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Saccade landing point selection and the competition account of pro- and antisaccade generation: The involvement of visual attention – A review

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This paper presents a review and summary of experimental findings on the role of attention in the preparation of saccadic eye movements. The focus is on experiments where performance of *prosaccades* (saccades *towards* a suddenly appearing item) and *antisaccades* (saccades of equal amplitude in the direction opposite to where the target moved) is compared. Evidence suggests that these two opposite responses to the same stimulus event entail competition between neural pathways that generate reflexive movements to the target and neural mechanisms involved in inhibiting the reflex and generating a voluntary gaze shift in the opposite direction to the target appearance. Evidence for such a competition account is discussed in light of a large amount of experimental findings and the overall picture clearly indicates that this competition account has great explanatory power when data on saccadic reaction times and error rates are compared for the two types of saccade. The role of attention is also discussed in particular in light of the finding that the withdrawal of attention by a secondary task 200 to 500 ms before the saccade target appears, leads to speeded antisaccades (without a similar increase in error rates), showing that the results do not simply reflect a speed-accuracy trade-off. This result indicates that the tendency for "reflexive" prosaccades is diminished when attention is engaged in a different task. Furthermore, experiments are discussed that show that as the tendency for a reflexive prosaccade is weakened, antisaccades are speeded up, further supporting the competition account of pro- and antisaccade generation. In the light of evidence from neurophysiology of monkeys and humans, a tentative model of pro- and antisaccade generation is proposed.

Key words: Saccadic eye movements, prosaccades, antisaccades, attention shifts, neural competition.

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INTRODUCTION

When we move our eyes over a visual scene, resulting in a shift in the center of gaze, we typically make a number of *saccades.* Those are relatively ballistic movements of the eye; their vectors and landing points are computed beforehand and once the command for the saccade has been made, relatively little influence can be had on the direction and landing point of the saccade (Leigh & Zee, 1999; Goldberg, 2000; Sparks, 2002); although there are examples of how shifting the intended landing point *during* the eye movement can result in slight online modifications of the saccade landing point (an effect known as *saccadic* adaptation, see e.g. Bahcall & Kowler, 2000; McLaughlin, 1967) and modification can occur for landing points based on previous target history, while everything else remains constant (Edelman, Kristjánsson & Nakayama, 2001; He & Kowler, 1989).

Saccades can occur voluntarily or involuntarily. We can have a plan to move our gaze to an item of interest in the visual scene, but saccades can also occur automatically in response to something that captures our attention in the visual field – an effect known as the *visuo-motor grasp reflex* (see e.g. Munoz & Everling, 2004). The other main type of eye movement are the so-called smooth-pursuit eye movements where a moving target is tracked with smoothly translating eye movements (as opposed to the jerky movements of saccades) but it is interesting that for these smooth eye movements to occur, a moving stimulus is required; in other words without a smoothly moving stimulus we *cannot* make smooth eye movements; the movement would be a collection of jerky saccades (see e.g. Leigh & Zee, 1999; Chen *et al.*, 1999; Krauzlis, 2004; Rashbass, 1961). Readers can easily try this out for themselves by tracking their moving finger with their eyes, and then trying to move their eyes in a similarly smooth manner across a stationary scene *without* a moving stimulus.

Selection of saccadic landing points

A hotly debated question in the experimental literature on saccadic eye movements is the question of how the upcoming landing point is selected, or in other words, what sort of mechanism guides or dictates this selection process. In the literature on psychology, selection – be it object based, location based or based on the features of a particular stimulus – is often thought of in terms of *selective* or *focal attention*

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(see e.g. Neisser, 1967; Posner, 1980; Pashler, 1998; Wang, Kristjánsson & Nakayama, 2005; Treisman & Sato, 1990; Kristjánsson, 2006).

