $p=0.16$ . Further, latencies were about 40 ms longer for low-contrast compared to high-contrast targets,  $F(1, 21)=148.5$ ,  $p<0.001$ , irrespective of response mode,  $F<1$ . The effect of target contrast is numerically larger than in Kingstone's (2003b) study. They reported a difference of 17 ms between dim and bright targets (calculated from their Table 4.1). Thus, our study accentuates effects of target contrast which may have increased our chances of finding interactions involving target contrast.

Importantly, the effect of validity was modulated by target contrast,  $F(1,21)= 17.1$ ,  $p <0.001$ , indicating greater IOR with low- compared to high-contrast targets (32 vs. 20 ms). This interaction was not modulated by response mode,  $F < 1$ .

Hunt and Kingstone's (2003b) most surprising result was the absence of a validity by target contrast interaction for saccadic responses. We ran separate ANOVAs (gap x target contrast x validity) for each response mode to follow-up on their results. The interaction between validity and target contrast was confirmed for saccades,  $F(1,21)=18.5$ ,  $p<0.001$ , and manual responses,  $F(1,21)=4.61$ ,  $p<0.05$ . IOR increased by 15 ms with low-contrast compared to high-contrast targets for saccades (37 vs. 23 ms) and by 7 ms for manual responses (25 vs. 18 ms). We also confirmed a significant gap effect for manual (9 ms),  $F(1,21)=27.4$ ,  $p<0.001$ , and saccadic responses (51 ms),  $F(1,21)=79.4$ ,  $p<0.001$ . A small but significant gap effect with manual responses is not without precedent (Bekkering et al. 1996).

#### **5.4.1 IOR as a function of responses time quantile**

The discrepancy between Hunt and Kingstone's (2003b) and our results may arise from two methodological differences. First, Hunt and Kingstone used means as a measure of the central tendency and we used medians. While means are frequently used, they will be strongly biased by long RTs when the distributions are skewed. Second, Hunt and Kingstone did not report any form of data trimming such that outlying data points may have contaminated the results.

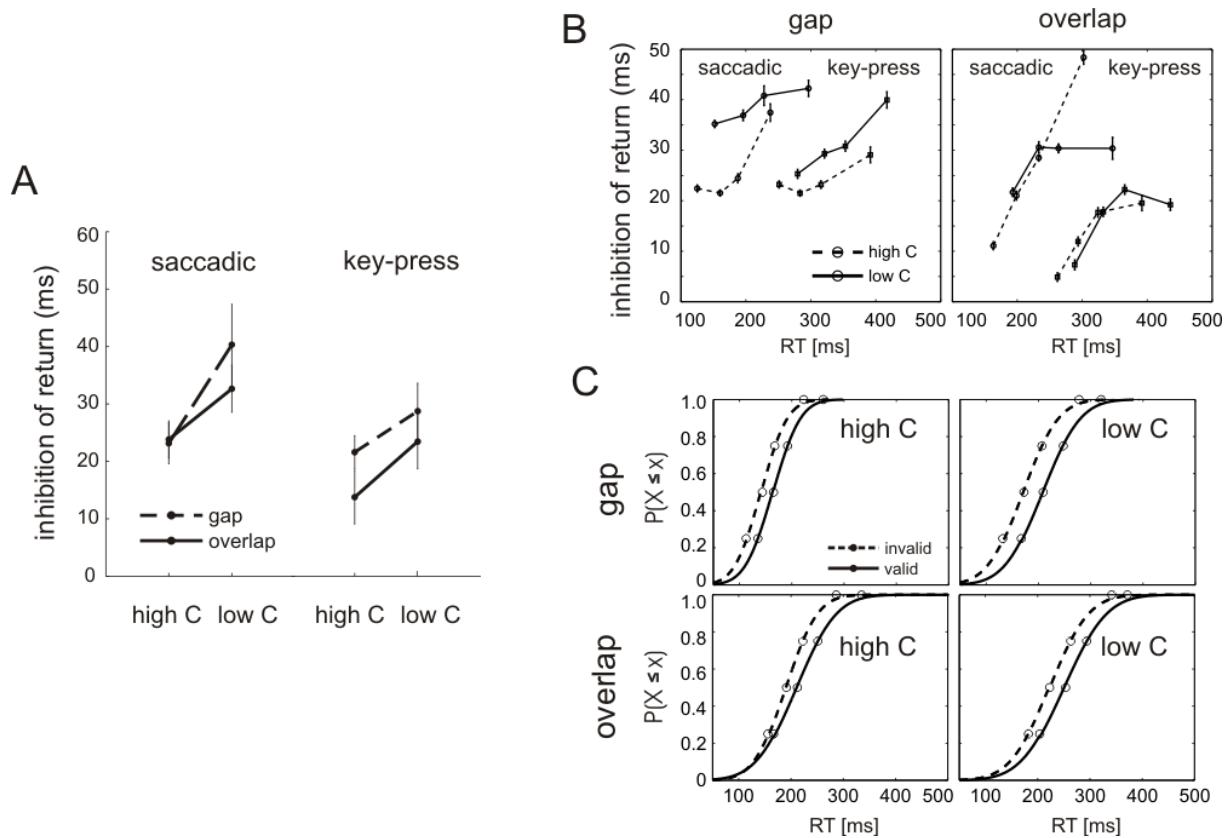
To look for effects of IOR as a function of RT (Ratcliff 1979), RTs were rank ordered separately for each participant and condition. Then, the observations were divided into four

quartiles, so that each quartile contained 25 % of the observations. IOR for each quartile is shown as a function of average quartile latency in Figure 5.2B. The pattern in Figure 5.2B may explain why the interaction between IOR and target contrast was missed when means were calculated. The difference between low- and high-contrast targets diminished with longer saccadic reaction times, and was even inverted in the overlap conditions, as indicated by nearly 20 ms greater IOR with high-contrast targets in the last quartile (*t*-test,  $p = 0.06$ ). In the gap condition, only the first three quartiles showed significantly larger saccadic IOR with low compared to high contrast ( $p < 0.02$ ). In the overlap condition, this was only the case in the first quartile ( $p < 0.05$ ). The tendency for effects of target contrast on IOR to diminish with longer reaction times is nearly absent with key-press responses (i.e., the shape of the distribution for high- and low-contrast targets is very similar), and thus the effect of target contrast on IOR may be harder to obfuscate by averaging. This might explain why Hunt and Kingstone (2003b) found an effect of luminance on IOR with manual responses, but not with saccades.

This relation is further illustrated in Figure 5.2C, by showing the ex-Gaussian<sup>13</sup> fits to the latency quartiles in valid and invalid trials for saccadic responses (IOR values in Figure 5.2B can be derived from the data points in Figure 5.2C). Shorter RTs are visible in a shift of the distribution to the left. It is evident that RT distributions in valid trials are shifted to the right compared to invalid trials (compare solid and broken lines). The lower left panel in Figure 5.2C shows the RT distributions underlying the sharp increase in IOR seen in the overlap condition with saccadic RTs and high-contrast targets (cf. Figure 5.2B, right panel). Put another way, the left shift for cued targets is not uniform across the RT distribution, but increases with increasing RT.

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<sup>13</sup> The SIMPLEX algorithm (MATLAB function *fminsearch*, with default parameters) was used to find the best fitting ex-Gaussian cumulative distribution that minimized the squared sum of the residuals. The ex-Gaussian distribution is widely used as it usually offers a good fit of reaction times data (Heathcote et al. 1991).



**Figure 5.2** Mean inhibition of return (IOR, valid RT minus invalid RT) as a function of response mode, gap, and target contrast (low C = low contrast, high C = high contrast) is shown in *panel A*. *Panel B* shows IOR as a function of quintile. For each quartile, IOR is computed and plotted against mean latency of invalid and valid RT. *Panel C* shows ex-Gaussian fits to the quartiles underlying *panel B*, but only saccadic responses are shown. Error bars represent the between-subject standard error of the mean.

## Experiment 2: effect of background luminance with saccadic responses

As we found effects contrary to those reported by Hunt and Kingstone (2003b) with saccadic responses, we replicated their display more closely. First, background luminance in their study was much darker than in our Experiment 1. Therefore, we added a condition with reduced background luminance. Second, we used a 0-ms gap/overlap paradigm as they did, instead of the 200-ms gap/overlap paradigm used in Experiment 1. In a previous study, the 200-ms gap led to somewhat larger IOR and shorter latencies than the 0-ms gap (Abrams and Dobkin 1994).

## 5.5 Method

### 5.5.1 Subjects

There were 18 observers ( $M = 24$  years,  $SD = 5$  years), 17 students naïve to the purpose of the experiment, and one experienced observer who already participated in the first experiment.

### 5.5.2 Stimuli and Procedure

Methods were the same as in the first experiment, except for the following. Instead of a 200-ms gap, a 0-ms gap was used, which will be referred to as "step". We added two background luminance conditions as a blocked variable. Only saccadic responses were tested. Background luminance was light gray ( $29.5 \text{ cd/m}^2$ ) as in our first experiment, or dark ( $6.8 \text{ cd/m}^2$ ), which is about the same as in Hunt and Kingstone's (2003b) study ( $6.7 \text{ cd/m}^2$ ). The targets in the light background condition were the same as in Experiment 1. The dim and bright targets in the dark background condition had a luminance of  $10.3$  and  $58.8 \text{ cd/m}^2$ , resulting in Weber contrasts of 51% and 764%, respectively. The low-contrast target had a higher contrast in the dark background condition than in the light background condition (51% vs. 7.1% Weber contrast), but matched the contrast value of 55% in Hunt and Kingstone (2003b). In the dark background condition, the placeholders, cue, and fixation target were white ( $58.8 \text{ cd/m}^2$ ). In both background luminance conditions, the cue was a thickening of the placeholder outline, not a dimming *and* thickening as in Experiment 1. With the exception of background luminance, all experimental factors (gap, target contrast, cue side, and cue validity) were randomized within a block. These differences are sketched in the insets of Figure 5.3. There were 20 trials per condition (2 background luminance  $\times$  2 gap  $\times$  2 target contrast  $\times$  2 validity). The RT distribution (i.e. quartiles) was not analyzed because of the lower number of trials per condition.

