Remote distractor effects in saccadic, manual and covert attention tasks

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To my mother

Abstract

The Remote Distractor Effect (RDE) is a robust phenomenon where a saccade to a lateralised target is delayed by the appearance of a distractor in the contralateral hemifield (Walker, Kentridge, & Findlay, 1995). The main aim of this thesis was to test whether the RDE generalises to response modalities other then the eyes. In Chapter 2, the RDE was tested on saccadic and simple manual keypress responses, and on a choice discrimination task requiring a covert shift of attention. The RDE was observed for saccades, but not simple manual responses, suggesting that spatially oriented responses may be necessary for the phenomenon. However, it was unclear whether distractor interference occurred in the covert task. Chapter 4 compared the effects of distractors between spatially equivalent tasks requiring saccadic and manual aiming responses respectively. Again, the RDE was observed for the eyes but not for the hands. This dissociation was also replicated in a more naturalistic task in which participants were free to move their eyes during manual aiming. In order to examine the time-course of distractor effects for the eyes and the hands, a third experiment investigated distractor effects across a wider range of target-distractor delays, finding no RDE for manual aiming responses at distractor delays of 0, 100, or 150 ms. The failure of the RDE to generalise to manual aiming suggests that target selection mechanisms are not shared between hand and eye movements. Chapter 5 further investigated the role of distractors during covert discrimination. The first experiment showed that distractor appearance did not interfere with discrimination performance. A second experiment, in which participants were also asked to saccade toward the target, confirmed the lack of RDE for covert discrimination while saccades were slower in distractor trials. The dissociation between covert and overt orienting suggests important differences between shifts of covert attention and preparation of eye movements. Finally, Chapter 6 investigated the mechanism driving the RDE. In particular it was assessed whether saccadic inhibition (Reingold & Stampe, 2002) is responsible for the increase in saccadic latency induced by remote distractors. Examination of the distributions of saccadic latencies at different distractor delays showed that each distractor produced a discrete dip in saccadic frequency, time-locked to distractor onset, conforming closely to the character of saccadic inhibition. It is concluded that saccadic inhibition underlies the remote distractor effect.

Sintesi

L’effetto del distrattore è un fenomeno oculare nel quale la produzione di un movimento saccadico verso un bersaglio visivo viene rallentata dalla presentazione di un distrattore nel campo visivo controlaterale a quello di presentazione del bersaglio (i.e. RDE: Walker, Kentridge, & Findlay, 1995). L’obiettivo di questa tesi è stato quello di verificare se l’effetto del distrattore viene generalizzato in altre modalità di risposta oltre quella oculare. Nel secondo capitolo, il RDE è stato testato su movimenti saccadici, risposte manuali semplici (pressione di un pulsante) e in un compito attentivo di discriminazione visiva (non foveale). Il RDE è stato osservato nei movimenti oculari ma non in quelli manuali, suggerendo che probabilmente, al fine di causare tale fenomeno, siano necessarie risposte manuali orientate nello spazio, come ad esempio un movimento di puntamento. Meno chiaro è stato il risultato riguardante l’interferenza del distrattore durante il compito attentivo di discriminazione. Dal momento che nel quarto capitolo vi era la necessità di registrare concomitantemente movimenti di puntamento e movimenti oculari, nel terzo capitolo si è verificata l’attendibilità delle latenze oculari registrate con la tecnica di elettro-oculografia (EOG), tramite una comparazione diretta di queste con le latenze registrate con l’EyeLink II. Tale comparazione ha dato esito soddisfacente, evidenziando come l’EOG sia un metodo preciso di registrazione delle latenze dei movimenti oculari. Nel quarto capitolo sono quindi stati comparati gli effetti del distrattore tra compiti spazialmente equivalenti che richiedevano movimenti saccadici e risposte di puntamento. Ancora una volta, l’effetto del distrattore è stato osservato per i movimenti oculari ma non per quelli di puntamento. Questa dissociazione è stata poi replicata anche in un compito più naturale nel quale i partecipanti erano liberi di muovere gli occhi durante le risposte manuali. Al fine di esaminare l’effetto del distratttore a diversi intervalli temporali, sia nei compiti di puntamento che in quelli saccadici, un terzo esperimento ha investigato il RDE usando una varietà di ritardi tra l’apparizione del bersaglio e quella del distrattore. Anche in questo caso non è stato registrato nessun effetto del distrattore per le

risposte manuali in nessuno degli intervalli temporali usati (0, 100 o 150 ms). Il fallimento nella generalizzazione del fenomeno per le risposte manuali suggerisce che i meccanismi di selezione del bersaglio non sono condivisi tra il sistema di movimento manuale e quello oculomotore. Nel quinto capitolo si è ulteriormente investigato l'effetto del distrattore durante il compito attentivo di discriminazione. Il primo esperimento ha evidenziato che il distrattore non interferisce con la performance discriminativa. Il secondo esperimento, nel quale ai partecipanti veniva richiesto di eseguire anche un movimento oculare verso il bersaglio visivo, ha confermato la mancanza di RDE nel compito di discriminazione ma la presenza di un effetto di interferenza nella produzione saccadica, per cui l'inizio dei movimenti oculari veniva ritardato nelle prove in cui il distrattore era presente. La dissociazione tra l'esecuzione del movimento oculare e la performance attentiva suggerisce importanti differenze tra la preparazione dei movimenti oculari e i processi attenzionali (spaziali). Nel sesto capitolo si è investigato il meccanismo che genera il RDE. In particolare è stato testato se l'effetto di inibizione saccadica (i.e. SI: Reingold & Stampe, 2002) sia responsabile per l'aumento delle latenze del movimento oculare indotto dalla presenza del distrattore. Un esame accurato delle distribuzioni di latenze saccadiche per differenti tempi di presentazione del distrattore ha evidenziato che ogni distrattore produceva una riduzione nella frequenza di produzione saccadica, effetto temporalmente vincolato all'apparizione del distrattore. Le caratteristiche di questa riduzione nella frequenza dei movimenti oculari sono risultate essere chiaramente conformi alle caratteristiche del fenomeno di inibizione saccadica. Si è quindi concluso che l'inibizione saccadica è il processo sottostante l'effetto del distrattore. Il settimo capitolo riassume i risultati e propone un'interpretazione riguardante la generalizzazione di questo particolare effetto oculare per altre modalità di risposta. La parte finale della tesi è dedicata alla presentazione di future linee di ricerca.

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And now let's have some distraction...

Declaration

I declare that this thesis is my own composition, and that the material contained in it describes my own work. It has not been submitted for any other degree or professional qualification. All quotations have been distinguished by quotation marks and the sources of information acknowledged.

(Antimo Buonocore)

List of acronyms and abbreviations

ANOVA: analysis of variance
CE: constant error
CRT: cathode ray tube
EOG: electro-oculography
FEF: frontal eye field
FDP: fix delay period
FOE: fixation offset effect
IOR: inhibition of return
IQR: interquartile range
L-ELII: EyeLink II latencies
L-EOG: EOG latencies
LCD: liquid crystal display
LED: light-emitting diode
LGN: lateral geniculate nucleus
LIP: lateral intraparietal
MRF: midbrain reticular formation
MRT: manual reaction time
MT: movement time
N.D: not determined
OMRH: oculomotor readiness hypothesis
OPN: omni-pause neurons
PPRF: paramedian pontine reticular formation
PS: peak speed
RDE: remote distractor effect
RDP: random delay period
RIP: nucleus raphe interpositus
RT: reaction time
RTE: redundant target effect
SC: superior colliculus

SI: saccadic inhibition
SIH: saccadic inhibition hypothesis
SOA: stimulus onset asynchrony
SRT: saccadic reaction time
T: target only
TD: target with distractor
TPS: time to peak speed
V1: primary visual cortex
VAM: Visual Attention Model
VE: variable error
VOR: vestibulo-ocular reflex

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Chapter 1

General introduction

As we explore the visual world, we move our eyes 2-3 times per second, making eye movements the most frequent behaviour in all of human life. We also accomplish a multitude of target-directed movements with our limbs with little conscious effort. The study of motor output and its interaction with the environment has a long history but it is only in the last 20 years, thanks to developments in recording technology, that it has been possible to study the motor output in detail, not only to inform about the motor system itself, but also as a window into higher cognitive processes involved in the preparation of motor output. It is the relation between the *motor system* and *attentional processes* that forms the overarching theme of this thesis, and provides its starting point.

1.1 Target selection

The complexity of the environment represents a continuous challenge for the nervous system. Every action, from the simple grasping of an object to the most skilled motor behaviour, such as playing an instrument, is an incredible computational feat. Specialised areas of the central nervous system are devoted to transforming sensory information from the environment into motor output. The chain of transformations starts from the *distal stimulus* (Neisser, 1976 - perception-action cycle), for example an object placed in front of us. Eyes and hands work in close concert during the execution of goal-directed manual actions. The oculomotor system and the limb motor system are tightly coupled both in time and space. When reaching for a target, eyes and hands usually move toward the same target (Gielen, van del Heuvel, & van Gisbergen, 1984). Moreover, eye movements usually begin about 60 to 100 ms before the hand movement (Angel, Alston, & Garland, 1970; Prablanc, Echallier, Komilis, & Jeannerod, 1979). This may be due principally to the lower inertia of the eye than the arm (Biguer, Jeannerod, & Prablanc, 1982), but it undoubtedly produces functional benefits. When foveation toward the object of interest is prevented, a decrease in the accuracy of the hand movement has been reported (Abrams, Meyer, & Kornblum, 1990; Mather & Fisk, 1985; Neggers & Bekkering, 1999; Prablanc et al., 1979; Vercher, Magenes, Prablanc, & Gauthier, 1994). The coupling of the two systems can be so strict that, for example, when engaged in a series of pointing movements the eyes can not move away from the target until the hand movement is at the final stage, an effect referred to as *gaze anchoring* (Neggers & Bekkering, 2000). The effect is not dependent upon online control of the ongoing hand movement since it persists even when the hand is not visible (Neggers & Bekkering, 2001).

A critical source of information we use during the transformation processes comes from the light reflected by objects. One possible problem the nervous system can encounter is that the visual array provides too much information (Broadbent, 1958) and, as already noted by William James, we are aware of only part of the visual array at one time (James, 1890). Taken together these two assumptions lead to the hypothesis that a *selection mechanism* able to discriminate one target among many others and to discard the irrelevant sensory stimulation is necessary. Selection processes are related to both object recognition (LaBerge & Brown, 1989) and action execution (Allport, 1987). When the final goal is to act upon an object, the spatial parameters of the target have to be specified (Neumann, 1987) in order to compute the appropriate motor program, and suppress others. Given that we rely on the visual system to extract spatial information, *visual-spatial attention* (i.e. the capability for an increased preferential processing at a particular location in space) will be central during these operations. The filtering is not only related to the discrimination of one target among others; sometimes it is necessary to suppress interfering information that was not present in the first instance. In fact, it often happens that a change in the environment elicits a modification of the motor program, for example when a new element, or even just a *flash of light,* perturbs the visual scene. In these cases, the central nervous system has the critical task of taking into account such changes and generating a new and appropriate motor output. One fundamental operation the selection mechanism is required to perform is to process target location in the visual scene. Most of the time, in order to discriminate target characteristics, we need to align the eyes with the object in such a way that the *fovea*, the part of the eye that contains the largest number of photoreceptors, maximises the sensitivity to the light available and provides the finest resolution of the target's intrinsic properties, such as shape and dimension.

1.2 Orienting behaviour

Selecting an object requires us to shift our attention onto the target object. The aligning of the attentional focus with the target is called *orienting behaviour.* There are two types of orienting that we can adopt to move the attentional focus to the target object. When an explicit eye movement is present in response to a stimulus in the environment we speak of *overt* orienting. The purpose of orienting eye movements is to get the relevant stimulation on the high-acuity fovea. Not only overt movements are used for target selection, however: it often happens that we can look *"out of the corner of the eye",* meaning that we can shift our attentional focus toward a particular location in space without moving our gaze. Although this does not change the retinal location of the stimulation, there is nonetheless an attentional enhancement, improving perceptual discrimination and sensitivity at the attended region. This second form of attention is often called *covert* attention (see Chapter 2 for more detail on orienting).

Another important distinction that it is necessary to introduce is *how* attention is moved toward a target. In fact, every one of us knows that we can intentionally dissociate our attentional focus from the direction of the gaze. In this case we speak of an *endogenous* shift of attention since it is dictated by an internal state. On the other hand, as reported in the examples above where a distracting element appears on the visual scene, a change in the environment can capture our attention. In this case we speak about an *exogenous* shift of attention, because it is an external change that is causing the shift.

As it will be discusses in section 1.7, motor theories of attention propose a strong link between attentional shifts and eye movements programming. To better understand the relation between these two forms of orienting behaviour it is necessary to briefly review eye movement characteristics and the physiology of their generation.

1.3 Types of eye movements

The eyes have a repertoire of movements that they can perform in different circumstances. Eye movements are restricted by the three opponent pairs of muscles that control the eyeball. The *lateral* and *medial rectus* are responsible for *abduction* and *adduction*, the moving of the eyes outwards or inwards on the horizontal plane; vertical movements are performed by the *superior* (for elevation) and *inferior* (for depression) *rectus.* Finally, the *inferior* and *superior oblique* muscles contribute to the eye's rotation, moving the eye toward or away from the nose, i.e. extorsion and intorsion. These muscles control eye movements in a very fine way.

There are four main types of eye movement we can execute in order to constrain target location on the fovea region: saccades, pursuits, vergence and vestibulo-ocular reflex (VOR). The saccadic movement is basically a reflex-like motor behaviour in which the eyes move quickly from one location to another. Pursuit movements are much slower and allow the eye to follow an object that is moving in the environment. Vergence is reserved for objects moving in depth. Differently from the other type of eye movements where both eyes move in the same direction (conjugate eye movements), during vergence movement the eyes involve disconjugate eye movements, producing a divergence or a convergence of the eyes on the line of sight. Finally, the last category of eye movements is the vestibulo-ocular reflex, VOR. This reflex is stimulated by the hair cells in the semicircular canals of the vestibular system, and it is used to stabilise the eyes relative to the external world, compensating for head movements (see: Purves, Augustine, Fitzpatrick, Katz, LaMantia, et al., 2001). The exclusive focus of the present thesis will be on the control of saccadic eye movements.

1.4 Saccadic eye movements

Saccadic eye movements are reflex-like motor outputs in which the eyes move quickly from one location to another. Saccades can be triggered by different events from visual, auditory or somatosensory input but also as a result of a voluntary effort to move to a particular location without the presence of a target. Saccades are necessary in order to bring to the fovea the object of interest in such a way that it can be better processed thanks to the higher sensitivity of this part of the retina.

These stereotyped and ballistic movements have a duration usually lasting less than 100 ms but that, due to its spatial-temporal dependency, can be easily modeled by the following equation (Carpenter, 1988):

$$Ts = 2.2As + 21$$

where Ts = saccade duration in ms and As = saccade amplitude in degrees. The general pattern of an eye movement starts with a fixation. Then the eye starts moving with a rapid acceleration until it reaches maximum velocity. Then a symmetric rapid deceleration happens to bring the eye to the new position (see: Findlay & Gilchrist, 2003). Even if highly stereotyped, saccades include a variety of amplitudes, ranging from 1-2 degrees of visual angle for the most commonly used to the wider movements of 18 to 20 degrees (Land, Mennie, & Rusted, 1999).

1.5 Saccade generation

A peculiar discharge pattern is responsible for saccade generation: the *“burst-tonic”* activity. At a muscular level, saccade generation happens when the motor neurons rapidly switch from a high firing rate related to the initiation of the movement to a lower but increased rate related to the new position. Premotor areas in the brainstem such as the *midbrain reticular formation* (MRF) and the *paramedian pontine reticular formation* (PPRF) form a specialised network of neurons that are dedicated to generating these patterns (reviewed by: Scudder, Kaneko, & Fuchs, 2002). A series of cortical areas are also involved in the circuitry of eye movement generation, of which the most important are the *lateral intraparietal* (LIP) area of the posterior parietal cortex and the *frontal eye field* (FEF) of the premotor frontal cortex. Moreover, subcortical areas like the *superior colliculus* (SC) are also responsible for controlling the brainstem, to which it sends most of its output. These areas are known to be responsible for eye movement activity since their electrical stimulation can elicit saccadic movements. The network for saccade generation is formed by multiple parallel routes. Although all of these areas may not be required in order to generate a movement, the loss of both SC and FEF makes monkeys unable to saccade (Schiller, True, & Conway, 1980). A more recent study by Hanes and Wurtz (2001) challenged the autonomous role of the FEF in generating saccades. In fact, the authors reported that when the SC was inactivated, FEF elicited saccades were eliminated or distorted. This finding puts more emphasis on the critical role of the SC in the eye movement circuitry, since the direct connection of the FEF to the brainstem saccade generator seems to be insufficient to trigger accurate saccades. One peculiarity of this system is that the eye movement network works in parallel, separating the initiation of the movement (when) from the information about the location (where) (Van Gisbergen, Gielen, Cox, Bruijns, & Kleine Schaars, 1981; see also Findlay & Walker, 1999).

Eye muscles are controlled directly by cranial nerves III, IV and VI and the cell bodies of these nerves are in corresponding oculomotor nuclei. SC is the main area passing the input to the nerves. Two classes of neurons have the key role in the burst-tonic activity. The *omnipause* neurons have the peculiarity of firing at a uniform rate until 5 to 15 ms before movement onset. These neurons have the same type of activity independently from the characteristics of the saccades. On the other hand, *burst* cells start to discharge in correspondence with movement onset and are responsible for coding the metric of the saccade. The cells that control the vertical component of the saccade are mainly located in the MRF while the cells that control the horizontal component are mainly located in the PPRF.

The light coming through the eyes hits the retina (i.e the back of the eyeball) where all the photoreceptors are placed. The visual information starts to be processed already at this level by a different number of specified ganglion cells and then it is carried by the *optic nerve* to the *optic chiasm* where a partial crossing of the axons takes place. The fiber bundle that emerges from the crossing at the optic chiasm is called the *optic tract*, see Figure 1A.

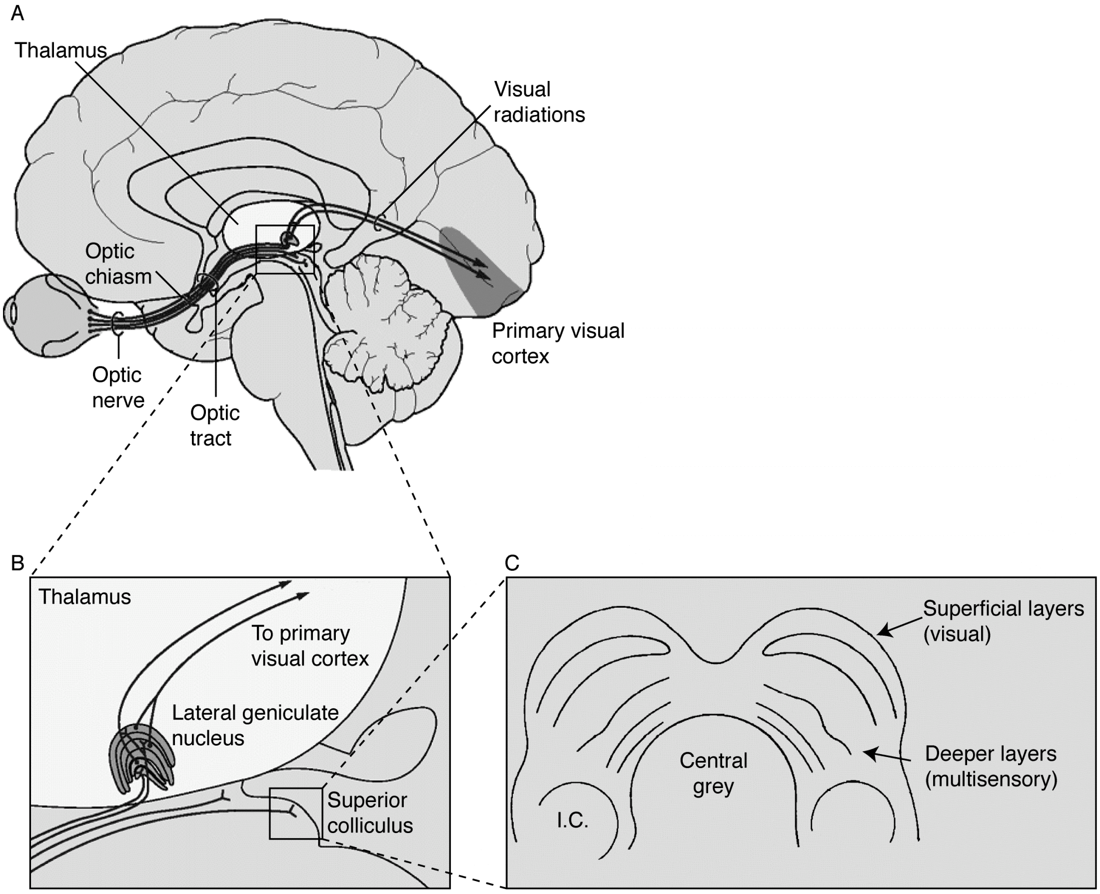

Figure 1.1 Visual pathways.
A. The projections from the retina to the visual areas of the thalamus and midbrain ending in the primary visual cortex (sagittal section). B. Subcortical structures (sagittal section) in the visual pathway, showing the terminal connections of the optic tract to the *lateral geniculate nucleus* of the thalamus, and to the *pretectum* and *superior colliculus* in the midbrain. C. Superior colliculus of the macaque monkey (coronal section). It is possible to appreciate the alternating fiber and cell layers of monkey superior colliculus and their subdivision in superficial and deep layers. I.C. denominates the Inferior Colliculus. Diagrams A and B adapted from Kandel, Schwartz and Jessel (2000). Diagram C adapted from Wurtz and Albano (1980; p. 190).

There are two main streams toward the first cortical areas that process visual information, the primary visual cortex (V1), from this point on. These two pathways are the phylogenetically older retino-tectal projections and the retino-geniculate projections. The retino-geniculate stream consists of most of the nerves (~90%) and goes to the *Lateral Geniculate Nucleus* (LGN) where it is connected to each of the six layers of this structure according to the dimension of the ganglion cells where it had its origin in the retina, Figure 1B.

The retinotectal projection instead consists in a small percent of fibers that terminate directly in a subcortical structure in the optic tectum of the midbrain, i.e. the superior colliculus in mammals, Figure 1C. This structure is a fundamental part of the oculomotor circuitry, performing computations for motor programming, especially those involved in saccadic movements. Moreover, the SC is connected to most of the cortical visual areas, especially FEF, working in close concert with them in the fine triggering of eye movements.

1.6 The Superior Colliculus

The SC is a subcortical structure that consists of multiple layers, Figure 1C. Each layer contains maps of visual and oculomotor space with each hemifield represented in the contralateral SC. The s*uperficial* layers receive direct input from the retina. Neurons in this layer have receptive fields that respond to contralateral visual stimulation and their activity is primarily related to vision. The output is mainly directed to the thalamus (Sparks & Hartwich-Young, 1989). The lower layers, the *intermediate* and *deep* layers, receive cortical projections. The cells within these layers also have visual responses but their discharge is mainly related to the onset of the saccade showing motor proprieties (Wurtz, Basso, Paré & Sommer, 2000). They have a movement receptive field that is activated only for a specific saccade to a location in space, defined by its amplitude and direction (Wurtz & Goldberg, 1972). The organization is topographic with visual and oculomotor maps in register (Robinson, 1972; Schiller & Koerner, 1971). The structure is anisotropic, with the foveal region represented largely in the rostral pole of the SC. One important structure of the SC is located in the rostral pole: the *fixation centre*. This region is active when the animal fixates a stimulus and stops its activity during saccadic movements (Munoz & Wurtz, 1993a; 1993b). There is a similarity between the cells in the rostral pole of the SC and the *omnipause* cells in the brainstem (Parè &

Guitton, 1994). In the deep and intermediate layers there are mainly two types of cells that show activity related to saccadic eye movements. The *build-up cells* (intermediate layer) show an increase in activity that initiates before the actual movement and that peaks just before the saccade is launched. On the contrary, *burst cells* show a very brief discharge just prior to saccade execution. Both build-up cells and especially burst cells are active in the region where the saccade's direction is specified.

Although the distinction between fixation and build-up neurons in the SC has been widely accepted, recent neurophysiological work suggests that this dichotomy may be somewhat artificial, with these classes of cells representing the endpoints on a continuum of build-up neurons coding for saccades of different amplitudes. This idea changes completely our view of the function of the rostral pole of the SC, originally identified as a fixation centre. According to Krauzlis and colleagues (Krauzlis, Basso & Wurtz,1997), the fixation centre is still part of a saccade zone but is only coding for microsaccades. In their experiment the authors showed that fixation neurons pause only during ipsiversive saccades but fire during small contraversive saccades that are involved in maintaining fixation for parafoveal targets. The authors clearly stated that:

> "[…] there are no fundamental differences between "build-up cells" in the caudal SC and "fixation cells" in the rostral SC […]" (Krauzlis et al., 1997, p. 1695).

Supporting this idea there is also the work of Anderson, Keller, Gandhi and Das (1998), who suggested that the classification of fixation neurons has to be dropped in favour of *tonic rostral* neurons. They argued that any cells within the rostral pole might have a saccade-related activity, instead of a pause, but that the size of the saccade and of the field to which the neuron respond is very small (<1°). According to this subdivision then, the density of such cells declines by moving caudally, since the size of the saccades increase for more caudal position. Testing the activity of these tonic rostral neurons could be problematic since it might be difficult to systematically obtain saccades with very small amplitudes (Anderson et al., 1998).

1.7 Neurophysiology of pointing

The previous sections described how visual information is carried along the visual pathway and how an oculomotor response is generated at the level of the SC. Of course, the same visual stimulation can elicit other types of orienting responses, such as a reaching or pointing movement. At the subcortical level, there is neurophysiological evidence that cells of the intermediate and deep layers of the SC represent arm movements (Fries, 1984; 1985; Lünenburger, Kleiser, Stuphorn, Miller, & Hoffmann, 2001; Stuphorn, Bauswein, & Hoffman, 2000; Werner, 1993; Werner, Dannenberg, & Hoffmann, 1997). In particular two types of cells have been described as firing before and during arm movements (Stuphorn et al., 2000). *Gaze-independent* cells specify the muscles related to the actual movement and operate in gaze-independent coordinates. The other type of cells is *gaze-dependent* and they fire preferentially in concomitance with the starting of the movement (Stuphorn et al., 2000), though it is not clear to what extent they code for motor preparation. In fact, another hypothesis is that these gaze-related neurons code for motor error, allowing online correction of the reaching movement toward the foveated target, given that they code the target in the eye centred coordinates.

At a cortical level, the dorsal visual stream, which runs from the extrastriate cortex to the superior parietal lobe, is most strongly implicated in the visuomotor transformations that support visually-guided limb movements. Ungerleider and Mishkin (1982) proposed a functional subdivision between ventral (occipito-temporal) stream and dorsal (occipito-parietal) stream processing. While the ventral stream was involved in processing the intrinsic properties of an object (*what*) (i.e. shape, colour etc.), the dorsal stream was involved in coding spatial location (*where*). Ten years later Goodale and Milner (1992) reinterpreted the function of the dorsal stream, suggesting that it is specifically concerned with the visuomotor tranformations required for goal-directed actions. This interpretation is strongly supported by a neuropsychological double dissociation between patients with damage restricted to the ventral or dorsal stream. Patients affected by optic ataxia, consequent to a lesion of the parietal lobe (dorsal stream), were unable to reach toward a peripheral target (Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003;

Perenin & Vighetto, 1988) despite a correct analysis of the intrinsic proprieties of the target object. On the other hand, visual form agnosia, consequent to a lesion in the ventro-lateral occipital region (ventral stream), revealed an inability to identify the object's intrinsic properties, whereas visuomotor transformations involved in the programming of a movement were intact and these patients showed skilful action guidance (Goodale & Milner 1992; Milner & Goodale 1995). This new interpretation of dorsal stream function focused interest on the role of PPC in the visual guidance of action.

At a neurophysiological level, studies on alert monkeys described a mosaic of regions within the PPC that behaved differently according to which effector was involved in the task (for a review see Culham, Cavina-Pratesi, & Singhal, 2006; Culham & Valyear, 2006; Snyder, Batista, & Andersen, 1997). The intraparietal sulcus subdivides the PPC into two lobules: the superior parietal lobule and the inferior parietal lobule. In monkeys, neurons that are selective for reaching movements are located mainly in the superior parietal lobe, while eye-movement selective cells are instead located mainly in the inferior parietal lobe. Two networks within the PPC are of particular interest for the experiments that will be described in this thesis: the LIP area, highly involved in eye movement control, and the parietal reach region (PRR), involved during reaching movements. The putative homologue in humans for the LIP is hypothesised to be the parietal eye field (Medendorp, Goltz, Vilis & Crawfor, 2003; Sereno, Pitzalis & Martinez, 2001) while the putative homologue for the PRR is hypothesised to be the precuneus (Connolly, Andersen, & Goodale, 2003), especially involved in pointing movements (Astafiev, Shulman, Stanley, Snyder, Van Essen, & Corbetta 2003). In area LIP, sensory attention and eye movement activations overlap (Corbetta et al., 1998; Kustov & Robinson, 1996) but can be dissociated (Andersen, Essick, & Siegel, 1987; Gnadt & Andersen, 1988; Zhang & Barash, 2000), making LIP the perfect candidate to exchange motor and sensory signals. Despite the bio-mechanical differences between the oculomotor system and the limb motor system (Soechting, Buneo, Herrmann, & Flanders, 1995) some authors (for a review see Buneo & Andersen, 2006) have hypothesised that PPC plays a similar role in the control of arm movements. PPC seems to be able to carry out visuomotor transformations, as highlighted by the selective discharge for sensory stimuli and for motor preparation.

One key problem that the PPC needs to solve in order to specify the correct motor output is to encode the target and the effector locations within a common spatial frame of reference. The PPC is well-equipped to do this, since it receives multimodal inputs from visual, somatosensory and kinaesthetic sources, and therefore has the possibility to support tranformations from eye-centred to body-centred frames of reference. One strategy to create a body-centred representation of a visual target would be to transform eye-centred coordinates into hand-centred coordinates (Flanders, Tillery, & Soechting, 1992; McIntyre, Stratta, & Lacquaniti, 1998). Since the position of the eyes in the orbit is known by proprioception (including motor efference), eye-centred coordinates can be transformed into head-centred-coordinates. This spatial representation could in turn be transformed into a body frame of reference by adjusting for the position of the head relative to the body. The final stage would be to convert the body-centred coordinates to a specific coordinate system shared by the effector involved in the task; for example, a shoulder-based frame of reference for arm movements. Recently, however, an alternative solution to this classical “transformation problem” has been proposed in which the arm position is instead coded in eye-centred coordinates, and the motor error (i.e. the difference vector that expresses the required movement) is derived by subtraction from the eye-centred target position. Buneo and Anderson (2002) found that in the PPC, both LIP and PRR neurons code in eye-centred coordinates, supporting the idea that the motor error is computed by vectorial subtraction within a common eye-centred reference frame. Medendorp, Goltz, Vilis and Crawford (2003) found evidence for this type of coding in the human PPC. In their study, they observed an area within the PPC with a contralateral topographic map containing information about the target for both eye and arm movements. This map was also updated in eye-centred coordinates according to the position of the eyes. In a successive study Medendorp, Goltz, Crawford and Vilis (2005) showed that the activation in this area (i.e. the intraparietal sulcus) was stronger when there was compatibility between target side and effector (for example stronger activation for pointing with the right hand to a right target), and then concluded that this area represented both target location and effector selection.

It is clear from these and many other studies, that the PPC contains networks coding space for the programming of an action. As proposed by Rizzolatti and colleagues (1987), these *pragmatic maps* are used to transform spatial information into movements. However, as the next section will document, Rizzolatti et al. (1987) went further and suggested that these *pragmatic* maps not only support visuomotor transformations for eye and hand movements, but simultaneously constitute the neural substrate for shifts of spatial attention. According to this view it becomes of great interest how target selection mechanisms act upon these maps, if covert orienting is directly mediated by them, and to what extent spatial selection mechanisms are shared between different effectors, such as eyes and hands.

1.8 The relation between eye movements, limb movements and attention

Section 1.1 introduced the concept of a *selection mechanism* by which an individual is able to suppress irrelevant information in favour of that which is more relevant. In fact, we face the problem that we are submerged by information coming from all different modalities, and in order to behave coherently we must select what is of interest. Attention helps us in achieving this coherence. But the concept of attention is very broad and may involve many cognitive functions. For the purpose of this thesis, I will refer specifically to *visual attention* (i.e. the selective enhancement of processing at an attended location). This definition of attention fully overlaps with what has also been defined previously as covert attention.

To give an example, imagine that you are preparing yourself to find an object in certain surroundings, like a red cap in your bedroom. In this case, an attentional mechanism will be useful to enhance the target characteristics, such as its colour and shape, and, at the same time, to suppress irrelevant competing information, such as the other objects present in the room that do not share the target characteristics. Once this filter is active, the behavioural consequences will result in your being faster in finding your target. Moreover, the visual array contains information not only about the target's intrinsic characteristics but also its location in space. In these terms, visual attention *moves* within the spatial map representing the visual information, and both target identity and location are processed. Once these operations are performed, another aspect of attention steps in: the state of readiness to prepare a motor response toward the object of interest. In this case, the enhancement of motor processing will be part of what I previously called overt attention, when the motor response is an eye movement.

Once your target object has been selected from among the others, you will be ready to trigger the appropriate motor response and act towards your target. In fact, it is now well known that once an object has been selected by means of spatial attention, processing at target location is enhanced in both the perceptual (Carrasco & Yeshurun, 2009) and motor domains (Posner, 1980). However, whether the attentional system is independent of eye movements (or other overt motor responses), or if these two functions are coupled, and if so how tightly, is an issue that is still highly debated. It is important to point out that in the example reported above there is a strong component of top-down processing, meaning the intention to actively select a particular object in space. This type of processing has the same characteristics as the endogenous shift described in section 1.2. Nonetheless, similar mechanisms may also apply for bottom-up processing, as in the case of attention being captured by an exogenous cue.

The first attempt to answer this question was made by investigating the relation between eye movements and shifts of attention. The existence of a strong link between the programming of an eye movement and an attentional shift was hypothesized. In 1980 Klein proposed the *oculomotor readiness hypothesis* OMRH, which stated that shifts of attention were accomplished through the same motor programs used in saccade generation. Some year after, following this idea, Rizzolatti and colleagues (Rizzolatti, Riggio, Dascola, & Umiltà, 1987) proposed the *premotor theory of attention*. According to this framework, overt and covert shifts of attention share that same neural substrate. Spatial attention was conceived to be the same as a motor program without its execution. Contrary to the classic theory of attention that hypothesised different mechanisms for motor control and attentional processing (Posner, 1980), Rizzolatti suggested that there is no need to postulate any superordinate system devoted to attentional control. Interestingly, according to premotor theory, it is not only the area responsible for eye movement programming that overlaps with covert attentional shifts: all motor areas can potentially subserve attentional processing, according to the motor activity in which the subject is engaged. Rizzolatti and colleagues then conceived covert attention as motor preparation toward the selected object.

Another interesting proposal comes from Schneider (1995). His model of attention incorporates both aspects of *selection-for-perception* (i.e. the enhancing of visual processing aimed at object identification), and *selection-for-spatial-motor-action* (i.e. the activation of a motor program toward the selected target). Of course these two aspects must be related to behave coherently, with the perceptual information that needs to be passed to the motor system in order to generate an action accompanied by the suppression of irrelevant stimulation. The “Visual Attention Model” (VAM) proposes a:

> “[…] common visual attention mechanism which selects one object at time for processing with high priority” (Schneider & Deubel, 2002, p. 610).

This model follows the ventro/dorsal distinction of the visual pathway described in section 1.7. In particular, the ventral stream carries on the selection-for-visual-perception operation. On the other hand, the dorsal pathway implements the selection-for-spatial-motor-action. This second operation is very similar to the mechanism proposed by premotor theory: in fact, selection-for-spatial-motor-action generates a motor program toward the target without any need for overt execution. A common visual attention mechanism is postulated to process the visual information and pass it for parallel processing to the ventro/dorsal streams, enhancing perceptual discrimination and activating motor programs toward the selected target. One important characteristic of the model is that these two functions are highly coupled. This assumption implies that perception for an object that is also the target for an action is processed with high priority. At the same time, the perceptual processing of the target object will be strengthened, leading to enhanced identification. The opposite is also true: attending an object for perceptual analysis will lead to motor preparation aimed at that object.

Even if VAM and premotor theory seem to have many points in common, there is an important difference that needs to be considered. While premotor theory assumes that visual attention is *identical with* motor preparation, VAM offers the opposite assumption, hypothesising that once visual attention processes are active, motor programming *follows* (Schneider & Deubel, 2002).

It is also worth briefly noting another influential theory of attention, proposed by Henderson (1992). This model is intermediate between an extreme view of a complete overlap of the covert and overt attentional systems, as Rizzolatti proposed, and the assertion of their complete independence. In the *sequential attentional model*, visual attention is firstly allocated at the locus of fixation where perceptual processes are carried out with the purpose of identifying the target stimulus. Once this operation is complete, a covert shift of attention is generated and visual attention is reallocated to a new location in space in order to process the new stimulus. Once the covert shift has been generated and visual attention reallocated to a new location, the motor programming for a saccade starts. The saccade is programmed to bring the eye to the location in space selected via the covert shift. The reallocation of attention to a new location will lead to enhanced visual processing at the location. Finally, the eyes move to the new location (Henderson, 1992).

In the last two decades since these motor theories have been proposed, influential results have been reported supporting the premotor hypothesis and the VAM (see Chapter 2 and Chapter 4 for detail on experimental support for these two models). Nonetheless, it is still not completely clear to what extent these two forms of orienting behaviour are linked one to the other. The study of saccade parameters, such as reaction times and trajectories, has been one of the favourite motor output to research these sort of interactions. In particular, researchers have focused on particular phenomena in order to understand to which extent they are a peculiarity of the motor system or reflect more general attentional processes.