## 5.6 Results

Results of the second experiment are summarized in Figure 5.3. Absolute latencies are shown in Table 4.1. As in the first experiment, a large effect of target contrast on IOR was confirmed for light and dark background conditions. However, there was an interaction between validity, gap, and background luminance that complicates the picture. With the light background, the effect of target contrast on IOR was much larger in the step than in the

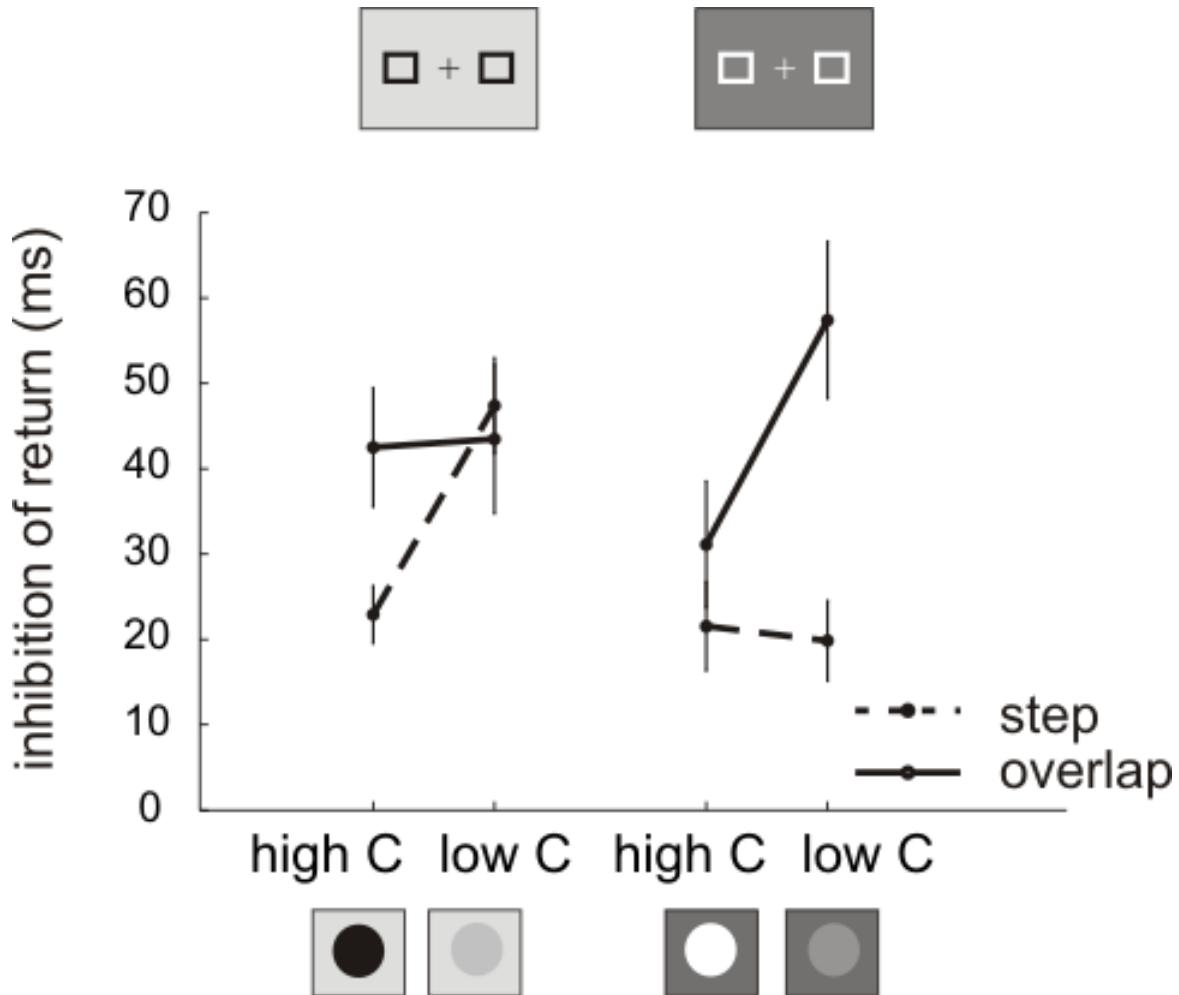
overlap condition. A similar tendency can be seen in Experiment 1, where the effect of contrast was larger in the gap than in the overlap condition. With a dark background, the difference between step and overlap was reversed. The effect of target contrast on IOR was much larger in the overlap than in the step condition. This triple interaction can also be described as an interaction of gap and validity that is specific to dark targets: Inspection of Figure 5.3 shows that the difference between step and overlap is largest for dark targets (leftmost and rightmost data points).

A four-way repeated measures ANOVA (background x gap x target contrast x validity) was run on median saccadic latencies. There was a gap effect of 37 ms (244 vs. 207 ms),  $F(1,17)=68.14$ ,  $p<0.001$ , and an effect of target contrast of 32 ms (242 vs. 210 ms),  $F(1,17)=137.5$ ,  $p<0.001$ . Gap and target contrast interacted,  $F(1,17)=16.93$ ,  $p<0.001$ , indicating that the gap effect was larger with low-contrast targets than with high-contrast targets (48 vs. 27 ms). Following the logic illustrated in Figure 5.1A, the interaction with target contrast suggests that attention is involved in the gap effect. In contrast, no interaction of gap and target contrast was observed in Experiment 1. Possibly, the different gap durations (200 vs. 0 ms) explain the discrepancy (see Discussion). Further, latencies were 20 ms shorter with the dark than the light background (216 vs. 236),  $F(1,17)=5.3$ ,  $p<0.05$ .

Background luminance and target contrast interacted significantly,  $F(1,17)=45.3$ ,  $p<0.001$ , indicating that the slowing of RTs with low- compared to high-contrast targets was stronger on the light background (261 vs. 212 ms) than on the dark background (213 vs. 193 ms),  $t(17)=6.34$ ,  $p<0.001$ . The latter difference of 20 ms is similar to the 17-ms effect of target contrast reported by Hunt and Kingstone (2003b) which confirms that we closely replicated their stimulus display.

The IOR effect was of 36 ms,  $F(1,17) = 87.8$ ,  $p<0.001$ . Importantly, IOR was modulated by contrast,  $F(1, 17)=18$ ,  $p=0.001$ , indicating larger IOR with low-contrast compared to high-contrast targets (43 vs. 30 ms). IOR was also considerably modulated by gap,  $F(1,17)=16.9$ ,  $p=0.001$ , indicating less IOR with the step compared to the overlap condition (28 vs. 43 ms). Finally, there was also a significant four-way interaction,  $F(4,68)=3.6$ ,  $p<0.02$ . To explore this interaction further, t-tests (Bonferroni correction applied) were run. With the light background, IOR was greater when target contrast was low

than when it was high, but only significantly so in the step condition (47 vs. 23 ms),  $t(17)=3.4$ ,  $p<0.05$ , and not in the overlap condition (43 vs. 42 ms). On the dark background, IOR was significantly greater with low than high contrast in the overlap condition (57 vs. 31 ms),  $t(17)=4.3$ ,  $p<0.001$ , but not in the step condition (22 vs. 19 ms).



**Figure 5.3** Mean inhibition of return (valid RT minus invalid RT) as a function of target contrast, gap and background luminance. Error-bars represent the between-subject standard error of the mean.

## 5.7 Discussion

We tested the effect of variables thought to tap the perceptual/attentional or motor stages on IOR. Contrary to a previous report (Hunt and Kingstone 2003b), we have found only little differences between ocular and manual responses. The following results will be discussed in turn:

1. Target contrast affected IOR with manual *and* saccadic responses.
2. The difference in IOR between low- and high-contrast targets decreased with increasing RT for saccades, but not manual responses (Figure 5.2B), suggesting that the measure of central tendency and the range of allowable RTs are important parameters in the data analysis.
3. We found no effect of gap on IOR with saccadic responses in the first experiment, but did so in the second experiment.
4. Significant modulation of the gap effect by target contrast with the 0-ms gap (Exp. 2) but not with the 200-ms gap (Exp. 1) suggests an additional attentional component in the former condition.
5. Effects of gap and target contrast on IOR depended on background luminance.

### 5.7.1 Effect of target contrast

Many studies have suggested that saccadic IOR may be different from manual IOR. For instance, IOR was shown to affect locations in an environmental reference frame for key-press responses (Posner and Cohen 1984; Maylor and Hockey 1985), but in a retinotopic reference frame for oculomotor responses (Abrams and Pratt 2000; Souto and Kerzel 2008b). Also, IOR with key-press but not with saccadic responses was observed for stimuli that do not reach the SC, such as isoluminant blue stimuli (Smith et al. 2004; Sumner et al. 2004). However, dissociation of oculomotor and manual IOR with respect to the attentional component seems implausible, because selective attention and the programming of eye movements are tightly coupled. We confirmed this coupling by showing that IOR was stronger for low-contrast targets that benefit more from signal enhancement than high-contrast targets. Further, the existence of a perceptual component in saccadic IOR was corroborated by a study reporting an IOR effect on temporal order judgments (Li and Lin

2002). The decreasing effect of target contrast on IOR with increasing saccadic reaction times may explain why target contrast was not found to interact with saccadic IOR in the study of Hunt and Kingstone (2003b). Alternatively, it may be that Hunt and Kingstone's contrast values resulted in a difference between dim and bright targets that was too small to produce significant interactions. Remember that their dim, low-contrast target had a (rather high) contrast of 55% whereas our low-contrast target with the bright background had less than 10% contrast. However, we replicated the interaction of contrast and IOR in the second experiment with a similar range of contrasts as in their study.

We also expected IOR to be greater with saccades than with key-press responses, as saccadic programming is more strongly coupled to attention than manual responses in general, and because saccades are more specifically directed at the cued location than key-presses. Indeed, we found significantly larger IOR with saccades compared to key-press responses, but this effect has not always been replicated (Reuter-Lorenz et al. 1996; but see Briand et al. 2000; Li and Lin 2002a; Pratt and Neggers 2008).

### 5.7.2 Gap effect

The modulation of IOR by gap with choice key-press responses is surprising at first sight, as key-press responses were not directed at the cued location, and therefore should not be sensitive to the motor bias component. However, it has been shown that IOR can under some circumstances affect responses that do not target the cued location. In one study, subjects were asked to press a key in response to a centrally presented arrow. Responses were slower when the direction of the arrow corresponded to a formerly fixated location (Taylor and Klein, 2000). It is unlikely that attention caused a deficit in the perception of one arrow direction or another. Rather, the previous saccade may have produced directional inhibition at the motor level.

Consistent with previous research (Kingstone and Klein 1993b; Reuter-Lorenz et al, 1991), Experiment 1 showed that the gap effect does not interact with target contrast, suggesting that the gap effect does not involve attention. On the other hand, there was an interaction between gap effect and target contrast in Experiment 2, which fails to replicate Hunt and Kingstone's (2003b) results.

If the gap were to facilitate attention to the target, the gap effect is expected to be larger with dim than with high-contrast targets (the same rationale as for the effects of

target contrast on IOR applies). Reuter-Lorenz et al. (1991) found no interaction of target luminance with the gap effect when using a 200-ms gap (replicated in our Experiment 1). The gap effect was also not modulated by requiring attention shifts to the periphery (Kingstone and Klein 2003b), which provides further evidence against the involvement of attention in the gap effect. However, a significant interaction between gap and target contrast was found when we used a step (0-ms gap, Experiment 2) instead of a 200-ms gap (Experiment 1). The motor-preparation account of the gap-effect states that there is advance preparation of the motor parameters when the fixation point disappears 200 ms before target onset (e.g. Rolfs and Vitu, 2007). This does not hold for the step condition, because the target appears at fixation offset and no advance preparation is possible. Therefore, it does not seem implausible that the processes underlying the 200-ms gap effect are not identical to the processes underlying the 0-ms gap effect. These differences may explain why there was an interaction between gap and target contrast with a 0-ms gap, but not with a 200-ms gap. Finally, the strict independence of the gap effect from attention is not uncontested. Pratt, Lajonchere, and Abrams (2006) have demonstrated that attention to the remaining or to the vanishing part of a cross can modulate the gap effect. Clearly, further research on the effect of gap duration and its interaction with target contrast is needed.

Further, there was an effect of gap on IOR with saccadic responses in Experiment 2 which is predicted by a motor bias account of IOR. However, it was not significant in Experiment 1. Previous studies show some inconsistencies with respect to this effect. Hunt and Kingstone (2003b) found larger IOR in the overlap compared to the gap condition which we replicated in both background conditions of Experiment 2, but not in Experiment 1. Abrams and Dobkin (1994) found the opposite relation, larger IOR with the gap, consistent with the tendency that we observed in Experiment 1. A difficulty in deciding which result may be more trustworthy is that no *a priori* prediction was formulated. Further, no significant effect of gap on IOR was found in our first experiment, even though statistical power was slightly higher than in Experiment 2 ( $N=22$  vs.  $N=18$ ), suggesting again different underlying processes in the 200-ms and the 0-ms gap. Alternatively, the absence of an effect with a true gap (200-ms gap) on IOR may also indicate that the ocular component of IOR is not as important as previously thought (see Fecteau and Munoz 2006).

In previous studies, the interaction of gap and IOR was taken as evidence for a motor component in IOR. This reasoning rests on the assumption that the gap effect has a purely

motor origin. The interaction of gap and target luminance in Experiment 2 casts doubts on this assumption, because it suggests that attention was involved in the gap effect, at least with the 0-ms gap. Because the presence of an interaction between gap and IOR in Experiment 2 goes with an attentional component in the gap effect, while the absence of an interaction between gap and IOR in Experiment 1 goes with the absence of an attentional component in the gap effect, we are reluctant to conclude that our experiments provide evidence for a motor component in IOR. When there was an effect of gap on IOR, the gap effect also reflected attentional components.

### 5.7.3 Effects of background luminance

A rather surprising result in Experiment 2 was that background luminance affected IOR. We rather expected very similar results on light and dark backgrounds. Contrary to our expectation, the effect of gap and target contrast on IOR changed as a function of background luminance. One may think that contrast polarity also plays a role in this interaction, as the polarity of our targets was opposite on light and dark backgrounds. On the light background, targets were darker than the background, whereas targets were lighter on the dark background (see Figure 5.3). To our knowledge, response asymmetries between the ON and OFF pathway (see Chichilnisky and Kalmar, 2002), which contribute respectively to the detection of increments and decrements of light, do not provide grounds to expect an effect of target polarity on IOR. Further, Posner and Cohen (1984) reported no difference in IOR when the cues consisted of a dimming or a brightening. There is a well documented advantage of light decrements over increments in reaction times, but it is confined to situations where background luminance levels are below those reported here (Cao et al. 2007). Therefore, it seems more plausible to look for explanations in terms of effects of mean luminance, although an independent variation of background luminance and polarity should be run to confirm this later point. The recent dissociation between magnocellular and parvocellular pathways in IOR (Sumner et al. 2004) may shed some light on the effect of background luminance. There is evidence showing that the contrast response of parvo (P) cells is weaker with low background luminance than the contrast response of magno (M) cells. It is also known that the intermediate layers of the superior colliculus (SC) receive their main input from the M-pathway (Schiller and Malpeli 1977; Schiller et al. 1979). Sumner et al. (2004) have recently used this property to unveil attentional components of IOR by using

isoluminant stimuli (optimal for S-cones) to which the M-pathway, and hence the SC, is blind. As measured in the lateral geniculate nucleus (LGN), the M-cell contrast response is higher and saturates at much lower background luminance levels than P-cells (Purpura et al. 1988). Thus, low luminance backgrounds promote the influence of the M-pathway, by silencing the P-pathway (to some extent), and thus may engage oculomotor structures like the SC and FEF more strongly than high luminance backgrounds. Even if the light and dark background luminance used here cannot fully dissociate the two contributions, they may strongly modulate their respective weights. Neurophysiological studies have shown that a decrease of activity of fixation cells of the rostral SC correlates with the gap effect (Dorris and Munoz, 1995). As for IOR with manual responses, it has recently been shown that the gap effect occurs also for stimuli that bypass the M-pathway (2006), suggesting parallel contributions of M- and P-pathways to the effect. Altogether, this indicates that the use of a dark background may favor the expression of the oculomotor components in gap and IOR effects. However, the effects of gap on IOR are not stronger on a dark background. Further research is clearly needed to tease apart effects of background luminance from effects of target contrast or contrast polarity.

More practically, the finding that background luminance generates partly unpredictable differences in IOR raises some concerns about the replicability of effects associated with IOR. Looking at some of the studies relevant to the questions tackled in this paper, we noticed that the background luminance varies greatly. The background luminance was on most occasions not reported (e.g. Abrams and Dobkin 1994; Gibson and Egeth 1994; Danziger and Kingstone 1999; Kingstone and Pratt 1999; Ro et al. 2000; Ro et al. 2003; Ivanoff and Klein 2006), even when details about the luminance of the stimuli were reported (e.g. Li and Lin 2002b). Values of  $0.15\text{ cd/m}^2$  (Chelazzi et al. 1995; Berlucchi et al. 2000), possibly about the same as with a “black background” (Taylor and Klein 2000; Godijn and Theeuwes 2002), were also reported. A minority of studies used a light gray background, of  $25\text{ cd/m}^2$  (Sumner et al. 2004; Sumner et al. 2006) similar to the one in our own experiments ( $29.5\text{ cd/m}^2$ ). The use of a gray background, approaching normal daylight conditions, seems preferable in further experiments. At least, background luminance should be reported for the sake of comparability between studies.

#### 5.7.4 Conclusion

Our finding that IOR measured with saccadic responses is affected by target contrast is in agreement with a large amount of evidence indicating that programming of saccades and spatial attention are closely coupled. Unexpectedly, we have found that relatively small variations in background luminance radically change the way gap and target contrast affect IOR. The differences possibly arise from the different contributions of the magnocellular and parvocellular pathways in the generation of IOR. We also fail to provide evidence for a motor component in saccadic IOR, which is consistent with recent proposals that IOR is mainly due to sensory/perceptual process.

## 6 Conclusions

Our objectives were to explore how attention relates to voluntary eye movements. In particular we wanted to know how results that are well established for saccades generalize to the initiation and maintenance of smooth pursuit eye movements. The results of the four studies that were presented are discussed in turn.

### 6.1 Attention for smooth pursuit initiation

Shifting attention to locations far away from the upcoming saccade target is known to delay saccade latencies. In contrast, we found that attention shifts cause a small interference on smooth pursuit onset. This was not due to the weakness of attention shifts, as we found a large delay in catch-up saccades, as well as an important reduction of pursuit velocity near closed-loop phase initiation (some 100 ms after movement onset).

Effects were different if attention was paid to placeholders that stayed on the screen or moved with the pursuit target. When the placeholders moved with the target, no reduction in pursuit gain was observed, but a delay of catch-up saccades. When the placeholders stayed on the screen, a delay of catch-up saccades latency happened and a reduction of pursuit gain, observed in velocity traces with no saccades, but could be observed when catch-up saccades were included in the analysis (data not shown in the paper).

From the latter findings it can be concluded that pursuit initiation does not require that attention is narrowly focused on the target, unlike saccades, which fits well with the ability to pursue targets defined by extra-foveal cues (Ilg and Thier 1999). Further, only allocation of resources to stationary objects seems to impair pursuit initiation, but only at a later stage of initiation, when the steady-state phase of pursuit begins.

The absence of interference between peripheral attention shifts and pursuit initiation does not necessarily mean that no attention is required for pursuit onset. The results can be well accommodated by supposing pursuit initiation requires much less attentional resources than saccades, or catch-up saccades in this case. The effect of orienting attention to the periphery is to remove some resources from fixation. If we are still fixating, it can mean that

some resources kept there. Certainly the amount of attentional resources that are on the fixated location cannot be neglected. At least, we have to acknowledge that we have no estimation of this amount. This is rather different than to say that no attention precedes pursuit onset, or that it is pre-attentive. This issue may be clarified with different paradigms, in which the difficulty of the peripheral perceptive task is varied, in order to reduce resources at fixation. Nonetheless, the pre-attentive nature of pursuit onset fits well with the results of Erkelens (2006) and the non-selectivity of pursuit initiation (e.g. Lisberger and Ferrera 1997).

Further, we did not show vertical deviations in pursuit initiation that could indicate inhibition of the locations that were attended before the eye movement onset – in either the first or second study, which was not reported. Those kind of effects were found by Spering et al. (2006a). There was a deviation of pursuit away from the stimuli that had to be ignored. One possible reason for these discrepant results is that a spatial overlap between distractor and target may be necessary to find this effect. This effect was thought to reflect inhibition of the distractor. A model of attention selection that supposes an inhibitory surround (the “Mexican hat”) of the attention focus can accommodate these results. While several distant objects may be selected without interference, when they are close together the inhibitory surrounds interfere with each other when they are close together (as suggested in Carlson et al. 2007). When the distractor is far from the target there may be no need to inhibit its influence for pursuit initiation. Sheliga et al. (1995) found that paying attention to a peripheral location deviated upcoming saccade trajectories opposite to the attentional bias. The reason given was that saccades were prepared in the direction of the previous attention locus, which is less likely to be the case for pursuit, as position is much less an input for the pursuit system. Thus, proximity (or overlap in Spering et al. 2006) of the attended distractor with the pursuit target seems a necessary condition to find significant deviations away from the distractor during pursuit initiation and maintenance.

## **6.2 Shared target selection for perception and for pursuit eye movements**

In the second study, we tested the possibility that target choice for pursuit could be different from what is selected from the “mind’s eye”. That the selection filter used for

perception is the same that the one that is used for selection of the next saccade has been shown with saccade programming (Kowler et al. 1995; Deubel and Schneider 1996) and with maintained pursuit (Khurana and Kowler 1987). As our first study suggested that attention may be accessory during smooth pursuit initiation, it is relevant to ask if that is the case for pursuit initiation.

Past research showed that pursuit is very unselective when presented with two possible targets. When they move 180° apart, some bias has to be applied in order to follow a designated target. Ferrera and Lisberger (1995) proposed that it is the role of attention to bias the competition between motion of the target and of the distractor. It could be that the amount of resources that are needed to start pursuit matters less than the fact that there is some bias in favor of the target. We should then see that improvements of perception are possible without a corresponding lengthening of pursuit latencies, indicating that only a bias is needed. We rather showed that the amount of attention paid to the distractor translated in a delay of pursuit latency or in the amount of wrong direction choices, indicating that the competition could be reduced or enhanced by the instructions to prioritize the distractor or the pursuit target.