1.9 The RDE and associated oculomotor phenomena

The literature on eye movements reports a large number of phenomena involving attentional processing. These have been widely used to study the characteristics of eye movements and attentional shifts. For example, the process of selection from among multiple targets has been approached systematically in experimental environments. A simple but extreme case is when two stimuli are presented simultaneously within the same hemifield or bilaterally. The experiments of Lévy-Schoen (1969) represent one of the first attempts to investigate saccadic behaviour in such circumstances. In their paradigm, participants were presented simultaneously with two numbers and were asked to move their eyes and discriminate one of the two (as soon as they were visible). The two numbers might be presented in the same or in the opposite hemifield and participants were let free to choose which one to saccade towards. The authors observed a pronounced tendency to look towards the more proximal target, and a slow down in saccadic reaction times (SRT) of about 30 to 40 ms under bilateral conditions. The delay in starting the saccade was interpreted as the additional time required to choose which direction to look in.

Interestingly, Ross and Ross (1980; 1981) found a similar increase in SRTs even when the choice between the two potential targets was removed. In their first experiment (Ross & Ross, 1980) the authors examined the effect of *onset/offset* and *change* warning events at different stimulus onset asynchrony (SOA) of 0, 100, 300 and 600 ms. They presented a lateralised target at 15° of visual angle and asked their participants to saccade toward the target as soon as it was presented. In some trials, an onset, offset or a change at fixation occurred according to the SOA. They observed that the warning events facilitated SRT in response to the peripheral target after about 10 ms. Moreover, the offset effect was much stronger than the onset/change (~40 ms in offset condition). What was also very interesting, and much more closely related to the findings reported by Levy-Schoen, was that at 0, 50 and 150 ms of SOA, fixation onset or change drastically increased SRT, an effect opposed to the facilitation recorded in offset conditions. The stimulus at fixation appearing simultaneously or after target onset reversed the pattern and the saccade latency increased ~10 to ~30 ms, with the effect being stronger for onset stimuli. The author (p. 255) concluded that there is an

> "[…] interfering effect on saccade latency of a stimulus occurring simultaneously with or, in the case of these additional data, up to 150 ms after the onset of a peripheral target."

In a follow-up study Ross and Ross (1981) also tested the effect of visual or auditory warnings. They observed that a non-specific warning signal preceding target onset also had an impact on RT. As with saccadic responses, manual reaction time also presented a modulation related to the fixation events but, differently from the oculomotor system, manual RT were not subjected to the increase of RT for events happening simultaneously or after target onset. This series of studies drew important conclusions regarding the mechanism of the oculomotor system. In the first place, warning events were able to decrease reaction times for both the saccadic and the manual system while onset events happening simultaneously or after target onsets were specific to the visual modality and the oculomotor system. Another important outcome was that visual events happening peripherally were able to slow down SRT in a similar way to events occurring at fixation. In fact, the interfering effect was present even when the onset warning was presented at 5.5° away from the fovea. The interpretation of the effect elicited at fixation was different from that for the effect due to peripheral distractors. The authors suggested two possible hypotheses for the effect at fixation. According to one view, the interfering effect was caused by the generation of microsaccades related to the appearance of the new stimulus. The other view posited that the interfering effect was due to the fact that the eye remained fixed when new information was presented (e.g., Potter, 1976; Potter & Levy, 1969; Senders, 1976). According to this second hypothesis, the slow down in SRT was caused by the encoding and buffering of this new information. Ross and Ross also proposed that in the case of a lateralised target the interfering process that was causing the slow down in SRT was due mainly to oculomotor processes, in particular the:

> "[…] competition between the programming of the saccade to the target and some initial programming for a saccade to the location of the warning event." (Ross & Ross, 1981, p. 437).

The abrupt onset of the non-target stimulus was hypothesised to elicit a new motor program or a shift of attention that was interfering with the ongoing program ready to be launched. Similar results were observed by Braun and Breitmeyer (1990) where the simultaneous reappearance of the fixation stimulus delayed the start of the saccade. The authors also investigated the effect of such reappearances in the contralateral hemifield, observing the same effect on SRTs, even if this effect was not as reliable. In these experiments, the location of the target was predictable, removing any effects due to high cognitive processes related to target selection (see also Weber & Fischer, 1994).

This peculiar increase in SRTs during bilateral stimulation is now known as the *Remote Distractor Effect* (RDE). Walker and colleagues thoroughly investigated such saccadic phenomena, systematically manipulating the spatial and temporal proprieties of the distractor, i.e. the secondary stimulus (Walker et al., 1995; Walker, Deubel, Schneider, & Findlay, 1997). To eliminate any effect of choice, participants were always aware in advance of target location and they were only requested to select the correct amplitude of the movement. For a distractor presented at fixation or in the opposite hemifield, they observed a delay in the initiation of the saccades of ~18 ms compared to target only condition. Moreover, they showed that the effect was present for a distractor presented 40 ms before and after target presentation with its peak at simultaneity. On the other hand, the appearance of the distractor in the same hemifield near the target location led to another category of effects, named the *Global effect*, where there was no change in the SRTs but only a modification in the landing position (Walker et al., 1997). According to these results the greater increase in SRT was found for distractors simultaneously appearing with the target and placed at fixation and reduced monotonically moving to a more eccentric position.

1.9.1 Physiological explanation of the RDE

The remote distractor effect has been hypothesised to take place at the subcortical level in the first relay structure to the visual cortex, the *Superior Colliculus*. The fitting by a single function of the inhibitory effects of distractors across the range of eccentricities led Walker and colleagues (Findlay & Walker, 1999; Walker et al., 1995; 1997) to propose a neurophysiological mechanism in terms of the stimulation of fixation neurons in the superior colliculus. Fixation neurons, antagonistic to saccade preparation, and showing sustained activity during active fixation, are found chiefly in the rostral pole region of the superior colliculus, which represents the central 2° of the visual field (Munoz & Wurtz, 1992, 1993a, 1993b). Gandhi and Keller (1997) subsequently found collicular neurons with similar properties beyond the rostral pole, with receptive fields extending to up to 10° eccentricity. Walker et al. (1997) suggested that the inhibitory effects of foveal and non-foveal distractors alike might derive from the stimulation of collicular fixation neurons within this extended network (see also Findlay & Walker, 1999). Olivier et al. (1999), however, have expressed scepticism about this mechanism. They suggest that a more likely source for the RDE is lateral inhibition between subpopulations of build-up neurons in the intermediate layers of the superior colliculus, coding for spatially incompatible saccades. Honda (2005) supported this idea, showing that in overlap condition the strength of RDE is reduced if compared to GAP condition (where the fixation cross was turned off simultaneously to target onset). The explanation for this modulation in magnitude of the RDE is related to the influence of the fixation neurons. When the fixation stimulus is turned off the inhibition from the fixation neurons stops as well. At this point the only source of inhibition is due to the activity of the saccade-related neurons firing for both target and distractor and leading to a strong RDE. In overlap condition the strength of the RDE is reduced by the constant activity of the fixation neurons, which causes inhibitory interaction between distractor and fixation stimuli, reducing the inhibitory interaction between target and distractor.

At a neurophysiological level, as reported in Section 1.6, the explanation of the RDE in terms of push-pull interactions between the populations of build-up neurons is supported by new findings that reclassify fixation neurons as build-up neurons (Andersen et al., 1998; Krauzlis et al., 1997). If rostral pole neurons have the same characteristics as the build-up neurons present in other parts of the SC, it would be possible to hypothesise that the main process causing the delay in saccade initiation is lateral inhibition. According to this view, lateral inhibition processes will also be active between rostral pole neurons (firing for parafoveal micro saccades aimed at maintaining fixation) and the population of build-up neurons preparing a saccade to the peripheral target. As noted earlier, this hypothesis is favoured by Olivier and colleagues and is in opposition to a view whereby the rostral pole neurons extend fixation by acting on omnipause neurons in the brainstem because they are stimulated by the new visual information presented at fixation (or within 10° of visual field) (Walker et al., 1997).

Neuropsychological studies also provided results similar to the interfering effect noticed by Ross and Ross (1980; 1981) and Walker et al. (1995; 1997) that can be referred to as RDE, providing more evidence that such an effect is taking place already at the subcortical level. In particular, Rafal Smith, Krantz, Cohen and Brennan (1990) tested the effect of distractor appearance in the *temporal* and in the *nasal hemifield* in hemianopic patients. The author presented the distractor stimulus at different SOA ranging from 250 before to 500 ms after target (500 ms used as baseline since no eye movements were recorded with such latency). Even if none of the three patients saw the box brightening in the hemianopic field, Rafal et al. observed an interaction of the irrelevant stimulus related to the hemifield where it was presented. In particular, there was no effect for a distractor presented in the nasal hemifield while in the temporal hemifield, the distractor presented at 0 and 50 ms before target onset increased saccade latency relative to the no distractor condition for all subjects. In a control experiment, the authors also recorded manual responses. In this condition, there was no impairment of RT due to distractor appearance. Moreover, the authors reported that distractor onset was inducing faster reaction times, a result compatible with the finding of Marzi and collaborators (Marzi, Tassinari, Aglioti, & Lutzemberger, 1986). This result was congruent with Ross and Ross's conclusion, suggesting that the interfering effect was specific to the oculomotor system and not due to covert orienting of attention. In a much more recent work on this topic, Walker, Maurer, Pambakian and Kennard (2000) reported results that contrast with Rafal's findings. Walker et al. found that SRT of hemianopic patients were not affected by a distractor presented in their hemianopic field. On the contrary, normal participants, used as a control group, showed an increase in SRT in distractor trials. Moreover, Walker reported that a distractor presented in the temporal hemifield had a greater effect than a distractor presented in the nasal hemifield. This tendency was in direct contrast with Rafal's study (1990) and supported the view that the distractor effect was related to normal processes involved in saccade target selection.

A very interesting study was carried out by Sumner, Adamjee and Mollon (2002) in which equiluminant stimuli were used as distractors. In particular, these s-cone coloured are named in reference to s-cone cells, a particular class of cone photoreceptors that are sensitive to the short wavelengths. These photoreceptors are connected to a different type of ganglion cell (Dacey & Lee, 1994) that does not project to the superior colliculus (Derrington, 2002), making as a consequence s-cone coloured stimuli *invisible* to the SC. In this way the author was able to test if collicular mediation was needed during RDE. The results showed that invisible stimuli were not able to slow down saccade generation as reported in the classic RDE paradigm. The same stimuli, on the contrary, were able to interfere with spatial shifts of attention in a choice keypress task. This result provided further evidence for the involvement of the SC in generating the RDE.

1.9.2 More studies on the RDE

A series of other studies were then run to test other peculiar characteristics of the RDE. Griffiths, Whittle and Buckley (2006), for example, investigated the contribution provided to the RDE by binocular vision. They tested participants with normal vision when distractors were presented to the dominant or non-dominant eye, or to both eyes. Binocular presentation led to a much stronger distractor effect compared to monocular presentation. Moreover, the contributions of the dominant and non-dominant eye were equivalent, generating RDEs of similar magnitude. The authors concluded that each eye provides equal input for saccade programming and the two signals come together in the case of binocular vision, driving a much stronger RDE.

Another aspect that was further investigated was related to target predictability. Two experiments carried out by Benson (2008), compared the effect of central and peripheral distractors (as in Walker et al., 1997) with no prior participant knowledge of the target presentation location. The author reported that there was a difference if participants were aware of target location in advance. In particular, they reported a reverse pattern of distractor effect for central as opposed to peripheral distractors, with the latter being stronger than the former. Benson implies that there is a choice component that modulates the effect, arguing that RDE is not just a low level oculomotor effect as reported in previous studies (Honda, 2005; Walker et al., 1995; 1997). Born and Kerzel (2009), carried out other experiments investigating the cognitive aspects of the RDE. To do so, they manipulated target-distractor similarity. The results showed that congruent distractors were more effective than incongruent distractors and the author concluded that the RDE can be modulated via top-down instruction. The authors also proposed that the structures underlying the RDE, such as the SC, receive bottom-up as well as top-down information.

1.9.3 Modulation of RDE related to target saliency.

The RDE has been studied not only in terms of the temporal characteristics of the distractor but also by manipulating its saliency. Born and Kerzel (2008) showed that distractor characteristics such as contrast can in fact influence the RDE. In three experiments they showed that RDE was not modulated only by distractor characteristics but was also significantly influenced by saccadic latencies to the target, with strong RDE recorded for shorter latencies. The author then proposed that there must be a temporal overlap with the neural signal for the distractor to inhibit the target, and this depends upon both target and distractor characteristics. This consideration has been taken further by Bompass and Sumner's (2009a) testing the competition framework (Trappenberg, Dorris, Munoz, & Klein, 2001). Bompass and Sumner showed that there is a relation between the latency to the target and the contrast at which the distractor is presented. In particular, measuring the SRT to a distractor of a certain intensity presented alone allows the prediction of the temporal window of maximum interference where this stimulus has to be presented when used as a distractor. According to this framework, it is important to account for the velocity of the two signals, related to the saliency of the target and the distractor, that have to temporally overlap in order to interfere. For example, if a low contrast stimulus is used as a distractor together with a high contrast target, the distractor will have to be presented before target onset in order to produce interference. This temporal lead can be calculated by measuring SRT to distractor alone. An important point that emerges from these experiments is that it is not safe to use only one SOA to measure the effect of distractors on saccade since it could lead to mistaken interpretations of the results.

1.10 Oculomotor effects and the limb motor system

The eye movement literature offered the opportunity to use well-known paradigms to investigate different motor domains, especially hand movement. In fact, as previously stated in section 1.7, the motor hypotheses of attention (Klein, 1980; Rizzolatti et al., 1987) proposed that attentional mechanisms rely on the motor structure involved in the programming of the movement. According to this idea, shifts of attention could interact with the *programming/execution* of the movement itself. The fact that eye movements were modulated in a particular way by warning signal and distractor events allowed researchers to hypothesize that a similar modulation might have taken place in other motor domains. Some examples are given by the studies on the role of fixation on RTs and the effect of distractors in the visual field. In particular, the previously mentioned Global effect and the GAP effect (Saslow, 1967) provided a framework within which to study the representation used by the oculomotor and manual motor system and their temporal coupling. Sailer and colleagues (Sailer, Eggert, Ditterich, & Straube, 2002) investigated the role of a distractor appearing near to the target on both eye and hand movements. In such cases it is well known that the final landing position of the eyes falls in the centre of gravity between the target and the distractor, and this *global effect* is attributed to incomplete target selection. Pointing movements seemed to mimic eye behaviour but only in some circumstances, with the target continuously displayed and especially when a distractor presented more eccentrically than the target, suggesting that the two systems are coupled during target selection but that they do not use the same target representation to achieve such coupling. Moreover, the global effect for the hand seems to be less stable and to depend more on the target-distractor configuration.

The GAP effect is an eye movement phenomenon where the disappearance of the fixation point before target onset causes a strong decrease in SRT and is independent of advance knowledge of the target location (Kingston & Klein, 1993a; Walker et al, 1995). As hypothesised by Ross and Ross (1980; 1981), the GAP effect applies to any events at fixation (offset, onset and change) and is formed by two different components, a *warning signal* and an effect specific to visual offset, i.e. *ocular disengagement.* Whereas the warning effect has been found in other modalities such as manual responses, the ocular disengagement was discovered to be a specific eye movement phenomenon (Tam & Stelmach 1993).

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One important consideration that has to be taken into account regards the difficulty of dissociating these two components of the GAP effect. In fact, the warning signal is just a motor preparation that alerts the system to release the response for the forthcoming target, and it is difficult to exclude the possibility that the removal of the fixation itself does not contain a general visual warning. The presence of these two different components in the GAP effect, then, needs a control condition to eliminate the general effect of the visual warning signal. One possible way to isolate the FOE is to balance the generalized motor readiness across conditions by providing an auditory warning tone in both GAP and *overlap* trials (usually GAP conditions are compared to overlap conditions where the fixation remains on screen for the length of the trial). In this way the general readiness to respond should be equally present in all experimental conditions, making it possible to assess the specific effect of fixation offset. For example, in the studies carried out by Iwasaki (1990) and Tam and Stelmach (1993), the authors reported a GAP effect for choice manual responses, but no warning tone was used. Without introducing the auditory signal, it is impossible to fully understand what was driving the reduction in manual RTs, especially when the reported GAP effect for the manual modality is smaller than that for the saccadic modality, as in the case of Iwasaki.

Nonetheless, even when this auditory warning tone is introduced, it may not be possible to completely exclude a contribution of the offset of the visual stimulation to the general warning signal. Therefore, that portion of the GAP effect normally considered as due to ocular disengagement alone (FOE) may include some residual contribution from this warning signal. To try to clarify the extent to which the visual warning signal is active, Pratt, Bekkering and Leung (2000) carried out a study whereby they deployed an intermediate condition in which just a partial offset of the fixation was used, by changing its size. In this condition the authors suggested that the partial-gap provides a visual warning effect related to the fixation offset, without providing the full GAP effect. When fixation was reduced in size SRT decreased, underlying a visual warning effect. On the contrary, when the fixation increased in size, SRT were slowed down. Importantly, the partial-gap condition was not modulated by the presence of a warning tone. While the decrease in SRT suggested a visual warning component to the fixation offset, the increase in SRT was probably related to remote distractor effects. For all these reasons, although I shall use the FOE throughout this thesis to refer to the component of the GAP that is due to ocular disengagement alone, it must be borne in mind that this component may nonetheless include some contribution from a generalised warning signal.

Another important aspect that has been highlighted regarding the specificity of the GAP effect is that aiming movements and choice keypress are also susceptible to the FOE component, whereas this did not apply to simple keypress responses (Bekkering, Pratt & Abrams, 1996; Pratt et al., 1999) underlining the importance of spatially oriented responses (see Chapter 4 for more detail on the GAP effect). In these studies the authors controlled the effect of the visual warning by introducing an auditory tone. These results are incongruent with previous studies by Reuter-Lorenz and colleagues (1991) and Tam and Ono (1994) which failed to find a GAP effect in choice manual keypress when an auditory tone was used. Bekkering and colleagues (1996) argued that the studies by Reuter-Lorenz et al. (1991) and Tam and Ono (1994) suffered from a lack of statistical power that made the data unreliable (even if a trend of faster RTs was present in GAP conditions). The fact that only spatially oriented responses such as saccades and pointing movements are susceptible to FOE conditions points toward the conclusion that the FOE is mainly due to processes within the SC (Pratt et al., 1999).

From these studies it emerged that a spatial and temporal coupling of the eye and hands was not obligatory. In particular eyes and hands may rely on different signal to initiate the movement (Salier, Eggert, Ditterich, & Straube, 2000). In the same way, Sailer, Eggert and Straube (2002) proposed that eyes and hands are not strictly coupled during aiming movements and that they probably use different target representation already at the level of target selection.

1.11 Research question

Despite the fact that lots of work has been carried out investigating similarities and differences between the oculomotor and the limb motor systems, there has been no systematic test of manual movements under bilateral stimulation accounting for effects on the RTs. In particular, there has been little investigation of RDE for response modalities other than eye movements. One possible research line would be to test if RDE is an eye-specific phenomenon or if it can be generalised to other effectors and tasks rather than the eyes, for example hand movements and covert discrimination tasks. In fact, it is already well known how the onset of visual stimuli can capture covert attention (Yantis & Jonides, 1984). This assumption implies that a covert shift is caused by distractor appearance, generating the slow down of SRT in the RDE paradigm. If the RDE is a general attentional phenomenon involving shifts of attention, and is not a peculiarity of the oculomotor system, then other modalities should be affected by distractors in a comparable way.

Such an investigation would have important implications for prominent theories of attention such as the *premotor theory of attention* (Rizzolatti et al., 1987) and the Visual Attention Model (Schneider, 1995). In fact, both theories make strong predictions about the attentional modulation caused by distractor appearance for both hand movements and covert discrimination tasks. According to the premotor theory, spatial shifts of attention are identical to eye movements, with the only difference being that the movement is not executed. A strict version of the theory states that the same neural circuit responsible for computing the execution of the eye movement is also involved in covert shifts of attention (Sheliga, Riggio, & Rizzolatti, 1994), and that spatial attention can sub-serve any pragmatic map, i.e. maps that transform spatial information into movements. The premotor theory would predict distractors to cause a shift of attention that would interfere with the motor programming (if a motor response is required) or with discrimination ability, since attentional shifts and eye movements overlap. A similar outcome is suggested by VAM. According to Schneider and Deubel, covert shifts of attention precede target-directed hand movements (Schneider & Deubel, 2002), predicting an increase in manual reaction times when distractors are present.

1.12 Structure of the thesis.

This thesis is structured around one precise question: is the RDE an eye-movement-specific phenomenon or will it transfer to modalities other than the eyes? This general problem is addressed in Chapter 2, where the RDE paradigm is tested on eye movements, hand movements and covert shifts. The RDE is observed for saccades, but not simple manual responses, and it is unclear whether distractor interference occurred in the covert task. The conclusions drawn from Chapter 2 allow us to break down this main problem into two further sub-questions. In particular, the research will be restricted to the investigation of RDE when (i) manual spatially-oriented responses or (ii) covert discriminations are required. The first question is investigated in Chapter 4, which tests the effects of distractors between spatially equivalent tasks requiring saccadic and manual aiming responses respectively. The second question is addressed in Chapter 5, which tests the role of distractors during covert discrimination. The final part of the thesis, Chapter 6, is dedicated to investigating the mechanism that underlies the RDE, suggesting a functional identity between RDE and another well-known phenomenon described in the reading literature, *Saccadic Inhibition* (Reingold & Stampe, 1999; 2002).

Chapter 2

The RDE in saccadic, simple manual and covert discrimination tasks

Chapter overview. The aim of the present chapter is to investigate the effect of abrupt-onset distractors not close to the target for different response modalities. It is well-known that distractors presented in the field contralateral to the target affect the *planning/execution* phase of eye movement generation, with the behavioral consequence of increasing saccadic reaction times. This phenomenon is often known as *Remote Distractor Effect* (RDE: Walker et al., 1995). So far in the literature, the RDE has been investigated only in the eye movement domain. However, other studies on the interaction between overt and covert attention provide grounds to predict that this phenomenon may generalize to other response modalities. For example, the *premotor theory of attention* (Rizzolatti et al., 1987) states that a covert shift of attention is the same as an eye movement to the attended location, the only difference being that the movement is not executed. This assumption, taken together with the fact that abrupt onsets of visual stimuli can capture covert attention (Yantis & Jonides, 1984), suggests that the RDE should generalise to other response modalities provided that the response requires a spatial shift of attention to the target.

The current experiment tested this prediction by using the RDE paradigm during a saccadic response task, a simple manual response task (i.e. keypress) and a covert location discrimination task. The results clearly replicated the typical RDE for saccadic reaction times and demonstrated how simple manual responses did not show such an effect. On the other hand, it remained unclear if covert attention was susceptible to distractor interference. A close consideration of the results from the covert discrimination task suggests that the ability of this experiment to unambiguously assess the RDE may have been compromised by *response compatibility effects* (Possamaï, 1991) peculiar to the specific task design. Further experiments are proposed to address the possible generalization of the RDE beyond saccadic responding to manual responding and covert orienting.

2.1 Introduction

Eye movements are the most common of all human behaviour. A great number of saccades is generated in order to acquire information about the environment that surrounds us. Of course, all these eye movements do not represent a random scanning of the visual scene. Instead, saccadic production represents a very fine and sophisticated example of integration between volitional and reflexive behaviour, aimed at orienting the attentional system to the source of stimulation (Posner, 1980). This orienting response has the scope to increase sensitivity at the location of the sensory input (James 1890; Titchener, 1966). It is possible to distinguish between two different types of orienting behavior. We can orient *overtly* toward an object, and this implies adopting a motor response such as a saccade to bring into the fovea the object of interest. On the other hand, we can *covertly* shift our attention, dissociating the direction of the gaze from the locus we are attending to, as when we continue to fixate an object in front of us while we monitor the periphery. This distinction was introduced by Helmholtz (1867/1925) in his studies on the ability of shifting attention while maintaining fixation. Moreover, it is possible to differentiate two ways in which we direct attention, according to the way it is controlled. For instance, we can intentionally generate a motor action to direct our attention toward a location in the environment. This form of orienting is also called *endogenous*. On the other hand, it could happen that an object captures our attention *exogenously*, meaning that the decision to orient the attentional system toward the source of stimulation derives from something happening in the environment, e.g. a sudden visual change in the eye periphery (Posner, Nissen, & Ogden 1978; Posner, 1980).

There has been a long tradition of research describing how overt and covert systems interact with each other and the neural substrates subserving the two attentional processes. One of the first hypotheses was that the oculomotor system was also involved during perceptual processing (Hebb, 1949; Festinger, Ono, Burnham, & Bamber, 1967; see Weimer, 1977 for a review). Moreover, Wurtz and Mohler (1976) had already proposed that a shift of attention was a program for an eye movement. In 1980, Klein formalised these assumptions and proposed the *oculomotor readiness hypothesis* (OMRH). The main claim of OMRH was that shifts of attention were accomplished with the same motor programs used in saccade generation. The OMRH allowed the formulation of two clear predictions:

> "[…] readiness to move the eyes to a certain locus produces an attentional bias toward that locus. […] attention to a location in space involves a readiness to move one's eye to that locus." (Klein, 1980, p. 264).

In his experiments Klein tested if a saccade was triggered faster when covert orienting responses were required throughout a block of trials. In particular, he presented an asterisk on 80 percent of the trials and a luminance increment on the other 20 percent of the trials. Participants were asked to make an eye movement when the asterisk was displayed and a simple manual response when there was the luminance change. Both the asterisk and the luminance change could happen on the left or right of the visual field (4° of visual angle) with the same probability. Klein assumed that participants were preparing an eye movement since this was the most likely response during the block of trials. The results showed that simple manual keypresses were not facilitated by the preparation of the eye movement, supporting the idea that *oculomotor* readiness was not accompanied by an attentional shift at target location. In a second experiment Klein used arrow cues to direct participant attention to a location where a luminance increment might occur (80 percent of the trials), requiring a keypress, or an asterisk might appear (20 percent of the trials), requiring an eye movement. The study showed that directing attention to the target location did not affect saccadic reaction times, meaning that covert orienting was not accompanied by oculomotor preparation. These results led the authors to refute both the predictions suggested above. When participants were engaged in a covert task, there was no advantage in saccade production. On the other hand, when participants were involved in a saccadic task, there was no advantage for covert responses. Similar results were subsequently achieved by Posner (1980) and Remington (1980). Moreover, almost fifteen years later, Klein and Ponterfact (1994) ran the same studies just described above, including verbal commands to prepare the eye movement when this was the primary task, and verbal commands when the eye movement should be executed. The results that they obtained were perfectly compatible with those of Klein's first study.

The results from Klein discouraged the motor hypothesis of attention. Nonetheless, only a few years later, Rizzolatti and colleagues brought new interest to the OMRH and, in 1987, they conceptualised a new framework, which they referred to as the *premotor theory of attention.* The aim of the premotor theory had the same foundation as Klein's oculomotor readiness hypothesis. In particular, Rizzolatti and colleagues (1994, p. 238) were interested in understanding whether attention consisted of:

> "[...] one superordinate system, different superordinate systems, or intrinsic mechanisms within the pragmatic and semantic representation."

According to Rizzolatti and colleagues (1987) the literature provided enough studies, coming from different areas - such as neuroimaging, neurophysiology and behavioral experiments - to dispute the notion of many independent systems controlling the attentional processes. The new framework assumed that overt and covert shifts of attention shared a common substrate with spatial attentional processing, relying on the same structures that carried out motor commands (e.g. Corbetta, Akbudak, Conturo, Snyder, Ollinger, et al., 1998; Rizzolatti et al., 1987). According to this view, attention was strictly related to motor preparation and it was not necessary to postulate any superordinate system specifically devoted to attentional control.

The premotor theory then defined three core assumptions, providing the ground for a new hypothesis and experimental setup (Rizzolatti et al., 1994, p. 240):

> "1. The mechanisms responsible for spatial attention are localised in the spatial pragmatic maps. There are no such things as selective attention circuits defined as anatomical entities separated from the spatial maps.
> 2. Spatial attention is a consequence of a facilitation of neurons in the spatial pragmatic maps. This facilitation depends on the preparation to perform goal-directed, spatially coded movements.
> 3. Different spatial pragmatic maps become active according to the task requirements. Spatial attention can be produced by any map that codes space. In humans and primates, as a consequence of the strong development of the foveal vision and the neural mechanism for foveation, a central role in selective attention is played by those maps that code space for programming oculomotion."

In a series of experiments Rizzolatti and colleagues provided strong support for the premotor hypothesis. In the first behavioural study testing the premotor theory (Rizzolatti et al., 1987), they asked their participants to perform a manual keypress in response to the occurrence of a visual imperative stimulus located in one of four boxes arranged vertically or horizontally, above or below a fixation cross. The location of the imperative stimulus was previously cued by the appearance of a number at the locus of fixation, indicating in which of the four boxes the imperative stimulus would appear. Valid, invalid and neutral (i.e. trials with no cue) trials were then analysed. The main outcome of the study was the presence of the *meridian effect.* When the stimulus appeared in the hemifield opposite to that cued, the time required to respond was longer then when the imperative stimulus appeared at the same distance from the cued location but in the same hemifield. The premotor interpretation of this result was quite appealing**.** Rizzolatti and colleagues argued that when the cue was provided, a motor program (i.e. a covert shift of attention) was prepared at the attended location. In invalid trials, this motor program had to be adjusted for the new location. Crossing the meridian required the complete deletion of the first motor program in favor of a new one, an operation that required more time than merely changing the final landing position for a program already prepared toward an imperative stimulus falling in the same hemifield as that cued.

New and stronger support for the theory came from a series of studies on the analysis of the spatial trajectory of the eyes in response to the imperative stimulus. Sheliga and colleagues (1994) asked their participants to fixate a central dot and subsequently to attend to the location cued by a number corresponding to one of the four boxes placed above the fixation cross where the imperative stimulus could appear. Participants were required to make a saccade toward a fifth box placed below the fixation cross, as soon as the imperative stimulus was presented. The results showed that the trajectories of the eye movements were modulated by the locus of attention. In particular, they deviated away from the field to which attention had been allocated. Moreover, this tendency was stronger when the imperative stimulus was presented at the attended location. In a second experiment the authors cued attention, through a line presented at fixation, toward one of two boxes, placed on the left or on the right of the fixation cross. The imperative stimulus could be a visual stimulus presented in one of the two boxes (50 percent of the trials) or a non lateralized sound. Half of the participants were asked to saccade toward the box placed above fixation when the imperative was visual or to saccade toward the box placed below the fixation cross when the imperative stimulus was a sound. The other half of the participants received the opposite instructions. The authors observed a deviation in saccadic trajectory that was contralateral to the location where attention was allocated via the cue. They also showed that saccades deviated contralaterally to the location of the imperative stimulus, even when such stimulus was an acoustic signal. According to the authors, the spatial allocation of attention was actually activating circuits controlling oculomotion, leading to interference with the online motor program generated in response to the imperative stimulus. In a subsequent series of experiments involving the same paradigm (Sheliga, Riggio, & Rizzolatti, 1995), the allocation of attention was manipulated in order to compare endogenous and exogenous allocation. Sheliga and colleagues observed that vertical saccades tended to deviate contralaterally to the focus of attention, irrespective of whether attention was allocated endogenously or exogenously. The effect was also stronger when attention was allocated in the same hemifield as the final location of the saccade. Sheliga and colleagues concluded that a strong oculomotor activation is responsible for this deviation and that the allocation of attention does not elicit eye immobility but a motor preparation for a saccade.

The results obtained by the Rizzolatti group represent a very strong core of research from which much subsequent work has been developed. For example, Craighero, Nascinben and Fadiga (2004) used an ingenious paradigm to test the premotor hypotheses. In the *frontal* condition, they asked their participants to attend monocularly to one of two locations - either on the right or on the left of the visual field - previously cued by a central pointer. As soon as the imperative stimulus appeared on screen, participants had to give a simple motor response by pressing a button. In the *rotated* condition, participants were asked to perform this identical task but with their eye rotated by 40° (in a control experiment it was assessed that the rotation was not affecting target discriminability). It is important to state that the retinal events were matched between conditions, but that the rotation of the eye in one condition was such that further rotation in one direction would not be physiologically possible. What they observed was that in the frontal condition there was a significant difference for valid and invalid cue both in the temporal and in the nasal hemifield. Surprisingly, in the rotated condition participants did not show any significant difference in the temporal condition, whereas a significant difference was still present in the nasal condition. The interpretation was that the impossibility to rotate the eye any further was precluding any saccade programming toward the temporal hemifield. Covert shifts of attention were then impeded in this condition, suggesting that the physical limitation of the eye movement system imposed a limitation of the covert allocation of attention. They concluded that the same oculomotor circuits were employed for spatial shifts of attention and eye movement programming.

Converging evidence also came from neuropsychological data. Smith, Rorden and Jackson (2004), for example, reported the case of AI, a patient with a congenital opthalmoplegia that made her unable to make eye movements (Gilchrist, Brown, & Findlay, 1997; Jackson, Newport, Osborne, Wakely, Smith & Walsh, 2005). She was tested in variants of the Posner cueing paradigm in which a peripheral cue predicted the location of target appearance. AI did not show any advantage given by the exogenous cue whereas when the cues was endogenous, she was able to shift her attention, showing that voluntary allocation of attention was intact. The authors concluded that the oculomotor system is highly involved in the covert orienting of attention, arguing also that cortical structures are not the only areas necessary for developing normal attentional reflexes: the ability to produce eye movements is also necessary for a normal development of spatial attention (see also Craighero, Carta & Fadiga, 2001).

In an attempt to generalise these phenomena to other motor responses, Sheliga and colleagues employed the same paradigm, comparing saccadic and pointing movements (Sheliga, Craighero, Riggio & Rizzolatti, 1997). What they observed was that the reaction times of goal-directed hand movements were also affected by attentional shifts, but in a different way to eye movements. In particular, the authors reported a directional effect in which both saccadic and pointing movements were faster when the imperative stimulus was presented in the same hemifield as the target location. In contrast, a difference between manual and saccadic reaction times emerged when an endogenous shift of attention was required. In this case, manual responses were not modulated by the attentional focus. Further analysis concentrated on the trajectory of the saccades where the authors replicated the finding that saccadic eye movements deviated away from the attended location. Nothing was possible to infer for manual movements since the trajectory of the hand movement was not recorded.

Tipper and colleagues also made important contributions to the premotor theory in the manual domain. In one of their experiments, Tipper, Lortie and Baylis (1992) asked their participants to perform a reaching movement finalised to press a button. In some trials, a visual distractor was also presented at a different location in space. The location of the distractor might interfere with the ongoing movement or not. The results showed that the relationship between the starting position of the hand and the distractor location was critical in determining the effect. In particular, a distractor close to the hand interfered more than a distractor placed far from the hand. Other experiments from Tipper, Howard and Jackson (1997) demonstrated that the hand trajectory veered away from a near distractor location during movements toward farther targets, whereas they hand veered towards a farther distractor during near reaches, replicating the inhibition effect already seen in saccade trajectories. An important factor of all these experiments was that distractors were not physical obstacles able to interfere with the path of the ongoing movement. A final study was run to test these results in a paradigm much more similar to the one employed by Sheliga and collaborators. In fact, the aforementioned studies by Tipper and collaborators were conducted using three-dimensional targets (like a button) and distractors (wooden cube). Howard and Tipper (1997) then showed that manual trajectories deviated from distractors in the same way that saccades deviated from the locus of attention even when the distractor stimuli were light-emitting LEDs. The authors concluded that distractor stimuli evoked competing responses. The final motor output was a result of an inhibition process adopted to resolve this competition, which generated as a behavioural consequence the modulation of the trajectories and of the kinematic parameters of the movement.

A critical experiment was carried out by Walker et al. (1995) in which the meridian effect was tested in the oculomotor domain. In particular, saccadic reaction times were recorded for a stimulus presented on the right/left of the visual field while the attentional focus was manipulated in three conditions: valid, invalid and neutral. The results from Walker and colleagues clearly supported the premotor hypothesis and the previous finding from Rizzolatti and colleagues, showing a small advantage for saccades made in the attended hemifield and a very large cost for saccades made in the unattended hemifield.

All these results provide full support and extension to other modalities for the premotor theory. Nonetheless, the predictions of the premotor theory have not been extensively investigated for responses other than eye movements. The aim of the present work was to test premotor theory assumptions using a well-known phenomenon described in the oculomotor domain, the *Remote Distractor Effect* (RDE). Moreover, since the RDE has been described only in the eye domain, testing the RDE on other effectors raises interesting empirical questions itself.

Before describing in detail the present study it is necessary to briefly review what is known about RDE and its characteristics. Preliminary work on bilateral stimulation was carried out by Lévy-Schoen (1969). In her studies participants were presented simultaneously with two targets, which might be in the same or in the opposite hemifield. Participants were requested simply to saccade toward one of the two targets, without any more specific instruction. From this design they observed two main important patterns of behaviour. Firstly, participants tended to saccade toward the more proximal target. Secondly, participants were faster to respond when the targets were presented in the same hemifield than when they were presented in opposite hemifields. The author interpreted these findings in terms of the time required to make the choice as to which target to saccade toward. Starting from these early studies, new experiments were carried out to investigate the role of the distractor per se. Interestingly, Ross and Ross (Ross & Ross, 1980, 1981) found a similar increase in SRTs even when the element of choice between the two potential targets was removed. In particular, they manipulated the onset of a stimulus presented at fixation, i.e. the warning signal, and varied the time between target onset and warning signal, presenting it *before*, *simultaneously* or *after* target appearance. They observed that when a warning signal was presented before target appearance, participants speeded up their SRT, whereas when the warning signal was presented after target onset the pattern was reversed and the saccade latency increased. Similar results were observed by Braun and Breitmeyer (1990) where the simultaneous reappearance of the fixation stimulus delayed the start of the saccade. The authors also investigated the effect of such reappearances in the contralateral hemifield, observing the same effect on SRTs, even if not as reliably. In these experiments, the location of the target was perfectly predictable, removing any effects due to high-level cognitive processes related to target selection (see also Weber and Fischer, 1994). This increase in SRTs during bilateral stimulation that occurs even in cases of complete target predictability is now known as the Remote Distractor Effect (RDE).