Similarly, Kowler et al. (1994) found that saccades needed only some share of available attentional resources, as large improvements in perceptual performance could go unnoticed on saccadic precision and latency performance. In contrast, pursuit choices seem to be a trustworthy indicator of the target that is being selected for perception.

We also show that a high perceptual performance is impossible while starting pursuit with a normal latency, even after intensive training, marking a limit to the dissociation of attention from eye movement programming. At least when there is no bottom-up bias, the competition cannot be resolved by other means than allocating more attention to the target.

Further, unlike what the results with monkeys suggest, human subjects are able to filter-out the influence of moving distractors when initiating pursuit, as shown by pursuit latencies similar with and without distractor in the conditions when the target was properly attended.

### 6.3 Cuing effects in oculocentric coordinates

In the third study, we compared the size of cuing effects during fixation and pursuit, under conditions of retinal motion or with cued objects moving with the pursuit target. The results suggested that involuntary cuing effects provoke enhanced and later on inhibited processing at the retinal location, because they are only found when cued objects go with the target or are immobile (the classic paradigm). A similar enhancement with retinal motion of the cued objects was expected if the object or the location in space was primed by the cue.

These results can be a bit puzzling if we consider the important task of keeping track of objects location across eye movements (implemented by spatial remapping of neurons' receptive fields in area LIP, for instance, Duhamel et al. 1992). Shouldn't we expect objects or spatial locations in world-coordinates to be enhanced, rather than retinal locations? A first guess is that the result lies in the involuntary nature of the task. Involuntary cuing effects may be due to exogenous activation of the SC saccadic map, which retinotopic organization is well known, and which activity may enhance perceptual as well as saccade preparation (Muller et al. 2005). Object- and location-based cuing effects may be expected when attention is voluntarily engaged, permitting trans-saccadic stability (see Melcher 2008a; Melcher 2008b).

A recent study published almost at the same time by Golomb et al. (2008) entitled "The native coordinate system of spatial attention is retinotopic" provides another piece of answer. They studied the maintenance of attentional facilitation across saccades. An interesting finding was that the facilitation at the same retinal location as the cue depended on how much time passed after the saccade. Right after the saccade there is a facilitation for targets appearing in the same retinal location over targets appearing in the same spatial location (the same place as the cue, but a different retinal coordinate after a saccade). After some time this effect inverts, the spatial location becomes more facilitated. Even when the task promotes spatial facilitation, they find a larger retinotopic effect.

It was proposed that facilitation in retinotopic coordinates is observed first because it takes time to "remap" the salience map (representing the distribution of attentional resources in space) to spatial coordinates after a saccade (unlike the rapid visual remapping

that takes place in the parietal cortex). The visual cortex being primarily retinotopic, it is the first available frame of reference.

This latter interpretation point suggests an interesting follow-up to our experiments. Because the remapping of the salience map in spatial coordinates takes time, we may observe the same cuing effects in every condition if the pursuit stops before the saccade target appears; which could reconcile our results with those of studies showing object-based cuing effects when cued objects move in-between the cue and target onset events.

Further, that we found no significant reduction in cuing effects during pursuit compared to fixation indicates that the influence of irrelevant, exogenous events is maintained during pursuit. However it can still be said that the cues were not completely task irrelevant, as they carried information about the time at which a saccade will be required, only their location was truly task-irrelevant. Would it be the same if, for instance, there were red cues having no time and no location information and black cues carrying timing but no location information? Would the influence of the red cues be the same as during fixation?

Finally, when there is relative motion of the fixation target and the peripheral objects, we interpret smaller cuing effects during fixation compared to pursuit as evidence for effects in retinotopic coordinates. This is an economic explanation. It can also be that during pursuit smaller cuing effects reflect the suppression of attention shifts to a direction opposite to the pursuit direction (an interpretation suggested by the first study). However, can we explain the reduced cuing effects when we fixate and peripheral objects move? It is not explained by the de-blurring advantage of pursuit<sup>14</sup> because latencies should be longer than during fixation with stationary cued objects. We reasoned that if the spatial cue is less effective in biasing attention, it should also be a less effective temporal cue. In addition, the results of Golomb et al. (2008), obtained in a very different setting, support our interpretation that the spatial coordinates of the effect explains the pattern of results.

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<sup>14</sup>Moving objects during fixation are more blurred than stationary objects moving at the same retinal speeds during pursuit or vergence (Bedell et al. 2004)

## 6.4 Failure to replicate independence

In the fourth study, we attempted to replicate the study of Hunt and Kingstone (2003b). Their study held the controversial view that attention has no special role in eye movements programming. Evidence was rather indirect, and supposes that attention orienting leads to cuing effects that are larger for low-contrast than for high-contrast targets. Therefore, if target contrast affects inhibition of return, there is evidence that an attentional component is involved inhibition of return, following Sternberg's additive factors logic. We have shown that their study may not have provided enough guarantees to accept a negative result as evidence of its absence. The main argument was that there was no effect of target contrast on inhibition of return when saccadic reaction times were measured but were present with manual reaction times. However, our analysis of the reaction times distributions revealed a clear effect of target contrast on IOR with saccades and manual reaction times, which is consistent with the important role of attention in saccade programming. The following interpretation is favored: in IOR, attention is oriented in the direction opposite to the cued side, causing larger benefits when probed with low-contrast targets.

The finding that background luminance makes a big difference on the effects that were found, needs to be explored further. Only tentative explanations could be offered. There are still many competing, but not incompatible, conceptions of IOR: it is sometimes conceived as resulting from a motor, attentional, or even sensory bias. In this context it would be of value to know if background luminance, usually not even reported, can explain some of the discrepancies that are found in the literature. As we suggested, it is possible that low background luminance may promote the magnocellular pathway, and thus entail different mechanisms than those that come into play under normal luminance conditions. This prediction can be tested and could complement results that show an IOR effect with stimuli which processing supposedly bypasses oculomotor areas.

## 6.5 Synthesis

*“Psychologists treat other people’s theories like toothbrushes – no self-respecting person wants to use anyone else’s”<sup>15</sup>*

It was shown in the Study 1, 2 and 3 that pursuit depends on different amounts of attentional resources at different moments. In our experiments, pursuit was tested in uncluttered environments, which may be far from the multitude of visual information available in everyday tasks, like when crossing the street and as such they only can be an estimate of minimal requirements. It cannot be said that pursuit always provides an overt readout of allocation of perceptual resources (Khurana and Kowler 1987). We have shown that it is likely to be the case during pursuit initiation. We also have shown that when presented with a choice, ocular decisions cannot be dissociated from perceptual decisions, even after training for many hours with the same instruction, with feedback about the ocular performance. I will briefly discuss a framework within which those results can make sense, in line with the recent view that the selection of targets for pursuit and for saccades can be coordinated in the superior colliculus.

First, we can suppose that saccades are triggered according to some saccade map, representing the readiness to execute a saccade at any location of the visual field (Godijn and Theeuwes 2003b). Activity within this map is raised according to a multitude of sources (bottom-up or top-down sources are integrated together). The coupling of attention and eye movements can be modeled by supposing that there is a direct connection between the saccade map and the salience of the neural representation of those locations in extrastriate visual areas (Hamker 2003; Schneider, 1995).

Second, there is a bidirectional relation between a salience map (or priority map) and preparation of the eye movements, meaning that motor preparation is facilitated by attention to a given location and that motor preparation itself raises activity on the priority map (e.g. Müller et al. 2005). Although we have seen that covert attention does not always deviate motor programs (Juan et al. 2004), this does not mean that attention does not raise the state of motor preparation at that location.

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<sup>15</sup> Walter Mischel cited by Gigerenzer (2009)

Third, we suppose that the same saccade map controls selection of the pursuit target, which is the main factor in the coordination of pursuit and saccade choices (together with the gate formed by the omnipause neurons downstream).

Why are saccades delayed by attention away from the saccade target, but not pursuit? It can be that the level of activity on the saccade map that is required for saccades is higher than what is required to initiate pursuit (Krauzlis and Dill 2002). Distracting information may delay the saccade because attentional resources to the distractor location compete with the high amount of attentional resources required at the saccade goal to reach some threshold value (as reaching some state of motor preparation is equivalent to raising the perceptual priority of the target). As we showed, pursuit can start with fewer resources, which may interfere less with allocation of attention elsewhere.

Further, we do not have to suppose that attention must be narrow or large around the saccade, only some activation at the saccade map is necessary. A plausible mechanism is that some activity above activity at non-target locations is required, and not an absolute threshold (see Krauzlis 2005). Winner-take-all or averaging will consequently depend on the suppression of distractors activity by progressive allocation of attention.

Target selection for pursuit and saccades can involve the same selection process. The low selectivity of pursuit reflects that it is initiated without the requirement that a majority of resources are allocated to the target. As we have shown, averaging of motion signals is not a mandatory behavior during pursuit initiation. It can be overridden if target priority is raised by a top-down signal. Within this framework selectivity of saccades and of pursuit should show similar trade-offs of precision with speed. For instance, for a similar latency range, we should see similar influences of the distractors on pursuit direction and saccade endpoint averaging. A more counter-intuitive prediction is that there should be a similar dependence with the distance of the distractor, as the two responses may depend on a similar “saccade map”. This latter point is well suited for an experimental test.

On the other hand, maintained pursuit does not seem to depend on a location signal, as suggested by the fact that even during maintained pursuit, attention can be allocated to the periphery at little cost when the movement of the attended object is in synergy with the movement. Therefore, pursuit maintenance may not depend in the same way as saccades on

narrow attention on the target, and could be considered separately from the initial target choice.

Finally, the same mechanisms can hold for involuntary and voluntary eye movements, as suggested in the first study (Godijn and Theeuwes 2003b). The saccade is executed when activity reaches some threshold, no matter whether it comes from bottom-up or top-down signals.

In summary, this framework is parsimonious, because it proposes similar selection mechanisms for the generation of pursuit and saccades, and contains a few testable assumptions.

## 6.6 Challenges for future research

We have reviewed research spanning over the past 30 years. There are certainly questions left for the next 30 years. I will point to some possible paths that may increase our understanding of how we control eye movements.

It was shown that many studies have tested the validity of the pre-motor theory. Although there is some convergence on certain issues, some other need further clarification. One aspect of the premotor theory that has not received close inspection is that attention shows some constraints that are believed to be specific to the oculomotor system. For instance, no exogenous cuing effects were found with targets appearing at locations that could not be reached by a saccade (Craighero et al. 2004). Another example is the meridian effect: supplementary costs in reorienting attention are attributed to the costs of reprogramming the eye movement (Rizzolatti 1987; Craighero et al. 2004). Recently it was reasoned that diminished effects of interference when attentively tracking motion of two objects across the horizontal meridian could be due to the anatomical organization of the visual cortex. Indeed, the part of V2 that represents the upper visual field is detached from the part of V2 that represents the lower visual field (Carlson et al. 2007). While this was not related to the meridian effects observed in the context of saccadic latencies (maybe because they found the task was easier when objects crossed the meridian), it offers a very different alternative explanation to the costs associated with crossing the horizontal meridian observed by Rizzolatti.

Recently, Findlay and Blythe (2008; Findlay 2009) have pointed out that the influence of distractors over saccades suggest a higher resolution for target selection than what is expected from estimates of the ability to individualize a target in the periphery by attending to them (Intriligator and Cavanagh 2001). It was suggested that saccades are selected by a perceptual process that is too selective to be mediated by attention for perception, bringing us back to the issue of whether selection for perception shares the same filters than selection for action. Estimations of the resolution of attention were based on the results of a task that required attentive tracking. It should be noted, however, that more recent estimations find higher resolution with simpler tasks (Moore et al. 2008). We have seen (Section 1.3.3) that measures of the speed of attention during fixation are problematic if we think that there is a special relation between covert orienting and preparation of eye movement. Shifting attention according to some instruction while holding eye movements may be effortful and slow (see Wolfe et al. 2000; Horowitz et al. 2004). However, it would be valuable to know if an estimate of attention resolution is different when allowing eye movements than when covertly attending with maintained fixation. One could then compare this measure to the saccade target selection inferred by the distractor influence (like in Findlay and Blythe 2008).

Another interesting path of research concerns the way attentional resources required for eye movements depend on distracting information and on difficulty of the task. For instance, during pursuit maintenance, attention seems to be enhanced at the pursuit target in the presence of distractors (Watamaniuk and Heinen 2007), indicating that there may be some flexibility in the way attention is allocated to the target. Unlike what is often assumed, the amount of attention to the target may vary as a function of the necessity to suppress surrounding signals. Effects of attention can be described in a number of ways, like the enhancing of the target representation by reduction of external noise, enhancement of the target signal or both (Carrasco et al. 2000; Dosher and Lu 2000). Monkey neurophysiology led also to the idea that attention may also be an emergent process that comes into play when two objects compete for selection by spatial proximity, for instance (Desimone and Duncan 1995). The role of attention is then to enhance the target and suppress the response to the distractor, but none of it takes place without the presence of a distractor. This does not mean that different conceptions are incompatible (Ghose 2009). However, they suggest

different predictions. A prediction of the “biased competition model” is that the amount of attention needed to resolve the competition depends to the extent that distractors are similar to the target, for instance (Beck and Kastner 2007; Torralbo and Beck 2008). In our context that could mean that the amount and distribution of attentional resources that are needed for saccades and pursuit initiation may represent what is needed to resolve competition between target and distractors. There is evidence that there is more than resolution of a competition for saccades, as the attention focus interferences with saccade initiation even there is a single target (e.g. Shepherd et al. 1986). However, studies that inferred a very narrow focus of attention around the saccade target (Deubel and Schneider 1996), may measure the outcome of competitive interactions due to the presence of surrounding distractors, plus the shift of attention that unconditionally accompanies the saccade. A simple prediction is that if the distractors are different from the saccade target in some dimension, there will be less competition between representations due to the perceptual grouping of distractors (Beck and Kastner 2007), and then we may have a different estimation of the requirements of attention for saccades.

Related to the previous point, Deubel and Schneider (1996) have emphasized that the spatial specificity of the attention shift represents the parallel mechanism of object recognition and target selection. If the object is the relevant scale we should also expect that the ability to process distant locations depends strongly on the size of the object. For instance, attention may be paid to an object that is 5° distant from the saccade target if its size is 3°, but equally to a 2° distant object of a 0.5° saccade target, for instance. Such a scaling would provide strong support to the VAM theory. In a similar vein, some authors have suggested that we can select task relevant features without selecting everything at the attended location (Remington and Folk 2001). To my knowledge, there is no evidence that the execution of a saccade towards an object does constrain the selection of task-irrelevant information at the targeted location. This would be interesting to know as the answer can constrain how we conceive the flow of information between the ventral and dorsal branch for selection of the saccade target. Does position come first and then objects are highlighted?

Finally, at the lowest-level of detail, a thrilling path of research that we have not alluded to is the investigation of information selection and tracking behavior in the

Drosophila. It might represent a unique chance to develop biologically plausible and precise computational models. The fly, although not equipped with mobile eyes, turns its body in sequences of smooth pursuit and saccadic movements in a very similar way to primates (Boeddeker and Egelhaaf 2005), and we can identify in it neural substrates of exogenous selection (van Swinderen and Greenspan 2003). Together with the fact the fly visual and motor system is certainly simpler than ours, the Drosophila genome has been intensively studied and permitted the inauguration of genetic manipulations to test precise hypothesis about the neural computations that underlie the selection of information for action (van Swinderen and Greenspan 2003).

## 6.7 The last word

We have reviewed recent advances that have unveiled neural sites involved in the control of spatial orientation and eye movements. We have discussed that structures involved in the control of covert attention have also a prominent role in the control of eye movement plans, although there might also be supramodal structures directing spatial and non-spatial attention to enhance information relevant for other kinds of goal-directed actions (e.g. Craighero et al. 1999). Our experiments similarly suggest that attention has a prominent role in planning pursuit and saccadic eye movements and, in particular, it is proposed that attention plays an important role in the necessary coordination of target choice for pursuit and saccades.

## 7 French abstract

Nous savons tous que l'attention peut être attirée par des évènements externes divers, tels qu'une lumière, le fait d'entendre son nom, un claquement de porte, etc. Nous pouvons aussi nous concentrer sur des objets, pensées ou actions qui sont organisées en fonction d'un plan interne. La question adressée dans ce travail est celle de savoir dans quelle mesure nous avons un contrôle volontaire sur le déplacement de nos yeux indépendamment de l'objet de notre attention. En d'autres termes, peut-on lire dans le déplacement de nos yeux une indication fidèle de ce qui fait l'objet de notre attention ?

Le rôle de l'attention dans la programmation des déplacements volontaires des yeux a été longuement débattu dans la littérature ces trente dernières années. Je commencerai par brièvement définir l'attention, ainsi que les mouvements oculaires étudiés, pour ensuite évaluer les travaux et théories qui ont été proposées liant le contrôle de l'attention et l'exécution de mouvements oculaires. Finalement, j'introduirais les travaux sur la poursuite oculaire, un système oculomoteur qui a été nettement moins étudiée dans ce domaine, et discuterais de la façon dont sont possiblement coordonnés les choix des saccades et de la poursuite oculaire.

### 7.1 Pourquoi déplacer les yeux?

Notre acuité visuelle décroît rapidement en s'éloignant de la partie fovéale du champ visuel. Cette limitation n'est pas seulement due à l'espacement des bâtonnets sur la rétine, lequel est de plus en plus grand avec l'éloignement en périphérie, mais trouve également son origine dans des étapes ultérieures du traitement visuel. En conséquence de cela, nous devons constamment déplacer les yeux.

Dans ce travail, deux types de déplacements des yeux de nature volontaire sont considérés : la saccade oculaire et la poursuite lente oculaire. Ces deux systèmes servent des buts bien différents, celui de ramener les objets sur la fovéa pour une analyse fine, et, pour la poursuite lente, celui de réduire leur déplacement sur la rétine. En effet le système visuel est également limité pour ce qui est de percevoir clairement des objets se déplaçant sur la

rétine. On estime qu'à partir de 2-3 degrés par seconde la vision d'un objet en mouvement est dégradée. D'où le besoin de stabiliser l'objet sur la rétine par le moyen de la poursuite lente ou par d'autres types de mouvements de nature reflexe (tels que le réflexe vestibulo-oculaire, le nystagmus optokinétique, ou l'« ocular-following response », voir p. ex. Leigh et Zee 2006).

## 7.2 L'attention

Selon la célèbre formule de William James, tout le monde sait ce qu'est l'attention. Le fait qu'il y ait un lien intime entre l'attention et les contenus de la conscience supporte ce point de vue. Faire attention à un objet particulier est une action que nous comprenons très bien, et qui correspond, comme James le suggère, à se saisir de cet objet pour en faire le centre de notre perception consciente, au détriment de tout autre. Ceci étant dit, le mécanisme cognitif par lequel cette sélection est opérée n'en est pas moins impénétrable et cela James le savait aussi.

Deux caractéristiques de l'attention sont presque unanimement acceptées par les chercheurs: le fait que nous pouvons porter d'attention qu'à un nombre limité d'objets en même temps, ce qui exclut tout autres stimuli d'un traitement poussé, et la fait que l'attention peut être sélectivement alloué à un endroit, objet, ou trait visuel, pour ce qui est de l'attention visuo-spatiale (Desimone et Duncan 1995).

Dans la littérature citée dans ce travail, il est d'usage d'utiliser des métaphores pour décrire les opérations de l'attention. Celles-ci sont utiles pour décrire bien des résultats, néanmoins il est important de ne pas les pousser trop loin et d'être éclectique dans leur utilisation, car elles décrivent toutes des effets différents que l'on peut attribuer aux mécanismes attentionnels. Ainsi on pourra parfois utiliser la métaphore du projecteur pour décrire les processus de sélection basés sur l'espace. Néanmoins on pourrait aussi bien admettre que le « focus » (métaphore photographique à rapprocher de la métaphore du zoom d'Eriksen) attentionnel est un filtre spatial (métaphore introduite par Broadbent) de type « chapeau mexicain » : avec un centre excitateur (facilitation) et un pourtour inhibiteur ; description d'une nature très différente de celle du projecteur.

Il faut aussi considérer le fait que les processus de sélection peuvent être basés sur l'objet ainsi que sur ses attributs (par exemple la couleur), et non seulement sur l'espace. Néanmoins la sélection basée sur l'espace est peut-être plus pertinente dans le cadre de la programmation d'une action orientée.

Au moment d'évaluer les résultats des études visant à tester le lien entre attention et mouvements oculaires, il est important de retenir que les mesures utilisées ne sont souvent que des indicateurs indirects de la sélection attentionnelle. Par exemple, les temps de réaction pour la détection d'un stimulus peuvent être réduits lorsque son emplacement a été indiqué au préalable par un indice (le paradigme d'indication introduit par Michael Posner). Néanmoins d'autres facteurs peuvent réduire les temps de réaction dans ce type de tâches, comme le déplacement du seuil à partir duquel on décide que le stimulus est apparu, ce qui tient plus de facteurs décisionnels que de l'attention.

Dans les paradigmes qui seront présentés, l'attention peut être contrôlée selon deux modes différents, le mode endogène et le mode exogène, selon que des événements en périphérie attirent l'attention ou que le déplacement se fait de façon volontaire par le moyen d'un indice symbolique (typiquement une flèche).