Walker and colleagues thoroughly investigated such saccadic phenomena, systematically manipulating the spatial and temporal properties of the distractor (Walker et al., 1995; 1997). To eliminate any effect of choice, participants were always aware in advance which hemifield the target would be presented in, and they were only required to select the correct amplitude of the movement. For a distractor presented in the opposite hemifield or at fixation, they observed a delay in the initiation of the saccades of ~18 ms compared to target only condition. Moreover, they showed that this effect was present for a distractor presented not only at simultaneity, where it was at its maximum, but also for a distractor presented 20 and 40 ms after target appearance. According to these results the greater increase in SRT was found for distractors appearing simultaneously with the target, placed at fixation and reduced monotonically moving to more eccentric positions. They also observed that when a distractor was presented near the target location, distractor interference was restricted to saccade metric, no longer modulating SRTs. In particular, the Global effect referred to a particular saccadic behaviour where the landing position of the eyes fell in the *centre of gravity* between the target and distractor (Walker et al., 1997).

2.1.1 Rationale for the experiment

We know that the RDE is a very robust phenomenon replicated in a variety of studies over the last 20 years. If the premotor theory of attention is correct, eye movements and spatial shifts of attention involve the same circuitries, making spatial shifts of attention identical to eye movements, with the only difference being that the movement is not executed. Concomitantly to this assumption, a great number of studies provide evidence that stimuli can abruptly capture attention (Yantis & Jonides, 1984). One of the possible interpretations of the RDE is that the abrupt onset of the distractor elicits a motor program toward it. In this way, the programming of the saccade toward the target is delayed by this conflicting motor program. If participants are required to respond to the appearance of the target covertly, given the identity between motor programs and shifts of attention, it should be possible to measure a similar interference effect during a covert discrimination task. On the other hand, the effect of distractor onset on simple manual reaction times depends upon the nature of the RDE. If the RDE is a general attentional phenomenon, we should expect an increase in reaction times related to distractor appearance. If the RDE is a specific effect related to spatial attention, then an abstract response as a keypress should not inherit the RDE.

In the present experiment I tested the above prediction in a within-subject paradigm where saccadic, manual and covert responses were compared. The covert location discrimination task was chosen because it was intended that the task should encourage a covert shift of attention to the target locations, and discriminating the location was considered to be a manipulation likely to encourage this. The results do not support a strict version of the premotor theory, with RDE being present only in the saccadic modality, leaving both manual and covert responses unaffected.

2.2 Experiment 1 method

2.2.1 Participants

Twelve volunteers from the University of Edinburgh, aged between 18 and 24 years, participated in this study. All participants were right-handed by self-report, and free from neurological and visual impairments. This experiment was conducted in accordance with the 1964 Declaration of Helsinki, and with the approval of the Ethics Committee of the School of Philosophy, Psychology and Language Sciences at the University of Edinburgh.

2.2.2 Apparatus and stimuli

White on black stimuli were presented on a 19-inch CRT monitor (1024 x 768 pixel resolution, 32-bit True Colour, 75Hz refresh rate) driven by a Pentium IV processor at 75Hz. A second computer was used to run the Eyelink II head-mounted system and record eyes movement at a sampling frequency of 500 Hz. The participants' responses were recorded with a standard joypad. Participants were seated in front of the monitor, with their heads immobilised upon a chin rest and their eyes horizontally and vertically aligned with the centre of the screen at a viewing distance of 75 cm. The height of the chin rest was adjusted appropriately according to the height of the participant. To facilitate fixation, a white cross (0.5°) on a black background was presented at the centre of the screen. When the participant was fixating, the experimenter performed a manual drift correction to start each trial by pressing the "return" key when he was happy that the subject was fixating the central cross, cueing the target and distracter to appear 1000 ms later.

The target stimuli (an outline square of 0.5° of visual angle formed by the white border of the square, 2 pixel thick, with a cross inside) appeared at either of two eccentricities, 4.5° and 9.0° to the right of fixation on every trial, except in catch trials, and were presented for a maximum of 1000 ms. Distracter stimuli consisted of a filled white square of 0.5°, filled to increase salience, which encouraged the occurrence of RDE.

2.2.3 Design

A repeated measures three ways design was used. The dependent variable was the reaction time to respond to the target, and three independent variables were manipulated: *Response Modality* (three levels: Saccadic, Manual, Covert), *Target Location* (two levels: Near, Far) and *Distractor* (three levels: Near, Far, and void, where no distractor was presented).

2.2.4 Procedure

The room was partially illuminated and light-sealed to prevent lighting changes during the experiment. Participants were instructed not to move their eyes during trials. There were two kind of stimulus presentation, bilateral and unilateral. When the participant was securely maintaining fixation the experimenter started the trial. Participants attended an experimental session for each of the three task conditions, saccadic, manual and covert. In each condition, a central fixation cross was presented and remained throughout each trial. After a short interval a target stimulus was presented on the right side of fixation at one of the two eccentricities, 4.5 or 9° from fixation and in most of the trials, a distractor stimulus was presented on the left side of fixation at either 4.5° or 9°, simultaneously with the target stimulus.

In the saccadic condition participants were instructed to make an eye movement to fixate the target as fast as possible and ignore the distractor stimulus. The manual condition consisted of responding as quickly as possible to target onset by pressing a button once while maintaining fixation. In the covert condition, participants pressed a left-fingered button when targets appeared on the near side of the right side of fixation, and a right fingered button when targets appeared on the far side of the right side of fixation, also without moving their eyes, and were also instructed to respond as quickly as they could.

In each experimental session, one practice block and six experimental blocks of 28 trials each were completed. Each block of 28 trials consisted of: eight trials with target alone, half at a near and half at a far eccentricity; four trials with distractor alone (catch trials), half at near and half at far eccentricity, included to discourage anticipatory saccades; four trials with a near target and near distractor; four with near target and far distractor; four with far target and near distractor; four with far target and near distractor; four with far target and far distractor. The trial type order was randomised throughout each block, and therefore between sessions. A total of 168 experimental trials per session per participant were generated; each participant therefore generated 504 trials in total. If an error (e.g. anticipatory saccade or button press) was detected online, the trial was automatically recycled at the end of the trial block, and the error was automatically recorded by the program. The order of the experimental sessions (Saccadic, Manual and Covert) was counterbalanced across subjects. The experiment lasted about 30 minutes for each session. Tasks and stimuli are displayed in Figure 2.1.

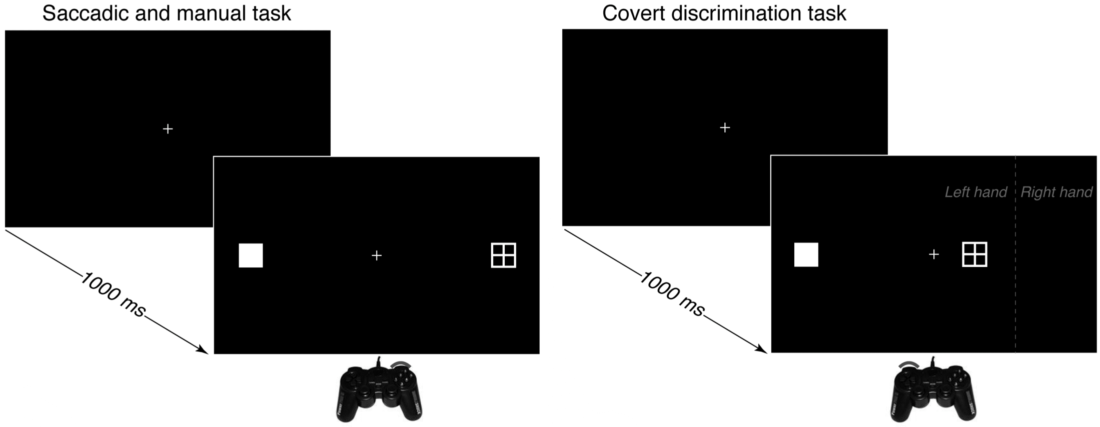


Figure 2.1 Experiment 1, task and stimuli.
Exerimental stiuli and tasks. On the left side the saccadic and the manual tasks are illustrated. After 1000 ms the target appeared on the right side of the screen and participants were required to saccade or to press a button of the response pad. The trial depicted represents the far target condition with a far distractor. On the right side, the covert discrimination task is illustrated. Participants were required to discriminate target location whilst maintaining central fixation. If the target was presented near the fixation cross a left button press was required. If the target was presented far from the fixation cross a right button press was required. The trial depicted represents the near target condition with a far distractor.

2.3 Experiment 1 results

2.3.1 Data screening

Saccades with a latency under 80 ms (~1%) or above two standard deviations of the mean (~4.6%), simple keypress RTs under 100 ms (N.D) or above two standard deviations of the mean (~4.7%), keypress RTs during covert discrimination under 100 ms (N.D.) or above two standard deviations of the mean (~4.7%) were excluded from the analysis.

2.3.2 Main analysis of Reaction Times

For each participant, the mean RT was taken as the measure of central tendency for each condition and entered into a 3x2x3 repeated-measures (*Response Modality * Target Location * Distractor*) ANOVA. The overall analysis showed a highly significant main effect the factor modality ($F(2,22) = 74.454$; $p < 0.001$) highlighting a difference in RTs according to the modality of response. Three planned paired t-test between the three conditions showed that there was a reliable effect so that the RTs recorded in the saccadic condition (257 ms) were faster than the manual (368 ms: $t(11) = -5.908$; $p < 0.001$) and also faster than the covert (465 ms: $t(11) = -10.136$; $p < 0.001$). The RTs recorded in the manual task were also significantly faster than the RTs recorded in covert task ($t(11) = -9.829$; $p < 0.001$). The difference between saccadic and manual RTs was not very surprising. The covert task, on the contrary, required a discrimination operation since the response was related to the location of the target in the right hemifield. According to this idea, it was foreseeable that, given the greater processing time required to take the decision, the RT would be affected when compared to the saccadic and manual performance. A marginal main effect of the target location factor was present ($F(1,11) = 4.773$; $p = 0.051$) with RTs to the far location (366 ms) being 6 ms faster than to the near location (360 ms).

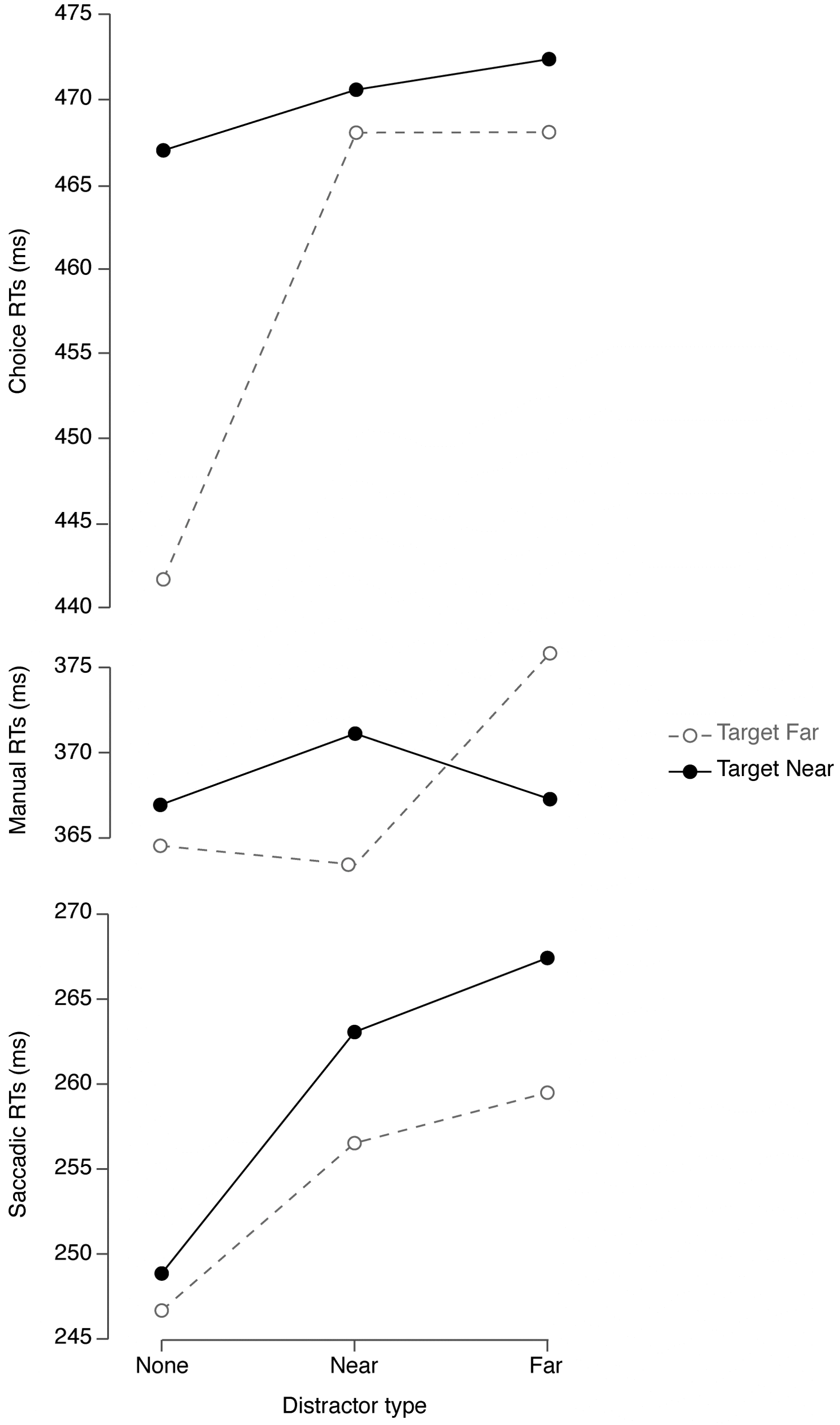


Figure 2.2 Experiment 1, interaction plot.
Saccadic, manual and covert RTs for the three distractor conditions (None, Near, Far) according to target eccentricity (i.e. solid line: Near, dashed line: Far).

Finally, the other significant main effect was related to the distractor condition (*F(2*,22) = 22.768; *p* < 0.001) showing how, in general, the baseline condition had the quickest RT (356 ms) followed by the condition where the distractor was in the near position (365 ms) and finally the condition where the distractor was presented in the far position (368 ms). The only other significant result was the 3-way interaction *Response Modality* * *Target Location* * *Distractor* (*F*(4,44)= 2.637; *p* = 0.046), Figure 2.2 (page above). For this reason, the three modalities were followed up separately. Measures of within-subject variability for all the conditions are reported in Table 1.

	Target near			Target far		
	T only	DN	DF	T only	DN	DF
Saccadic	53	44	48	50	43	44
Manual	60	65	67	60	66	64
Covert	75	71	75	78	74	79

Table 2.1. Experiment 1 data variability.
Average within-subject SD (ms) for all combinations of target and distractor locations in the three different modalities. DN: Distractor Near; DF: Distractor Far.

An additional analysis in order to assess the within-subject variability of RTs in the different task conditions has been run. For each participant, the SD for each condition was taken as the measure of within subject variability and entered into a 3x2x3 repeated-measures (*Response Modality* * *Target Location* * *Distractor*) ANOVA. The overall analysis showed a significant main effect of the Response Modality (*F*(2,22) = 11.744; *p* < 0.001). To further investigate the main effect, three paired t-tests (Bonferroni corrected) between the three conditions showed that the effect was driven by variable RTs being significantly higher in the covert (74 ms) that in the saccadic (47 ms: *t*(11) = 4.464; *p* < 0.003) task, though not different from the manual (64 ms: *t*(11) = 2.389; *p* < 0.108). The manual and the saccadic modalities were not significantly different one to the other (*t*(11) = 2.652; *p* < 0.069). This pattern is unsurprising, given that RTs were also generally highest in the covert task, and considering the greater cognitive complexity of this task, as discussed in section 2.4.

2.3.3 Analysis of Saccadic Reaction Times

A 2x3 repeated-measures (*Target Location * Distractor*) ANOVA. The analysis did not show any main effect of target location ($F(1,11) = 1.797$; p = N.S.) but a highly reliable effect of the distractor factor ($F(1,11) = 14.530$; $p < 0.001$). The baseline condition was faster (248 ms) than both the condition where the distractor was Near (260 ms) and the condition were the distractor was Far (263 ms). Two planned paired t-test confirmed that a significant difference was present only between the baseline condition against the near ($t(11) = -3.973$; $p = 0.002$) and the far ($t(11) = -5.126$; $p = 0.001$). These results replicated the findings of Walker and colleagues (1995) demonstrating that it was possible to reproduce the RDE effect with this specific experimental set up. The interaction between target location and distractor was not significant.

2.3.4 Analysis of Manual Reaction Times

A 2x3 repeated-measures (*Target Location * Distractor*) ANOVA was run. The analysis of manual RT did not show any main effect for the target location factor ($F(1,11) = 0.17$; $p = 0.899$) or the distractor factor ($\mathrm{F}(1,11) = 1.022$; $p = 0.376$). Also, the interaction between the two factors did not reach significance ($F(2,22) = 2.289$; $p = 0.125$). The data showed that manual reaction times were completely invulnerable to distractor appearance, a result comparable to that reported by Rafal et al. (1990) in a group of hemianiopic patients.

2.3.5 Analysis of Covert Reaction Times

A 2x3 repeated-measures 2x3 (*Target Location * Distractor*) ANOVA was run. The analysis of covert RT revealed a main effect of the target location factor ($F(1,11) = 6.588$; $p = 0.026$). Responses to the near location (470 ms) were slower than responses to the far location (459 ms). Also, the data showed a main effect of the distractor condition ($F(1,11) = 9.572$; $p = 0.001$) with the baseline condition being the fastest (454 ms) followed by the near condition (469) and then from the far condition (470 ms). However, this was modified by the interaction between the two factors (i.e. target location and distractor location) which reached significant levels ($F(2,22) = 3.801$; $p = 0.038$).

Follow up analysis with two repeated measure ANOVAs was performed to test the effect of the distractor for each target location. For the Near target location, the effect of the distractor was absent ($F(2,22) = 0.386$; $p = 0.684$). In contrast, there was a highly significant effect of distractor when the target was presented at the far eccentricity ($F(2,22) = 12.673$; $p < 0.001$). In particular, the baseline condition produced the fastest RT (442 ms) while in the Far and Near distractor eccentricity the RT were identical (468 ms). Two planned paired t-test confirmed that the difference between the baseline condition was significantly different from the Near distractor condition ($t(11) = -4.228$; $p < 0.001$) and from the Far distractor condition ($t(11) = -4.058$; $p < 0.002$).

2.4 Experiment 1 discussion

In the present experiment, the well-known distractor effect (Walker et al., 1995; 1997; see also Findlay & Walker 1999), in which the sudden appearance of a contralateral distractor interferes with the planning/execution of a saccade to a target, was replicated. The RDE recorded has a magnitude of ~14 ms, comparable to that recorded by Walker and colleagues (1995) of ~18 ms for a distractor presented simultaneously with the target, as in the present experiment. Nonetheless, we failed to replicate the finding that a distractor presented at larger eccentricities affect the SRT more than a distractor presented more centrally, as reported in Walker et al. (1997). In this experiment, in fact, distractor eccentricity did not have an effect upon SRT. It is worth pointing out that the distractors used in this experiment were different to those used by Walker and colleagues. In particular, the present distractors were more salient, i.e. filled squares, compared to the target, i.e. unfilled squares.

The other main finding was that RDE did not apply to manual responses. In particular, the effect of a distractor on a simple keypress was tested where no directional response, as in the case of an eye movement, was required. The task required participants to respond only when the target was on screen and to retain the response when only the distractor was presented (catch trials). This result is congruent with the idea that the RDE is not a general attentional phenomenon. If that were the case, RDE should have been inherited by a manual responses. This result negates some of the premotor theory assumptions. According to Rizzolatti et al. (1987; 1994), if a covert shift of attention is directed toward the distractor, the motor response, even if produced with different effectors, i.e. eyes and hands, should behave in a comparable way. The extent and the magnitude of the RDE could be compromised according to different neural pathways and substrate where attentional shifts are generated, but at least a comparable delay was expected. On the other hand, if we assume that a simple button press detection response does not require a spatial shift of attention it is not necessarily inconsistent with the premotor theory. In this case it is possible to argue that in order to elicit the RDE in manual responses, tests should require a goal-directed movement rather than an abstract response such as a keypress. This argument is also brought forward by Sheliga and colleagues (1997), who hypothesised that simple keypress responses, such as the button press used here, are not sufficient to demonstrate a link between motor programming and spatial attention because are considered to be abstract and arbitrary. The correct way to investigate the relationship between attention and motor preparation is to use goal-oriented responses. As Sheliga and colleagues reported (1997, p. 346):

> "[...] a link between spatial attention and motor programming should appear once attention is investigated, not in an abstract way using arbitrary responses as probes for attentional processes (i.e., key pressing), but using behaviorally relevant goal-directed actions. Under such conditions, attention should appear linked to motor responses and not any more disembodied from basic sensorimotor processes."

Consistent with the idea that spatially-oriented responses might play a fundamental role in the study of attentional shifts are the results on the GAP effect for manual responses. It has been showed that the GAP effect is constituted by two components: one refers to the offset of the fixation stimulus that provides a warning signal common to different modalities; the other is a component specific to fixation offset (*fixation offset effect,* i.e. FOE; Kingstone & Klein, 1993), which influences target-directed saccades but has no effect upon simple manual reaction times (Bekkering, Pratt & Abrams, 1996), and little (Bekkering et al, 1996; Iwasaki, 1990; Tam & Stelmach, 1993) or no effect (Reuter-Lorenz, Hughes, & Fendrich, 1991; Tam & Ono, 1994) on choice manual reaction time. Also, Bekkering et al. (1996) demonstrated that FOE was absent for a simple keypress, but they showed that it was present for target-directed movements of the hand. Pratt and colleagues (Pratt, Bekkering, Abrams, & Adam, 1999) subsequently replicated the FOE for manual aiming with a perfectly predictable target location. Given the temporal similarity between the eyes and hands RTs during different gap intervals, Pratt et al. (1999) concluded that the FOE is not saccade-specific, but applies to spatially-oriented manual responses.

The results on manual responses are also consistent with previous data reported in a study by Rafal, Smith, Krantz, Cohen, & Brennan (1990). In that experiment, three hemianopic patients were asked to saccade toward a target presented in the intact visual field while in some trials a distractor was presented contralaterally in the blind visual field. Rafal et al. reported an effect of distractor appearance in saccadic reaction times, but when the three patients were asked to perform the same task under a manual condition consisting in a simple keypress, no distractor appearance effect was reported. In another control experiment run by Sumner, Adamjee and Mollon (2002), participants were asked to make a choice manual response, i.e. keypress, according to the side of presentation of a target stimulus. In some trials a contralateral distractor was presented. Even in this condition of choice keypress no distractor effect was found.

The present results are coherent with the past literature and support the idea that the RDE is not a general attentional phenomenon but that it is probably related either only to the saccadic system or to spatially-oriented responses. This hypothesis will be taken further in Chapter 4, where manual aiming will be tested under distractor conditions. In particular, in the next series of experiments participants were asked to point with their finger toward a lateralised target while maintaining a central gaze. In another block of trials they were asked to make a saccade toward the target and to maintain their hand on the central fixation cross. In a second experiment they will also left free to execute eye movements during the pointing task. This set-up was conceived in such a way that hand movements were mimicking saccadic movements; Bekkering (1996) and Pratt (1999) studied the FOE in a similar way.

The third result regarded the effect of a distractor on covert attention. In this case the pattern of the data was not as clear as in the other conditions. At first glance, it seems that whereas for a near target there was no effect of distractor appearance, for the far target an increase in reaction times during distractor conditions was recorded. This result superficially looks like a RDE, but the fact that it was so specific to the far target is not compatible with the RDE, and suggests an alternative explanation. The simpler explanation for the slowing in RTs is in terms of *compatibility effects.* In the Figure 2.2 it is possible to see that the only point different from the others is the baseline condition for the far target. In this particular condition, participants were required to respond to a right target with their right hands in absence of distractors; we will call this the condition of *full compatibility*. As reported in the literature (Possamaï, 1991) the congruency between response hand and target side elicits very fast reaction times (i.e. *motor compatibility effect*). In all the other conditions of the experiment it is possible to notice that an element of choice was introduced in the criteria of hand response selection**.** When the target was far and the distractor was present (either in the near or far location), the participants' task was to covertly discriminate whether the target was presented near the fixation cross, and press the left button, or far from the fixation cross, and press the right button. To correctly complete this task, participants were forced to align the midline of their body with the imaginary midline that divided the left half of the screen in two. According to this reasoning, it is plausible to think that a distractor, that was always presented on the left side of the screen, could have been interpreted as a *near target.* This incongruency probably led to the increment of reaction times in this condition, due to the cognitive process of discrimination of target location, not to a pure motor activation elicited by the distractor presence, as reported in the original RDE study. In the case of the near target, the baseline RT increased compared to the baseline for far targets since there was a strong incompatibility between responding hand (left) and target side (right). This incompatibility led to slower reaction times. When a distractor was appearing in concomitance with the near target, the response incompatibility had already taken effect and any other effect related to distractor appearance should therefore have been present on top of this baseline incongruency effect. On the other hand, if we suppose that the RDE was playing a role in this condition, we are in the position that it is impossible to differentiate between the pure RDE and the incompatibility effect related to the target location (right side of the screen) and responding hand (left). In summary, if the RDE were responsible for the delay recorded during the covert discrimination task, it should be possible to see an increase in RT on top of the incompatibility effect. Since such an increase was not recorded we can either assume that it was confounded with the incompatibility effect or that it was not the cause of the slow-down in RTs. The former hypothesis is supported by the idea that the only condition that had a different set was the baseline for far targets, where full compatibility was accomplished, resulting in faster responses. These unforeseen, and rather complex, compatibility effects reflect a clear limitation of the design and suggest that an alternative, simpler, design might be required to answer the covert question.

Nonetheless, the results for the covert condition are ambiguous. According to the premotor theory, in fact, it would have been expected that the RDE generalised to covert responses, since covert shifts of attention are assumed to be identical to motor preparation for an eye movement. The current data cannot respond to this question and for this reason it was necessary to run a follow-up study on covert shifts under distractor appearance (Chapter 5). As has been already proposed in the previous paragraphs, the manual condition also needed to be investigated using oriented motor responses and this is the starting point of the next series of experiments (Chapter 4).

Chapter 3

Validation of EOG against Eyelink II measures of saccadic latency

Chapter overview. The aim of this chapter is to validate a specific electro-oculography (EOG) set-up for use in the experiments that will be described in Chapter 4. In order to ensure validity and cross-comparability with the modern eye-tracking methodology used in the saccadic studies in other chapters, the EOG will be used in concomitance with the Eyelink II system (SR research) during a pro-saccade task. The Eyelink II is one of the most commonly used commercially available systems employed to record eye movements. It is based on the recognition of the pupil by the reflection of an infrared signal. On the other hand, EOG is one of the first techniques used to measure eye movements. For historical context, this chapter will give a brief overview of the development of eye-movement recording technologies, and will then present a small-scale validation trial of our EOG set-up against Eyelink II. Concurrent recording of EOG and Eyelink II data in a pro-saccade task was carried out with two participants. The data clearly demonstrate the accuracy and reliability of the EOG system in detecting saccadic reaction times. The close correspondence between the results gives confidence in the validity of the EOG data, at least for the recording of saccadic latencies.

3.1 A practical problem

The Visuomotor laboratory at Edinburgh University, where all the studies reported in this thesis took place, provides a modern eye-tracking system (i.e. Eyelink II) to record eye movements. Nonetheless, the empirical project that will be explored in the next chapter (Chapter 4) required the ability to record manual responses and eye movements concurrently within a single experimental set-up. However, pilot trials investigating this set-up found that (i) the recording of eye movements simultaneously with hand movements induced large artefacts in the eye movement traces due to head vibrations that would only have been eliminated by using a bite bar, a solution excluded from the experimental set-up in order to avoid subject discomfort; (ii) for comfort of the arm, a far preferable set-up would have been to have the stimulus plane more inclined to the horizontal plane, giving it support. This inclination is incompatible with the standard Eyelink II algorithms. Therefore, a possible solution was to revert to using EOG, and this was made possible when a physiological amplifier and surface electrodes were made available by an ERP lab in the Department. However, because this equipment had not previously been used to record EOG signals, it was first necessary to run a validation study, in order to directly confirm correspondence of the EOG traces with Eyelink II recordings. This not only validated EOG data, but provided a basis for cross-comparisons of saccadic results between experiments employing EOG and those employing Eyelink II. Prior to reporting the validation results, the methodological investigation will be contextualised through a brief history of the development of eye-movement recording technologies.

3.2 Brief history of eye movements recording devices

The anatomy of the eye, with the eyeball constrained in the eye cavity, and the peculiar characteristics of an eye movement, such as its rapid onset and velocity, made the study of eye movements extremely challenging and the recording of its rotation in the horizontal and vertical plane difficult to achieve. Eye movements, in fact, have always been a very interesting form of behaviour to investigate since they can reveal relevant underlying cognitive processes in different research tasks such as reading, the exploring of visual scenes, memory and so on. Starting from the end of the nineteenth century, a great effort has been put into the development of methods to achieve a precise recording of eye movements.

One of the first instruments developed to record eye movements used a lever directly connected to a device attached to the eyeball in such a way that the rotation of the eyes was mechanically translated onto a recording surface (see: Wade & Tatler 2005). Apart from the discomfort to which the participants were subjected, a major problem with this device was that the lever added inertia to the natural movement of the eye, forcing the subject to perform in an unnatural way. Nonetheless, this system was actually used and one example is reported by Young and Sheena (1975), where in 1898 a pair of rings of plaster was directly connected to the cornea and from the cornea to a recording pen. One year later, in 1899, Orschansky proposed that instead of using a lever or a mechanical device, better recordings could be achieved using a small mirror attached to an aluminium eye cup. Measurements were taken by recording the light reflected by this mirror. Ditchburn and Ginsborg (1952) modified this methodology using more sophisticated contact lenses. This last experimental methodology opened up a new way of recording eye movements at the start of the twentieth century: corneal reflection (Robinson, 1968). Yarbus (1967) used a scleral contact lens, where a mirror was attached to a rubber suction cup. He then recorded the light that was reflected by the mirror. The next step was to record the light that was directly reflected by the eyes. This was achieved with photographic methods, introduced by Dodge (1907) and others in the early twentieth century (Wade et al., 2003). The results obtained from this methodology were not as good as expected, since the images were very blurred and it was difficult to distinguish the different components of the eye, such as the pupil from the iris. Dodge and Cline (1901, p. 148-149) by using:

> “[…] a bright vertical line as it was reflected from the surface of the cornea”

managed to achieve more precise recordings. This technique was quite successful and it was used in many different types of experiments, for example where participants were asked to explore a visual scene. Another attempt was carried out by filming the movement of the eyes. Of course this technique, even if useful for certain paradigms, revealed itself to be tedious and prone to error when it came to scoring recordings consisting of a large number of images in each of which the eye position needed to be measured.

Electro-oculography (EOG) was one of the first techniques to have been used to measure eye movements. EOG measures the variation of the difference in electrical potential between front and the back of the eye (Mowrer et al., 1936). This system is based on one of the properties of the eyes, in particular on the different potential between the cornea, that remain 0.40 to 1.0 mV positive, with respect to the back of the eye, which is negatively charged (du Bois-Reymond, 1848). The difference in potential is called *corneo-retinal* potential. According to simple physical rules the eye may be considered a battery which, as it rotates, carries with it a potential field, or dipole, which can be measured by placing electrodes on the adjacent tissue. It is possible to record the change from the resting position (when the eyes have 0° angles the difference between the cornea and the back is close to 0 mV) and to correlate it to the eye movement, Figure 3.1.

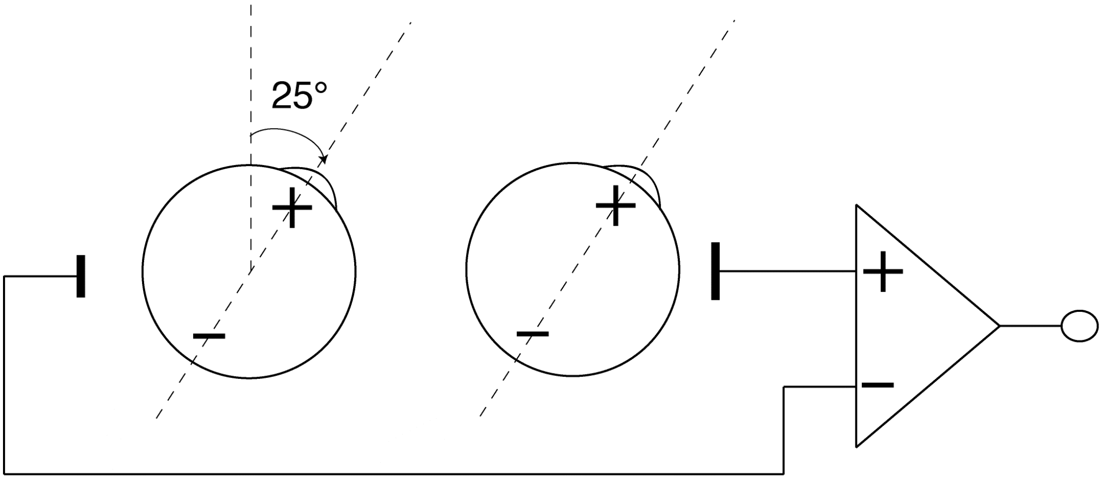


Figure 3.1 Electro-oculography.
Schematic of the corneo-retinal circuit.

In fact, as the eye moves, the potential at the electrode becomes more positive or negative depending upon the direction of movement. EOG can be used to record eye movements up to 70°. Schott (1922), Meyers (1929) and Jacobson (1930) were the first to use this type of eye tracker.

Nowadays with improvements in material and technology, it is possible to create contact lenses that are very sophisticated and allow the most sensitive recordings, measuring even very small movements and microsaccades. One of these methods uses a scleral coil (recently used by Collewijn et al., 1997; Findlay, 1997; McConkie & Loschky, 2002; Steinman & Collewijn, 1980) consisting of two perpendicular wire coils embedded in the contact lens. The participant is situated within two perpendicular electromagnetic coils. As the eye moves, the potential difference in each coil changes and this change in potential difference can be used as a measure of the eye position.

Modern eye trackers can use also corneal reflective systems. For example, the Eyelink II - SR research - uses a combination of corneal reflection and pupil tracking. Infrared light is used to illuminate the eye so that it is not interfering with normal vision. A special camera is then used to record the light reflected by the cornea and the pupil, and an algorithm detects the pupil and tracks it during the eye movement.

3.2 Aim of the study

The aim of this study is to validate saccadic latencies recorded by EOG in the experimental set-up that is used in Chapter 4. To do so, the Eyelink II system (SR research) has been used as the standard reference. The primary advantages of EOG for present purposes are comfort and flexibility of set-up with ease of recording alongside arm movement (the head must be fixed, but does not need to be aggressively restrained); the disadvantage is likely to be far poorer spatial accuracy. However, for present purposes, this is acceptable, as the experiments are primarily concerned with saccadic latencies. Therefore, analysis will be restricted to SRT.

3.3 Method

3.3.1 Participants

The participants were the author of the thesis (AB) and his first supervisor (RDM) from the University of Edinburgh. Both AB and RDM had normal vision and were free from any neurological or visual impairment. The study was approved by a University ethics committee and was performed in accordance with ethical standards.

3.3.2 Apparatus and stimuli

Participants sit in front of a 19-inch CTR monitor (1024 x 768 pixel resolution, 32-bit True Colour) driven by a Pentium IV processor at 75Hz at a viewing distance of 50 cm with their eyes horizontally and vertically aligned with the centre of the screen. A second computer was used to run the Eyelink II head-mounted system to record eye movements at a sampling frequency of 500 Hz. Horizontal eye movements were monitored using electro-oculography (EOG), with a passive electrode placed on the outer canthus of each eye, and a reference electrode on the forehead. To favour electric conductivity, the skin was cleaned at the spot where the electrodes were to be placed. The electrode cup was filled with electrode paste and then attached to the skin with surgical tape. The leads were then connected to the preamplifier and amplifier. The most commonly used electrodes for recording eye movements are miniature type (11 mm) silver-silver chloride electrodes. The electrodes were carefully placed as near to the eye as possible, since the DC potential tends to decrease as the electrodes are placed farther from the eye. When placing the electrodes the experimenter was careful to align the two in the horizontal plane in such a way as to eliminate any vertical component during the horizontal measurement.

EOG voltage were sampled at 500 Hz, with sampling data streams mutually time-locked to stimulus presentation, which triggered the onset of both recordings via the Optotrak Data Acquisition Unit (ODAU) (Northern Digital Inc., Waterloo, Canada) and the Eyelink II recordings. Although accurate only to within one screen refresh, with respect to the true time of stimulus onset, they are perfectly time-locked to one another. A chin rest was used to keep the head still during the stimulus presentation. The height of the chin rest was adjusted appropriately according to the height of the participant. With this set-up it was possible to record eye movements simultaneously with the two systems, as showed in Figure 3.2.

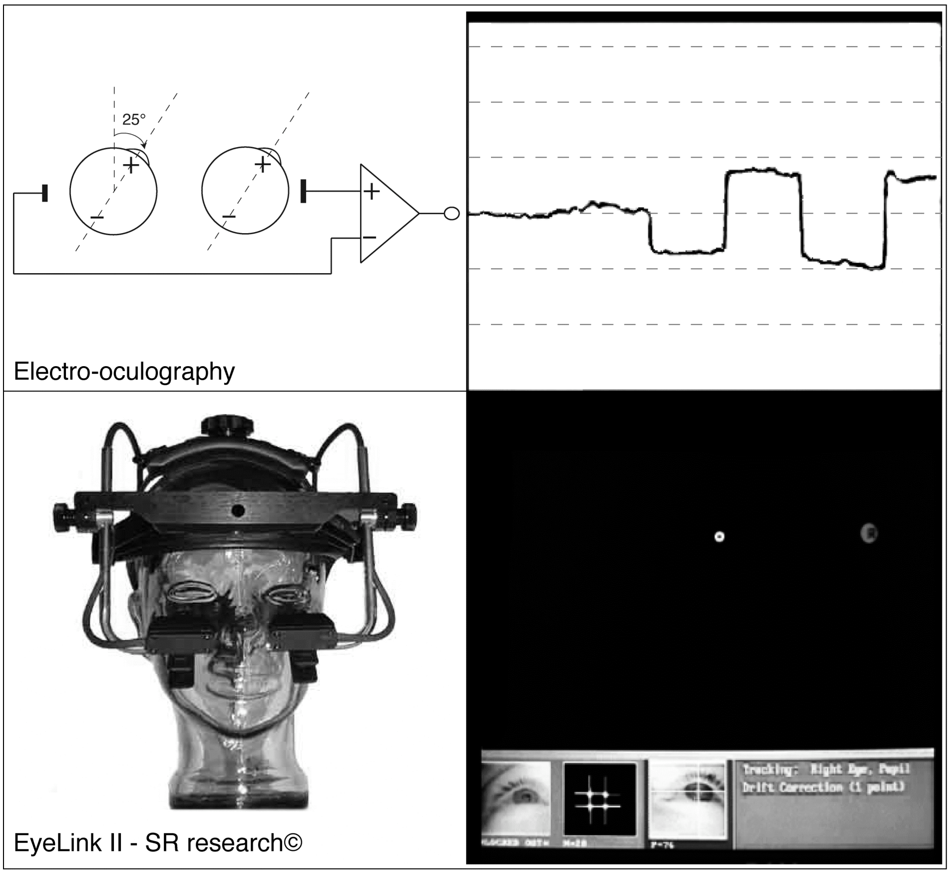


Figure 3.2 EOG and EyeLink II.
The upper left panel shows the electrical circuit of the eyes generating the corneo-retinal potential. The upper right panel shows the EOG voltage signal generated by a leftward (negative) and rightward (positive) saccadic sequence. The bottom left panel shows the EyeLink II head mounted system. The bottom right panel shows a screenshot of the experimenter's view during recording of a rightward saccade.

To facilitate fixation, a white cross (0.5°) on a black background was presented at the centre of the screen and remained present for the whole length of the trial. When the participant was fixating, the experiment performed a manual drift correction to start each trial by pressing the “return” key when happy that the subject was fixating the central cross. After a variable time of between 500 - 1000 ms a dot (0.8°) appeared for 1000 ms in one of the three locations on the right or on the left of the display. Data were analysed offline.

3.3.3 Design

There were a total of 120 trials, 20 for each of the three distances of visual angles (5°, 10° and 15°) presented on the left and right side of the screen. A recycling routine was used to re-run trials in which the subject moved his eyes before the dot appeared on the screen. The dependent measure was the latency of the saccade calculated from the onset of the stimulus on screen.

3.3.3 Procedure

Each trial started with a fixation cross on the centre of the screen that remained present for the whole length of the trial. The task of the subject was to move his eyes as soon as the dot appeared at one of the six locations.

3.3.4 Analysis

A series of analyses was run to compare the data collected with the EOG technique and that collected with the Eyelink II. A custom program was written to analyse the electric signal recorded from the eyes. To detect eye movements, the raw EOG voltage data were filtered by a dual-pass through a second-order Butterworth filter with a cut-off frequency of 10 Hz. The velocity of the EOG signal was then computed for each sample and saccade onset was estimated as the point at which the EOG velocity exceeded 5% of its peak value for that saccade.

3.4 Results

3.4.1 Data screening

For subject AB, a total of ~4% of trials were discarded from the saccadic analysis due to corruption of the signal. Saccadic RTs faster than 70 ms (SRT <1%), longer than 500 ms (N.D.), or made in the wrong direction (N.D.), were excluded from the analysis. For subject RDM, a total of ~14% of trials were discarded from the saccadic analysis due to corruption of the signal. Saccadic RTs faster than 70 ms (N.D.), longer than 500 ms (N.D.), or made in the wrong direction (N.D.), were excluded from the analysis.

The latencies recorded with the EyeLink II (L-ELII) and the latencies recorded with the EOG (L-EOG) were then compared.

3.4.2 Analysis of SRT.

For participant AB, the best fitting straight line between L-ELII and L-EOG accounted for ~98% of the variance (i.e. $R^2 = 0.976$), with a slope of $\alpha = 1$. A constant $\beta = -32.932$ indicated that the latency recorded with the EOG, based on the peak velocity of the electric signal, was about ~33 ms earlier than that recorded with the Eyelink II.

Participant RDM showed an almost identical pattern to participant AB. The best fitting straight line in this case accounted for ~91% of the variance (i.e. $R^2 = 0.916$). The slope was almost identical to participant AB with $\alpha = 0.967$ and close to 1. The constant value $\beta = -30.998$ ms was different by only 1.93 ms from the constant recorded for participant AB.

Figure 3.3 shows the correlation of L-EOG against L-ELII for participants AB and RDM respectively.

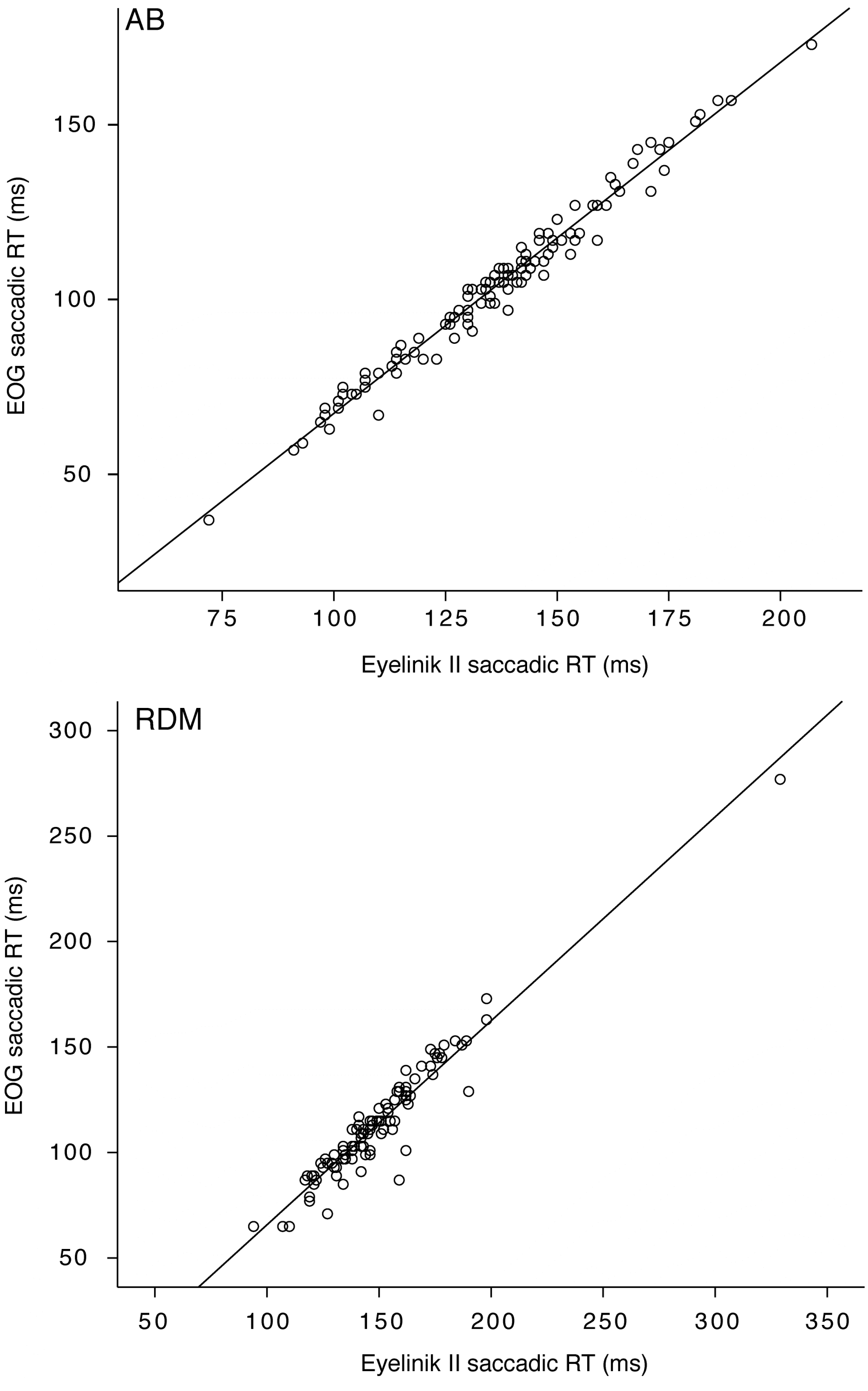


Figure 3.3 Scatterplot EOG vs EyeLink II.
Scatterplot between SRTs recorded with the Eyelink II and the EOG system for participant AB and RDM and the respective regression lines.

3.5 Conclusion

The results from this validation study indicate that the present EOG setup provides a valid measure of saccadic latency. There is a constant difference of about 30 ms between the SRTs detected from the Eyelink II algorithm and those detected by the EOG algorithm. This is probably attributable to the EOG signal being sensitive to muscular activity preceding movement of the eyeball itself. Nonetheless, SRTs were detected with confidence, making it possible to proceed with the empirical project of the thesis, comparing the effect of distractors on saccadic and manual responses.

Chapter 4

The RDE in saccades and manual aiming

Chapter overview. The aim of the present chapter is to investigate the effect of abrupt-onset distractors on manual aiming. As previously described, it is well known that distractors presented in the contralateral field to the target slow down SRTs (RDE: Walker et al., 1995). In Chapter 2 the RDE has been investigated in different modality of response, including the manual modality. The results clearly showed that the RDE was not present when participants were required to make a general response such as a button press. Nonetheless, it was not possible to exclude that the limb motor system was immune to distraction since it has been accepted that keypress responses are not strictly involved in attentional shifts. More appropriate to study this phenomenon is manual aiming. Already Bekkering et al. (1996) and Pratt et al. (1999) clearly demonstrated how the GAP effect was present for pointing movement but it was absent for simple keypress. Moreover, Sheliga and colleagues (1997) also proposed that to study attentional shifts in the arm domain an aiming response was required.

The current experiment compared the effects of distractors between spatially equivalent tasks requiring saccadic and manual aiming responses respectively. The RDE was observed for the eyes but not for the hands. This dissociation was also replicated in a more naturalistic task in which participants were free to move their eyes during manual aiming. In order to examine the time-course of distractor effects for the eyes and the hands, a third experiment investigated distractor effects across a wider range of target-distractor delays, finding no RDE for manual aiming responses at distractor delays of 0, 100, or 150 ms. The failure of the RDE to generalise to manual aiming suggests that target selection mechanisms might not be shared between hand and eye movements.

4.1 Introduction

While scanning our environment, we move our eyes systematically from one location to another; because we can fixate only one location at a time, we are required continually to select between candidate targets competing for our overt attention. These mechanisms of selection among multiple targets have been approached systematically in experimental environment. A simple but extreme case is when two stimuli are presented simultaneously within the same hemifield or bilaterally. Lévy-Schoen (1969) experiments represent one of the first attempts to investigate the saccadic behaviour in such circumstances, focusing on the time involved to solve the conflict. In their studies, participants were presented simultaneously with two stimuli in the same or in the opposite hemifield and were asked to move their eyes to one of the two. The author observed a pronounced biased to look towards the more proximal target and a slow down in saccadic reaction times (SRT) under bilateral conditions. The delay in starting the saccade was interpreted as the additional time required to choose which direction to look in. Despite this conclusion, the cognitive effect of choice was not the critical factor to elicit such effect on SRT under double stimulation. In a series of experiment by Ross and Ross (Ross & Ross, 1980, 1981) a similar increase in SRTs was evident also without any conflicting information between targets. Ross and Ross investigated the role of warning signal related to *offset*, *onset*, and *change* of stimuli presented at fixation. They observed a pronounce modulation of SRT related to the onset asynchrony (SOA) between the appearance of the target and the fixation stimulus. The direction of the effect was dependent on the SOA and it was also interacting with the kind of stimulus at fixation (offset, onset, change). In particular, they showed that onset stimuli caused an increase in SRTs for SOA of 150, 100 or 50 ms *after* target onset. On the contrary, offset stimuli caused a decrease of SRTs at 50 ms *before* target onset acting as a warning signal. If the stimulus at fixation was a change, for example changing from the letter “O” to an “#”, the result resembled the pattern of the onset condition. The interesting point is that in these experiments the directional choice between stimuli was removed since the interfering stimulus was presented at fixation. Nevertheless the same pattern of result was also obtained for irrelevant bilateral stimuli presented peripherally in the horizontal or in the vertical plane. Similar results were also obtained by Braun and Breitmeyer (1990). In their experiments they were investigating the effect of the reappearance of a stimulus at fixation on SRTs. Congruently with Ross and Ross results, they observed that when stimuli at fixation reappeared *before* target onset (up to 100 ms before target onset) the mean latency was smaller if compared to *overlap* condition (where the fixation stimulus stayed on continuously). Interestingly, when the fixation stimulus reappeared in the time window of 100 ms before to 150 ms *after* target onset, SRTs drastically increased to a value comparable to overlap condition. Moreover, the authors investigated the effect of distractors in the contralateral hemifield, observing that they also increased SRTs, albeit less severely than distractors at fixation. Crucially, the location of the target in these experiments was perfectly predictable, excluding effects of cognitive choice related to target selection. Weber and Fischer (1994) run a series of studies investigating the effect of distractors on express saccades, i.e. target directed saccades with extremely short latencies (80 to 100 ms). To rule out any cognitive interference and investigate the effects of distractors *per se,* the authors used completely predictable target presentation. In such condition they noticed that the generation of express saccades was modulated by the presentation of competing non-target stimuli. They also observed a big reduction of express saccades when a contralateral distractor was presented simultaneously with target onset. Such delay was described by a change of frequency in the production of express saccades corresponding to an increase of SRT of about 30 ms. They concluded that (p. 1887):

> “[...] the introduction of the distractor seems to have no effect in some trials - where the subjects still make express saccades as if there was no distractor - but in other trials the distractor delays the saccades by about 30 msec”

This highly replicable increase in SRTs during bilateral stimulation, persisting even with complete target predictability, is now known as the Remote Distractor Effect (RDE).

Walker and colleagues explored the saccadic RDE systematically, manipulating the spatial and temporal proprieties of the distractor (Walker et al., 1995; 1997). To eliminate the effect of directional choice, participants were always aware in advance in which hemifield the target would be presented. For distractors presented in the opposite hemifield or at fixation, they observed a delay in the initiation of saccades by comparison with the target only condition. The effect was maximal (~18 ms) for distractors presented simultaneously with the target, but also reliable for distractors appearing 20 or 40 ms after the target (Walker et al., 1995). Simultaneous distractors were found to exert their greatest effect when presented at fixation, the RDE reducing monotonically with increasing eccentricity (Walker et al., 1997). Interestingly, distractors presented within a window of 20° around target axis modulated the amplitude but did not influence the latency, such that the landing position of the eyes tended to deviate towards the centre of gravity between a target and distractor. The *global effect* was the term given to this tendency (Walker et al., 1997). The fitting by a single function of the inhibitory effects of distractors across the range of eccentricities led Walker and colleagues to propose a neurophysiological mechanism in terms of the stimulation of *fixation neurons* in the superior colliculus. As already described in the introduction (sections 1.6 and 1.8.1) fixation neurons represents a class of neurons mainly present the rostral pole of the SC (Munoz & Wurtz, 1992, 1993a, 1993b). This region is active when the animal fixates a stimulus and stops its activity during saccadic movements A possible extended zone of the rostral pole has been documented by Gandhi and Keller (1997) which described neurons with similar proprieties up to 10° of eccentricity. The characteristics of these neurons led Walker et al. (1997) to suggest that the delay recorded in saccadic latency when distractor were presented at fixation or within 10° of eccentricity was due by the activity of these fixation neurons which is antagonistic to saccade preparation (see also: Findlay & Walker, 1999). Another hypothesis is that the distractor effect is a consequence of lateral inhibition interactions between subpopulation of build-up neurons in the intermediate layers of the superior colliculus, coding for spatially incompatible saccades (Olivier et al., 1999). Behavioural evidence supporting the second view was provided by Honda (2005). In his experiment, participants are required to perform a saccadic movement at the onset of a laterlised target. The author compared GAP (where the fixation cross was turned off simultaneously to target onset) and overlap condition showing that the strength of the RDE was reduced in the latter. In fact, during overlap condition the stimulation of fixation neurons caused inhibitory interaction between distractor and fixation stimuli reducing the inhibitory interaction between target and distractor, and consequently reducing the strength of the RDE. On the contrary, in GAP conditions the inhibition deriving from the fixation neurons stops. At this point the only source of inhibition was due to the activity of the saccade-related neurons firing for both target and distractor and leading to a strong RDE.

Walker et al's (1997) proposed explanation of the RDE in terms of the stimulation of fixation neurons by distractor stimuli would imply a close kinship with an even more intensively studied saccadic phenomenon: the *gap effect*. This refers to a speeding of SRT that is obtained by the offset of a fixation stimulus simultaneously with, or shortly before target appearance (Saslow, 1967). Like the RDE, the gap effect persists even when target location is predictable (Kingston & Klein, 1993; Walker et al., 1995). The gap effect consists of two components. First, the offset of the fixation stimulus provides a warning signal that enhances readiness to make any kind of response to the target, and similar benefits are obtained from alternative warning signal such as (non-offset) visual changes at fixation (Ross & Ross, 1980), or auditory tones (Bekkering et al., 1996; Forbes & Klein, 1996; Reuter-Lorenz et al., 1991, 1995; Ross & Ross, 1981; Tam & Stelmach, 1993). Second, there is a component, specific to fixation offset, which influences target-directed saccades but has no effect on simple manual reaction time (Bekkering et al., 1996), and little (Bekkering et al., 1996; Iwasaki, 1990; Tam & Stelmach, 1993) or no effect (Reuter-Lorenz et al., 1991; Tam & Ono, 1994) on choice manual reaction time. This more specific component, called the *fixation offset effect* (FOE; Kingstone & Klein, 1993), is believed to result from a release from stimulation of rostral pole fixation neurons, with a consequent facilitation of saccade preparation (Dorris & Munoz, 1995; Dorris et al., 1997; Findlay & Walker, 1999). According to the hypothesis of Walker et al (1997), this is the exact obverse of the mechanism underlying the RDE: whilst the release of fixation neurons from stimulation produces the facilitatory FOE, stimulation of the same fixation network would produce the inhibitory RDE.

In addition to offering insight into the mechanisms of saccade generation, the FOE component of the gap effect has provided a salient behavioural marker for investigating the coupling between eye- and hand-movements. Many goal-directed movements of the hand are visually-guided, so the eyes and hands often work in close concert (e.g. Neggers & Bekkering, 2000). A fundamental issue in understanding the co-ordination of these response systems concerns the extent to which response mechanisms are shared between them. Kingstone and Klein (1993) characterised the FOE as specific to the oculomotor system, implying that only saccadic responses should be prone to the effect. However, neurophysiological evidence implicating intermediate and deep layers of the superior colliculus in the representation of arm movements (Fries, 1984, 1985; Lünenburger, Kleiser, Stuphorn, Miller, & Hoffmann, 2001; Stuphorn, Bauswein, & Hoffman, 2000; Werner, 1993; Werner, Dannenberg, & Hoffmann, 1997) raises the possibility that such oculomotor phenomena may generalise to manual responses. Consistent with this, Bekkering et al. (1996) showed that, whilst the FOE was absent for a simple keypress, it was present for target-directed movements of the hand, even when participants maintained gaze centrally. In fact, most of the previous studies on the GAP effect on the manual system were recording just a general motor response, usually a button press. The main difference between a button press and an aiming hand movement is that the latter is spatially oriented, not requiring only the detection of the target appearance but also its location in space. This sort of response provides much greater overlap with the saccadic eye movements that have been intensively study in this research field. In support of this idea, Pratt et al. (1999) subsequently replicated the FOE for manual aiming with a perfectly predictable target location. Moreover, the modulation of FOE with the temporal gap between fixation offset and target onset was closely similar for the eyes and the hand, suggesting a common underlying mechanism. Pratt et al. (1999) concluded that the FOE component of the gap effect is not saccade-specific, but applies to spatially-oriented manual responses, which may similarly reflect the functioning of the superior colliculus. At this point, it becomes much more interesting to do a direct comparison between saccadic and manual movements during bilateral stimulation.

The effect of fixation offset on manual responses has been well studied, but there is little information available concerning the effect of remote distractors. Walker et al's (1997) hypothesis that the RDE derives from the same network of fixation neurons as the FOE clearly predicts that a similar pattern should be observed for the RDE as for the FOE (Bekkering et al., 1996; Pratt et al., 1999). Specifically, whilst remote distractors should not retard simple keypress responses to visual targets at predictable locations, they should slow spatially-oriented aiming responses in the same manner as for saccades. The first part of this prediction is already confirmed, as remote distractors do not increase simple (Rafal et al., 1990) or choice (Sumner et al., 2002) manual reaction time. However, there has been no experimental study of the effect of remote distractors on manual aiming responses. The aim of this study is to test for the RDE in manual aiming, in order to reveal whether it is a saccade-specific phenomenon or, like the FOE, generalises to spatially-oriented manual responses.

4.2 Experiment 2

4.2.1 Method

4.2.1.1 Participants

Eight volunteers from the University of Edinburgh, aged between 18 and 24 years, participated in this study. All participants were right handed by self-report, and free from neurological and visual impairments. This experiment was conducted in accordance with the 1964 Declaration of Helsinki, and with the approval of the Ethics Committee of the School of Philosophy, Psychology and Language Sciences at the University of Edinburgh.

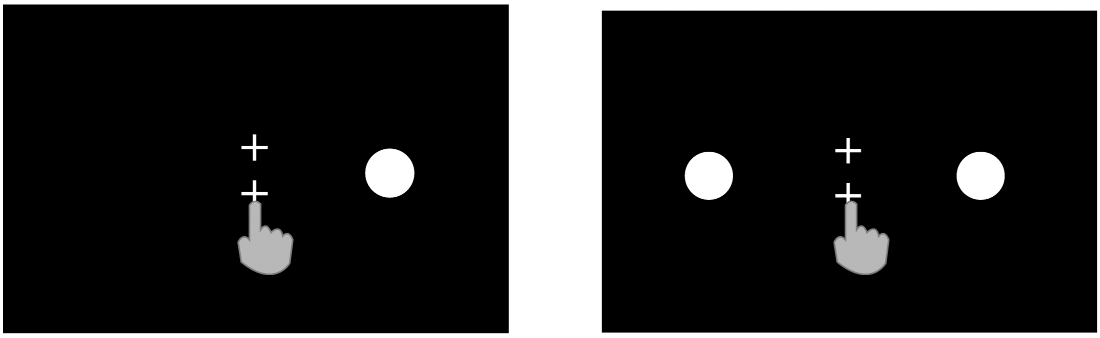
4.2.1.2 Apparatus and stimuli

Stimuli were presented on a 17 inch LCD flatscreen monitor (resolution 1024 x 768 pixels; refresh rate 60 Hz) driven by a Pentium IV processor. Participants sat centrally in front of the monitor, with their head immobilised in a chin rest, at a viewing distance of 50 cm. The monitor was tilted 60° away from the participant to permit the comfortable resting of the right index finger on its display surface. Hand movements were recorded by the Optotrak Certus system (Northern Digital Inc., Waterloo, Canada), which sampled the 3D spatial position of an infrared emitting diode (IRED) attached to the nail of the right index finger. Horizontal eye movements were monitored using electrooculography (EOG), with a passive electrode placed on the outer canthus of each each eye, and a reference electrode on the forehead. IRED position and EOG voltage were sampled at 500 Hz, with sampling time-locked via the Optotrak Data Acquisition Unit (ODAU). Data were analysed offline.

Stimuli were white on black. Two 0.5° fixation crosses, one centred 0.67° above the other, occupied the middle of the screen throughout the experiment. The upper cross defined the fixation position for the eyes, and the lower cross a home position for the finger. Target and distractor stimuli were 0.8° diameter circles, presented at 5° or 10° to the left or right of the screen centre.

4.2.1.3 Procedure

Participants were tested according to a 2x2x2x2 experimental design created by the factorial combination of four factors: *Modality* of response (saccadic, manual), *Side* of target (left, right), *Eccentricity* of target (near, far) and *Distractor* condition [target only (T), target with distractor at the mirror image location in the opposite hemifield (TD)]. Each participant performed four blocks of 70 trials. Modality was blocked according to an ABBA schedule, side was blocked according to an ABAB schedule, and block order was counterbalanced fully across participants. Within each block, trials were shuffled randomly, and each combination of target eccentricity and distractor condition occurred 15 times, with ten catch trials in which a stimulus was presented in the non-target hemifield alone (five times each at the near and far eccentricities). Prior to each block, the participant was informed of the response required (saccadic or manual) and the target side (left or right) for that block. In saccadic blocks, the participant was required to move their eyes to the target, keeping their finger on the lower cross throughout each trial. In manual blocks, the participant was required to slide their index finger along the screen to the target, keeping their eyes fixed on the upper cross throughout each trial. Prior to each trial, participants were required to fixate the upper cross and place their right index finger on the lower cross. Trial onset was signaled by a 500 ms warning tone. Following a delay that varied randomly between 1000 and 1500 ms from tone onset, stimuli appeared for 1000 ms in one or both hemifields. The participant was required to respond as rapidly as possible to stimuli on the target side, making no response to stimuli on the non-target side.



Target

Target and Distractor

Figure 4.1 Experiment 2, tasks and stimuli.
Experimental set up in the two conditions: target alone and target with distractor. In the manual task, participants slid the right index finger from the lower cross to target, without moving the eyes from the fixation (upper) cross. In the saccadic task, participants moved their eyes to the target, without moving the hand from the lower cross.

4.2.1.4 Analysis

Hand and eye-movement data were analysed offline using custom LabVIEW routines. For hand movements, the raw IRED position data were filtered by a dual-pass through a second-order low-pass Butterworth filter with a cut-off frequency of

20 Hz. The tangential speed of the IRED was computed for each sample and this series was used to estimate movement onset and offset. Movement onset was estimated using the algorithm developed by Teasdale et al (1993; algorithm b), and movement offset was estimated using a simple threshold of 50 mm/s. For eye-movements, the raw EOG voltage data were filtered by a dual-pass through a second-order Butterworth filter with a cut-off frequency of 10 Hz. The velocity of the EOG signal was computed for each sample and saccade onset was estimated as the point at which the EOG velocity exceeded 5% of its peak value for that saccade.

Several additional variables were extracted for hand movements: movement time (MT) was calculated as the time between movement onset and offset; peak speed (PS) was the highest speed reached during the movement; time to peak speed (TPS) was calculated as the time between movement onset and the moment of peak speed; constant error (CE) was the horizontal distance of the final finger position from the target, with undershoot errors signed negatively and overshoot errors signed positively; variable error (VE) was calculated for each condition as the within-subject standard deviation of CE.

4.2.2 Experiment 2 results

4.2.2.1 Data screening

A total of ~13% of trials were discarded from the saccadic analysis due to blinks or to corruption of the signal. A total of ~10% of hand movements were discarded due to failures to maintain central fixation or to corruption of the signal. Saccadic RTs faster than 70 ms and manual RTs faster than 100 ms (SRT ~1%; MRT ~ 1%), longer than 500 ms (SRT ~1%; MRT ~1%), made in the wrong direction (less than 1% and ~1% respectively), were excluded from the analysis.

4.2.2.2 Analysis of RT

For each participant, the median RT was computed for each condition and entered into a 2x2x2x2 (*Modality * Side * Eccentricity * Distractor*) repeated-measures ANOVA. The main effects of modality, side and distractor were not reliable, but the main effect of eccentricity was reliable ($F(1,7) = 12.87$; $p < 0.01$), reflecting slightly shorter RTs to the near than to the far target (243 vs. 247 ms). The most notable effect was the reliable interaction between modality and distractor ($F(1,7) = 11.21$; $p < 0.05$), which reflects the fact that distractors in the non-target hemifield increased SRTs but not MRTs. The typical RDE was thus observed for the eyes, but not for the hand, as shown in Figure 4.2.

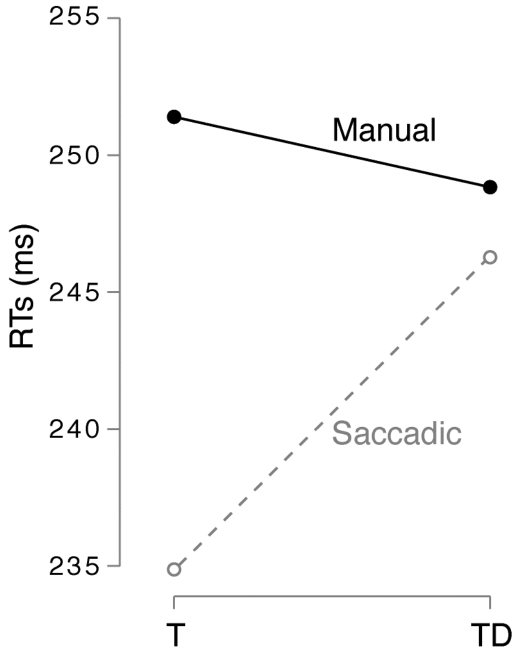


Figure 4.2 Experiment 2 results.
Saccadic and Manual RTs for target only (T) and target with distractor condition (TD).

The interaction of modality and distractor was modified further by a three-way interaction with eccentricity ($F(1,7) = 15.24$; $p < 0.01$), and a four-way interaction with side and eccentricity ($F(1,7) = 11.59$; $p < 0.05$). The interaction terms were explored via 2x2x2 (*Side * Eccentricity * Distractor*) repeated-measures ANOVAs performed for each response modality separately, with an adjusted alpha criterion of 0.025. For saccadic responses, the main effect of distractor ($F(1,7) = 10.89$; $p < 0.025$) was modified by the interaction with eccentricity ($F(1,7) = 13.08$; $p < 0.01$), such that the increase in SRT induced by the distractor was large for the near target (19.4 ms) but negligible (3.3 ms) for the far target. Note that, because the distractor always appeared at the mirror image of the target location, it is not clear whether the modulation of distractor effect by eccentricity is determined by the target eccentricity, the distractor eccentricity, or both (cf. Walker et al., 1997). The equivalent ANOVA for the manual condition found no reliable effects except for a three-way interaction of side by eccentricity by distractor ($F(1,7) = 14.57$; $p < 0.01$). There was insufficient statistical power to support a formal investigation of this interaction, though it appears to reflect an interaction between eccentricity and distractor that arose for right-sided targets only, whereby the distractor induced a slight slowing of MRTs (~9 ms) at the far location, and an equivalent speeding of MRTs (~9 ms) at the near location. It is hard to ascribe any theoretical significance to this interaction, but it should be noted that apparent influence of the distractor for targets at the near location would in any case be opposite to the RDE for saccades.

Table 4.1 reports the measure of within-subject variability for both the saccadic and manual modalities in the target only and target with distractor condition as previously presented in the interaction plot.

	T	TD
Saccadic	70	58
Manual	66	70

Table 4.1. Experiment 2 data variability.
Average within-subject interquartile range (ms) for target only (T) and target with distractor (TD) condition in the Saccadic and Manual modalities.

An additional analysis in order to assess the within-subject variability of RTs in the different task conditions has been run. For each participant, the interquartile range (IQR) was computed for each condition as measure of within subject variability and entered into a 2x2x2x2 (*Modality * Side * Eccentricity * Distractor*) repeated-measures ANOVA. The analysis did not show any significant effects.

4.2.2.3 Analysis of manual kinematics

Given the absence of RDE for manual responses, it is important to consider the possibility that distractors may instead have affected the speed and/or accuracy of the *execution* of manual responses. To evaluate this possibility, median values of each kinematic variable (MT, PS, TPS, CE, VE; see Methods section) for each participant for each manual response condition were submitted to seperate 2x2x2 *(side * eccentricity * distractor*) repeated-measures ANOVAs. Main effects of target eccentricity were observed for MT ($F(1,7) = 89.15$; $p < 0.001$), PS ($F(1,7) = 26.03$; $p < 0.001$) and TPS ($F(1,7) = 59.49$; $p = 0.001$) since, unsurprisingly, movements made to the more eccentric target were of a longer duration, and reached a higher peak speed at a later time than movements to the near target. The side of target presentation similarly influenced MT ($F(1,7) = 30.02$; $p < 0.001$), and marginally influenced PS ($F(1,7) = 5.35$; $p = 0.054$), as movements made to the right side were briefer and reached a higher speed. This pattern would be expected for the right hand, since movements to ispilateral targets are typically more efficient than to contralateral targets (e.g. Fisk & Goodale, 1985). Critically, however, distractors had no significant impact upon MT, PS or TPS. Similarly, neither the accuracy (as measured by CE) nor the precision (as measured by VE) of manual responses were affected by distractor presence. Target eccentricity did affect VE, however ($F(1,7) = 12.90$; $p = 0.009$), with movements being more precise for the near than for the far target (mean VE 4.49 vs. 5.08 mm). These kinematic data give no indication that MRTs are preserved in the presence of distractors by sacrificing the accuracy of motor programming. The data from Experiment 1 thus indicate that neither the initiation nor the execution of manual responses is influenced by distractors in this task.

4.2.3 Experiment 2 discussion

The appearance of a distractor dot in the unattended hemifield, simultaneous with target onset, caused eye movements to be delayed relative to the condition where the target was presented alone. This replicates the well-documented RDE (Walker et al., 1995, 1997). In contrast, manual aiming-movements were unaffected by distractors. This was true both for response initiation, and for the kinematic character and terminal accuracy and precision of the executed movement. The lack of modulation of MRTs by distractors therefore did not result from a speed-accuracy trade-off, in which the participant preserved response latencies by sacrificing motor programming accuracy. Experiment 2 thus found that eye movements were susceptible to distraction where manual aiming movements were not. This result is perhaps surprising, given prior demonstrations that the FOE component of the gap effect does generalise to manual aiming (Bekkering et al, 1996; Pratt et al, 1999). Moreover, these studies demonstrated the FOE even for manual responses made whilst eye movements were constrained, equivalent to the manual condition of our Experiment 1. The lack of RDE for manual aiming in Experiment 2 thus questions the idea that the saccadic RDE and FOE share a common neurophysiological basis (Walker et al., 1997; Findlay & Walker, 1999).

Notwithstanding the clear contrast with earlier findings (Bekkering et al., 1996; Pratt et al., 1999), it may be noted that the strict requirement for participants to maintain central gaze during manual aiming is somewhat unnatural. It is conceivable that this demand for uncoupled responses of the hand and eyes critically influenced the outcome of Experiment 2, by forcing participants to uncouple response systems that would be coupled under more naturalistic conditions. In order to assess this possibility, Experiment 3 replicated the basic procedure in a more naturalistic task, in which participants were free to move their eyes during manual responding.

4.3 Experiment 3

4.3.1 Method

4.3.1.1 Participants

Ten volunteers from the University of Edinburgh, aged between 18 and 24 years, participated in this study. All participants were right handed by self-report, and free from neurological and visual impairments. This experiment was conducted in accordance with the 1964 Declaration of Helsinki, and with the approval of the Ethics Committee of the School of Philosophy, Psychology and Language Sciences at the University of Edinburgh.

4.3.1.2 Apparatus and stimuli

Apparatus and stimuli were identical to those used for Experiment 2.

4.3.1.3 Procedure

The procedure was identical to that of the manual condition of Experiment 2, except that participants were free to move their eyes as soon as the target appeared, although they were not required to do so. Each participant completed two blocks of 70 trials each. Within each block, trials were shuffled randomly, and each combination of target eccentricity (near, far) and distractor condition (T, TD) occurred 15 times, with ten catch trials in which a stimulus was presented in the non-target hemifield alone (five times each at the near and far eccentricities).

4.3.1.4 Analysis

Analysis of hand and eye movement parameters was performed as for Experiment 2.

4.3.2 Experiment 3 results.

4.3.2.1 Data screening

A total of ~36% of eye movement trials were discarded from the initial analysis due to no saccade being executed, blinks or corruption of the signal. A total of ~5% of hand movements were discarded due to corruption of the signal. SRTs faster than 70 ms or longer than 500 ms (~3%), MRTs faster than 100 ms or longer than 500 ms (~ 2%), and saccadic and manual response made in the wrong direction (~1%, and 0% respectively) were excluded from the analysis.

4.3.2.2 Analysis of RT

Since participants were required always to move their hand, but were free to move their eyes or not, we recorded a substantially smaller number of saccades than manual responses. Entire datasets were rejected for two participants, who produced insufficient numbers of saccades for reliable estimation of central tendency per cell (<2 saccades in each cell). For the remaining participants, median SRTs and MRTs were entered into a 2x2x2 (*Modality* * *Eccentricity* * *Distractor*) repeated-measures ANOVA.

There was no main effect of Modality ($F(1,7) = 0.45$; $p = 0.52$) or target location ($F(1,7) = 4.40$; $p = 0.74$) on RT. Distractor condition did not produce a reliable main effect ($F(1,7) = 3.705$; $p = 0.096$), but did interact reliably with modality ($F(1,7) = 5.621$; $p < 0.05$). This interaction is shown graphically in Figure 4.3. Post hoc analysis revealed that SRTs were marginally lengthened (~25 ms) in the distractor condition ($t(7) = 2.30$; $p = 0.06$), while the slight reduction in MRTs

(~7 ms) did not approach significance (t(7) = 1.71; *p* = 0.13). Although the RDE for the eyes was only marginally reliable, presumably due to the relatively small number of saccades available, the interaction pattern in Figure 4.3 clearly replicates that observed in Experiment 1, with the RDE being specific to saccadic responses.