Dans ce travail il sera essentiellement question de savoir comment la sélection implicite s'articule avec le mode de sélection explicite, c'est-à-dire avec le déplacements des yeux, et dans quelle mesure cette mesure explicite est un bon indicateur de la distribution des ressources attentionnelles. Il sera aussi essentiellement question d'attention orientée dans l'espace plus que d'attention orientée sur l'objet ou sur un trait visuel.

### 7.3 L'attention et la programmation des saccades oculaires

La problématique autour de laquelle un grand nombre de recherches se sont penchées est celle du partage des processus de sélection pour la perception et pour l'initiation des mouvements oculaires. Peut-on décider de faire attention à un objet situé à gauche de notre champ visuel et en même temps programmer un déplacement des yeux vers la droite?

La théorie prémotrice de l'attention avancée par l'équipe de Rizzolatti (Rizzolatti et al. 1987) propose que non seulement qu'un mouvement de l'œil est préparé par le

déplacement de l'attention vers la cible, mais aussi que tout déplacement de l'attention implicite est équivalente à un programme oculomoteur implicite, à la seule différence qu'il est ultérieurement avorté. Cette théorie a été très influente jusqu'à aujourd'hui, bien que certains de ses aspects n'aient pas reçu de support empirique. Un point plus général de cette théorie est qu'elle s'oppose à ce que l'attention soit conçue comme contrôlée par une entité supramodale (un point de vue attribué à Posner). Elle propose plutôt que les circuits neuronaux impliqués dans l'action sont les mêmes à être impliqués dans la sélection des informations qui relèvent de cette action. Le lien privilégié entre attention spatiale et mouvements oculaires est dû à l'importance des mouvements oculaires dans la vision. Avec un autre système moteur, cela suppose, par exemple, que lorsqu'une action de préhension est engagée, les objets préhensibles vont être sélectionnés par les mêmes structures qui sont responsables de cette action, sans l'entremise d'un centre dévolu à d'orientation de l'attention.

Les premières études à avoir adressé empiriquement la question du lien entre saccades oculaires et attention ont eu lieu dans les années quatre-vingt (Klein 1980; Posner 1980; Remington 1980). Elles avaient toutes conclu à l'époque que les déplacements des yeux pouvaient être découplés de l'emplacement du focus attentionnel. Il était accepté qu'habituellement ce couplage est maintenu, car "l'œil" et l'attention sont attirés pareillement par des stimuli saillants. Lorsque la tâche le requiert, on peut dissocier l'œil et l'attention, démontrant leur indépendance. Néanmoins, plus récemment, des études ont contesté les méthodes utilisées par ces premières, et ont conclu à leur tour à un lien étroit entre attention et mouvements oculaires, tendant parfois vers l'autre extrême, à l'identité des processus qui contrôlent la sélection pour la perception et pour le déplacement des yeux (Shepherd et al. 1986; Crawford et Muller 1992; Reuter-Lorenz et Fendrich 1992; Hoffman et Subramaniam 1995; Deubel et Schneider 1996).

Le point de vue le plus controversé, défendu par les tenants de la théorie prémotrice, est que tout déplacement de l'attention implicite génère un programme oculomoteur. Cette idée a reçu un certain support à partir d'expériences montrant que des contraintes qui semblent appartenir au domaine oculomoteur se retrouvent dans le domaine de l'attention spatiale. Les effets de méridien découverts par Rizzolatti et al. (1987) tombent dans cette catégorie. On avait trouvé que lorsque l'indice et la cible se trouvent dans des positions qui

traversent le méridien horizontal ou vertical, les effets d'indication sont plus importants (en comparant les temps de réaction lorsque l'indice endogène est valide aux temps de réaction lorsqu'il est invalide) que lorsqu'indice et cible se trouvent dans le même quadrant. Les effets de méridien vertical peuvent trouver une explication dans la séparation entre les deux hémisphères. Pour ce qui est des effets de méridien horizontal, il semblait que seule une explication oculomotrice pouvait expliquer les résultats: lorsqu'un méridien est traversé, les coûts attentionnels sont plus importants, car dans un premier temps le déplacement de l'attention génère un programme oculomoteur vers l'endroit indiqué. Le mouvement doit être reprogrammé lorsque l'indice apparaît du côté opposé, car dans cette situation le couple fléchisseur-extenseur doit être modifié, ce qui devrait prendre plus de temps que de moduler la force de la commande motrice, situation rencontrée lorsqu'on se trouve toujours dans le même quadrant.

Une autre série d'expériences en faveur de la théorie prémotrice a montré que l'emplacement de l'attention pouvait dévier la trajectoire des saccades oculaires dans la direction opposée (Sheliga et al. 1994; Sheliga et al. 1995; Sheliga et al. 1997), probablement par la nécessité d'inhiber la tendance à diriger les yeux sur l'emplacement préalablement sélectionné.

Des recherches plus récentes ont néanmoins montré qu'il n'est pas toujours vrai qu'un déplacement de l'attention est suivi d'un programme oculomoteur. Ainsi on a montré que des neurones des champs oculomoteurs frontaux peuvent indiquer la sélection d'une cible sans pour autant que cela ne génère d'interfère avec la génération d'une commande motrice provoquée de façon artificielle, par micro-stimulation de neurones moteurs dans la même aire (Juan et al. 2004). A contrario, lorsqu'une saccade est volontairement programmée, la commande volontaire est combinée à la commande artificielle, si elle est générée au niveau des champs oculomoteurs frontaux, résultant dans un compromis entre les deux.

### 7.3.1 Spécificité spatiale

Une question importante est de savoir dans quelle mesure les mouvements des yeux sont des bons indicateurs des déplacements de l'attention (et *in fine* du niveau de traitement de l'information fixée). Qu'elle est la spécificité spatiale du déplacement de l'attention qui semble être nécessaire à l'exécution des mouvements oculaires? Pour répondre à cette

question, certaines études ont comparé la performance perceptive à l'emplacement visé par la saccade avec celle obtenue à des emplacements proches, peu avant l'exécution d'une saccade. Deubel et Schneider (1996) avaient ainsi trouvé que la performance perceptive pouvait chuter au niveau du hasard à des emplacements aussi proches qu'un degré d'angle visuel.

Les études qui ont testé l'emplacement de l'attention lorsqu'une série de saccades est programmée ont montré que l'attention est distribuée en parallèle sur les différents buts, mais à divers degrés en fonction de l'ordre d'exécution. Le plus intéressant est qu'il ne s'agit pas seulement d'un élargissement du focus attentionnel, car la performance perceptive aux emplacements intermédiaires entre les buts indique qu'ils ne sont pas sélectionnés (Baldauf et Deubel 2008).

### 7.3.2 Compensation

Que se passe-t-il lorsque l'attention allouée vers le but de la saccade est insuffisante? Une possibilité est que la saccade soit exécutée avec une latence normale mais qu'elle ne soit pas aussi précise. C'est ce qui arrive lorsque des distracteurs sont proches de la cible de la saccade. Une autre possibilité est que la saccade soit reportée jusqu'à ce que les ressources attentionnelles soient suffisantes, ce qui est peut-être ce qui arrive lorsque qu'on requiert un découplage dans des directions opposées.

Kowler et al. (1995) ont montré que le déplacement de ressources attentionnelles sur d'autres emplacements que celui de la saccade à venir ne se traduisait pas toujours par le prolongement des latences, ni par une perte de précision, indiquant que les besoins attentionnels sont de nature limité (voir aussi Montagnini et Castet 2007).

### 7.3.3 Décours temporel

Le développement des ressources attentionnelles en préparation des mouvements oculaires prend un certain temps. Les études qui ont essayé d'estimer la vitesse à laquelle l'attention pouvait être déployée ont typiquement trouvé des valeurs qui sont parfois trop grandes pour qu'elles s'accordent avec le fait que l'attention précède les saccades. Néanmoins celles-ci peuvent refléter le fait que les déplacements de l'attention implicite sont plus lents lorsqu'ils ne sont pas accompagnés par un mouvement oculaire qui doit être inhibé. On estime que l'essentiel des ressources attentionnelles pour la préparation de la

saccade sont allouées environ 150 à 200 millisecondes après présentation du signal impératif (Castet et al. 2006), dans des conditions dans lesquelles un découplage entre focus attentionnel et le but de la saccade est encouragé; entre 50 et 150 millisecondes dans d'autres conditions (Deubel 2008).

## 7.4 La poursuite lente oculaire

Comme il a été dit précédemment, la poursuite lente oculaire a pour but de réduire le déplacement des objets jugés intéressants sur la rétine, afin d'en améliorer la perception. Comme le système saccadique, la poursuite lente peut être déclenchée de façon volontaire. A un niveau très basique, on peut concevoir que ce mouvement est contrôlé par une boucle de rétroaction négative dont la principale entrée est le mouvement de la cible sur la rétine. Cette boucle se ferme avec un certain délai, estimé à environ 100 ms. Par conséquent on peut diviser l'initiation de la poursuite lente en deux phases: une première phase en boucle ouverte, les 100 premières millisecondes du mouvement, suivie d'une phase en boucle fermée, dite de « poursuite maintenue ». Contrairement aux saccades, le début du mouvement semble peu sélectif, ce n'est qu'au début de la poursuite maintenue que la poursuite reflète la seule influence de la cible et non celle de la cible et d'un éventuel distracteur. Les latences de la poursuite lente sont nettement plus rapides que celles des saccades, ce qui peut s'accorder avec l'idée que les mécanismes de sélection ont un déroulement similaire à celui des saccades, en supposant un critère de déclenchement plus laxiste pour la poursuite lente.

### 7.4.1 Poursuite vers le vecteur moyen

En présence d'un distracteur qui se déplace en même temps que la cible, la réponse de poursuite suit ce qui peut être décrit comme le vecteur moyen, calculé en moyennant les vecteurs de vitesse des deux objets. Après une centaine de millisecondes, c'est uniquement la cible qui est poursuivie. La transition se fait généralement par une saccade (Ferrera et Lisberger 1997). Ce qui a été dit du déroulement temporel dans l'allocation des ressources attentionnelles peut être s'appliquer à ce comportement. La réponse moyenne peut refléter le fait que l'attention prend plus de temps à sélectionner la cible que le temps qu'il faut typiquement pour démarrer la poursuite. Bien que cette hypothèse semble raisonnable, des études sur le singe ont montré que, même lorsque la cible se déplace toujours dans la même

direction, la poursuite est encore dirigée vers le vecteur moyen, indiquant qu'il s'agit d'une réponse indépendante de l'attention que l'on met sur la cible. Néanmoins la même manipulation avait montré la capacité d'ignorer le distracteur chez l'homme (Spering et al. 2006), ce qui tendrait à indiquer des différences l'homme et le singe dans la capacité à adapter la distribution de l'attention en fonction de différentes tâches. Néanmoins, des différences importantes entre les paradigmes et protocoles d'expérience utilisés chez le singe et chez l'homme rendent cette comparaison difficile.

#### **7.4.2 Attention et poursuite oculaire soutenue**

La distribution des ressources attentionnelles pendant la phase de poursuite maintenue a fait l'objet de quelques études. Ces dernières montrent que l'attention a un rôle important pour le maintien de la poursuite lente (Khurana et Kowler 1987). Ainsi, il semble impossible de continuer de poursuivre une cible lorsque l'attention est portée sur d'autres objets. Néanmoins un certain nombre de ressources peut être alloué ailleurs sans compromettre la performance de poursuite. Il a été également prouvé qu'une condition importante pour le maintien de la poursuite lente est que l'attention n'est pas portée sur des objets statiques, qui vont se déplacer sur la rétine en sens inverse du mouvement (Kerzel et al. 2008). Inversement, la sensibilité au contraste est meilleure pour un objet en mouvement dans le sens de la poursuite que pour un mouvement opposé (Schutz et al. 2007b). Prises ensemble, ces études suggèrent un rôle de l'attention dans la suppression des signaux de mouvement pouvant entrer en conflit avec la poursuite de l'objet d'intérêt.

#### **7.4.3 Partage des mécanismes de sélection**

Lorsqu'une cible est poursuivie, elle est également centrée sur la rétine par le moyen du système saccadique. Il n'est dès lors pas étonnant de constater que la poursuite lente et les saccades partagent un système de sélection qui leur permet de coordonner le choix de la cible. Néanmoins on a longtemps considéré les substrats neuronaux de la poursuite lente et des saccades comme deux entités séparées.

Des études psychophysiques et neurophysiologiques ont permis d'établir que les saccades et la poursuite lente pourraient partager des mécanismes de sélection de la cible. Au niveau neurophysiologique, on a montré que l'activité des cellules motrices des couches intermédiaires du collicule supérieur corrèle avec les choix saccadiques et de la poursuite

lente, dans des situations dans lesquelles un distracteur et la cible peuvent être présents dans le champ récepteur du neurone (Krauzlis et Dill 2002; Cariello et Krauzlis 2004). L'attention spatiale peut être un facteur qui coordonne le choix de la cible pour la saccade et pour la poursuite lente simultanément, et dont l'activité au sein des couches intermédiaires du collicule supérieur serait un des corrélats neuronaux.

## **7.5 Le rôle de l'attention dans l'initiation de la poursuite lente oculaire (Etude 1)**

L'idée qu'un déplacement de l'attention précède nécessairement l'exécution d'une saccade est bien établie. Nous avons voulu tester la validité de cette hypothèse pour ce qui est de l'initiation de la poursuite lente. Comme nous l'avons rappelé plus haut, il se pourrait également que les besoins attentionnels pour l'initiation de la poursuite lente soient bien moindres, ce qui expliquerait la poursuite du vecteur moyen en présence d'un distracteur en mouvement. Pour ce faire, nous avons supposé que, si la poursuite lente dépendait fortement de l'attention sur la cible, des demandes attentionnelles concurrentes devraient prolonger les latences de la poursuite. Nous avons utilisé un paradigme de double-tâche pour découpler l'emplacement de l'attention de celui de la cible de la poursuite. Il était requis que les participants fassent attention à la périphérie en fonction d'indices endogènes (Expérience 1 et 2) ou d'indices symboliques (Expérience 3). La performance de discrimination à l'emplacement indiqué indiquait que la tâche perceptive était bien réalisée. La deuxième tâche était de commencer à poursuivre la croix de fixation aussitôt qu'elle commençait à se déplacer. La croix se déplaçait horizontalement, alors que les stimuli perceptifs étaient situés en haut et en bas de la croix de fixation. Une variable importante était l'intervalle de temps qui séparait la présentation de l'indice (indiquant de déplacer de l'attention en périphérie) du début du mouvement de la croix de fixation. Cet intervalle était de 500 à 0 ms. En comparant les latences dans une simple tâche (poursuivre seulement) aux latences dans la double-tâche, on peut évaluer dans quelle mesure le déplacement de l'attention interfère avec l'initiation de la poursuite. Lorsque l'intervalle de temps est le plus long, on peut supposer que l'attention a eu le temps de revenir sur la croix de fixation. Pour des intervalles de temps entre 200 et 50 ms, on peut supposer que l'attention est encore en périphérie lorsque la cible doit être poursuivie. On peut noter que des différences de latence peuvent être constatées par le simple fait que le début du mouvement de la cible est perçu

plus tard dans la tâche double que dans la tâche simple, lorsque l'attention se trouve en périphérie.

Les latences de la poursuite dans la tâche simple et dans la tâche double sont étonnamment similaires dans les trois expériences. Les seules conditions dans lesquelles un délai sensible est constaté sont celles où l'attention doit être portée sur un objet qui reste statique alors que la poursuite doit être engagée. Ces résultats indiquent donc une certaine indépendance de l'initiation de la poursuite lente par rapport à l'emplacement de l'attention.

On pourrait aussi penser que les déplacements de l'attention qui étaient demandés en périphérie n'étaient pas suffisants pour interrompre la programmation du mouvement. Les effets sur le début de la phase en boucle fermée montrent le contraire. Ainsi on trouve que les saccades qui accompagnent l'initiation de la poursuite lente sont prolongées de plus de 40 ms. Dans les cas dans lesquels la poursuite est initiée sans l'exécution d'une saccade correctrice, la vitesse de la poursuite est grandement diminuée, mais seulement lorsqu'on approche de la phase de poursuite maintenue, et que l'on doit fixer l'attention sur un stimulus statique. L'ensemble des résultats indiquent d'une part que les besoins en ressources attentionnelles sur la cible de la poursuite sont assez faibles lorsque la poursuite démarre, mais également que le début de la phase de poursuite maintenue requiert que l'attention soit allouée au moins vers des objets qui se déplacent dans le sens de la cible. En même temps, il est intéressant de constater que des saccades qui ne sont pas déclenchées de façon volontaire, telles que les saccades qui sont générées pendant l'initiation de la poursuite lente, semblent requérir des ressources attentionnelles. Bien qu'on puisse rétorquer que la latence de ces saccades dépend de la vitesse de l'œil avant leur exécution, celles-ci devraient être exécutées plus rapidement lorsque l'œil est en retard sur la cible, ce qui est davantage le cas dans les conditions de double-tâche. Donc, on devrait s'attendre à ce que ces saccades soient exécutées avec des latences plus courtes et non plus longues, si elles dépendaient strictement de la vitesse pré-saccadique.

En résumé, le besoin en ressources attentionnelles pour la poursuite oculaire est constaté au début de la phase de poursuite maintenue. Bien qu'on ne puisse affirmer que l'initiation de la poursuite se fait de façon pré-attentionnelle, car il est clair que seule une

partie des ressources est déplacée vers la périphérie, les besoins attentionnels semblent être bien moindres que ceux nécessaires à l'initiation des saccades.

## **7.6 Attention et sélection de la cible de la poursuite lente oculaire (Etude 2)**

Comme il a été dit précédemment, la première réponse de la poursuite lente reflète la moyenne des vecteurs de vitesse, ce qui pourrait suggérer qu'un processus de sélection attentionnel n'a pas le temps de supprimer l'influence du distracteur. Alternativement il pourrait s'agir d'un comportement indépendant des mécanismes de sélection endogènes, comme cela a été suggéré chez le singe.

Bien que l'étude précédente suggère que l'attention n'est pas nécessaire à l'initiation de la poursuite lente en présence d'un seul objet mobile, cela ne veut pas dire que l'attention ne peut pas déterminer le choix de la cible de la poursuite en présence de deux objets en mouvement.

Dans cette étude nous avons utilisé un paradigme expérimental dans lequel les sujets reçoivent différentes instructions à chaque bloc, la tâche oculaire étant de démarrer la poursuite de la cible en présence d'un distracteur qui se déplace en même temps en direction opposée. La position de la cible de la poursuite est désignée par un indice central. Dans différents blocs on doit soit porter son attention sur l'objet opposé, soit partager son attention entre l'objet à poursuivre et l'objet à percevoir, soit porter l'attention majoritairement sur l'objet à poursuivre. Ces différentes instructions permettent d'avoir un aperçu de la quantité de ressources qui est suffisante pour sélectionner la cible en présence d'un distracteur, en comparaison les performances dans la tâche double et la tâche de poursuite lente ou de perception réalisées isolément.

Les résultats montrent qu'une performance qui s'élève au-dessus du hasard pour la tâche perceptive a pour conséquence la prolongation des latences de la poursuite et une augmentation du nombre d'essais dans lesquels la poursuite était engagée dans la direction de la cible à percevoir. Il semble impossible de trouver des performances perceptives et des latences oculaires approchant la performance en simple tâche, ce qui indique l'impossibilité de dissocier totalement les décisions oculaires et perceptives.

Un autre point intéressant est que, lorsque l'attention doit être portée sur la cible à poursuivre, les latences peuvent être très peu prolongées par la présence d'un distracteur en mouvement, voire pas du tout chez certains sujets. Ce dernier point est en contradiction avec ce qui avait été montré chez le singe. Chez le singe les encouragements à porter l'attention de façon endogène sur la cible ne changent pratiquement pas les délais en présence d'un distracteur.

Nous avons testé la possibilité que les limitations observées sur nos sujets (qui étaient néanmoins préalablement entraînés) pourraient ne pas refléter pleinement l'incapacité de partager des ressources entre perception et mouvements oculaires mais la difficulté de passer d'une instruction à une autre. Nous avons donc également entraîné deux sujets sur la même tâche sur six sessions, pendant lesquelles un feedback était donné après chaque bloc sur leur performance oculaire (sous la forme d'un histogramme des temps de réaction) et leur performance perceptive. On constate que même dans cette condition, il n'est pas observé de progrès dans le sens d'une performance qui s'approcherait de l'indépendance (amélioration de la performance perceptive et oculaire en même temps), mais à chaque fois une compensation de la performance perceptive par les latences oculaires et inversement.

## **7.7 Effets d'indication involontaires pendant le maintien de la poursuite lente (Etude 3)**

Lorsque des indices sont présentés en périphérie, et qu'ils ne sont pas informatifs quant à la position de la cible, les temps de réaction sont facilités pour des cibles présentées au même endroit que l'indice; c'est ce qu'on appelle l'effet de facilitation. Pour des intervalles de temps longs entre l'indice et la cible, les temps de réaction sont prolongés pour une cible apparaissant à l'endroit indiqué, ce qu'on appelle l'effet d'inhibition de retour. Il est bien établi que pendant la poursuite lente l'attention est concentrée sur la cible poursuivie (ou en tout les cas dans la même direction, voir l'étude 1). On s'est demandé si les effets d'indication étaient préservés à un niveau similaire pendant la poursuite lente et pendant la fixation. Dans une condition, les indices et les cibles périphériques apparaissaient au même endroit sur la rétine. Dans une autre, ceux-ci se déplaçaient sur la rétine: pendant la poursuite ils étaient statiques et pendant la fixation ils étaient en mouvement. Si on

trouve des effets d'indication exogènes pendant la poursuite et que les effets de facilitation et d'inhibition sont rétinocentrés, on devrait s'attendre à ce que ceux-ci soient plus faibles lorsqu'indice et cible occupent des positions différentes sur la rétine. Certaines études ont montré que l'effet d'inhibition était centré sur l'objet. Néanmoins elles avaient utilisé des paradigmes différents, dans lesquels l'indice apparaît puis le mouvement de la cible est engagé. Nous avons plutôt voulu savoir si la capacité à s'orienter vers des informations exogènes pouvait être préservée pendant la poursuite lente. Nous avons utilisé les temps de réaction de saccades dirigées vers la cible pour tester ces effets.