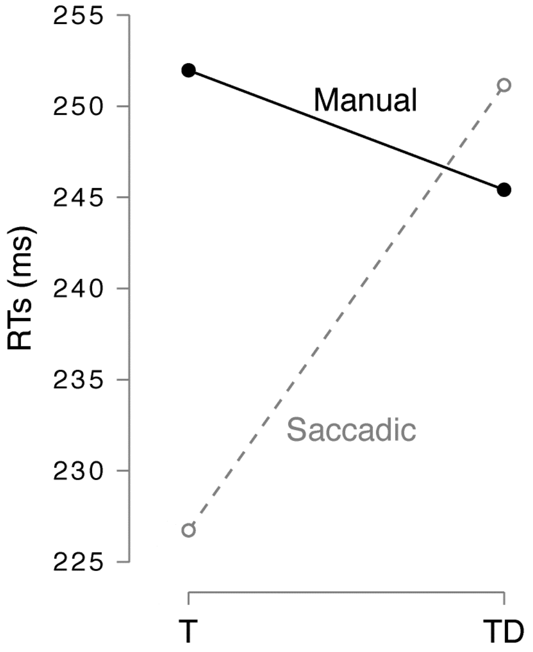


Figure 4.3 Experiment 3 results.
Saccadic and Manual RTs for target only (T) and target with distractor condition (TD).

Table 4.2 reports the measure of within-subject variability for both the saccadic and manual modalities in the target only and target with distractor condition as previously presented in the interaction plot.

	T	TD
Saccadic	105	84
Manual	71	73

Table 4.2. Experiment 3 data variability.
Averae within-subject interquartile range (ms) for target only (T) and target with distractor (TD) condition in the Saccadic and Manual modalities.

For seven of the eight participants (one participant did not have enough trials in one of the condition to compute the IQR, so was excluded from this analysis), the IQR was computed for each condition as measure of within subject variability and entered into a 2x2x2 (*Modality* * *Eccentricity* * *Distractor*) repeated-measures ANOVA. As for Experiment 2, the analysis did not show any significant effects.

As an additional check on the absence of RDE for manual responses, a further 2x2 (*Distractor* * *Eccentricity*) repeated-measures ANOVA was run only on the MRTs, including also the two participants that were excluded from the main analysis for producing too few saccades. This analysis, with improved power, found no reliable main effects or interactions, further confirming the invulnerability of MRTs to distraction.

4.3.2.3 Analysis of manual kinematics.

To maximise power, the analysis of the kinematics parameters was carried out on all ten participants. For each parameter a 2x2 *(Eccentricity* * *Distractor*) repeated-measures ANOVA was run. As in Experiment 2, target location exerted predictable influences on movement kinematics, with longer duration movements to the far target than the near target (MT 383 vs. 319 ms: $F(1,9) = 24.71$; $p < 0.001$), reaching a higher peak speed (PS 528 vs. 368 mm/s: $F(1,9) = 38.63$; $p < 0.001$) at a later point in time (TPS 222 vs. 187 ms: $F(1,9) = 10.04$; $p = 0.011$). Distractor condition had no reliable influence on any kinematic parameter, and nor were there any reliable interactions.

CE of the movement was affected both by target location ($F(1,9) = 78.36$; $p < 0.001$) and distractor condition ($F(1,9) = 19.76$; $p = 0.002$). In aiming for the near target, participants overshot by more than in reaching for the far target (4.5 vs. 1.2 mm), but the tendency to overshoot was reduced in the distractor relative to the no-distractor condition (2.5 vs. 3.3 mm). The precision of the movement (VE) was marginally affected by target location ($F(1,9) = 5.07$; $p = 0.05$) being less precise for the far than the near target (4.95 vs. 4.01 mm), as also observed in Experiment one, but was unaffected by distractor condition. Overall, as in Experiment 2, there was no indication of a speed-accuracy trade-offs for manual movements in the presence of distractors. The only anomalous result is the reduced tendency for overshooting when the distractor is present. There is no principled account to offer for this finding, which was not observed in Experiment 2 (and is not replicated in Experiment 4), but the direction of this effect is in any case opposite to that predicted by a speed-accuracy trade-off. The data strongly confirm the absence of an RDE for manual responses, even when fixation is unconstrained.

4.3.3 Experiment 3 discussion

Experiment 3 replicated the key outcome of Experiment 2: eye movements were susceptible to distractor interference while hand movements were not. In this second experiment, participants were free to move their eyes during the manual movement. Even under these more naturalistic conditions, manual and saccadic response systems were not tightly coupled, since the distractor was able to interfere selectively with the saccadic response. These experiments clearly point towards the conclusion that the RDE, unlike the FOE, is a saccade-specific phenomenon.

Following the running of Experiments 2 and 3, however, a discovery that modified our understanding of the RDE in an important way (see Chapter 6) was made, and prompted to design a third experiment to test the above conclusion further. Previous research has emphasized the critical importance of simultaneity, or near-simultaneity, between target and distractor, in determining the RDE (Walker et al., 1995, 1997). However, it was discovered that the critical temporal factor governing the RDE is not the timing of distractor onset relative to the target, but the temporal relationship between distractor onset and the expected time of saccade execution for the baseline (target-only) task (see Chapter 6). Specifically, remote distractors induce a reduction in the frequency of saccadic responses within a temporal window spanning from around 70 to 125 ms after distractor onset, with the maximum depression around 90 ms post- onset, with the suppressed saccades being delayed. These characteristics precisely match those of the well-described ‘saccadic inhibition’ phenomenon, whereby transient visual changes induce just such a temporally-specific dip in saccadic frequency during text reading, scene exploration, and pro- and anti-saccade tasks (Reingold & Stampe, 1999; 2000; 2002; 2003; 2004), implying that the classical RDE is in fact a consequence of saccadic inhibition.

The idea that saccadic inhibition underlies the RDE entails that the optimal timing of a distractor to produce a robust RDE will depend critically upon the character of the baseline SRT distribution for a given task. In the saccadic tasks of Experiments 2 and 3, a median target-only SRT of around 230 ms suggests that, in these tasks, distractors presented around 100-150 ms after target onset might have induced a larger RDE than distractors simultaneous with the target. More importantly, since the baseline reaction times were on average later for manual aiming than for saccades, the RDE might have emerged for manual responses if the distractors in the manual task had been delayed relative to their timing in the saccadic task. To test this possibility, Experiment 4 manipulated distractor timing, to check whether the absence of RDE for manual aiming is upheld across a wider range of distractor delays (0, 100 and 150 ms after target onset).

4.4 Experiment 4

4.4.1 Method

4.4.1.1 Participants

Fourteen volunteers from the University of Edinburgh, aged between 18 and 24 years participated at the study. All participants were right handed by self-report, and free from neurological and visual impairments. This experiment was conducted in accordance with the 1964 Declaration of Helsinki, and with the approval of the Ethics Committee of the School of Philosophy, Psychology and Language Sciences at the University of Edinburgh.

4.4.1.2 Apparatus and stimuli

Apparatus and stimuli were identical to those used for Experiment 2, except that only the far (10°) target position on the right side was used, making the target location perfectly predictable and invariant across trials and blocks. The use of a single target location is consistent with the method adopted by Pratt et al (1999), and additionally allowed us to keep trial numbers within reasonable limits, given the inclusion of two extra distractor delays in this experiment. Similarly, for reasons of efficiency, distractor-only catch trials were excluded.

4.4.1.3 Procedure

The procedure was similar to that of Experiment 2, except that, in addition to the target only condition (T), three distractor delay conditions were used, with the distractor presented simultaneously (D0), 100 ms (D100) or 150 ms (D150) after target onset. Each participant completed two blocks of 200 trials each. Modality of response (saccadic, manual) was blocked and the order was counterbalanced across participants. Within each block, trials were shuffled randomly, and each condition (T, D0, D100, D150) occurred 50 times, with no catch trials. Prior to each block, the participant was informed of the response required (saccadic or manual).

4.4.1.4 Analysis

Analysis was as for Experiment 2.

4.4.2 Experiment 4 results

4.4.2.1 Data screening

A total of ~13% of records were discarded from the saccadic analysis due to blinks or to corruption of the signal. A total of ~6% of hand movements were discarded due to failures to maintain central fixation or to corruption of the signal. SRTs faster than 70 ms and MRTs faster than 100 ms (SRT less than 1%; MRT ~1%) and longer than 500 ms. (SRT ~1%; MRT ~1%), made toward the wrong direction (less than 0.5%), were excluded from the analysis.

4.4.2.1 Analysis of RT

For each participant, the median RT was computed for each condition. Figure 3 shows the mean of median RTs for each modality and distractor condition. For the eyes, SRT was overall increased relative to baseline in the distractor conditions, with the largest effects at the longer distractor delays (D100 and D150). For the hand, MRT was overall reduced relative to baseline, with the largest effect at simultaneity. Surprisingly, then, the inhibitory effect of distractors was not only absent for the hand, but reversed to become facilitation, at least for the simultaneous distractor.

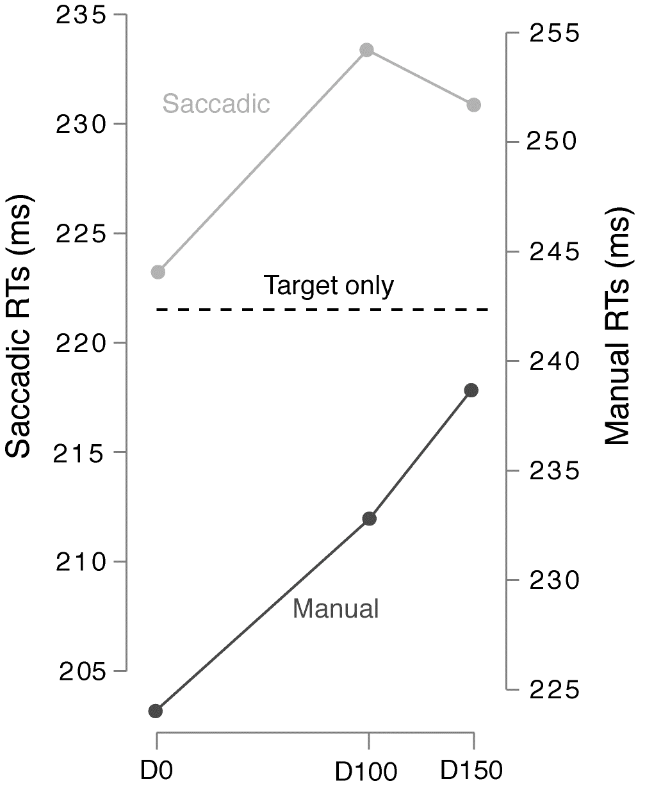


Figure 4.4 Experiment 4 results.
Saccadic and manual RTs for the three distractor delay conditions (D0, D100, D150). Note that this figure uses separate ordinate axes for the two modalities: the left ordinate represents SRT and the right represents MRT. The two scales are offset such that the dashed line representing the baseline (T) condition is aligned across modalities. In this way, the effects of distractors can be compared more directly between hand and eyes.

The patterns described above were confirmed by statistical analysis. A 2x4 (*Modality * Distractor condition*) repeated-measures ANOVA showed no main effect of modality ($F(1,13) = 1.18$; $p = 0.30$) , but a significant main effect of the distractor condition ($F(1,9) = 4.47$; $p < 0.01$), modulated by an interaction between the two factors ($F(3,39) = 6.38$; $p < 0.005$). Six planned paired t-tests were conducted to assess the reliability of the distractor effect, relative to baseline, for each distractor delay in each modality, with alpha adjusted to 0.008. For saccadic responses, the distractor induced a reliable slowing (RDE) in the D100 condition ($t(13) = 5.05$; $p < 0.001$), a marginal RDE in the D150 condition ($t(13) = 2.78$; $p = 0.016$), but no RDE in the simultaneous distractor (D0) condition ($t(13) = 0.30$; $p = 0.766$). For manual responses, MRTs were reliably facilitated in the D0 condition ($t(13) = 3.53$; $p <$

0.004), but were not reliably different from baseline in the D100 ($t(13) = 2.46$; $p = 0.03$) or D150 condition ($t(13) = 0.90$; $p = 0.39$).

Table 4.3 reports the measure of within-subject variability for both the saccadic and manual modalities in the target only and target with distractor condition as previously presented in the interaction plot.

	T	D0	D100	D150
Saccadic	83	60	75	89
Manual	77	60	74	78

Table 4.3. Experiment 4 data variability.
Average within-subject interquartile range (ms) for target and distractor conditions in the Saccadic and Manual modalities

As for the Experiment 2 and 3, for each participant, the IQR was computed for each condition as measure of within subject variability and entered into a 2x4 (*Modality * Distractor condition*) repeated-measures ANOVA. The only significant effect was the main effect of distractor condition ($F(1,13) = 7.511$; $p = 0.001$). Six paired t-tests (Bonferroni corrected) between the four conditions suggested that the effect was driven by a significant difference between the baseline (80 ms) and the D0 condition (60 ms: $t(13) = 4.544$; $p < 0.003$). Another significant difference was found between the D0 and the D150 (84 ms: $t(13) = -4.805$; $p < 0.002$). All the other comparisons did not reach significant level. There is no obvious hypothesis to explain why the D0 condition should have lower variability than the baseline and the D150 condition.

4.4.2.1 Analysis of manual kinematics

MT, PV, TPV, CE and VE of the reaching movements were all unaffected by distractor condition.

4.4.3 Experiment 4 discussion

Experiment 4 provides a third replication of manual resistance to remote distraction. Moreover, by testing across several distractor delays, it is possible to exclude that, because manual aiming responses tend to have longer latencies than saccades, a slightly later distractor is required to produce the same interference. The data from this experiment also reinforce the recent demonstration that the maximal saccadic RDE does not necessarily arise from simultaneous target and distractor onsets (Bompass & Sumner, 2009a; see Chapter 6). The critical insight is that the RDE reflects the inhibition of saccades within a window 70-125 ms after distractor onset. It is therefore to be expected, given a baseline median SRT of ~220 ms in Experiment 4, that distractors delayed by 100 and 150 ms should be more disruptive than a distractor at simultaneity (D0). In fact, the simultaneous distractor produced no reliable increase in SRT. At first sight, this may seem to conflict with the reliable RDE for simultaneous distractors in Experiments 2 and 3. However, Experiment 4 used only the far (10°) target and distractor positions, the equivalent stimuli to which produced a negligible effect of simultaneous distractors in Experiment 2. Therefore, the character of the saccadic RDE in the present experiment is perfectly consistent with the prior experiments. The results suggest that the RDE is a saccade-specific phenomenon, which does not generalize to other spatially-oriented responses. This idea will be further considered in section 4.5.

First, however, consider another striking feature of the data of Experiment 4: not only were manual reactions not inhibited by any of the distractors, they were *facilitated* significantly by a simultaneous distractor. This is reminiscent of the well-documented facilitation, known as the redundant target effect (RTE), induced by the presentation of multiple targets when participants must issue a simple detection response, such as a key-press (Hershenson, 1962; Raab, 1962). It is possible to hypothesise that the speeding of manual reactions in Experiment 4 is indeed a form of RTE, and that it arises because of the very high target predictability in this particular design. Spatial predictability, at least for target direction, is required in order to observe the RDE independently of cognitive discrimination of target from distractor (Braun & Breitmeyer, 1990; Walker et al., 1995; Walker et al., 1997;

Weber & Fischer, 1994; Walker et al, 1995). As noted by Pratt et al. (1999), spatially predictable targets make a manual aiming response more similar to a simple key press, in that it could be preconfigured ‘offline’ and initiated on the basis of target detection, rather than being configured *de novo* on the basis of online target selection. In Experiment 4, this was compounded by the absence of distractor-only catch trials, such that a preconfigured response could be issued upon detection of either the target or the distractor. In the last experiment participants exploited simultaneous distractors as imperative stimuli for manual responding, thereby showing a redundancy gain (RTE). In Experiments 2 and 3, a trend towards manual facilitation from simultaneous distractors can be discerned (see Figures 4.2 and 4.3). In Experiment 4, the use of an invariant target location, and the elimination of catch trials, may have transformed this incipient trend into a robust facilitation.

The fortuitous finding of an RTE for manual aiming but not saccades highlights one potentially key difference between these two responses. For predictable targets, manual aiming may be amenable to off-line control, with pre-configured movements being initiated in response to target detection, whilst saccades are more tightly bound to processes of online target selection. Support for this proposal can be found within the literature. In a series of elegant experiments, Deubel and Schneider have shown that covert shifts of spatial attention precede saccadic (Deubel & Schneider, 1996) or manual aiming (Deubel, Schneider & Paprotta, 1998) movements (see Schneider and Deubel, 2002, for a review). This is revealed by an enhancement of perceptual discrimination, spatially specific to the target location. This coupling of attention to the intended target of an action may be obligatory, since the effect persists even when participants are cued to make a perceptual discrimination at locations remote from the action target. However, a subsequent experiment assessed the coupling of attention and action under immediate and delayed action conditions (Deubel & Schneider, 2003). Discrimination was selectively enhanced at the target location at the time of initiating saccades, irrespective of the delay since target onset, suggesting that spatial attention is obligatorily coupled to the saccadic target at the time of response. However, when manual responses were delayed by 300 ms or more from target onset, attention was no longer pinned to action target, but could be deployed elsewhere. These effects of temporal delay may be directly analogous to those of target predictability in our Experiment 4, since both manipulations provide perfect foreknowledge of the target location. Such foreknowledge may allow manual responses to be executed ‘off-line’, on the basis of a prepared motor plan, whilst saccades are always ‘on-line’, requiring target selection at the time of initiation.

Experiment 4 provides a third replication of the main result, the absence of RDE in manual aiming, and additionally suggests a looser relation between target selection and response initiation for the hands than for the eyes (Deubel & Schneider, 2003; Schneider & Deubel, 2002). The data also illustrate the robustness of the saccadic RDE. Even with an invariant target location, saccadic responses cannot resist distraction from an onset stimulus in the opposite field, confirming that the basic RDE is strongly automatic, immune to top-down influences.

4.5 General discussion

These three experiments establish that the RDE is specific to saccadic responses, in that it does not generalise to a spatially-oriented manual response. This is in direct contrast to the FOE component of the gap effect, which does apply to manual aiming in a similar way as to saccades (Bekkering et al., 1996; Pratt et al., 1999). This contrast undermines the hypothesis that the RDE arises from the same neurophysiological substrate as the FOE, namely the activity of fixation neurons in the superior colliculus (Walker et al., 1997; Findlay et al., 1999). By exclusion, the results support the alternative view that the RDE arises from the stimulation of saccade *build-up neurons* coding for the distractor location, which competitively inhibit *build-up neurons* stimulated by the target (Olivier et al., 1999). The RDE may be related to competitive target selection, and the FOE to response initiation. Neurophysiological data better support the idea of competitive target selection. In fact, it is well known that fixation neurons have been found predominantly for stimuli acting in the central region of the visual field. Walker and colleagues in their work refer to studies which demonstrate the presence of fixation neurons up to 10° of visual angle (Gandhi & Keller, 1997) and that the RDE is a result of an extended fixation zone (Walker et al., 1997). On the other hand, according to Everling et al.

(1998), even if up to 50% of *omni pause* neurons (OPNs - located near the midline in the caudal pontine reticular formation within the *nucleus raphe interinterpositus* - Buttner-Ennever et al., 1988; Langer & Kaneko, 1990) responded to visual target presented in the periphery up to 10° of visual angle, only a small percentage of fixation neurons responded to such stimuli, making the idea of an extended fixation zone less probable. On the other hand, the work by Honda (2005) provides more evidence for the competition hypothesis. In his paper it is shown how a continuously presented fixation point reduced the strength of the RDE. His explanation for the reduction lies in the inhibitory activity of the saccade-related neurons against other population of saccade-related neurons at remote location (Munoz & Istavan, 1998; Wurtz, Basso, Pare, & Sommer, 2000). Such inhibitory activity is weakened when the fixation is on, stimulating fixation neurons. In contrast, GAP paradigms creates the perfect condition for the lateral inhibition activity between saccade related neurons, strongly decreasing SRT to target location. This interpretation is also endorsed in the competitive integration model proposed by Godijn and Theeuwes (2002). The model hypothesised that saccade related activation is enhanced at neighbour location, leading to spatial and temporal modulation, whereas it is inhibited for remote ones. Moreover Trappenberg et al. (2001) provided physiological evidence that the SC is the locus where these sorts of interactions can take place, explaining effects such the global effect and the RDE.

As pointed out by Olivier et al. (1999), understanding the RDE in terms of competitive target selection suggests a unified account of the effects of remote distractors with those of distractors close to the target. Whilst the former increase saccade latency, the latter primarily affect saccade metrics, biasing the saccade toward the centre of gravity between target and distractor (*global effect*; Walker et al., 1997). This spatial averaging of saccade plans might arise for near distractors because the build-up activity associated with the target and the distractor may overlap spatially, whilst a winner-takes-all competition would emerge between the non-overlapping populations created by remote distractors. Consistent with our hypothesis, a study of the global effect on hand movements (Salier et al., 2002) showed that pointing movements seemed to mimic the eye behaviour when a distractor is presented nearby the target, but only in some circumstances, suggesting that the two systems are coupled during target selection but that they do not use the same target representation to achieve such coupling. Moreover the global effect for the hand movements seemed to be less stable and depending more on the target-distractor configuration. This result is compatible with the suggestion of a non completely shared target representation within the superior colliculus.

A second benefit to the identification of the RDE with competitive inihibition between saccade build-up neurons is that this corresponds closely to the mechanism of saccadic inhibition envisaged by Reingold and Stampe (2002). As described in Chapter 6, since it is argued that the RDE is identical with the phenomenon of saccadic inhibition, the two phenomena require a single neurophysiological explanation. Nonetheless, it must be emphasised that the present conclusions apply strictly to the relatively eccentric distractors used in the present experiments (5-10°). The contribution of fixation neurons to the RDE may increase for distractors within the central 2° of the visual field. If so, we would predict that manual responses would become prone to inhibition by central distractors. On the other hand, there are already data indicating that this may not be the case. In a control experiment carried on by Ross and Ross (1981 - Experiment 2, pp. 432) participants were asked to move a lever left or right as soon as a peripheral target was presented. As in their previously experiments, a warning signal at fixation was presented (onset or offset) at different SOA. They clearly demonstrate that in such circumstances there was no increase of manual reaction times for stimuli presented after target onset. Surprisingly, manual reaction times were reduced for both warning onset/offset presented at simultaneity. This unexpected outcome is perfectly congruent with the data of Experiment 4, where it is possible to observe a decrease of manual reaction times for distractor presented with target onset. These results could be associated with the redundant target effect already mentioned in the discussion of Experiment 4.

If we accept Olivier et al's (1999) account of the RDE as arising from competitive target selection processes within the intermediate layers of the superior colliculus, we must still ask why such effects should not generalize to manual aiming responses. One possibility is simply that manual responses do not share these target selection mechanisms, despite evidence for the representation of arm movements within these layers (e.g. Stuphorn et al., 2000; Werner, 1993; Werner et al., 1997).

The present study, however, cannot provide evidence either to support or refute this possibility, because our use of highly predictable target locations may have promoted dissociated manual and saccadic responses, regardless of whether these responses normally share target selection mechanisms.

In summary, the present study showed that eccentric remote distractors interfere with saccade initiation even for highly predictable targets, but that this does not apply to manual responses. Whether or not manual responses will continue to resist distraction when target location is less predictable, or distractors are closer to fixation are issues for future research. However, these unresolved questions do not obscure the clear contrast between the present results and previous demonstrations that the FOE affects manual aiming to predictable targets (Bekkering et al., 1996; Pratt et al., 1999). This contrast undermines the idea that the RDE, like the FOE, is due primarily to the activity of fixation neurons in the superior colliculus (Walker et al., 1997; Findlay & Walker, 1999). The RDE may instead reflect competitive interactions between collicular build-up neurons during saccadic target selection.

4.5 Future directions

As discussed in the previous sub-section, foreknowledge of target location may allow manual, but not saccadic responses, to become independent of online target selection (cf. Deubel & Schneider, 2003). Accordingly, even if the RDE operates at the level of saccadic target selection, and even if these selection processes are normally shared by manual responses, manual responses to predictable targets may nonetheless be decoupled from target selection, and thus immune to distraction. At this stage the remaining question is if attentional processes are prone to RDE. As previously stated, in the experimental design used for this study, participants were aware of the direction of target appearance, as in Experiments 2 and 3, or even perfectly reliable knowledge of the target location, as in Experiment 4. In these specific conditions the saccadic system could not resist distraction, showing it to be immune to top-down modulation. However, within the attentional literature is reported that covert attentional capture by abrupt visual onsets is not similarly immune to top-down modulation. Yantis and Jonides (1990) showed that advance knowledge of target location can eliminate the deleterious effect of distractor onsets upon target identification. Theeuwes (1991) similarly concluded that visual onsets outside of the focus of attention do not attract attention automatically, and showed that the size of the attentional focus is sensitive to the certainty of participant's expectations about target location. These experimental observations relate to circumstances that are closely equivalent to the previously described situation of perfect target predictability used in this experiment. These data suggest that attentional processes could be immune from distractor appearance in a classic RDE paradigm. On the other hand, an influential theory of attention would predict a different outcome. According to the premotor theory (Rizzolatti, 1987; 1994), attentional shifts are considered to be identical to eye movements with the only difference being that the movement is not executed. Moreover, the same circuitry responsible for the programming of the movement itself it is hypothesised to underly the attentional processes, in this particular case the neurophysiological substrate is identified in the SC. The premotor theory then would predict that a covert shift of attention will inherit all the characteristics of an eye movement, including the RDE. In order to test this hypotheses, it has been designed an experiment to measure the impact of remote distractors upon covert attention in a standard remote distractor set-up (see next chapter). The outcomes from the experiment will help to discern between these conflicting hypotheses and will further clarify the relationship between overt and covert attentional processes.

Chapter 5

The RDE during covert discrimination

Chapter overview. As has been extensively investigated in the previous chapters, one problem the visual system has to deal with is the distinction between targets and distractors. So far, it has been observed that there is a cost for the visual system to inhibit a contralateral distractor. In both Chapter 2 and Chapter 4, the RDE was replicated for saccadic responses (Walker et al., 1995). On the other hand, in Chapter 2, simple manual responses were not slowed down by distractor appearance. Moreover, as shown in Chapter 4, pointing movements were also immune to distractor onset; indeed, participants were actually faster during bilateral stimulation. Preliminary conclusions support the idea that the RDE is not a general attentional phenomenon but could be a peculiar characteristic of the oculomotor system. Consistent with this assumption, it has been hypothesised that the oculomotor system and the limb motor system might not share target selection mechanisms, and that the two systems can be successfully decoupled, as has already been shown by Sailer et al. (2002) in the case of the Global Effect. Whether spatial shifts of attention will inherit the RDE remains an open question. This problem has already been introduced in Chapter 2, but the set-up used to investigate the RDE during covert discrimination did not provide a clear solution. The aim of the present chapter is to respond to the question, defined as follows:

Does an irrelevant onset capture attention even when the target location is perfectly predictable?

In order to answer this, the effect of distractors was tested during a covert discrimination task. In contrast to the study reported in Chapter 2, in the present experiment covert discrimination was required to identify a letter briefly flashed inside a dot. In some trials, a contralateral dot was presented. The results demonstrate that covert discrimination was not impaired by distractor appearance. On the contrary, the same experimental set-up and stimuli led to a strong and consistent RDE when saccadic instead of covert responses were required, supporting the idea of the dissociation of the covert and overt systems.

5.1 Introduction

In the previous chapters the behaviour of the oculomotor system in the presence of multiple targets was reviewed. In particular, we examined an interesting effect that consists in the delay of SRTs when a contralateral distractor was presented simultaneously with target appearance. The effect was first explained in cognitive terms, referring to the time needed to choose which target to look at (Lévy-Schoen, 1969), but further investigation provided a different explanation. In fact, the delay persisted both for distractors presented at fixation (Ross & Ross, 1980; 1981) and when the target was presented in one hemifield at a predictable location (Braun & Breitmeyer, 1990; Weber & Fisher, 1994), removing in this way the cognitive component of choice. The most complete work on this topic has been carried out by Walker and colleagues (1995; 1997). In particular, they showed that the delay in SRT persisted even for completely predictable targets (Walker et al., 1995). Moreover, they observed that the effect was stronger for foveal distractors and decreased for distractors presented further into the periphery, at up to 10° of visual angle (Walker et al., 1997). This Remote Distractor Effect (RDE) was hypothesised to develop in the circuitry of the superior colliculus involving stimulation of the *fixation neurons* (Walker et al., 1997, Findlay & Walker, 1999). These particular neurons are mainly present in the rostral pole region of the SC that represents the central 2° of visual field (Munoz & Wurtz, 1992, 1993a, 1993b), but neurons with similar properties have been recorded at up to 10° of eccentricity, beyond the rostral pole (Gandhi & Keller, 1997). An extended fixation zone was believed to be responsible for the delay in SRTs (Findlay & Walker, 1999). However, other authors (Olivier et al., 1999) hypothesised that a more likely source of inhibition for the RDE came from a mechanism of lateral inhibition at the level of the sub-population of *build-up neurons* that coded for incompatible saccades in the intermediate layers of the SC (see Chapter 1 for a more detailed explanation of RDE mechanisms).

The empirical contribution on the RDE reported in the previous chapters provided more data on the generalization of such phenomena to other modalities. In particular, the distractor effect was tested on saccadic movements, simple manual responses, manual aiming responses and in a covert discrimination task. The results showed that manual movements were not affected by distractor appearance. When either a general response such as a simple keypress (Chapter 2), or an aiming movement (Chapter 3) such as a pointing movement was required, no distractor effect was recorded on RTs. On the other hand, saccadic responses were always susceptible to distractor interference (Chapter 2 and 4). More complex was the interpretation of the findings on the covert task tested in Chapter 2, where an increase in RTs was recorded during bilateral stimulation. Nonetheless, it has been argued that the increase in RTs was not a pure motor effect, as the RDE is hypothesised to be, but an increase related to higher-level cognitive processes (i.e. discrimination of target location). In fact, the attentional task used to measure the RDE in Chapter 2 introduced a compatibility effect between distractor appearance and the responding hand (see section “2.4 Discussion” for more detail), making the interpretation of the data harder. In that case, in fact, participants were asked to discriminate the target location in order to produce the correct response. The right or left button was pressed according to whether the target location was on the right or on the left side of the right section of the display.

To correctly measure the RDE during a covert discrimination task, it was necessary to design an experiment without the ambiguity of that described in Chapter 2. For this reason, a psychophysical experiment was run whereby, instead of a discrimination based on target location, participants were asked to discriminate target *identity* (letter “E” from the mirror-reversed letter “E”). In this way the compatibility between the responding hand and the target locations was eliminated. Before entering into the detail of the experiment it is necessary to review some of the literature on the relationship between attention and eye movements.

5.2 Relation between eye movements and attention

Attentional processes are one of the most commonly investigated mechanisms of the neural system. In particular, the ability to devote attention to a specific location in space without moving the eyes has given rise to much interest among scientists. This ability has been named *covert attention* and it differs from the *overt* process, whereby a stimulus presented in the visual field elicits an orienting response, i.e. the movement of the eyes toward the object to bring it into the fovea. One of the main questions that scientists have been interested in answering is the relationship between these two forms of attention and their degree of independence. In 1987 Rizzolatti and colleagues proposed one of the most influential hypotheses on this topic, the *premotor theory of attention*. Starting from the observation that there was a close relationship between the brain structures controlling eye movements and spatial attention (Matelli, Olivieri, Saccani & Rizzolatti, 1983; Rizzolatti, 1983) Rizzolatti argued that there was a complete identity of the overt and covert attentional systems. In fact, the neural circuitries that support the motor control of the eyes were hypothesised to also be responsible for attentional shifts, making covert attention an integral part of the motor system. A covert shift of attention was then redefined as a motor program for the preparation of an eye movement. A central role in these processes was played by the *pragmatic maps*. Rizzolatti et al. (1994) referred to pragmatic maps as neural representations of space that are used to produce motor outputs. According to premotor theory, spatial attention can avail itself of any pragmatic map within the motor system in order to compute a location in space. In humans and primates, given the central role of the oculomotor system, spatial attention is restricted to those areas that code for oculomotion. For instance, an example of a pragmatic map might be the motor map within the superior colliculus, as described by Wurtz (1996).

In the first experiment carried out to support these ideas, Rizzolatti and colleagues used a modification of the classic Posner paradigm (Posner, 1980) whereby participants were asked to respond manually to the occurrence of a visual stimulus, ignoring the previously presented spatial cue. The possible target locations were displayed across the horizontal and the vertical line in relation to the fixation point. The results showed that valid trials were faster than invalid ones, implying that re-orienting the attentional system entailed a significant cost, as already noted by Posner (1980). Moreover, this cost was dependent on the distance between target and cued location and, more importantly, the cost was greater for reorienting between hemifields than within a hemifield, i.e. *the meridian effect*. Rizzolatti and colleagues concluded that the covert shifts of attention elicited by the cue were in fact oculomotor programs prepared to the attended location. The cost they observed represented the time needed to delete this program in favor of a new one. In a subsequent series of experiments, Sheliga et al. (1994) used a similar paradigm to investigate these attentional shifts directly in terms of motor programs, analysing the trajectory of the eyes to the target. In their experiment participants were asked attend to one of the four boxes presented above the fixation cross according to a cue presented at fixation. When the imperative stimulus appeared in one of the four boxes, participants were asked to make a saccade to the box placed under the fixation cross. Sheliga and colleagues (1994) observed a contralateral deviation in the trajectory of the saccade in respect to the hemifield where the imperative stimulus was presented. In valid trials, where the imperative stimulus was presented in the attended hemifield, the deviation was larger. In a second experiment they observed that the deviation to the contralateral hemifield occurred not only when the imperative stimulus was a visual target but also when the imperative stimulus was a sound. Sheliga and colleagues concluded that the spatial allocation of attention induced activation in motor areas devoted to saccadic control. Other experiments followed, supporting the findings of Rizzolatti and colleagues, replicating such effects of trajectory deviation related to the manipulation of spatial attention (see Chapter 2 for more detail). Other than behavioural data, neurophysiological recordings also supported the rationale proposed by the premotor theory. In particular, it is worth reporting the findings on the activity of the superior colliculus (SC) during the allocation of covert attention. Desimone, Wessinger, Thomas, and Schneider (1989; 1990) reported that deactivating small zones of the SC was reflected in the inability to covertly attend to targets when distractors were present in the impaired visual field. The author proposed that the overt and covert systems share a common neural network. Kustov and Robinson (1996) demonstrated that saccades generated by electrical stimulation in the superior colliculus were modulated in their trajectory via manipulation of both endogenous and exogenous attentional shifts. Interestingly, the deviation occurred also in pointing movements. Via single-unit recordings from the brains of rhesus monkeys, Ignaschenkova, Dicke, Haarmeier and Thier (2004) also found that a particular population of neurons in the SC (i.e. the *visuomotor neurons*) that is highly involved in the preparation of saccades was also active during attentional shifts. Finally, Müller and colleagues (2005) demonstrated that microstimulation of the SC was reflected in an improvement during a covert discrimination task for stimuli presented in the part of the visual field congruent with the stimulation site.

Neuropsychological data also provided intriguing evidence for the premotor theory. For example, Smith, Rorden and Jackson (2004) reported the case of a patient, AI, with a congenital opthalmoplegia that made her unable to make eye movements (Gilchrist, Brown, & Findlay, 1997; Jackson, Newport, Osborne, Wakely, Smith, & Walsh, 2005). She was tested in variants of the Posner cueing paradigm in which a peripheral cue (reflexive condition) predicted with a 50% of confidence the location of target appearance. This set-up was used in both the horizontal and vertical planes. In a further experiment endogenous cueing was also tested using a central arrow that was pointing to the target location with 50% of confidence. For the reflexive condition there was no advantage given by the cue. On the contrary, in the endogenous condition AI was able to use the cue, showing that voluntary allocation of attention was intact. The authors concluded that AI did not show a normal pattern of covert attention. The data supported the idea of a strong relationship between the ability to generate eye movements and covert shifts of attention, as proposed by the premotor theory. They also suggested that eye movements might play a critical role in the development of spatial attention.

Of course, there are theories that have conceived overt and covert attentional shifts as two separated systems. Posner, for example, proposed that different neural circuitries have been independently developed to sustain covert and overt processing (Posner, 1980; Posner & Petersen, 1990). According to Posner (1980), the link between spatial attention and saccade generation is only functional. In fact, even if there are strong similarities between the covert attentional system and the oculomotor system, the two systems are conceived of as independent. Attentional processes were hypothesised to be completely modular and anatomically separated from the data processing system, with specific brain regions devoted only to attentional control (Posner & Petersen, 1990). According to this view, the attentional system is similar to other sensory and motor areas, interacting with them but maintaining its identity and operating in a superordinate manner. Finally, the authors proposed that the areas involved in attentional processes can carry out different functions, each one specified in cognitive terms (Posner et al., 1988). According to this view, covert shifts of attention represent (Posner, 1988, p. 5; Fischer & Breitmeyer, 1987; Posner & Cohen, 1984):

> "[…] a way of guiding the eye to an appropriate area of the visual field"

and the mechanism underlying these attentional processes entails the capacity to enhance processing for attended locations (Posner, Nissen, & Ogden, 1978; Mangun et al., 2001). This view of spatial attention as a modular system that interacts with the low-level sensory and motor areas is supported by experimental data (Hunt & Kingstone, 2003b; Klein, 1980; Klein & Pontefract, 1994; Posner & Petersen, 1990). In particular, in a recent work Hunt and Kingstone (2003a) also showed a distinction between the motor programming related to eye movement generation and attentional shifts in the case of reflexive orientation. The authors used *inhibition of return* (IOR) to demonstrate that in such effects it is possible to isolate a motor-based component from an attentional one. In their task, participants were asked to make a saccade to a lateralised target in half of the blocks and to make a button press, left or right congruently with target location, in the other half of the blocks. Previous literature, in particular Reuter-lorenz, Jha and Rosenquist (1996), already showed that IOR interacts with target luminance but not with response modality, providing grounds for an attentional effect on target processing. On the other hand, Abrams and Dobkin (1994) showed that IOR interacts with the FOE (i.e. reduction in IOR during overlap condition), interpreting this result as proof that a motor-based component of IOR is working in a similar way to the inhibition generated by the foveation of the fixation point in the overlap condition. Hunt and Kingstone used a 2x2 design to factorially cross fixation manipulation (Overlap vs. Gap) with a manipulation of target luminance (bright target vs. dim target). They demonstrated that the motor-based component of IOR was present only when the response was oculomotor and the attention-based component was present only when the response was manual, successfully dissociating the two components of IOR and providing support for the distinction between attentional shifts and motor programming. In another study, Hunt and Kingstone (2003b) asked their participants to perform a dual task experiment in which they had to prepare an eye movement to one of two peripheral targets and then perform a discrimination task (i.e. discriminate between an horizontal or vertical line). In these circumstances they observed that even if participants were correctly using the cue to prepare the eye movement they did not improve during the discrimination task (the paper actually reports that the trend was in the opposite direction). When the order of tasks was reversed, and participants had to first perform the discrimination task and then the eye movement, Hunt and Kingstone observed that there was no improvement in the reaction time needed to prepare eye movements to the attended location. This pattern of data was interpreted as signalling a strong dissociation between voluntary shifts in overt and covert attentional processes.

The pattern of data described by Hunt and Kingstone (2003b) seems to contrast with the observation made by Deubel and Schneider (1996). In a series of studies the authors reported that discrimination was better at locations congruent with the location to which an eye movement was planned. Schneider and colleagues used a double task paradigm similar to the one used by Hunt and Kingstone (2003b), whereby participants were asked to perform a target-directed saccade in combination with a discrimination task. They observed that visual discrimination improved when the discrimination stimulus and the saccade target were the same object. Moreover, even when the location of the target to be discriminated was predictable, it was not possible for the participant to correctly saccade toward a nearby target. The authors concluded that there was a strong coupling between overt and covert processing and only a single attentional mechanism was needed to execute both selection and motor programming. The data reported by Deubel and Schneider strongly supported the sequential theory of attention proposed by Henderson (1992), which states that an eye movement starts with a shift of attention to the intended location, which is followed by the eye movement itself. In this way, attentional shifts always precede the generation of a saccade. In a similar way, Deubel and Schneider (1996) suggested that a selection process is required to bring information about the target location in space before a saccade can be generated. This selection process could be subserved by attentional shifts, as proposed by Henderson (1992).

Some neurophysiological data also support the idea of dissociation between eye movements and shifts of attention (Awh, Armstrong, & Moore, 2006 for a review). Juan, Shorter-Jacobi, and Schall, (2004) reported that, in the *frontal eye field* (FEF), shifts of attention toward a target were not accompained by saccade preparation. Moreover, Thompson, Biscoe and Sato (2005) showed that the activity of visually responsive neurons in the FEF is dissociated from the activity of saccade-related responsive neurons, that are on the contrary inhibited. The author proposed that the visually responsive neurons represent the attentional spotlight.

The attentional theories described above provide the ground for a strong hypothesis regarding the effect of distractors during the performance of a covert task. In particular, according to the premotor theory of attention, if the covert system is completely overlapped on the overt system, and the same pragmatic maps are used to compute a motor program for a target, the covert system should behave in a similar manner to the overt system, inheriting all the properties of an eye movement, including the RDE. On the other hand, if the two systems were independent, as Posner suggested, it would be possible to dissociate the covert response from the overt one, relegating the RDE only to the oculomotor system. One problem that still remains to be discussed is whether distractor appearance is able to capture attention.

5.3 Attentional capture by distractor onset

In the previous section we reviewed part of the literature indicating how an irrelevant distractor interferes with the planning/execution of an eye movement, even when top-down processes, such as the prior knowledge of target location, are available in advance. There are mainly two types of event that can capture the attention: these are *offset* and *onset*. Many experiments have been run to see how onset/offset relate to the attentional state during, for example, a discrimination task. Usually in these experiments a participant is required to discriminate one stimulus among others that briefly appear on the screen. The strongest effect obtained in the attentional capture paradigm occurs when abrupt onset stimuli are used. Yantis and Jonides (1984) showed that in a visual search task, when one of the items had an abrupt onset, it was processed and consequently identified faster than other items in the visual array that were revealed on the screen without an onset, being introduced by gradually removing parts of a mask that was covering them. The authors concluded that abrupt onset caused a shift of attention toward the new object.

Further investigation (Jonides and Yantis, 1988) showed that other characteristics of the target stimulus, such as difference in luminance and hue, were not able to elicit the same shifts of attention as abrupt onset. Strong results on the effect of shifts of attention in response to cues were observed by Müller and Rabbit (1989). In a series of experiments it was shown that peripheral cues (flash) can interrupt and interfere with spatial endogenous orienting induced by a central symbolical cue (arrow). Even if abrupt onset has been reported to be the most powerful way to capture attention, other studies demonstrated that attentional capture can be overridden by top-down influences. The first to test this hypothesis were Yantis and Jonides (1990). In their study participants were asked to search for a letter in an array. In some trials a distractor letter appeared abruptly on the display (in contrast with the non-abrupt condition whereby the letters were revealed by removing the masking). A fundamental manipulation of this experiment was that a cue pointing to the target letter with 100% accuracy was presented at different SOAs (200 ms before, simultaneously with, or 200 ms after target appearance). When the cue was presented 200 ms before target appearance, participants were able to suppress the distracting effect caused by the abrupt onset of the distractor. For simultaneous and +200 ms SOA, abrupt appearance impaired performance relative to the classical study. In a recent review, Yantis (1998, p. 252) commented that:

> “When an observer directs attention to a spatial location in advance of a display, then visual events that would otherwise capture attention will generally fail to do so.”

Similar results were also obtained by Theeuwes (1991). In his experiment participants had to identify a letter in a display of four letters placed in an imaginary circle around the fixation cross. An arrow cue was also presented before (600 or 300 ms) or after (200 ms) the letters were unmasked. In some trials, a bar was abruptly displayed near one of the letters. When the bar was presented peripherally, and the cue was presented in advance, there was no modulation of RTs in the letter identification task. Only when the bar was presented near the target, the performance was affected, increasing the RTs. According to these data it seems clear that foreknowledge of the target position allows the focussing of the attention at the target location, eliminating any effect of the distractor appearing in the periphery. This idea has been conceptualised by Folk, Remington and Johnston (1992), who explained how a particular *set mode* can reduce the interference from distractors.

Schneider and Deubel (2002) reported an interesting experiment (Experiment 3) whereby they investigated the optimal condition for decoupling eye movements from covert processing and to what extent abrupt peripheral cues can involuntarily attract attention. In this experiment, participants knew in advance the location of the discrimination stimulus and they were instructed to wait for the appearance of the saccadic stimulus to make a response. In another condition, participants were asked to maintain fixation and ignore the irrelevant cues that were presented either ipsilaterally or contralaterally to the discrimination stimulus. The authors observed that participants were able to ignore controlateral peripheral cues. Instead, when the cue was used as a signal to generate a saccade, the cue was bound to the perceptual processing, and discrimination performance dropped for contralateral cues. The first conclusion was that irrelevant cues for saccade production were successfully suppressed. This observation fits nicely with the study previously described by Yantis and Jonides (1990), Theeuwes (1991) (see also Koshino, Warner & Juola,1992). Moreover, the author also added to the classic interpretation of irrelevant abrupt onsets that:

> "[…] it is not the abrupt appearance of the cues per se that generates the coupling of perception and action but its function to direct the saccade." (Schneider & Deubel, 2002, p. 624).

implying that the spatial relationship between target location and cue location is fundamental in determining whether the cue can be inhibited or not.

Nonetheless, new findings challenge this view of top-down suppression of irrelevant information. Recently a study by Christ and Abrams (2006) reviewed the two main experiments by Yantis and Jonides (1990) and Theeuwes (1991), arguing that confounding variables could have influenced their results. In particular, they pointed out that in these experiments there was no direct control of eye movements, and they relied only on verbal instructions in order to maintain fixation. In Christ et al. participants performed a task very similar to that used by Yantis and Jonides (1990), in which they were asked to discriminate a target that was revealed from behind a mask. A pointer predicted the location of the target's appearance with 100% reliability. In some trials, an abrupt onset occurred at a non-attended location. The results clearly showed that the abrupt onset was interfering with the discrimination response, increasing RTs. In a second experiment they replicated this pattern of data, even using a set-up whereby participants were induced into a highly focused state and pushed to use the central cue. In a third experiment, more similar to the Theeuwes (1991) study, the distractor stimulus they presented was a square (i.e. different from the letter the participants had to discriminate) and it appeared on the peripheral side of the letter. Even in the case of a general distractor the interference effect was still present, increasing RT in the abrupt onset condition. Only when participants were left free to fixate the target in order to accomplish discrimination did the effect disappear. Christ and collaborators argued that in the previous studies participants focused in advance on the target location, giving them an advantage deriving from foveal acuity. In Christ's experiment, in contrast, fixation was monitored by an eye-tracker and the results challenge previous findings on top-down influences and the ability to ignore abrupt stimuli. In fact, the authors suggested that abrupt onsets always capture attention.

5.4 Rationale for the experiments

A detailed analysis of the attentional literature highlights some uncertainty regarding the likely outcome of the present experiment. On one hand, abrupt stimuli seem automatically to catch attention, but on the other hand there are data that suggest an ability to suppress distractor influence via top-down control (Yantis & Jonides, 1990; Theeuwes, 1991; Koshino, 1992). Moreover, more empirical data are needed to support either the identity hypothesis proposed by Rizzolatti in the premotor theory or the modularity of the attentional system proposed by Posner. The following experiments were run to disentangle these issues. In particular, a discrimination task was designed to test the effect of a distractor on covert attention in a classic RDE paradigm.

5.5 Experiment 5

5.5.1 Method

5.5.1.1 Participants

Eleven volunteers from the University of Edinburgh, aged between 18 and 24 years, participated in this study. All participants were right handed by self-report, and free from neurological and visual impairments. This experiment was conducted in accordance with the 1964 Declaration of Helsinki, and with the approval of the Ethics Committee of the School of Philosophy, Psychology and Language Sciences at the University of Edinburgh.

5.2.1.2 Apparatus and stimuli

White on black stimuli were presented on a 19-inch CRT monitor (1024 x 768 pixel resolution, 32-bit True Colour, 75Hz refresh rate) driven by a Pentium IV processor at 75Hz. A second computer was used to run the Eyelink II head-mounted system to record eye movements at a sampling frequency of 500 Hz. Participants' responses were recorded with a standard keyboard. Participants were seated in front of the monitor, with their heads immobilised in a chin rest and their eyes horizontally and vertically aligned with the centre of the screen at a viewing distance of 90 cm. The height of the chin rest was adjusted appropriately, depending upon the height of the participant. To facilitate fixation, a white cross (~0.25° by ~0.25°) on a black background was presented at the centre of the screen. Two visual stimuli were used. The saccadic stimulus (SS) was a white dot (~1°). The discrimination stimulus (DS) was a white dot with the letter "E" (~0.3° by ~0.6°), or a mirrored "Ǝ", placed in the centre. Both the visual stimuli appeared in the same position, 4.5° from the fixation cross.

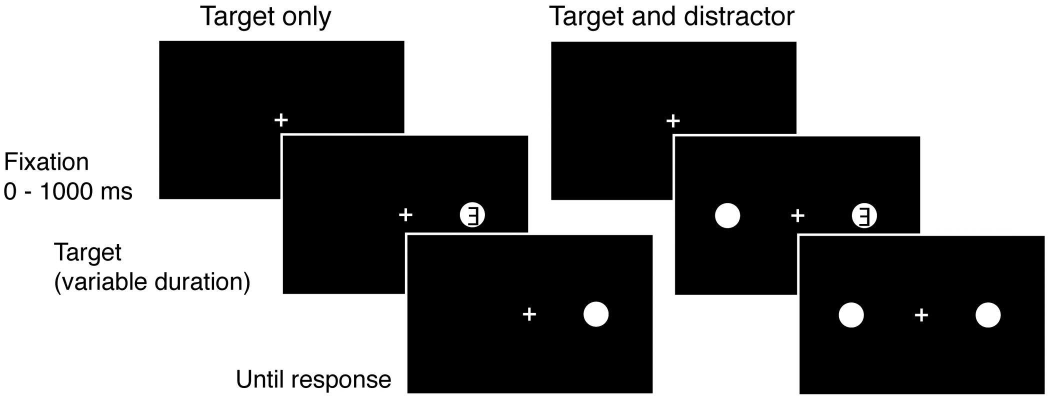


Figure 5.1 Experiment 5, task and stimuli.
Diagram displaying the task in target only (left) and target with distractor condition (right). Participants were required to discriminate the letter flashed inside the dot without moving the eyes from fixation.

5.2.1.3 Design

A 2x2x8 (*side * distractor * duration*) repeated measure design was run. The task of the subject was to fixate the central cross and, without moving his eyes, press the "YES" key if the letter "E" was present or the "NO" key if the letter was a mirror-reversed “E”. Participants were aware that the letter would always appear on the right/left side of the screen according to the block. The experiment consisted of two target conditions, target only (T) and target with distractor (TD) and of eight duration conditions for the DS (79, 106, 133, 159, 186, 212, 239, 266 ms). Each participant completed 512 trials: these were divided into four identical blocks of 128 trials (16 trials for each condition).

5.2.1.4 Procedure

Participants were seated in front of a monitor with both hands on the keyboard ready to answer. The right index finger was placed on the "M" key for "YES" responses and the left index finger was placed on the "Z" key for the "NO" responses. The room was partially blacked out to prevent changes in light levels and sources affecting the experiment. Participants were instructed not to move their eyes during the trial. There were two kinds of stimulus presentation, bilateral and unilateral. In both unilateral and bilateral trials, the fixation cross was presented at the centre of the screen for the whole length of the trial. When the participant was securely maintaining fixation the experimenter started the trial. The discrimination stimulus appeared on the right/left side of the screen according to the block, and for a particular time determined by the duration condition. After the disappearance of the discrimination stimulus only the saccadic stimulus remained on the screen until the participant responded. In the bilateral condition, the sequence of the event was the same as in the unilateral condition, but an identical dot was presented on the opposite side of the screen to that of the target location. At the beginning of each trial a drift correction routine was run to adjust the position of the eyes according to the fixation cross. For the whole length of the trial the subject could not move his or her eyes.

5.2.2 Experiment 5 results

5.2.2.1 Data screening

For each of the eleven participants two sigmoid curves, one for target condition and the other of distractor condition, were fitted to the relation between duration interval and mean proportion of correct responses. This procedure was used to determine whether there was a reliable increment in discrimination performance. Only one participant was excluded from the analysis since his sigmoid fit did not reach a significant level either in the target only or in the distractor condition.

5.2.2.2 Analysis of proportion of correct responses

For each participant, the proportion of correct responses was computed at each condition and entered into a 2x2x8 (*side* * *distractor* * *duration*) repeated-measures ANOVA. The main effect of side was reliable ($F(1,9) = 9.818$; $p < 0.012$), reflecting a better discrimination performance in the case of targets presented on the right side than on the left side. The most notable effect was the main effect of duration ($F(7,63) = 31.928$; $p < 0.001$), showing that the performance improved with the lengthening of the time the target was presented. There were not any other reliable main effects of a distractor ($F(1,9) = 0.095$; $p = 0.765$) or interactions among the three factors. For the purpose of this study, it is most relevant to emphasize the absence of a significant interaction between distractor condition and target duration ($F(7,63) = 0.755$; $p = 0.626$). As shown in Figure 5.2, the onset of the distractor did not interfere with the ability to discriminate the target.

A 2x8 (*distractor* * *duration*) repeated-measures ANOVA was run on the discrimination sensitivity (d'), confirmimng that there was a general effect of target duration ($F(1,7) = 2.856$; $p = 0.012$), no main effect of distractor ($F(1,9) = 0.500$; $p = 0.497$) and that distractor appearance had no influence at any target duration ($F(7,63) = 0.553$; $p = 0.791$).

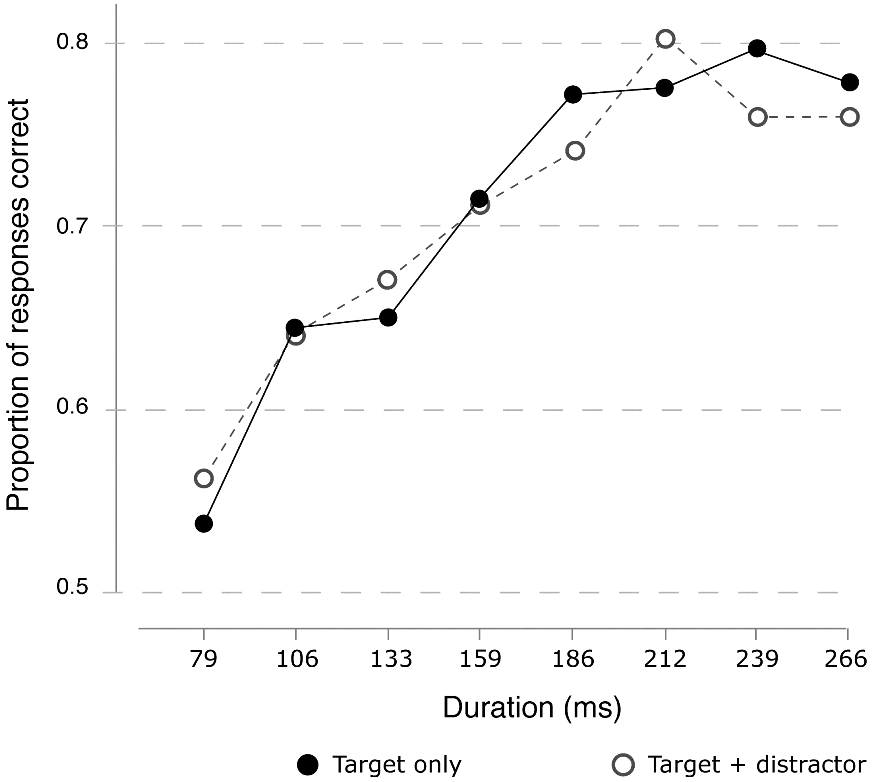


Figure 5.2 Experiment 5 results.
Interaction plot between *distractor* condition and stimulus *duration.* The two lines overlaps for all duration intervals, showing how distractor appearance was not interfering with target discrimination.

5.2.3 Experiment 5 discussion

The outcome of the experiment clearly demonstrates that distractor appearance does not influence discrimination performance, and contradicts the hypothesis based on the rationale of the premotor theory of attention (Rizzolatti et al., 1987; 1994). As previously reported, if covert shifts of attention are identical to eye movements, with the only difference being that the movement is not executed, we should have expected that if the distractor interfered with motor preparation, as it does in the RDE, it would also have interfered with the discrimination process. If attention was drawn away from the locus of the target display, then at short duration intervals the time required to discriminate the briefly presented letter should have lengthened. Overall the performance curve in Figure 5.2 should have shifted rightwards, with more time needed to reach the threshold for target discrimination. The findings of this study suggest that abrupt-onset distractors do not interfere with target discrimination, supporting the idea that shifts of attention do not inherit all the properties of an eye movement. In fact, in this particular case, no RDE was recorded.

This result is also highly congruent with the findings of Yantis and Jonides (1990) and Theewes (1991), who reported that previous foreknowledge of target appearance results in a suppression of the effect of an abrupt distractor during a covert discrimination task. In this particular case, there was a strong top-down influence that allowed participants to focus on just one side of the screen at the precise location where the target would be presented for the whole length of the block. Spatial location was in this way highly concentrated at one target location. Moreover, not only target appearance but also distractor characteristics were entirely predictable. Participants were aware that the distractor would always be presented on the contralateral side in respect to the target and the opposite eccentricity. Not only the spatial location remained constant, but also the temporal factor, since the distractor was always abrupt in concomitance with target onset. This highly predictable set-up for target and distractor presented the possibility for participants of attending to just that portion of the screen in which the target was located and completely suppressing stimuli presented in the periphery. The outcome contrasts with the findings reported by Christ and Abrams (2006). In fact, these authors suggested that the reason why Yantis and Jonides (1990) and Theewues (1991) did not find any distractor effect was because of a lack of eye movement control in their methodology. Christ concluded that it is impossible to suppress abrupt onset in a pure covert task. The present experiment contradicts this finding, since in the described task eye movement was checked via the eye tracking system, and only trials in which the eyes remained still at fixation were analysed. The outcome of this experiment points to the conclusion that abrupt onset does not always capture attention, and that top-down influences, such as foreknowledge of target location, distractor location and the temporal characteristics of these events, can provide enough information to suppress an irrelevant onset.

At this point though, there is still not enough information to fully support the dissociation between covert and overt processes, since the participants only performed the covert task. Even if in the previous chapters we found the RDE on saccadic movement, (Experiment 1 Chapter 2, Experiments 2, 3 and 4 in Chapter 4), we need to test saccadic movements in this particular design in order to confirm the expected RDE for this precise experimental configuration. The following experiment was run in order to do this. In particular, participants have been asked to saccade toward a target presented in the left/right hemifield and report whether the letter that was flashed inside the saccadic stimulus was the letter E or the mirror-reversed E.

5.3 Experiment 6

5.3.1 Method

5.3.1.1 Participants

Eleven volunteers from the University of Edinburgh, aged between 18 and 24 years, participated in this study. All participants were right-handed by self-report, and free from neurological and visual impairments. This experiment was conducted in accordance with the 1964 Declaration of Helsinki, and with the approval of the Ethics Committee of the School of Philosophy, Psychology and Language Sciences at the University of Edinburgh.

5.3.1.2 Apparatus, stimuli and design

Apparatus, stimuli and design were identical to those used for Experiment 1.

5.3.1.3 Procedure

The procedure was identical to that of Experiment 5, except that participants were asked to move their eyes as soon as the target appeared and to report the letter inside the saccadic stimulus. Discrimination performance and SRTs were recorded and analysed in this experiment.

5.3.2 Experiment 6 results

5.3.2.1 Data screening

SRTs faster than 70 ms (~4.9%) or longer than 500 ms (~0.6%), saccadic responses smaller than 1° of visual angle (~1.8%) and saccadic responses made in the wrong direction (~0.3%) were excluded from the analysis.

5.3.2.2 Analysis of RT

For each participant, the median RT was computed for each condition and entered into a 2x2x8 (*side * distractor * duration*) repeated-measures ANOVA. Only the main effect of the distractor was reliable ($F(1,10) = 26.464$; $p < 0.001$) reflecting that distractors in the non-target hemifield increased SRTs. The slowing down in SRTs was congruent with the effect described by Walker et al. (1995; 1997) and it persisted even with complete target predictability. Numerically, SRTs were ~7 ms slower in the distractor condition (140 ms) compared to the target-only condition (133 ms).

5.3.2.3 Data screening

For each participant an analysis was performed restricted to trials in which the SRT plus duration of saccade was smaller than discrimination stimulus duration. This was done because there was the necessity to exclude any trial in which the DS could have been foveated. Then the mean proportion of correct responses was calculated for each subject at each condition and only those conditions with at least 10 trials (over 16, 62.5% of trials for each cell) were used for statistical analysis. Only the first 3 duration conditions contained enough trials to carry on a complete ANOVA.

5.3.2.4 Analysis of proportion of correct responses

For each participant, the mean of the proportion of correct responses was computed for each condition and entered into a 2x2x3 (*side* * *distractor* * *duration*) repeated-measures ANOVA. In contrast with Experiment 5, the main effect of side was not reliable ($F(1,10) = 0.091$; $p = 0.769$), meaning that the discrimination was comparable for stimuli presented either in the right or in the left visual field. In addition, the overall effect of the distractor did not reach significant levels ($F(1,10) = 0.575$; p = 0.466). As reported for Experiment 5, the most notable effect was due to the manipulation of the duration ($F(2,20) = 20.194$; $p < 0.001$), showing that performance improved with the lengthening of the time the target was presented. There were not any other reliable effects of interaction between the three factors. For the purpose of this study, it is relevant to report the absence once more of a significant interaction between distractor condition and target duration ($F(2,20) = 3.010$; $p = 0.072$). As is shown in Figure 5.3 the onset of the distractor did not interfere with the ability to discriminate the target.

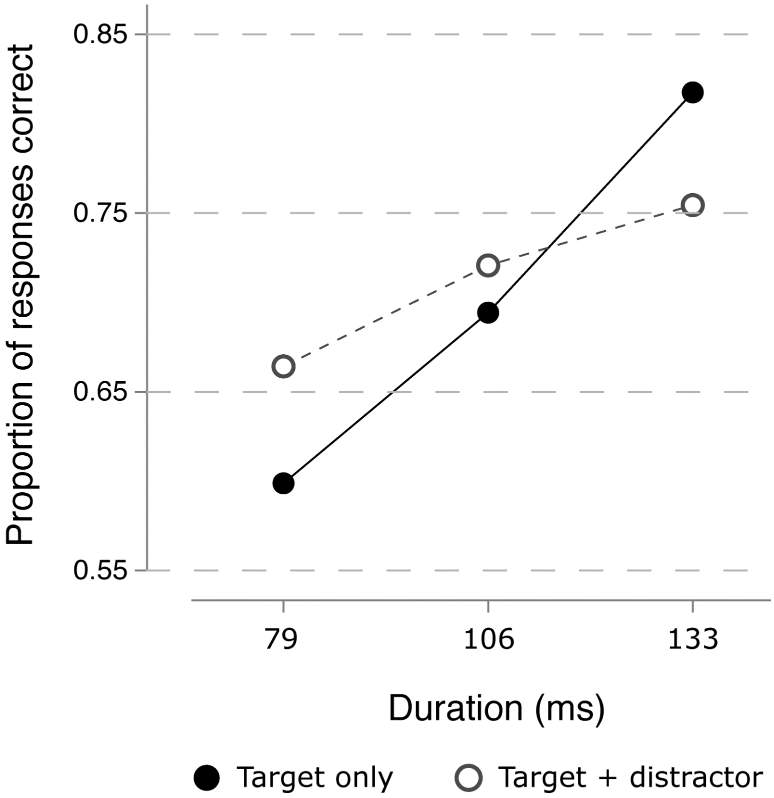


Figure 5.3 Experiment 6 results.
Interaction plot between *distractor* conditions and stimulus *duration.* The two lines overlaps for the three duration intervals, showing how distractor appearance was not interfering with target discrimination.

5.3.3 Experiment 6 discussion

The findings from Experiment 6 perfectly confirm the prediction of a dissociation between saccadic performance and discrimination performance under the influence of distractors. A reliable RDE was recorded for eye movements (Walker et al., 1995) even when the target location remained constant. Despite the fact that participants knew in advance in which hemifield the target was going to appear, they were unable to suppress the effect of distractor onset, supporting the idea that the RDE is a low-level phenomenon uninfluenced by top-down influences. On the other hand, discrimination performance in the covert task was unaffected by distractor appearance, replicating the results of Experiment 5 and supporting the idea that top-down influences provide useful information to focus attention only on target location, suppressing irrelevant events in the periphery (Yantis & Jonides, 1990;

Theeuwes, 1991). It is necessary to stress that in both Experiment 5 and Experiment 6 both the location of the target and of the distractor were known in advance, making top-down information as reliable as possible. This consideration is very important when we compare these results to Christ and Abrams (2006) results. It may be possible that in order to successfully inhibit distractor onset there is a need for a longer period of time to sustain attention at one location and also to keep location constant. All these criteria are missing from Christ's paper.

The most important outcome from the study regards its implications for the premotor theory of attention (Rizzolatti et al., 1987). As previously discussed, the premotor theory states that covert shifts of attention are identical to eye movements. According to this statement, we should have expected that if saccadic movement were interfered with from distractor onset, the same should have happened in the covert discrimination task. The result from Experiment 6 clearly contradicts this hypothesis: in fact, a strong dissociation emerges in the two tasks. While saccadic movements are impaired by distractor onset, resulting in longer SRTs, covert discrimination remains stable across conditions. This finding has a strong theoretical impact because it clearly demonstrates that the overlapping of the overt and covert attentional systems is only partial, and depends on the particular circumstances the visual system has to deal with. In particular, while the attentional system is open to top-down influences, the overt system, and in this case the part of the oculomotor system related to saccade generation, conserve a more reflex-like behavior. These findings fit nicely with the data reported by Hunt and Kingstone (2003a; 2003b), who were able to dissociate saccadic and covert processes.

5.4 General conclusion

These two experiments clearly demonstrate that the RDE does not generalise to tasks other than overt oculomotor responses. In particular, they show that while eye movements are susceptible to distraction (Experiment 6), presenting a robust RDE (Walker et al., 1995) in the saccadic response modality, covert attention can resist distraction (Experiment 5 and 6). The present data are in line with the findings reported in the previous chapter, where it was showed that the manual system was immune to distractor appearance, revealing a strong dissociation between the motor limb system and the oculomotor system. In this case, the dissociation was present between the overt system (i.e. oculomotor system) and the covert one.

The results from Experiment 5 and Experiment 6 provide more information about the link between the oculomotor and the attentional system. The data are in direct contrast with the predictions made by the premotor theory of attention (Rizzolatti et al., 1987). According to Rizzolatti and collaborators, covert shifts of attention are identical to eye movements, with the only difference being that the movement is not executed. Following this idea, if the saccadic system is susceptible to distraction, and the delay in SRT reflects the time taken to resolve conflicting motor programs generated by target and distractor appearance, the same processes should affect the covert task. In particular, the delay caused by the cancellation of the program generated by distractor appearance should be reflected in a decrease in the time necessary to accomplish the letter discrimination task. More generally, the data suggest that, depending on the particular circumstances in which attention is involved, it is possible to dissociate the overt and the covert system.

At this point, then, it is possible to respond to the question highlighted at the start of the chapter: *Does an irrelevant onset capture attention even when the target location is perfectly predictable?* Experiments 5 and 6 point to the conclusion that when participants are engaged in a covert discrimination task and enough information is provided about target/distractor location, irrelevant onset can be suppressed. This conclusion is also paralleled by behavioural and neurophysiology data. Hunt and Kingstone (2003a; 2003b) showed how it is possible to dissociate covert and overt systems in both reflexive and voluntary attentional tasks. In particular, Hunt and Kingstone (2003a) showed that IOR is made up of two components, i.e. attentional and motor. In their experiment, the authors successfully dissociated the motor component from the attentional component, suggesting that the former is a peculiarity of the oculomotor system. A similar dissociation has been proposed for the GAP effect, where the general warning signal, i.e the attentional component, had been dissociated from the pure motor component, later renamed the FOE (Klein & Kingstone, 1993). This has been demonstrated to have no effect on simple manual reaction times (Bekkering et al, 1996), and little (Bekkering et al, 1996; Iwasaki, 1990; Tam & Stelmach, 1993) or no effect (Reuter-Lorenz et al, 1991; Tam & Ono, 1994) on choice manual reaction time. Rather, it only affects aimed manual responses (Bekkering et al, 1996; Pratt et al, 1999). The literature, then, allows us to speculate regarding the possibility that the RDE too is a peculiarity of the oculomotor system, being a pure motor effect. An attentional component to this effect may be expressed when less top-down information is provided (Benson, 2008).

Coming from a different perspective, studies on the effect of abrupt onset during covert discrimination provide intriguing findings for the interpretation of the results of Experiments 5 and 6. It has been reported that top-down processes play a fundamental role in the modulation of such effects. For example, when foreknowledge of the target location was available to participants, it was possible for them to focus their attention on the cued hemifield, ignoring distractor appearance. Yantis and Jonides (1990) and Theeuwes (1991) all reported that when the target location was known at least 200 ms before target onset, the effect of an abrupt distractor was completely negated. In both the experiments described in this chapter, both target and distractor location were known in advance. Moreover, the location was kept constant for the whole length of the block, and was restricted to just one spatial location. The same was true of the distractor. In these particular circumstances it is reasonable to think that participants were in a highly focused state of sustained attention restricted to the spatial location of the incoming target. A strong misalignment of the oculomotor system and the covert was then induced in participants. This source of top-down control was present in both the experiments, even if less markedly so in Experiment 6, where the onset of the target triggered both the saccade and the discrimination. Experiment 6 highlights the nature of the dissociation, showing how saccade movements are delayed by distractor appearance, whereas the covert system does not inherit such delays, leaving attentional performance unaffected by distractor onset.

Another interesting parallel can be drawn with the results of Schneider and Deubel (2002). In their case, irrelevant cues presented 60 ms before target onset did not interfere with target discrimination and were successfully inhibited. The peripheral cue can be thought of as equivalent to the distractor of the present experiments (bearing in mind that in the present experiment the distractor was presented simultaneously with target onset). In both set-ups, participants knew the target location in advance, and this factor was critical for the inhibition process. As noted by Klein (2009, p. 245):

> "Normally when we want to move our attention without moving the eyes, the oculomotor system is simply suppressed. If it were not, our effort to keep orienting covert would likely fail."

This statement synthesises the idea of the possibility of dissociating covert and overt processing, especially when top-down information, such as the target location (and, in the case of the present experiments, distractor location), is available.

Finally, a clear dissociation between overt and covert shifts has been highlighted by single cell recordings. Thompson and colleagues (2005) reported that in the FEF spatial attention signals are independent of explicit saccade command signals, referring to these visually responsive neurons as the mental spotlight (Posner, 1980). Moreover, Juan et al. (2004) demonstrated that the FEF sensory-motor structures can covertly orient attention without preparing a saccade. Taken together, neurophysiological data and behavioral data support the idea that under certain circumstances dissociation between the overt and covert systems is possible.

Chapter 6

Saccadic inhibition and remote distraction

Chapter overview. The previous chapters investigated whether the RDE generalises to systems other than the oculomotor system. In particular, whether simple manual responses, spatial-oriented and covert discrimination responses are affected by distractor appearance was tested. The pattern of data supported the view that the RDE is a peculiar characteristic of the saccadic system, leaving both the limb motor (Chapter 2 and Chapter 4) and the covert system unaffected (Chapter 5). The results suggest that the oculomotor system may not share target selection processes with the limb motor system. Moreover, visuo-spatial attentional processes can be decoupled from overt responses when enough top-down information, such as target/distractor predictability, is provided in advance. Even if inconclusive as yet, these results challenge motor theories of attention, such as OMRH and premotor theory, where identity of attentional and motor processes is hypothesised.

The following question regards the identity of the RDE and *saccadic inhibition* (SI). SI is a more recently discovered phenomenon whereby a transient change to a scene during a visual task induces a depression in saccadic frequency beginning at 70 ms, and reaching a maximum of around 90-100 ms (Reingold & Stampe, 1999). SI has mostly been investigated in relation to the reading and exploring of visual scene but it has been hypothesised that it is a general phenomenon, relevant to all saccadic behaviour. Moreover, Reingold and Stampe (2002) speculated regarding the possibility that SI is the underlying cause of the RDE. The principal aim of the present chapter is to assess this relationship between SI and the RDE. In order to do so, participants were asked to perform a simple saccadic task in which the delay between target and distractor was varied between 0, 25, 50, 100 and 150 ms. Examination of the distributions of saccadic latencies showed that each distractor produced a discrete dip in saccadic frequency, time-locked to distractor onset, conforming closely to the character of saccadic inhibition. The data suggest that saccadic inhibition underlies the remote distractor effect.

6.1 Introduction

In the previous chapter it was shown how the sudden appearance of a distractor contralateral to the target location does not interfere with covert discrimination. On the other hand, the same paradigm elicited slower saccadic responses when participants were asked to move their eyes toward the target in order to perform the discrimination. These findings - together with the findings of chapters 2 and 4, - provide more information about the generalization of remote distraction. In particular, the RDE seems to be a saccadic-specific phenomenon, with the superior colliculus being the possible neurophysiological substrate accounting for the effect. An open question on which this chapter is going to focus regards the identity of RDE and SI. Detailed research work to date on the RDE allows us to rule out some hypotheses. Firstly, it has already been shown that the increase in saccade latency during bilateral stimulation is not just a cognitive phenomenon, as was suggested in the preliminary work by Lévy-Schoen (1969). In fact, the cognitive element of choice is not critical since comparable increases in SRT were induced by the onset of a stimulus at fixation, 50-150 ms following the onset of a single lateralized target (Ross and Ross, 1980, 1981). Braun and Breitmeyer (1990) obtained similar interference from stimuli at fixation, or in the contralateral field, when the target location was predefined and constant (see also Weber & Fischer, 1994). In two papers by Walker and colleagues (Walker et al., 1995, 1997), the effect was found to be present even when target location was predictable. Moreover, a recent work from Benson (2008) addressed directly the question of target predictability, and her results showed that when the location of the target was completely predictable, the effect of distractor appearance was less detrimental than when participants did not know the target location in advance. These results suggest that distractor effects do have a cognitive component, but that there is a residual inhibitory effect that is immune to top-down influences and presumably low level. This low-level component identifies the RDE that is of interest for the purposes of this thesis.

From a detailed scrutiny of the literature on the RDE it clearly emerges that one critical factor for the understanding of this phenomenon is distractor onset. In their 1995 paper (Experiment 3), Walker et al. examined the consequences of manipulating target-distractor asynchrony for a contralateral distractor. Walker et al. (1995) observed reliable increases in SRT when the distractor was simultaneous with, or within 40 ms after, the target, with a diminishing influence thereafter. Numerically, the effect was greatest (~18 ms) with a simultaneous distractor. Comparing the SRT frequency distribution in the simultaneous-distractor condition with that for the target alone, Walker et al. suggested that the RDE results from a reduction in the frequency of "fast-regular" saccades relative to "slow-regular" saccades. Interestingly, in a great number of the studies investigating the RDE, even if the simultaneous presentation of target and distractor was considered *a priori* to be the best time relation to generate the effect, a distractor presented after distractor appearance also seemed to be highly influential in modulating the saccadic response. To better understand these incongruences between studies it will be helpful to discuss a more recent finding that has emerged from within the eye-movement literature.

Some studies used a transient visual event briefly presented while participants were involved in a cognitive task such as reading or exploring a scene. In these *"display change"* studies the presence of a *dip* in the fixation duration distribution was reported (e.g. Blanchard, McConkie, Zola, & Wolverton, 1984; McConkie Underwood, Zola, & Wolverton, 1985; van Diepen, De Graef, & d'Ydewalle, 1995). One hypothesis put forward to explain this phenomenon is that the dip was:

> "[…] reflecting the disruption to automatic, parallel encoding or registration processes that are time locked to the onset of the visual pattern on the retina." (Reingold & Stampe, 1999, p. 249).