Les résultats montrent des effets de facilitation et d'inhibition de retour similaires pendant la fixation et pendant la poursuite lente consistants avec l'idée que ces effets ont des coordonnées rétiniennes. Il se pourrait que contrairement à ce qui avait été montré avec d'autres paradigmes les effets d'inhibition basés sur l'objet ou sur la position dans l'espace soient absents lorsque l'on mesure des temps de réaction saccadiques.

Une étude récente suggère que les cartes de saillance sont d'abord codées en coordonnées rétiniennes, puis un recodage en coordonnées spatiales a lieu après une saccade. Ce processus prenant du temps, ce n'est que quelques centaines de millisecondes après la saccade que l'on retrouve des effets attachés à la position dans l'espace, par un mécanisme de recodage analogue à celui qui est observée dans l'activité des neurones du cortex pariétal, censés sous-tendre la stabilité perceptive. A contrario de celui-ci, le recodage de la carte de saillance est lent et supposerait que des effets centrés sur la rétine sont superposés avec des effets centrés sur l'espace, qui émergent après ces premiers. Nos résultats pourraient bien s'accorder avec ce point de vue. On pourrait supposer que si la poursuite s'était arrêtée avant la présentation de la cible, ce processus de recodage aurait peut-être eu lieu et on aurait alors observé une plus grande facilitation et peut-être une plus grande inhibition centrées sur l'espace.

Il reste aussi à déterminer si le fait que les indices contiennent tout de même des informations temporelles sur l'avènement de la cible peut modifier leurs effets, étant donné que les intervalles de temps entre indice et cible étaient fixes dans un bloc.

## 7.8 L'inhibition de retour possède un composant attentionnel (Etude 4)

Bien qu'il soit bien établi que l'attention est nécessaire à l'exécution des saccades, quelques études ont montré des données incompatibles avec cette idée. Notamment, l'étude de Hunt et Kingstone (2003b) avait trouvé une dissociation entre saccades et attention dans le domaine de l'IOR. Comme il a été dit plus haut, l'inhibition de retour désigne l'inhibition des réponses vers l'endroit indicé. Cet effet est manifeste après quelque 300 millisecondes après la présentation de l'indice. Plusieurs hypothèses quant aux mécanismes en jeu dans l'IOR sont en compétition et sont en complémentaires, chacune étant supportée par un grand nombre d'études. L'une d'entre elles suppose que l'effet d'IOR est dû à une inhibition d'ordre oculomoteur. La présentation de l'indice provoquerait la préparation d'une saccade vers l'endroit indicé. Cette activation serait ensuite inhibée, car on exige de maintenir la fixation. C'est cette inhibition oculomotrice qui provoquerait l'effet d'IOR. Une explication alternative voudrait que cet effet soit de même nature que l'effet de facilitation et qu'il pourrait être dû, selon certains auteurs, au fait que l'attention, après avoir été captée par l'indice, retourne vers la fixation puis par inertie est biaisée vers la direction opposée.

En suivant la logique des facteurs additifs de Sternberg (1969), si un effet connu pour avoir lieu à un niveau oculomoteur interagit avec l'effet d'IOR, on a une indication que cet effet possède un composant oculomoteur. C'est ce qu'on pense de l'effet de « gap ». Lorsque le stimulus fixé disparaît avant la présentation de la cible, les temps de réaction saccadiques sont réduits, et on pense que l'effet est dû à un désengagement au niveau des structures oculomotrices. Selon la même logique, on pense que la relation inverse entre la taille des effets d'indication et le contraste de la cible est un effet de l'attention, étant donné que des stimuli de faible contraste bénéficient plus de l'attention que des stimuli à contraste élevé.

Hunt et Kingstone (2003b) avaient constaté que l'effet d'inhibition de retour n'interagissait pas avec le contraste de la cible quand il était mesuré avec des temps de réaction saccadiques, mais que c'était le cas lorsqu'il était mesuré avec des temps de réaction manuels (réponse de choix-forcé sur le clavier). Ce résultat avait été interprété comme indiquant que l'attention n'influençait pas les temps de réaction oculaires, les deux

étant indépendants. Les auteurs avaient aussi constaté que l'effet de « gap » interagissait avec l'effet d'IOR saccadique mais pas l'effet d'IOR manuel. Ils ont conclu de cette double dissociation qu'il existe deux sortes d'inhibition de retour, l'une d'origine oculomotrice et l'autre d'origine attentionnelle. Cette dernière est manifeste sur les temps de réaction manuels, mais pas avec des temps de réaction saccadiques, démontrant l'indépendance entre l'attention et la préparation des mouvements oculaires.

Etant donné que cette étude est contraire à ce qu'on se serait attendu d'après les expériences citées plus haut, nous avons tenté de répliquer l'expérience en examinant de plus près la distribution des temps de réaction, étant donné que les auteurs ont été très peu prolixes à ce sujet. Nous n'avons pas reproduit leurs résultats. Bien au contraire nous avons constaté un effet du contraste de la cible sur l'inhibition de retour très marqué avec des réponses saccadiques et manuelles. Nous n'avons pas non plus constaté d'effet de « gap » sur l'inhibition de retour, que ce soit pour les réponses manuelles ou saccadiques.

L'étude de la distribution des temps de réaction des saccades indique que l'effet du contraste sur l'IOR décroît avec les temps de réaction les plus longs, jusqu'à devenir inexistant. Ceci suggère que l'utilisation de la moyenne et le fait de ne pas employer de critère d'exclusion pour les temps de réaction les plus longs pourraient être les raisons pour lesquelles des effets du contraste n'ont pas été trouvés dans un premier temps. Supportant cette idée, l'effet du contraste sur l'IOR obtenu avec des temps de réactions manuels subsiste même pour des temps de réaction longs, contrairement à ce qui est observé avec les saccades.

Dans une deuxième expérience, nous avons voulu répliquer au plus près les qualités visuelles des stimuli utilisés dans l'étude de Hunt et Kingstone (2003b). Nous avons constaté que la luminosité moyenne provoquait d'importantes différences dans l'effet de « gap » et de contraste sur l'effet d'IOR. Ce dernier résultat nécessite une plus ample exploration, néanmoins il suggère que des facteurs de bas niveau, tels que la luminance moyenne, peuvent avoir une grande influence sur les effets étudiés. Ils sont également supportés par des études récentes critiquant l'identification qui a été faite entre l'inhibition de retour et l'oculomotricité à partir de preuves très indirectes de l'implication du collicule supérieur.

## 7.9 Perspectives

Nous avons vu que les déplacements des yeux sont dans certaines conditions de bons indicateurs de l'emplacement des ressources attentionnelles, et en tant que tels ils peuvent être considérés comme des indicateurs explicites du déplacement de l'attention. On a vu également que, dans d'autres conditions, l'attention pouvait être dévouée à des stimuli qui ne sont pas la cible des déplacements oculaires sans que ceux-ci s'en trouvent modifiés de façon significative.

Certains auteurs avaient émis l'idée que la poursuite oculaire est initiée de façon pré-attentive, et que l'attention n'est engagée sur la cible que lorsque la phase en boucle fermée de la poursuite lente est entamée (Erkelens 2006). Nos données s'accordent avec cette idée et suggèrent que les mêmes mécanismes de sélection sont en jeu lors de l'initiation de la poursuite lente et l'exécution des saccades, à la différence que la poursuite lente est enclenchée selon un critère de déclenchement moins strict (à un niveau de préparation précoce).

Nous avons également montré que l'attention était nécessaire pour sélectionner la cible de la poursuite lente en présence d'un distracteur, ce qui se manifeste par des latences plus courtes ou plus longues en fonction des ressources allouées au distracteur ou à la cible. La deuxième étude supporte l'idée que la sélection de la cible par le système oculomoteur partage les mêmes filtres que pour la perception. Dans le modèle de Schneider (1995) cela pourrait se traduire par l'interaction entre les branches pariétales et ventrales du système visuel (p. ex. Webster et Ungerleider 1998).

On a aussi vu que, pendant la phase de poursuite lente maintenue, on peut observer des effets d'indication involontaires à un niveau similaire à celui obtenu pendant la fixation. La présentation de l'indice a pour effet de faciliter ou d'inhiber (selon l'intervalle de temps entre indice et cible) une position sur la rétine et non l'objet en lui-même ou bien sa position sur l'espace, comme d'autres études l'avaient suggéré.

Il reste des questions ouvertes. Parmi celles-ci on peut se demander si la quantité de ressources attentionnelles nécessaires aux mouvements oculaires dépend fortement de la tâche étudiée. D'après certains modèles, l'attention peut être envisagée comme un phénomène émergeant de la compétition entre signaux (p. ex. Desimone et Duncan 1995).

L'attention aurait pour effet de renforcer la représentation de la cible et de supprimer la réponse au distracteur, mais uniquement lorsqu'il y a un conflit, dû par exemple à la proximité des deux objets. Appliquée à notre problématique, cette idée pourrait impliquer que le couplage entre attention et mouvements oculaires dépende fortement de la présence de distracteurs. Cela reviendrait à repenser le problème en termes relatifs. Comme on l'a vu à plusieurs reprises dans le cas de la poursuite, cette interprétation s'impose à nous lorsque la poursuite doit être initiée en présence de distracteurs qui se déplacent dans des directions opposées à celle du mouvement. C'est d'autant plus tentant que l'on sait qu'en absence de distracteur l'attention semble jouer un rôle mineur dans l'initiation de la poursuite. Dans cet esprit, d'autres auteurs ont constaté que la perception d'une cible poursuivie était améliorée par la présence de distracteurs (Watamaniuk et Heinen 2007). Il serait intéressant toutefois de tester cette idée pour ce qui est des saccades, pour lesquelles on semble concevoir un couplage en termes absolus de l'attention sur la cible et la programmation du mouvement. Par conséquent, une étude complète des ressources nécessaires à l'exécution des mouvements oculaires aurait requis que celles-ci soient évaluées relativement à la saillance de la cible – telle que définie par ses caractéristiques visuelles ou par la proximité de distracteurs – ou relativement à la compatibilité entre le mouvement des distracteurs et le mouvement des yeux requis.

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