The disruption process was then reflected in a delay in the execution of the eye movement (McConkie, Reddix, & Zola, 1992). On the other hand, another hypothesis was also introduced to explain the dip in the distribution. Reingold and Stampe (1999; 2000; 2004) proposed that the large transient visual event presented during text reading or visual search tasks produced *"saccadic inhibition"*: a characteristic dip in saccade frequency, visible as early as 60-70 ms after the change, with its nadir around 90-100 ms, and returning to normal levels within 120-130 ms. Essentially, the *saccadic inhibition hypothesis* (SIH) and the disruption hypothesis differed because while SIH predicted the same pattern across different delay conditions, the disruption hypothesis predicted different results among conditions, since the transient event would have interfered at different stages in the processing. To directly test this hypothesis Reingold and Stampe (1999) developed a gaze contingent paradigm whereby while a participant was reading or exploring a visual scene a transient visual event was displayed for 33 ms. In the first condition the transient event was time locked to the beginning of the fixation period with a delay of 110 or 158 ms, replicating the condition of McConkie and colleagues' paradigm (1992). In the second condition a *random delay period* was used to present the transient visual event randomly after the fixation period. The outcomes from this experiment were very interesting. Analysis of the distribution of fixation duration showed that in the fix delay period condition two dips were present, i.e. a decrease in saccade frequency, about 90 ms after the flash onset. In contrast, the distribution in the random delay period condition did not show any dip. A more accurate analysis of the distribution highlights that when the histograms were aligned according to the flash onset, the random delay period condition revealed a clear dip appearing as early as 60 ms after flash onset and with a peak at ~90 ms. These results clearly showed that this effect was related to the relation between the start of the saccade and the onset of the flash.

Although saccadic inhibition was initially demonstrated in a free viewing during exploration of visual scenes, Reingold and Stampe (2000) suggested it was a low-level saccadic phenomenon and therefore should be found in any saccadic task. Subsequent experiments by the same authors tested the generability and the characteristics of the saccadic inhibition. In a later paper, Stampe and Reingold (2002) reported that the latency of inhibition onset was modulated by the spatial frequency content of the display change. They observed longer latencies when the change affected the high spatial frequency content of the display and shorter latencies for low spatial frequencies. Moreover, luminance changes were able to induce the fastest inhibition onset independently of the spatial frequency content of the display change. Further experiments (Reingold & Stampe, 2004) also demonstrated that saccadic inhibition was influenced by both low and high level modulation. In particular, the saliency of the flash modulated the magnitude of the dip, with stronger inhibition at higher saliency levels. Finally, peripheral flashes were shown to have as strong an effect as foveal flashes. But more importantly, an auditory event was not sufficient to produce any sort of inhibition. Nonetheless, the characteristics of the flash modulate the latency by about 14 ms only, ranging from 95.4 ms in the case of a luminance change to 109.8 ms with a 6.0 c/deg grating (Stampe & Reingold, 2002).

As previously noted, Reingold and colleagues suggested that SI generalised beyond the specific tasks first tested. To relate this interesting phenomenon to the classic literature on eye movements, the authors developed a discrete version of the task. In this way they demonstrated that the same effect was also present in target-elicited saccadic tasks (Reingold & Stampe, 2002). Participants responded to a lateralized visual target, and online analysis of the eye-tracking data from each trial enabled a running computation of the median SRT. On 'flash' trials, a dramatic but brief visual change was applied (on average) 100 ms in advance of the current median SRT, with the top and bottom thirds of the screen turning from grey to white for 33 ms. As in reading and visual searches, there was a pronounced dip in saccadic frequency beginning 60-70 ms after the flash, with its nadir around 90 ms. The dip was time-locked to the flash, and independent of the asynchrony between target and flash, showing a comparable character across wide variations in baseline saccadic latencies associated with gap, overlap, prosaccade and antisaccade tasks.

In discussing their findings with regard to this, Reingold and Stampe (2002) hypothesised that saccadic inhibition might cause the slowing of SRTs observed in the RDE. The RDE is usually elicited by a small, localized visual change, whilst saccadic inhibition has been studied using a large flash, but this superficial difference might belie common mechanisms of influence. The SIH (saccadic inhibition hypothesis) implies that the key factor governing the RDE would not be the temporal relationship between target and distractor, but that between the distractor and the planned saccade. Of course, to the extent that the timing of saccades depends upon the timing of target presentation, there will be a relationship between RDE magnitude and the target-distractor asynchrony. However, this relationship would be indirect and task-specific, determined dually by the SRT distribution for the baseline task and the time-course of saccadic inhibition. As Reingold and Stampe note (2002, p.380):

> "If saccadic inhibition caused by the presentation of the visual change […] is responsible for the observed slowing of SRTs, then whether or not such an effect is predicted depends on two important factors: the latency between the onset of the target and the onset of the distractor […] and the characteristics of the SRT histogram obtained when a distractor is not presented."

Under this interpretation, the fact that different authors have found the RDE to be maximal at different target-distractor asynchronies might be due to differences in the SRT distributions for the baseline (no-distractor) tasks. Ross and Ross (1980) found the RDE to be maximal when the distractor followed the target by 100 ms, whereas Walker et al. (1995) obtained their maximum effect with a simultaneous distractor. Consistent with the SIH, the former observation was made in the context of a relatively late baseline SRT distribution (mean ~290 ms); the latter with a much earlier distribution (mean ~168 ms). Moreover, we can speculate that the selective reduction in fast regular saccades that Walker et al. (1995) identified might just reflect the portion of their baseline distribution most visibly affected by the dip induced by a simultaneous distractor, rather than the RDE being characterised universally by the attrition of fast-regular saccades. The SIH predicts that different portions of the baseline SRT distribution should be impacted by distractors presented at different times, with the dip time-locked to distractor onset.

What is really lacking in these papers is a description of the time dependency needed to correctly enter in the time window for motor competition. For this reason the work by Reingold and Stampe provides a perfect design to test the SIH under the remote distractor paradigm. For the present chapter a task based upon that of Walker et al. (1995) was used, in which the asynchrony between target and distractor is varied. As expected, the data show a robust RDE for distractors presented simultaneously with or shortly after the target. However, the main concern regarded the character of the changes to the baseline SRT distribution associated with the different distractor onsets. The SIH predicts that the RDE will invariably be accompanied by a discrete dip in the frequency distribution, developing within about ~70 ms of distractor onset. The outcome of the experiment provides unequivocal support for this prediction, suggesting that saccadic inhibition does indeed underlie the RDE.

6.2 Experiment 7 method

6.2.1 Participants

Fourteen volunteers from the University of Edinburgh aged between 18 and 24 years participated. All participants were free from neurological and visual impairments. This experiment was conducted in accordance with the 1964 Declaration of Helsinki, with the approval of the Ethics Committee of the School of Philosophy, Psychology and Language Sciences at the University of Edinburgh. All participants gave informed consent prior to testing.

6.2.2 Apparatus and stimuli

Stimuli were white on black, presented on a 19 inch CTR monitor (1024 x 768 pixels) driven by a Pentium IV processor at 120 Hz. Participants were seated in front of the monitor, with their head immobilised in a chin rest and their eyes horizontally and vertically aligned with the centre of the screen at a viewing distance of 90 cm. Eye movements were recorded with the EyeLink II head-mounted system (detection algorithm: pupil only, 500 Hz sampling). A 0.50° fixation cross occupied the centre of the screen throughout each trial (overlap design). The saccadic stimulus was a circle of 0.57° diameter, presented at 4.5° eccentricity in the right visual field. The target appeared after a fixation interval that varied randomly between 500 and 1000 ms. The target was presented alone or accompanied by a mirror-image distractor on the left. Distractor onset was simultaneous with target onset, or delayed by 25, 50, 100, or 150 ms. The target was presented for 400 ms followed by a blank screen for 100 ms. Distractors were presented for 100 ms.

6.2.3 Procedure

Each trial began with drift correction and a tone signaling the onset of the fixation cross. Participants were required to fixate the cross and to move their eyes to the target as soon as it appeared on the right side of the screen. The target could be presented alone (T) or with a distractor (D), presented under five delay conditions (D0, D25, D50, D100, D150). Each participant completed 1440 trials split into three sessions comprising ten blocks of 48 trials each. Within each block, eight trials for each of the six conditions were shuffled randomly. A three point-calibration on the horizontal axis was run at the beginning of each session and after three consecutive blocks; additional calibrations were run if the participant moved their head from the chinrest. After each session the headset was removed and the participant took a short break. The experiment lasted ~90 minutes in total per participant.

6.3 Experiment 7 results

6.3.1 Data screening

Saccades to the left (1.55%), saccades of less than 1° amplitude (1.68%), and saccades with a latency under 70 ms (2.39%) or over 400 ms (1.51%) were excluded.

6.3.2 RDE analysis

For each participant, the median SRT was taken as the measure of central tendency for each condition and entered into a repeated-measures ANOVA by condition (T, D0, D25, D50, D100, D150). The means of these medians are displayed in Figure 6.1, showing a robust elevation of SRT for distractors presented simultaneously with, or within 50 ms after the target. The overall effect of condition was highly reliable ($F(5,65) = 13.170$; $p < 0.0001$). Planned contrasts comparing each distractor condition against the baseline (T) confirmed a reliable RDE for the first three delay conditions (D0: $F(1,13) = 9.283$; $p < 0.009$; D25: $F(1,13) = 27.598$; $p < 0.0001$; D50: $F(1,13) = 35.110$; $p < 0.0001$), but not for the last two (D100: $F(1,13) = 3.497$; $p < 0.084$; D150: $F(1,13) = 0.801$; $p < 0.387$). Numerically, the maximum RDE arose with a distractor delay of 50 ms.

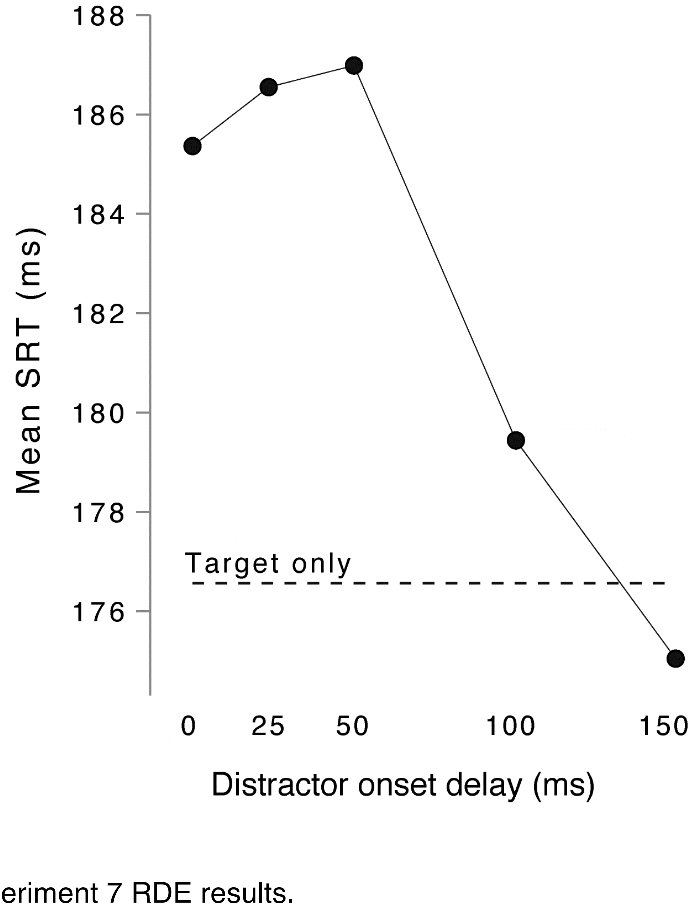


Figure 6.1 Experiment 7 RDE results.
Means of the median SRT for each distractor condition (*solid line*) and target only baseline (*dotted line*)

Measures of within-subject variability for SRTs in target only and target with distractor condition at each delay as previously presented in the interaction plot have been analysed. For each participant the IQR was computed for each condition as measure of within subject variability and entered into a repeated-measures ANOVA by condition (T, D0, D25, D50, D100, D150). The overall effect of condition was reliable ($F(5,65) = 3.4$; $p < 0.03$). In order to further investigate the main effect of conditions, planned contrasts compared the baseline (T) against each of the distractor delay conditions. According to this analysis, the baseline (57 ms) was significantly different from the D50 (64 ms: $F(1,13) = 5.064$; $p < 0.042$) and the D100 (65 ms: $F(1,13) = 9.436$; $p < 0.009$) while D0 (56 ms: $F(1,13) = 0.087$; $p = 0.773$), D25 (55 ms: $F(1,13) = 0.300$; $p = 0.593$) and D150 (58 ms: $F(1,13) = 0.521$; $p = 0.483$) did not differ significantly different from baseline. A differential increase in within-subject variability in these conditions may be related to the fact that the D50 and D100 distractors seem most likely to cause a split in the baseline distribution, thereby increasing the overall range of SRTs (see Figure 6.2 SI by distractor).

6.3.3 Saccadic inhibition analysis

The presence of saccadic inhibition was assessed via the character of the changes in the baseline SRT histogram induced by distractor presentation. Saccadic inhibition manifests as a clear dip in saccadic frequency, occurring at a relatively constant interval after the responsible visual change. In a prosaccade task with fixation overlap, as used here, Reingold and Stampe (2002) estimated the peak of inhibition to occur at 91.3 ms. This analysis had several stages. For each participant, for each condition, a percentage frequency histogram of SRTs was created, with a bin-width of 2 ms (the maximum temporal resolution of EyeLink II). A nine-point moving-window-average smoothing function was then applied. The smoothed histograms were then averaged, bin-by-bin, across participants, for each condition. The mean SRT histogram for the baseline (T) condition is shown in the top panel of Figure 6.2. The five lower panels show the difference histograms for each of the distractor conditions, computed via the bin-by-bin subtraction of the baseline histogram from the mean histogram for that condition. For each difference histogram, the interval between the distractor onset and the histogram minimum is reported below the grey shaded area. A discrete dip is present in each difference histogram, occurring later as the distractor onset is progressively delayed. The dip is thus roughly time-locked to the distractor onset: the estimated interval to maximum inhibition ranges between 87-113 ms. In reality, the timing of the dip is even more stable than this. Because the difference histograms in Figure 6.2 represent absolute differences, a bias arises, whereby the nadir of each dip is pulled towards the peak of the baseline distribution. This causes an overestimation of the latency of dips arising before the peak of the baseline distribution, and an underestimation of those arising after. If the plotted differences are normalised as percentages of the baseline, the estimated latencies all lie between 88 and 101 ms. In the D50 condition, in which the maximal RDE was observed, the normalised dip represents a 35% reduction in the baseline frequency. The patterns in Figure 6.2 provide compelling evidence that saccadic inhibition is responsible for the RDE.

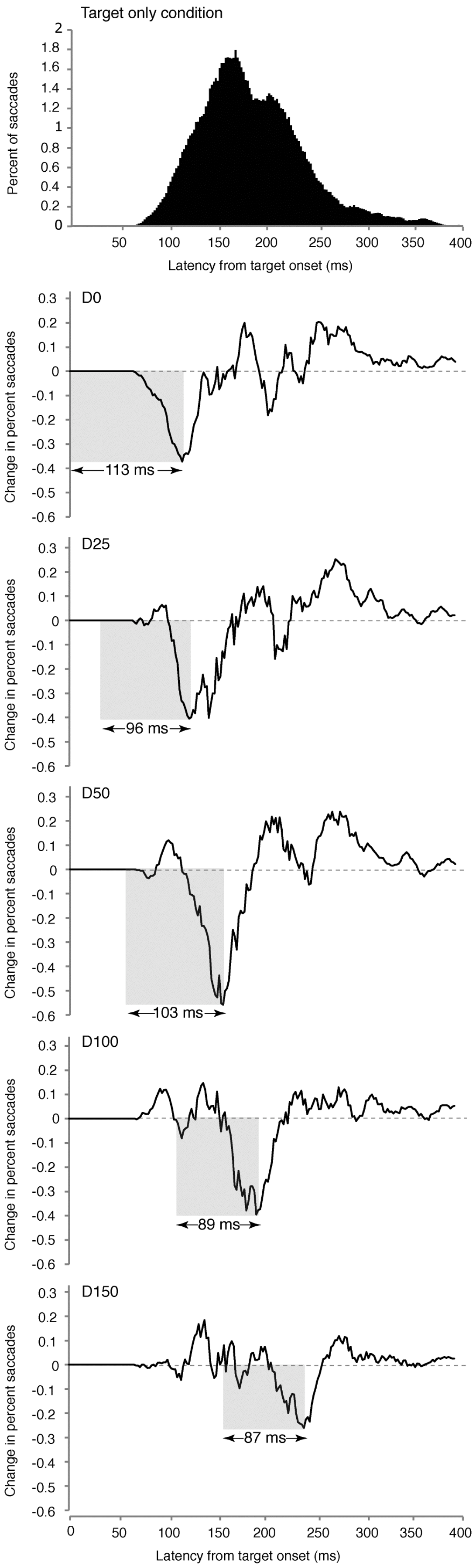


Figure 6.2 Experiment 7 SI results. Percentage frequency histogram of SRTs for target only condition (*top panel*), and difference histograms for each of the distractor conditions (*lower panels*), representing bin-by-bin subtraction of baseline histogram from frequency histogram for that condition. For each difference histogram, the interval between the distractor onset and the histogram minimum is reported below the *grey shaded* area.

However, the difference histograms per condition are somewhat noisy. To better characterise the timing of the dip, the difference histograms for each condition were temporally aligned to distractor onset, then averaged bin-by-bin to create a grand mean difference histogram. This histogram, shown as Figure 6.3, bears the hallmarks of saccadic inhibition: saccadic frequency drops reliably below baseline levels by 67 ms after distractor onset, reaching its nadir at 93 ms, and persisting below baseline levels until 125 ms, with a phase of relative elevation thereafter.

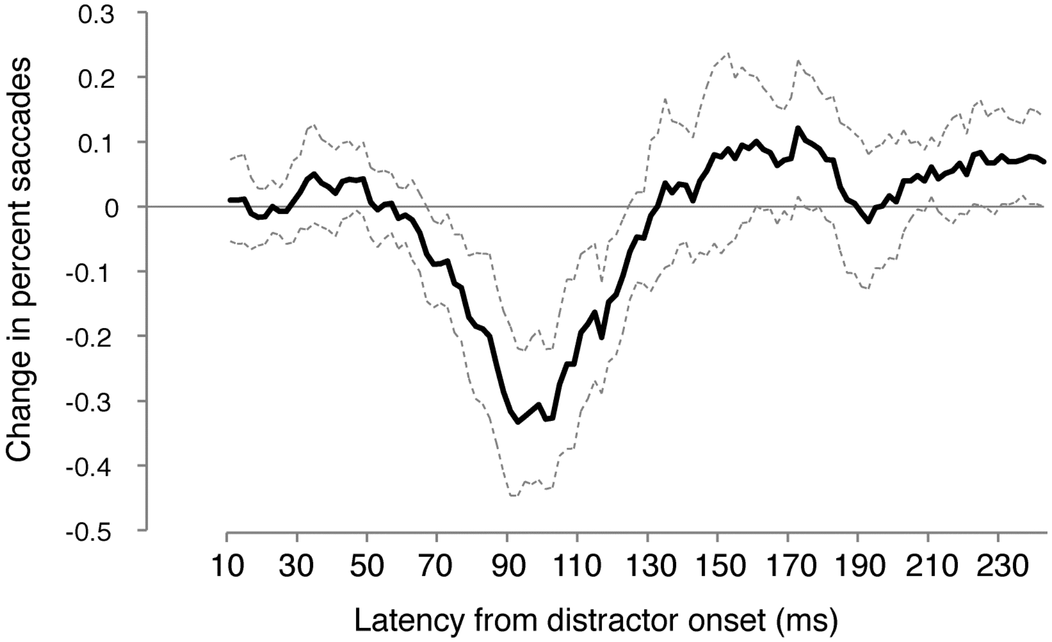


Figure 6.3 Experiment 7 mean SI results.
Grand mean difference histogram across all distractor conditions, time-locked to distractor onset, showing 95% confidence intervals (*dashed lines*) around the mean (*solid line*).

6.4 Experiment 7 discussion

The present study replicates the RDE, confirming that the onset of a distractor increases SRTs compared to unilateral target presentation (cf. Braun & Breitmeyer, 1990; Ross & Ross, 1980, 1981; Walker et al, 1995; Weber & Fischer, 1994). The size of the RDE was related to the timing of the distractor, being pronounced when the distractor was presented simultaneously with, or within 50 ms after target onset, but not reliable when the distractor was delayed by 100 ms or more. These results correspond closely with those of Walker et al. (1995), with a minor difference being that the present RDE was numerically greatest for a distractor presented with 50 ms delay, rather than at simultaneity. This pattern falls between those of Walker et al. (1995) and Ross and Ross (1980, 1981), since the latter authors found that the RDE was still large with a distractor delay of 100 ms. Moreover, the present results are in accordance with the findings reported in chapters one, two and three regarding saccadic behavior under the distractor condition.

The main purpose, however, was to assess whether the effect of remote distractors is consistent with the character of saccadic inhibition (Reingold & Stampe, 2002). As predicted by the SIH, a clear dip relative to the baseline SRT distribution was present in all five distractor conditions, emerging within ~70 ms of distractor onset and returning to baseline levels within 125 ms. The best estimate for the duration from latency to the peak of inhibition was 93 ms, closely comparable to the 91.3 ms estimated by Reingold and Stampe (2002), using a similar baseline task (prosaccade, overlap fixation). This temporal equivalence arose despite large differences in the distracting visual events, which in their task was a flash of two-thirds of the screen, and in ours was the onset of a small dot in the unattended field. The relative saliencies of the events, however, may have been reflected in the degree of inhibition, which was 89% of the baseline frequency for Reingold and Stampe's flash, but only 35% of baseline for the D50 condition, in which the RDE was maximal.

One major implication of these findings is that the proximal factor governing the RDE is not the temporal relationship between target and distractor (Ross & Ross, 1980, 1981; Walker et al., 1995), but the more complex relationship between the distractor onset and the baseline SRT distribution. The characteristics of baseline SRT distributions may thus be key to understanding differences between RDE results from different studies. As noted in the introduction, Walker et al. (1995) found a maximal RDE with a simultaneous distractor in the context of a relatively early baseline SRT distribution, whilst Ross and Ross (1980) observed large effects with a distractor delay of 100 ms in the context of a relatively late baseline distribution. In the present study, the RDE was maximal with a distractor delayed by 50 ms, presumably because the maximum saccadic inhibition, following this distractor by 103 ms, coincided with the peak of the baseline SRT around 150 ms (see Figure 6.2). Extrapolating from these data, one would expect that the earliest distractor that could affect the SRT distribution would precede the left tail of that distribution by ~125 ms; conversely, for a late distractor to have an influence, it should onset at least 70 ms before the right tail of the baseline distribution falls to zero. Whether or not a distractor's effect on the SRT distribution will translate into a reliable RDE is less predictable, and may depend on further factors including statistical power and the measure of central tendency chosen. Notably, in these data, the RDE was not reliable with distractor delays of 100 or 150 ms, despite demonstrable dips in the SRT distributions for these conditions.

The present findings are also comparable with new literature that is investigating the effects of distractors on saccadic reaction times. In particular, there are three main studies recently published that address the timing issue of distractor onset. The first study worth mentioning is by Bompass & Sumner (2009a). In a series of experiments the authors manipulates the onset of distractor according to target presentation in the same way as Walker et al. (1995) and the present experiment, varying the SOA from 80 ms before to 80 ms after target onset. Bompass's rationale was that, as already noted in the literature (Rafal et al., 1989; Ross & Ross, 1980; 1981), the simultaneous onset of target and distractor is not always necessary in order to maximize the RDE. What is really important is the *time* necessary for both target and distractor to reach the locus of inhibition where the RDE arises, hypothesized to be the superior colliculus (Findlay & Walker, 1999). It is worth noting that even in cases in which both target and distractor present the same physical characteristics (eccentricity, size, colour, etc.), other factors, such as top-down influences, could modulate the saccadic response to target onset. In such cases, it would be necessary to give a lead to the distractor to maximise the RDE. The important point emerging from Bompass and Sumner's paper is that there is a particular time-window in which it is necessary to present the distractor in order for it to inhibit saccade-related activity and produce the typical slow down in saccadic reaction times: this has also been suggested by Trappenberg and colleagues (2001) and Godjin & Theeuwes (2002). The concept of motor competition within a particular time window is an important aspect of the competition framework. The idea is that to obtain the maximum RDE the visual stimulation elicited by the distractor has to reach a processing level at the same time as the visual stimulation elicited by the target. The model proposed by Trappenberg et al. (2001) tested this idea by running a simulation network able to account for different visual phenomena such as the gap effect and the RDE. According to Trappenberg and colleagues, the temporal relation of target and distractor was crucial in determining the effects. There was only a short temporal window in which the distractor would have been able to interfere with the saccadic planning toward the target, delaying the start of the saccade. In the Trappenberg model, the locus where this temporal effect will be active is the superior colliculus and, in particular, the intermediate layer. Lateral inhibition processes triggered by build-up neurons activated by distractor appearance at remote locations would account for the inhibition of neural activity at target location. The results of the simulation showed that the maximum interference occurred when the distractor was presented in close temporal proximity to the target.

According to Bompass and Sumner (2009a), the dimension of this time window is determined by target/distractor characteristics that will modulate the time needed to reach the visual areas along the visual pathway. Low saliency distractors will need a temporal lead in respect to target presentation to maximally interfere with saccade latency, while high saliency distractors will need to be presented after target onset. Bompass and Sumner proposed that the latency difference between two stimuli when they are used as targets will correlate with the delay in the maximum RDE obtained when one is used as a distractor and the other as a target. In fact the results showed a strong correlation between the optimal SOA used to produce the maximum RDE and the latency difference between target and distractor. This correlation provides further support for the hypothesis that the time of arrival of the visual signal in the area where the inhibition processes take place is critical in determining the interference, which strongly depends upon target and distractor characteristics such as contrast. This idea is also supported by earlier work by Sumner et al. (2002), in which s-cone distractors were used to test the RDE. In this study Sumner failed to report RDE but in a subsequent review of the same paper (Bompass & Sumner, 2009b) demonstrated that the absence of any distractor effect was not due to s-cone stimulation but to the use of an inappropriate SOA between target and distractor (in that particular study target and distractor were presented simultaneously, while the distractor signal may have been slower than the target signal, which was of higher luminosity). In particular, given the low velocity of the s-cone pathway, Sumner and collaborators argued that it might be that the s-cone distractor needed to be presented with a certain lead, for each particular subject, in order to maximise the effect. In his follow-up study Bompass and Sumner showed that, using a range of SOA (from 80 ms before to 80 ms after target onset), it was possible to induce the RDE with s-cone stimuli in at least one of these conditions.

It is interesting in this regard to highlight the relation between Sumner's assumption and the SIH. Even if these two methodologies seem to overlap, an accurate analysis will reveal some differences. In particular, in the studies using different flashes reported by Reingold and Stampe, it is striking that the time of SI was quite stable across conditions, whereas there were substantial changes in the magnitude of the inhibition process. Reingold and Stampe reported a difference in the latency of the dip in the order of less than 20 ms. This observation suggests that while in Bompass and Sumner's method the velocity of the signal along the visual pathway is emphasized, the SIH maintains a constant relation between the saccadic distribution for the target alone and the flash onset. The modulation highlighted in Bompass and Sumner's paper could be a reflection of modulations in SI magnitude. Only an accurate analysis of the distribution would demonstrate the exact temporal characteristics of the RDE. The calculation of the RDE in terms of means could hide the true nature of the temporal profile in those particular conditions. Distractor characteristics may modulate dip amplitude rather than dip latency.

To give a clear example: according to Bompass and Sumner, if a target generates a population of saccades centered on 200 ms and a distractor generates a population of saccadic responses centered on 240 ms, then to maximise the effect it will be necessary to present the distractor 40 ms before target onset, in order to increase the probability of the two signals arriving in an overlapping time window within the motor map in such a way that the distractor will be able to inhibit saccadic activity. On the other hand, given the characteristics of SI, a distractor appearing ~90 ms before the median of the distribution will likely hit a large part of the distribution.

In this particular case it will be a distractor at ~110 ms after target onset, a very different prediction from that made by Bompass and Sumner. Interestingly, a step forward in the understanding of these phenomena would be to develop a capacity to account for the effects of different distractor characteristics, such as colour and size, in order to expand the SIH into a more generalizable model able to account for not only the temporal aspects but also for the magnitude of the effect in terms of both the RDE and SI. The suggestion proposed by Bompass and Sumner of recording SRTs toward a distractor could be a necessary step toward modelling the time and magnitude of SI for a particular pair of target/distractor.

Finally it is worth mentioning that a study independent from that described in this chapter used a very similar methodology to the RDP of Reingold and Stampe to onset distractor at different location in space. Edelman and Xu (2009) showed a very similar pattern to the one described in the results section above, with remote distractors abolishing saccades 90 ms after distractor onset. This pattern of results overlaps with the data previously presented and provides more support for the saccadic inhibition hypothesis. In fact, these considerations, together with the outcome of the present study, imply that the effects of distractors may be characterised more informatively by the shape of SRT distributions, than by any single measure of central tendency. For instance, a late distractor affecting the right tail of the baseline SRT distribution might increase the mean SRT, but leave the median unchanged; on the other hand, the reshaping of SRT distributions by saccadic inhibition may render calculation of the mean SRT inappropriate, as the resulting distributions may be far from normal. An obvious example is the bimodality that will tend to emerge when distractor onset precedes the peak of the baseline SRT distribution by around 100 ms. This was precisely the pattern obtained by Reingold and Stampe (2002) when they timed their distractor to precede the median SRT by (on average) 100 ms. In the present study, we observed similar instances of bimodality in individual participants, most commonly in the D50 and D100 conditions, when the distractor happened to precede the peak of their baseline SRT distribution by around 100 ms. With this in mind, it is possible to pinpoint likely examples of the same effect within the prior literature on remote distraction. For instance, Braun and Breitmeyer studied the effects of re-introducing the fixation stimulus in a gap paradigm, and observed a split in the SRT distribution, with the separation point roughly 100 ms after the return of fixation (Braun & Breitmeyer, 1990, p. 321, Figure 3). A similar split was obtained by Weber and Fischer (1994), 100 ms after the presentation of a simultaneous distractor.

The identification of the RDE with saccadic inhibition is a clear step forward in the eye movement literature. Integration of evidence and theories from these two previously separate sub-literatures should accelerate the quest for a full account of saccadic inhibition, which must necessarily encompass what is known about the RDE. Both effects have been hypothesised to depend upon inhibitory interactions in the intermediate layer of the superior colliculus (see Findlay & Walker, 1999; Reingold & Stampe, 2002), marking this as the likely locus of their common neurophysiological basis. Distractor onset may stimulate saccade *build-up neurons* coding for the distractor location, and/or *fixation neurons* if the distractor is not too eccentric (Findlay & Walker, 1999; Reingold & Stampe, 2002, 2003). This distractor-related activity would impede target-directed saccades, either directly by lateral inhibition of the *build-up neurons* coding for the target location (e.g. Reingold & Stampe, 2002, 2003), or indirectly by stimulating brainstem omnipause neurons, antagonistic to saccade execution (Findlay & Walker, 1999). The present data do not distinguish between these proposed mechanisms, and they need not be mutually exclusive. However, the present findings do imply that distractors can affect saccade generation only within a limited time -window post-onset, estimated across trials as ~65-125 ms. The lower limit may be imposed by minimum neural delays in the pathway of inhibition, whilst the upper limit presumably reflects the maximum persistence of inhibitory activity. Saccades in preparation within this time-window are vulnerable to distraction.

6.5 Future directions

The marriage of the SI and RDE literatures suggests that each of these phenomena needs to be understood in terms of the other. This identification of the RDE with the SI mechanism immediately implies that the saccade generation model of Findlay and Walker (1999) will be incomplete until it incorporates what is known about SI. For this purpose it is possible to generate a series of experiments with the primary aim of unifying the SI literature with the classical saccadic phenomena (RDE, gap effect, global effect) underlying Findlay and Walker's model. For example, Walker et al. (1997) observed the RDE to be maximum for distractors presented at the locus of fixation. One simple question would be to better understand what is special about distractors presented at fixation. According to the SIH the strength of inhibition is modulated by the location of the flash in the visual scene. Since SI underlies the RDE, it should be possible to predict that the effect of inhibition would be maximal for a flash presented at fixation. This point would be of great interest since Reingold and Stampe already found that central flickers (of big dimension, 18°) produce a similar SI profile to peripheral flickers (of the same dimension). As is also suggested below, the size and position strongly modulate these effects, making the study of central distractors (of different sizes) a very interesting topic (see also White, Gegenfurtner, & Kerzel, 2005). Nonetheless, with a closer look at the profile of the distribution recorded by Reingold and Stampe for peripheral and central flickers it is possible to see that the recovering phase after the inhibition is very different for the two types of visual interference. In particular, central flickers generate a steeper and higher recovery profile after the dip. In this case, the results reported by Walker et al. (1997) on the mapping of distractors in the visual field could improve our understanding of the difference between the two conditions. In fact, it could be that a central distractor, having a greater magnitude, modifies the parameters of the dip. This example demonstrates the validity (and necessity) of intermingling research on these two well-described phenomena in order to understand each one better. A similar approach could result in a better understanding of the GAP effect. In fact, if the GAP effect relies on SC, it may be possible to predict a similar modulation of saccadic distribution for a distractor presented before target onset.

The experiments where Walker and colleagues manipulated distractor location (1997) showed an interesting phenomenon for distractors presented within the same hemifield as the target. In that case, the presence of the distractor affected the amplitude (spatial parameters) rather than the latencies of the eye movements. Since in this case the latencies are not affected, it would be interesting to investigate whether there is any evidence of SI in the saccade distribution. The data of the experiment described above in this chapter has already demonstrated that SI can be present without giving rise to large changes in average SRT. Walker's (1997) conclusion, that ipsilateral distractors do not influence SRT, thus needs to be re-evaluated by a detailed examination of the effect of ipsilateral distractors on SRT distributions.

A similar rationale could be applied to the *congruency effect* described by Reingold and Stampe (2003). According to the authors, SI was stronger when a large (10°) distracting stimulus was displayed on the same side as the saccade target (congruency effect), but this effect was reversed when a small distractor (1°) was flashed. In fact, the authors reported that the effect was stronger when the flicker happened at the same location as the direction of the current saccade. Nonetheless, a larger flicker produced a stronger inhibition when occurring in the same location as the current saccade, whereas a small flicker was more effective at a remote location. This particular point is very relevant when SI is compared to the RDE explored by Walker and colleagues. In Walker et al. (1997), in fact, it is reported that a distractor presented in the same hemifield as the target does not affect SRT but only the landing position. The idea would be to test the SI congruency effect by flashing a distractor of increasing dimensions on the same side of the target. If the SIH applies to the RD paradigm, the inhibition elicited by the distractor should override the effect on the landing position and affect the SRT as well.

This chapter has described how the RDE and SI are really two different ways of looking at the same phenomenon. However, probably the most important contribution of this empirical work is that it opens up a new research framework within which SI and the oculomotor effects (i.e. RDE, GAP and Global effect) described by Findlay and Walker (1999) in their model can be used to better understand each other, with the final aim of producing a better model for saccade generation.

Chapter 7

General conclusion

7.1 Context of empirical work

The aim of this thesis was to investigate whether RDE generalises to other response modalities, in order to provide a window on relations between saccadic and manual response systems, and covert orienting. The starting point for the empirical work took advantage of the rich literature on the effects of distractors upon the oculomotor modality. On the other hand, motor theories of attention (Klein, 1980; Rizzolatti et al., 1987) provided the ground for predictions on the generalisation of these distractor-related effects on other response modalities. Among the many paradigms employed for the study of eye movements *bilateral stimulation* (i.e. RDE: Walker et al., 1995; 1997) stands out for its simplicity and clearness. As extensively reported in the previous chapters, during bilateral stimulation visual distractors, presented at remote locations with respect to the target of the saccade, slow down saccadic reaction time. This well-known effect was chosen as a useful empirical vehicle in order to investigate the extent to which properties of the saccadic orienting system are shared by other response modalities.

It is possible to highlight many reasons why the RDE was preferred to other oculomotor phenomena. Firstly, the RDE on the visual modality has been intensively investigated, and there is a consistent body of work providing information about its mechanisms at different levels: behavioural (Walker et al, 1995; 1997), neuropsychological (Rafal et al., 1989; Walker et al., 2000) and neurophysiological

(Bompass & Sumner, 2009b; Olivier et al., 1999; Trappenberg et al., 2001). This conspicuous body of research made it possible to define the most interesting characteristics of the phenomenon, which might then be tested across different response modalities. The apparently ineradicable saccadic effect, which cannot be explained simply in terms of cognitive choice, was chosen as the focus for this thesis. In fact, maintaining target and distractor locations blocked during the experiments provided top-down information enabling participants to reduce the effect related to discrimination between target and distractor in order to respond.

Secondly, while many research studies have used this paradigm, there are still various aspects of the phenomenon that have not been investigated in depth, such as, for example, the temporal relation between target and distractor onset. This aspect has also never been extensively explored in the visual domain. The literature reports that a distractor appearing simultaneously with the target is the most disruptive. Regarding this point, interesting findings emerge from a different literature, that investigating the exploring of visual scenes, where the saccadic inhibition effect has been described in detail (Reingold & Stampe, 1999). In fact, as has been explained in more depth in Chapter 6, study of saccadic inhibition introduced a new idea about the relation between the onset of distractors and the particular *family* of saccades affected, shadowing the hypothesis that simultaneity is always the preferred SOA choice. The possible linkage between saccadic inhibition and remote distraction represented a new niche worth exploring.

Finally, only in recent years the eye movement literature has started to be more connected to the literature on motor limb systems, thanks especially to the motor theories of attention proposed no more than 25 years ago. At present, there is only a small group of studies using the oculomotor paradigm to test different response modalities, such as pointing movements. In the particular case of RDE, this paradigm has been used in the manual domain only for control experiments (Ross & Ross 1981; Rafal et al., 1980; Sumner et al., 2002). Moreover, to the best of my knowledge there are no studies in the literature addressing the problem of covert discrimination responses during remote distraction, as proposed by Walker and colleagues (1995; 1997). For all these reasons a series of experiment were planned, testing remote distraction across different modalities and tasks.

7.2 Summary of the experiments and general conclusions

The present thesis has investigated the RDE in three response modalities, subdivided as follows: (i) saccadic eye movements; (ii) manual responses - divided between simple motor responses (i.e. keypress) and spatially-oriented responses (i.e. pointing movements); (iii) covert discrimination responses. After assessing the extent to which the RDE generalised to other response modalities, (iv) a deeper inspection of the phenomenon was carried out, based on the hypothesis that saccadic inhibition may be a functional basis for the RDE (i.e. that these two phenomena are really the same thing). The review of the results is grouped according to these four categories.

7.2.1 General experimental set-up

The experimental set-up used throughout the thesis was selected specifically to reduce the RDE to a low-level effect, removing as much as possible any source of high-cognitive processes related to target selection. In particular, the target side was always blocked and, in some of the experiments, the target was always presented on the right side of the display screen at just one eccentricity. The other important constraint that was imposed in the experimental set-up referred to distractor eccentricity. The distractor was always presented in the opposite hemifield to the target, at the mirror location (with the exception of the experiments discussed in Chapter 2, where distractor eccentricity was fully crossed with target eccentricity). Finally, the last important manipulation regarded the SOA at which the distractor was displayed. In most of the experiments, distractor onset was simultaneous with target onset (in accordance with the findings reported by Walker et al. (1995) where the maximum effect was for a distractor appearing simultaneously with the target – Experiment 3).

However, more recent findings suggested that the SOA is a critical variable in determining the magnitude of the RDE, and that in order for the distractor to have an effect, it has to be presented at a certain time according to the SRTs recorded in the baseline condition for target-alone presentation (Bompass & Sumner, 2009). For this reason it is worth exploring a greater range of SOAs. Experiment 4 (Chapter 4) applied this reasoning to map distractor effects in the manual system too, and the experiment design in Chapter 6 had the specific aim of testing the SIH, where Reingold and Stampe successfully demonstrated the relation between the start of the saccade and the onset of a transient. To carry out this test, a range of SOAs, from 0 ms to 150 ms after target onset, was used in these experiments.

7.2.2 The RDE in saccadic responses

Before reporting the novel findings of this empirical work, it is worth comparing the RDE recorded across all the experiments of this thesis and the RDE described in the literature, with particular reference to the results of Walker and colleagues (1995; 1997).

The RDE was replicated across all the experiments. The magnitude of the RDE ranged from ~7 ms (Chapter 5 – Experiment 6) to ~25 ms (Chapter 4 – Experiment 3): magnitudes approximating those recorded in other remote distractor studies of ~18 ms (Walker et al., 1995; 1997). Moreover, even if the testing of a different range of distractor eccentricities was not the focus of the thesis, the RDE reported here presents a similar modulation related to distractor location. This modulation is congruent with that reported by Walker et al. (1997), with an increase in RDE magnitude for a distractor presented closer to fixation. Nonetheless, these experiments did not fully support the findings of Walker et al. (1997). Though the RDE itself was robust, the modulation by eccentricity was not so, and was sometimes present (Experiment 2 - Chapter 4 but marginal) and at other times absent (Chapter 1). Unfortunately, there is no particular reason evident why such differences emerged with the stimuli used for these experiments.

7.2.3 The RDE in manual responses

The first novel conclusion is an answer to the question addressed at the start of the thesis regarding the generalisability of the RDE. In summary, the recorded RDE was not a general phenomenon and it was not inherited by the other response modalities tested.

Firstly, support for this conclusion is provided by the keypress task (Chapter 2). According to the assumption that distractor onset causes a shift of attention, if the RDE was a general attentional phenomenon, it should have been possible to record a delay in button press responses related to distractor appearance, reflecting an alteration of the attentional mechanisms. The data revealed that when the task required a simple, non-directional, motor response (keypress), there was not any increment in reaction time related to distractor appearance. The results are also in accordance with the previous literature, in particular the experiments of Rafal and colleagues (1989) and Sumner and colleagues (2002). In both of these experiments it is reported that distractor appearance did not impair manual performance either in simple keypress or in choice responses. One possibility is that the absence of the RDE for simple button-press (under top-down control) reflects the absence of a general attentional component, indicating only a pure motor effect.

Another possible interpretation explaining the absence of the RDE would be that shifts of attention are not involved in simple manual responses, as proposed by Sheliga and colleagues (1997; see Chapter 2). On the contrary, they are involved in spatially oriented responses, and it could be the case that these would provide a better basis for investigating remote distraction. When a movement is spatially oriented it is possible to directly compare the manual with the saccadic system. The same rationale was already applied in the study of the FOE component of the GAP effect in the manual domain. As described in Chapter 4, Bekkering et al. (1996) showed that the FOE was present for target-directed movements of the hand and absent for keypress responses. Moreover, Pratt et al. (1999) replicated the FOE for manual aiming with a perfectly predictable target location. Following this line of thought, to proceed further in trying to understand at which level the RDE operates (e.g. attentional or motor), it was necessary to test manual-aimed responses under the distractor condition (Experiments 2, 3 and 4 of Chapter 4). The data showed that the RDE was present during saccadic movements but not during pointing movements (Experiment 2). This dissociation was also replicated in a more naturalistic task, in which participants were free to move their eyes during manual aiming (Experiment

3). The outcome of these experiments represents a novel finding, suggesting possible implications for theories on target selection mechanisms.

Two possible explanations are proposed to account for the hand behaviour. The first hypothesis posits that motor programs for the limbs can become automated under particular response-setting constraints. In this particular case, as already suggested in section 7.2.1, the top-down information provided to participants about target and distractor location could have been strong enough to generate stereotyped motor responses for the hand. This assumption is congruent with the previous work from Schneider and Deubel (2003), where aiming responses were tested under a complete target predictability paradigm. In that case, perceptual performance (stimulus discrimination) was not dependent on manual movement. On the other hand, when participants were responding with saccadic eye movements, perceptual performance was seriously impaired when the location of the saccadic target was different from the location of the discrimination stimulus. The author concluded that:

> "[…] movements in the saccadic system are always controlled "on-line", i.e. involving selective attention" (Schneider & Deubel, 2002, p. 612)

while hand movement can be pre-programmed and stored. According to this interpretation, a shift of attention to target location is always necessary and coupled to the eye movement (see also Henderson, 1992), and it is this shift (that in terms of premotor theory *is* a motor program) that is susceptible to distractor interference (that in terms of premotor theory represents a competing motor program). On the other hand, in the manual domain hand movements can avail themselves of stored motor programs, dissociating covert shifts from movement generation. In this case, a distractor interfering with covert shifts will not impair the manual response, since the motor program is not generated online but retrieved from the memory. The hypothesis of the automatisation of hand responses is perfectly commensurate with the outcome of the experiments in Chapter 4. In fact, in those experiments, distractor onset was interfering with the saccadic response but leaving hand performance intact. The results imply that manual responses do not share target selection mechanisms with saccades. However, it is not possible to confirm this conclusion as a general fact, because it may depend upon the specific experimental constraints, and therefore apply only to fully predictable movements.

This rationale leads to the other possible conclusion for the results reported in Chapter 4. In fact, it could be that manual responses might not share target selection mechanisms with the oculomotor system. This assumption could clearly explain the dissociation recorded in Chapter 4, to the extent of the results of Experiment 4, where complete target/distractor predictability led to an advantage for the manual system in generating faster responses during the distractor condition, a result also compatible with the literature on the *Redundant Target Effect* (Hershenson, 1962; Raab, 1962). Even in this case it is not possible to draw a parallel with the GAP effect for hand movements. It has been reported that the modulation of the FOE related to the manipulation of the gap interval between fixation offset and target onset had a similar pattern for eye and hand movements, suggesting a common mechanism. This conclusion is not supported by the results of Experiment 4, in which the pattern of latencies related to the SOA was opposite for the two response modalities, suggesting that the two systems might rely on different mechanisms for the initiation of the movement. Moreover, this conclusion is also supported by the evidence that, even if the oculomotor system is highly coupled with the manual system, the two can be decoupled with the appropriate task demands. Examples of these decouplings are reported by Sailer et al. (2000; 2002). According to the authors (2000), the degree of coupling for eye and hand movements decreases in the case of reflexive movements (compared to endogenously generated movements such as anti-pointing and saccade tasks). The decrease in the correlation between hand and eye movements supports the idea of a possible dissociation of the two motor systems. Moreover, the authors noted that in the anti-saccade task there was a much higher percentage of errors for the oculomotor system (i.e. pro-saccades instead of anti-saccades) than for the manual system. The different behaviour recorded for the two systems points again to the hypothesis of separate mechanisms for target selection. Nonetheless, these possible explanations are not mutually exclusive. If we assume that hand movements can be automated, the present experiments are unable to definitively assess the sharing of target selection mechanisms between hands and eyes under more normal conditions. This argument raises the possibility that these mechanisms could be *shared* or *separate*.

A first step towards disentangling these hypotheses would be to determine whether the manual system is using a target selection mechanism but the actual selection process is not impaired by distractor onset. One way to test this hypothesis would be by using a larger set of target locations. In this way, the capability of the manual system to pre-configure responses would be reduced by decreasing the predictability of the target location, whilst keeping direction constant (and thereby excluding cognitive choices over the target). In this scenario, participants would be forced to select at every single trial the appropriate target location (or incur trade-off effects between reaction times and movement accuracy) and the possibility of storing a motor program would be compromised. This experimental design could be improved by the use of more distractor locations. This manipulation will help to map - as has already been done for the eyes - which distractor location it is necessary to use in order to better interfere with target selection mechanisms.

A further conclusion it is possible to establish is that the outcome of the experiments described above strongly supports the idea that the slow down recorded in the oculomotor modality is related only to saccade execution. Nonetheless there are some ambiguities: the covert study (Experiments 5 and 6 - Chapter 5) points in the direction of the conclusion that RDE might arise at the level of saccade generation.

7.2.4 The RDE in covert responses

The first attempt to test covert discrimination responses under remote distraction was not successful. The results of Experiment 1 - Chapter 2, which involved the covert discrimination of target location, presented a modulation of reaction times that at first sight could have been confused for the RDE. In fact, slower responses were recorded when the target was presented at the far eccentricity and accompanied by a distractor (near or far). Nonetheless, deeper investigation of the interaction between target and distractor location demonstrated that the recorded increment was probably due to compatibility of response between target location and responding hand.

Unfortunately, the experiment did not provide enough information to dissociate the compatibility effect from the pure RDE. For this reason, a better experiment using covert discrimination of target identity was run. In this second attempt, participants were asked to discriminate a letter that was briefly flashed inside a dot. In some trials, a contralateral distractor was presented. No effect of the distractor was found on participant performance in discriminating the letter. The data clearly suggested that the RDE was not affecting covert discrimination of the target (while the same stimuli were producing reliable RDE on saccadic eye movements).

In the literature there are findings on the absence of interference during covert discrimination reported by Yantis and Jonides (1990), Theweeues (1991), and Kosino (1992), where complete target predictability made covert discrimination responses invulnerable to abrupt distractor onsets. This could be one possible explanation of the results described in Chapter 5. Covert attention could be modulated by top-down information a consequence being that peripheral stimulation (i.e. cues or distractor) can be successfully inhibited. If this is the case, the natural consequence is that the RDE is not impairing the ability to covertly shift attention to the target location, but it is affecting the generation of the saccadic movement itself. This would explain why, in the same paradigm, eye movements are always inhibited but covert discriminations are not. At the same time, this proposal explains why the manual system can resist distraction with this particular visual stimulation (it is worth reporting that it is not always the case that manual movements are immune to distractor interference (see: Castiello, 1999; Tipper et al., 1992).

Interesting support for this conclusion comes from an experiment run by Warner, Juola and Koshino (1990). The authors reported that after 4,500 trials, participants involved in a Posner paradigm came to be able to direct:

> "[…] attention to a location opposite the cue very efficiently". (Yantis, 1998, p. 241).

The authors concluded that in this particular experimental setting it was possible to :

> "[…] overcome the natural tendency for attention to be captured by a peripheral cue". (Yantis, 1998, p. 241),

This finding, taken together with the results from Schneider and Deubel, raises the possibility that both the manual system and the oculomotor system can be dissociated from covert shifts when either enough top-down information or the possibility to automate movements is provided.

As speculated above, it would be possible to conclude that the RDE has a pure motor component that is specific to the oculomotor system, plus a general attentional component that could also interfere with other response modalities (similar to the warning signal of the GAP). The experiment described in Chapter 6 provides further confirmation of the motor nature of the RDE.

7.2.5 The RDE and SI

In Chapter 6 the relation between saccadic inhibition and the RDE was tested. Contrary to many studies reporting simultaneity as the most powerful condition in generating the RDE, an accurate examination of the distributions of saccadic latencies at different distractor delays revealed that each distractor produced a discrete dip in saccadic frequency, time-locked to distractor onset. This pattern was closely related to the character of saccadic inhibition (Reingold & Stampe, 1999; 2002). It was then concluded that saccadic inhibition underlies the RDE.

The finding that saccadic inhibition underlies the RDE puts an emphasis on the fact that such distractor effects have a strong reflex-like motor component. In the previous chapter it has been proposed that the RDE arises at the level of the SC. Rizzolatti et al. (Rizzolatti, Buchtel, Camarda, & Scandolara, 1980) hypothesised that the visual inputs arrive at this subcortical structure after 35 – 47 ms. The experiments reported by Reingold and Stampe (1999; 2000; 2002; 2003; 2004) showed that SI latencies can be as early as 60 -70 ms, approaching the limits imposed by neural delays in the visual system (Reingold & Stampe, 2002). Such small latencies suggest the pure motor nature of the effect of SI, and consequently, according to the results described in Chapter 6, of the RDE.

A final interpretation would be to follow the line suggested by Klein (1980; Klein & Ponterfact, 1994), accepting that the covert and overt systems are actually two separate mechanisms. In this scenario, the RDE could affect the oculomotor system and not interact with the attentional mechanisms, conceived as independent (or dissociable). On the other hand, it could also be plausible that the covert system relies on the same structure as the overt one (as premotor theories of attention propose). Embracing this view, the RDE can be conceived of as acting only at the saccadic execution level and not interfering with covert processes (for example, during target selection). Unfortunately, the data presented at the moment do not allow us to disentangle these two opposing hypotheses, and follow-up studies are necessary to better understand the underlying mechanisms.

7.2.6 Neurophysiological interpretation of the RDE

The general introduction to this thesis described the general characteristics of the superior colliculus, with a particular interest in the three classes of neurons that represent most of the varieties of neurons in this subcortical structure. The classical interpretation of the RDE prosposed by Walker and collaborators (1995; 1997; Findlay & Walker, 1999) was that distractor onset affects the nonspecific fixate system. In particular, both distractors presented at fixation and distractors presented peripherally can affect the fixate system, (up to 10° of visual angle) as is supported by neurophysiological data (Gandhi & Keller, 1997), with a strength that depends on the eccentricity at which distractors are presented. The behavioural conseqence of this stimulation is a delay in the triggering of the saccade (level 2 of the model described in Findlay & Walker 1999). The outcome of the experiments described in this thesis puts an emphasis on other possible mechanisms that can drive the RDE.

One hypothesis is that distractor onset may also stimulate saccade *build-up neurons* coding for the distractor location that, competing for target selection, would generate the delay in triggering the saccade. This idea is supported by neurophysiological evidence, such as that described by Olivier et al. (1999), suggesting that a more likely source for the RDE is lateral inhibition between subpopulations of *build-up neurons* in the intermediate layers of the superior colliculus, coding for spatially incompatible saccades, an account also favoured by the saccadic inhibition hypothesis (e.g. Reingold & Stampe, 2002, 2003). Moreover, in the paper in which they raised the possibility of an extended fixation zone, Gandhi and Keller (1997) also reported a strong decrease from the rostral SC to the caudal SC in the number of build-up neurons that could be excided antidromically from the OPN area. This result was also reported by Buttner-Ennever, Horn, Henn and Cohen (1999) who described a lack of input to the nucleus raphe interpositus (RIP) from the caudal SC, especially in the caudal zone of the SC devoted to the generation of *large horizontal saccades,* favouring the view of lateral inhibition between subpopulations of build-up neuron as main cause for the RDE.

To better understand the collicular mechanism underlying the RDE, there is also the need to take into account the proposal from Krauzlis et al. (1997). As already described in section 1.6, there may be no absolute distinction between fixation and build-up neurons: instead, the superior colliculus may be populated by a continuum of build-up neurons coding for saccades of different amplitudes. According to this idea, the fixation neurons code for microsaccades around the current point of fixation. This view of the architecture of the SC favours the hypothesis that the mechanism responsible for the RDE is the same for distractors both at fixation and at remote locations (i.e. the lateral inhibition processes arising between population of neurons coding for competing target in different parts of the SC map). A possible supplementary role for the rostral pole of the SC could derive from its more direct connection with brainstem OPN cells, as is suggested by the strongest effect of a distractor presenting at fixation. This direct connection could have an effect on top of the lateral inhibition processes involving build-up neurons. Neurophysiological recordings comparing the discharge properties of fixation neurons and OPNs, though, reported that these two classes of cells, despite having similar properties, behave differently. In particular, the activity of OPNs is higher and more regular during fixations, the onset of the pause is sharper and better correlated with the onset of the saccade and also better synchronised with the end of the saccade (Everling et al., 1998). These results suggest that the fixation neurons probably are not the only input controlling the activity of OPNs and ultimately the triggering of the saccade. Nonetheless, this hypothesis is only speculative, because at the moment there is no experimental evidence designed to specifically test this prediction. One way to proceed would be to compare the SI profile for distractors presented at fixation and at remote locations. This idea will be expanded upon in section 7.4.

The different behaviour of manual movements under the RDE and the FOE paradigms, with hand movements inheriting the FOE (Bekkering et al., 1996; Pratt et al., 1999) but not the RDE, points in the direction of a qualitative difference between these two phenomena. As previously stated, the model proposed by Findlay and Walker (1999) unifies these two phenomena as different expressions of the stimulation of the same underlying neural mechanisms (both take place at level 2 in the fixation/move centre). Nonetheless, it could be that there is an effect related to fixation onset/offset *per se*, explained by direct interaction of omnipause neurons in the brainstem via the fixation centre of the SC. On the other hand, remote distractor effects could be related to active competition between populations of build-up neurons. This could explain why the FOE was inherited by the hand, given all the neurophysiological evidence implicating intermediate and deep layers of the superior colliculus in the representation of arm movements (Fries, 1984, 1985; Lünenburger et al., 2001; Stuphorn et al., 2000; Werner, 1993; Werner et al., 1997) whereas the lack of the RDE in manual responses could be due to the fact that neurons that code for arm-movements in the SC are generally linked to the onset of the arm movement rather than the onset of the target (Stuphorn et al., 2000). This could explain why distractor onset was not interfering with the triggering of the movement.

This hypotheses clearly points to the necessity of running follow up studies in order to try to understand if there is something special about fixation. It could be hypothesised, for example, that a distractor at fixation will have an impact on manual movements, paralleling the outcomes for the FOE (Pratt et al., 1999). On the contrary, the lack of the RDE for a distractor presented at fixation too would suggest that the FOE and the RDE rely on different structural bases, or that the connection between the fixation zone and the areas devoted to triggering manual responses is not as direct as for the oculomotor system.

7.3 Scope and limitations of the paradigm

The present thesis investigated the effect of the RDE on different response modalities. As previously described in section 7.2.1, the entire study was carried out using a very simple experimental design, trying to exclude cognitive components. This reductionistic approach led the RDE to express mainly its pure motor component, the apparently ineradicable saccadic effect, which cannot simply be explained in terms of cognitive choice. This approach has advantages and limitations for the subsequent interpretation of the data.

One main advantage offered by removing the cognitive element of choice related to target/distractor discrimination was that it was then possible to link any effect caused by distractor onset to a low-level modulation. As suggested in the section above, the RDE is supposed to take place in the SC where the inhibitory processes are very well documented (Dorris et al., 1997; Dorris & Munoz, 1998; Munoz & Istavan, 1998; Munoz, Dorris, Parè & Everling, 2000; Munoz & Wurtz, 1992, 1993a, 1993b, 1995a, 1995b). The study of the pure motor component helps in the characterization of the neural aspect underlying the phenomenon.

Another positive aspect of its use was that it helped to dissociate the attentional from the motor component of the RDE. In fact, like other oculomotor phenomena, it is likely the RDE is formed by these two different components. As previously discussed, in this study the pure motor component is highlighted. By way of contrast, an example of the attentional component is provided by the work of Benson (2008) where a condition in which target direction was pre-specified is compared to a condition where the target could have appeared on either side of fixation. Benson reported that in the bilateral condition the magnitude of the RDE was greater than in the unilateral condition, suggesting that a cognitive component of choice between motor programs elicited by target and distractor played a role in the RDE.

Previous literature has already shown that in some cases of the oculomotor effect it was possible to dissociate the cognitive from the motor component using different response modalities. An example is provided by the GAP effect, where the general warning signal (inherited by other response modalities) was separated from the pure motor component, the FOE (peculiar of directional responses) (see Chapter 4 for more detail on the GAP effect). A similar dissociation has been also reported in the case of the IOR (Hunt & Kingstone, 2003a), where the motor component of the IOR was dissociated from the attentional component, with the former being a visible during a saccadic task and the latter during a manual task. In the experiments reported in the thesis, top-down influences could have eliminated the cognitive attentional component, isolating the pure motor element of the effect.

Although this reductionistic approach has been very useful in isolating the phenomenon, some problem arose at the interpretation level. For example, it is impossible to know, for certain, whether the manual resistance to the RDE was due to studying non-representative manual responses (i.e. that bypass online target selection processes). In fact, it could be that the manual responses that have been analysed are the pre-programmed ones, since participants were instructed regarding target/distractor locations in advance. In such a particular case, it may be that manual responses bypassed target selection processes, the mechanisms that I was most interested in studying, retrieving instead programs for the manual movement from memory. As suggested in section 7.2.3, manipulating target/distractor predictability would help in the understanding of hand behaviour during distractor interference.

Finally, one problem that this reductionistic approach generates is that it limits the study of the RDE to the particular paradigm employed (with complete top-down information provided). The natural consequence is that the results described in the previous chapters cannot be generalised to a broader category of distractor effects. In everyday life, there are many situations in which a distractor can interfere with normal behaviour, but in many of these circumstances distractor effects are a product of an attentional modulation, such as the discrimination between relevant and irrelevant information. The filter mechanism described in the introduction generally refers to the ability to make these sorts of distinction. It is indubitable that low-level mechanisms play a central role in the filtering of information, but yet, at an ecological level, it is likely that top-down processes play the key role. Moreover, in a more ecologic paradigm, irrelevant information is not always a source of interference that has to be suppressed. In many circumstances of everyday life what is classified here as irrelevant stimulation is actually an element that we have to take into account to generate a reponse. Most of the time, this means including top-down information in the process of choosing the best behaviour.

In brief, the reductionistic approach used in this thesis to investigate the effect of distractors limits its conclusions to the pure motor aspects of the phenomenon, probably arising at an early stage of processing in subcortical structures such as the superior colliculus. Of course, this simplification served to enable us to better understand the phenomenon, but an unavoidable consequence has been that in some aspects the study does not fully reflect the complexities of real life, making it more difficult to generate an interpretation referring to normal behaviour. This phenomenon, under the particular settings used throughout the thesis, is not ecologically valid. It is suggested, then that in normal behaviour the systems that here have been dissociated are generally coupled, and effects due to irrelevant stimulation would probably co-occur across different modalities.

7.4 Future research

The following section presents a program of research based on the outcomes of the experiments described in this thesis. In the third year of my doctorate some of these experiments were already planned and the experimental set-up was started. This is the case, for example, with the experiments involving s-cone stimulation. Nonetheless, none of these studies has been carried out yet and they represent a research program to pursue after the completion of this Ph.D.

7.4.1 Behaviour: a new approach to the model of saccade generation

The first aim of this series of studies is to understand the RDE in terms of SI and vice-versa. The RDE has been intensively studied by Walker and colleagues and different effects on SRTs and the amplitude of eye movements have been observed, manipulating the spatial and temporal characteristics of the distractor. On the other hand, SI has been studied under different conditions, manipulating the size, location and colour of the visual transient used during the saccadic task. Each of these manipulations has its own peculiar parameters, which are described in detail. To pursue this idea, the first manipulation will regard the intrinsic and extrinsic characteristics of the distractor, such as its location and size. Before describing the experiments in detail, there is the need to also frame the classic oculomotor effects (i.e. the RDE and Global effects in this case) according to the Findlay and Walker model (1999). This is important in order to better understand SI as part of the model.

Walker et al. (1995; 1997) observed that the RDE was maximal for distractors presented at fixation, and decreased monotonically for distractors at more eccentric locations. By contrast, distractors presented within the same hemifield as the target modulated the metrics of the saccade instead of its latency, as in the Global effect. Both these effects are well captured by Findlay and Walker's model (1999). The structure of the model separates the processing of the information between *where* and *when* parallel streams. While the "where" pathway influences the landing position of an eye movement, the "when" pathway determines the time of start of a saccade. The interaction between the two streams is only present at a very low level of processing (motor command and movement decision) and is of a reciprocal competitive inhibitory nature (Findlay & Walker, 1999). One example is the push-pull interaction between the *fixate* centre and the *move* centre that will determine the exact time of the triggering of the saccade. The two saccadic effects described earlier are explained within this model. In particular, the RDE is hypothesised to be due to activation of the fixate system (*"direct visual influences"*) that qualitatively refers to the fixation centre of the SC. The distracting visual stimulation affects thereafter the fixate-move balance and slows down the triggering of the saccade. On the other hand, in the Global effect the "direct visual influences" lead to a distributed spatial coding in the salience map (i.e. summation processes within the SC), without interfering with the fixate-move balance but generating a motor program directed to the centre of gravity between target and distractor. According to this interpretation, it is possible to explain why SRTs in the global effect remain unaffected.

Experiment A. The purpose of the first experiment is to better understand SI in the light of the RDE. In particular, my aim is to describe how the SI profile changes according to distractor location. We already know that increasing distractor eccentricity reduces RDE magnitude, but how this decrease is translated within SI parameters it is still unknown. SI presents three main parameters: the *magnitude*, the *wideness* and the *timing* of the dip (all these three parameters are fully explained in Chapter 6). A change in any of these parameters could influence the average SRT, and thus modify the RDE, but each parameter might suggest a different mechanism operating on the inhibition. For example, we can hypothesise that increasing distractor eccentricity will be translated simply into a change in the magnitude of the dip. This would suggest that the underlying mechanism of inhibition is unchanged, but the probability that a saccade in preparation will be inhibited is increased. This type of change would suggest that there is a continuum between fixation and more eccentric locations in terms of the population of neurons coding for different target/distractor locations, in accord with the lateral inhibition hypothesis. On the contrary, a change in the timing or the width of the dip would suggest that the underlying mechanism of inhibition is changed, implying a discontinuity somewhere in the effect of the visual transient, for example between fixation neurons and more eccentric build-up neurons.

The experiment will be set up as the classic RDE experiment, with a target presented at one eccentricity always on the same side (to avoid the interference of cognitive processes related to choice). On the contralateral side, in some trials a distractor will be briefly displayed. The eccentricity of the distractor will be manipulated and it will increase from 0° for fixation to 9°, at increments of 1.5°, for a total of 7 distractor locations. The step of 1.5° is suggested in order not to pass abruptly from foveal to parafoveal vision (giving the opportunity for SI profile to reflect the transition between different zones within the SC). The time of distractor onset will also be critical and for this reason, given our knowledge about the relation between baseline SRT and RDE, distractor onset will be time-locked to the baseline SRT collected for target only in preliminary block trials. The distractor will be presented at the median SRT minus 90 ms, following the methods of Reingold and Stampe (2002).

Experiment B. The second experiment is based on the same assumptions as Experiment A and also aims to better characterise SI according to our knowledge of the RDE. As previously stated, Walker and colleagues (1997) showed that distractors presented within the same hemifield as the target modulated the metrics of the saccade instead of its latency (i.e. Global effect). Since in this case a change in latencies is not captured by measures of central tendency, it becomes relevant to apply the SI analysis on the global effect paradigm in order to investigate if there are more subtle changes that instead can be described as a change in the SI profile. In fact, Chapter 6 already demonstrated that SI might be present without giving rise to large changes in average SRT. Walker's (1997) conclusion that ipsilateral distractors do not influence SRT thus needs to be re-evaluated, and it would be interesting to investigate whether there is any evidence of SI in the saccade distribution and how the SI profile changes for a distractor presented ipsilaterally. On one side, as discussed in Chapter 6, it could be that SRTs are in fact modulated for ipsilateral target but that such modulation is not reflected in mean SRTs. This could be due to a very weak dip or to a different type of rebound phase. Knowledge of SI in this case will help us to better understand the nature of the global effect. The experiment will also aim to map the ipsilateral space, as for experiment A, to see any eventual discontinuity in the visual field and also to cross-compare the results from experiment A, comparing ipsilateral and contralateral space. The methodology used will be identical to that of experiment one, with the only exception being that the distractor will be presented ipsilaterally.

Consequences for the Findlay and Walker model. The first two experiments will help in further understanding the RDE and the global effect in terms of SI. Moreover, as previously stated, both the RDE and the Global effect are well captured by the Findlay and Walker model. But where is SI acting within this framework? As noted earlier, Olivier et al. (1999) suggested the RDE is due to interactions between a subpopulation of build-up neurons coding for different spatial locations. Moreover, Olivier proposed that the same mechanisms driving the RDE also act upon the spatial parameters of saccade preparation, explaining the Global effect. In particular the authors suggested that the only mechanism that can provide a unitary explanation of the two phenomena is the interaction between zones within the SC salience map coding for different saccades (Olivier et al., 1999). The type of interaction between the different populations of build-up neurons will lead to inhibition in the case of contralateral distractors (RDE), and excitation in the case of ipsilateral stimulation (Global effect). Olivier et al. then proposed that these interaction processes are described by the interaction in the fixate-move balance (level 2). According to Reingold and Stampe (2002), the same processes are also responsible for SI.

This interpretation is very appealing and fits well with the Findlay and Walker model. Moreover, if we accept the neurophysiological findings described by Olivier and the neurophysiological interpretation of SI provided by Reingold and Stampe (2002), we can then assume that SI is also acting at level 2 in the salience map (and we should ask how SI is modulating the spatial parameters like the saccade amplitude). The only incongruent prediction within this new framework is that SI has an effect on SRTs for both controlateral and ipsilateral visual transients. The processes described in the SC, though, would suggest that ipsilateral stimulation will lead to excitation, which should be reflected in faster SRTs. A close inspection of the distributions is therefore necessary to discriminate between these different hypotheses.

Experiment C. This experiment is complementary to Experiment B. In fact, another point of contact between the RDE and SI is that Reingold and Stampe (2003) reported that SI is stronger when a large (10°) distracting stimulus is displayed on the same side as the saccade target (congruency effect), but that this effect reverses when a small distractor (1°) is flashed. Walker et al. (1997) reported that a distractor presented in the same hemifield as the target does not affect SRT but only the landing position, as already mentioned above. We can use these predictions in an experiment testing the SI congruency effect by flashing distractors of increasing size on the same side of the target. This manipulation of target size will help to better modulate the SI profile and, as a consequence, the RDE. Understanding which parameter of the SI profile changes according to the size of the visual transient will help to model how the dip translates in measures of central tendency.

The experiment will be designed according to the findings of Experiment B, selecting the best location in which to present the distractor in order to have a clear SI profile. The size of the distractor will be manipulated, increasing from 0.5° to 3°

in steps of 0.5° of visual angle. The timing of distractor onset and the type of analysis will be identical to that used in Experiments A and B. It is important to underline this congruency between experiments because the overarching aim of these experiments is to characterize the SI profile and how this changes in response to the manipulation of different stimulus parameters. Keeping the non-manipulated parameters constant across experiments will help in comparing the outcomes across different experiments.

The new findings coming from the merging of the two literatures will offer the opportunity of recasting classical eye movement phenomena in the light of more detailed models of saccadic behaviour. These findings could also be incorporated into the model proposed by Findlay and Walker (1999), which still lacks a common explanation to account for all these different phenomena.

7.4.2 Neurophysiology: the role of the SC

The second aim of the follow-up studies is to test the involvement of the SC hypothesis in the RDE. The better understanding of the relation between the RDE and SI and related interactions will enable me to test the role of the SC. The model will be used in conjunction with two other very accurate methodologies: S-cone stimuli and naso-temporal asymmetries (NTAs). These paradigms have been investigated by Rafal and colleagues (1990) and Sumner at al. (2002) respectively: nonetheless, some aspects of their research are not sufficiently well structured to answer certain hypotheses, i.e. the role of the SC in the RDE and Gap effects, and their relation to covert attention.

Experiment D. My prediction is that if the RDE relies on subcortical pathways, then bypassing the SC with S-cone stimuli will cause the effect of the distractor to disappear. Moreover, the role of SI under these paradigms is another interesting question in itself. The SI analysis will help us to better understand the results, eventually highlighting more subtle variations that are not captured by the measure of central tendency. For this experiment, the timing of the dip (if there is a dip) will be critical. Previous experiments using S-cone stimulation reported inconsistent results. Sumner et al. (2002) did not report RDE for S-cone distractor stimuli but in a subsequent study Bompass and Sumner (2009b) were able to find an effect of S-cone distractor by using different SOAs for distractor onset. In fact, these contradictory results were attributed to the idea that the velocity of the signal, due to distractor characteristics (and in this particular case to the fact that S-cone stimulation is weaker), needs to be controlled in order to have both target and distractor signals arriving at the same time for competition. Given the presence of RDE with S-cone distractors (Bompass & Sumner, 2009b), the authors excluded subcortical involvement of the SC from a role in driving the effect with this type of stimulation, and preferred an explanation where FEF or the parietal eye movements area might have been involved.

So it is not completely clear yet how S-cone stimulation is involved in the RDE. For the purpose of this experiment, the timing of the dip will help us to better understand if a different route, maybe cortical, is involved in this type of stimulation. If a different route is used to carry the visual signals, the time of arrival of the dip will be delayed. Otherwise, if it is only a matter of the strength of the signal, it will be the magnitude of the dip to vary. Moreover, it could be that the SI signature will have completely different characteristics when a cortical route is involved, changing the width of the dip or the rebound phase. A point that is important to remember is that when dealing with S-cone stimulation the absence of retinal projections to the SC from the ganglion cells coding for short wavelengths affects mainly the superficial layers (White, Boehnke, Marino, Itti, & Munoz, 2009). According to this idea, the timing of the dip will be critical to infer at which level the RDE might arise.

The experimental design will be the classic one used in the other experiment. The eccentricity of the distractor will be chosen according to the findings of experiment A. The temporal aspect will be controlled in two ways. In one condition, the onset of the distractor will be time-locked to the median SRT for luminance targets. In a second condition, taking into account the more recent findings made by Bompass and Sumner (2009a) and the different velocity of the signals (luminance vs. S-cone; see Chapter 6 for more details), baseline SRTs will also be recorded for S-cone target and this measure will be used to estimate a second onset time for the distractor.

Experiment E. SI inhibition will also be investigated under monocular conditions. According to the naso-temporal asymmetry, given that the nasal hemiretina contains more projections to the SC temporal hemiretina, a distractor presented under monocular viewing conditions in the temporal hemifield (nasal hemiretina) will have a stronger effect than a distractor presented in the nasal hemifield (temporal hemiretina). This experiment, in addition to testing the involvement of the SC in the RDE will be very useful in characterizing the SI profile. In fact, different SI profiles would support the idea of an asymmetry between the nasal and temporal hemiretina. This aspect could have an effect on both the timing and the magnitude parameters of the SI profile.

After understanding how S-cone stimuli are treated by the SC, a final series of studies will focus on the Global effect, looking at how the metric of saccades is modulated using S-cone stimuli in a similar way to that described for Experiment B, above.

7.4.3 Neuropsychology

The third aim of this series of follow-up experiments is to test the RDE with neglect (UVN) and hemianopic patients, and extend previous finding regarding the elderly population. The encorporation of SI in the Findlay and Walker (1999) model for saccade generation, and the clarification of the neural substrates involved during eye movement behaviour, will be followed by a series of studies entirely dedicated to the study of the damaged brain. These classical paradigms offer a powerful tool to test people with neuropathologies, since they have been tested for more than 20 years on people without brain disorders. The hypothesis is that if the RDE relies on the retinotectal pathway (as discussed by Rafal 1990 and supported by NTAs) it will possible to elicit the RDE with a distractor presented in the blind visual field in both UVN and hemianopic patients. Some research has already been carried out on this topic (Rafal et al., 1990; Walker et al., 2000), with inconsistent results possibly due to the assumption that the stronger effect is obtained when distractors are presented simultaneously with the target, without considering the baseline SRT in the no-distractor condition (highly slowed in brain-damaged patients and elderly people). It has been demonstrated in Chapter 6 how saccadic distribution can be more precise than mean reaction times. According to this consideration, all of these previous findings need re-assessment in the light of SI methodology.

The experiments described above will be of great help at this point to design an experimental set up to test UVN and hemianopic patients. At this stage, both the RDE and SI will be much better understood and a model of how SI translates into RDE will be accomplished. This new knowledge will be critical in planning the type of stimuli to use, their timing and their locations.

7.4.5 RDE and the manual system

The previous chapters already described many hypotheses regarding the effect of distractors on the motor limb system. To clarify the ambiguous points that arose during my doctoral years testing manual moments, a series of studies has been planned. Among them, the more relevant regard the effect of central distractors during manual aiming (and a possible relation between GAP, the RDE and the RTE with particular interest in the superior colliculus circuitry); to what extent the saccadic and manual systems overlap during target selection; and which aspects of top-down information are more relevant during manual aiming.

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