Many researchers have, in fact, investigated the relationship between the selection of an upcoming landing point and attention. They have asked whether an attention shift to an upcoming landing point precedes the direction of gaze; in other words, is attention allocated to the locus of the landing point of an upcoming saccade, and if so, is this coupling obligatory? A case in point is a study by Deubel and Schneider (1996), where observers had to perform a perceptual discrimination task while also making a saccadic eye movement to a particular target. The greater the degree to which the stimulus for the discrimination task coincided spatially with the upcoming landing point of the saccade (even though the target stimulus disappeared before the centre of gaze settled on the target following the saccade), performance on the discrimination task was improved, compared to when the discrimination stimulus was located to the left or right of the fixation point. Since attending to the locus of a discrimination target (for example following a spatial cue) is known to improve performance compared to a discrimination task presented at an unattended location (cf. Carrasco, Williams & Yeshurun, 2002; Kristjánsson & Nakayama, 2003, Posner, 1980), Deubel and Schneider reasonably assumed that attention had shifted to the locus of the landing point before the saccade was made and that attention had improved performance on the secondary task.

Others have reached conclusions similar to that of Deubel and Schneider in related experimental paradigms, for example Kowler, Anderson, Dosher and Blaser (1995) found that if a discrimination task was presented at the location of an upcoming target, shortly before the target appeared performance on a discrimination task was improved. Findings that point towards similar conclusions have also been reported by Hoffman & Subramaniam (1995) and Shepherd, Findlay and Hockey, (1986) who showed that saccade latencies to a suddenly appearing peripheral stimulus could be shortened both by advance knowledge of the upcoming landing point and also by the preparation of a saccade to that position. In other words, it seems that attention is shifted to the upcoming saccade landing point – attention "precedes" the center of gaze to the saccade landing point. A similar relationship has been proposed for the relationship between attentional orienting and smooth-pursuit eye movements (Chen *et al.*, 1999; Khurana & Kowler, 1987).

Many have thus argued for a tight coupling of attention and saccadic eye movements in that attention necessarily precedes the saccade, and some have even argued that a presaccadic shift of attention to a particular location entails a plan to shift gaze to that location, independently of whether the eye movement is actually executed or not (Schneider, 1995; Schneider & Deubel, 2002; see also Rizzolatti, Riggio, Pascola & Umilta, 1987), something that one might call a "premotor" conception of attention. This seems intuitively to often be the case, as readers may have experienced on themselves, since attending to an interesting stimulus in the visual field *without* looking at it is often very effortful (although possible), and this is of course quite reasonable since shifting the center of gaze to the stimulus puts its image on the region of the retina where the resolution of the visual field is highest (the fovea). So attending to something may entail an "urge" to look at that same thing. In relation to this, it is of interest that overlapping neural mechanisms seem, at least partly, to be involved in saccade generation and attention at least in the cerebral cortex (Kustov & Robinson, 1996; see also discussion by Schall & Thompson, 1999). Note that this proposal of the obligatory coupling of covert attention shifts and overt shifts of attention and gaze has not escaped some criticism and recent reports of neurons in the frontal cortex of monkeys that are involved in covert attention shifts but *not* eye movement planning complicate the picture somewhat (Schall, 2004; Juan, Shorter-Jacobi & Schall, 2004). There is also some evidence that attentional effects (such as those following a symbolic precue) mainly facilitate *voluntary* (or *endogenous* saccades such as *antisaccades*, which are introduced below; cf. Seidlits, Reza, Briand & Sereno, 2003; see also Reuter-Lorenz & Fendrich, 1992). If precueing does indeed mainly facilitate "endogenous" saccades, it does not, however, rule out that attention shifts to the upcoming landing point of a reflexive saccade. It may simply be that the prosaccade cannot "reap the benefits" of a symbolic precue to the same degree as voluntary saccades. There is indeed evidence that precues that are more likely to elicit "reflexive" attention shifts facilitate saccades especially if the stimulus onset asynchrony between cue and saccade is short (e.g. 100 ms; cf. Crawford & Müller, 1992), a result that suggests that the main benefits of attention upon prosaccades come from the so-called *transient* attention system (Nakayama & Mackeben, 1989; Kristjánsson, Mackeben & Nakayama, 2001; see also discussion in Fischer & Weber, 1998).

What this means essentially, if true, is that attention may be *required* for a saccade to be made. In other words, attention shifts to the locus of the upcoming saccade before it occurs, and if attention is withdrawn from that locus the saccade is slowed or disrupted. This proposal immediately raises the question of what the effect on saccade performance would be if a secondary attentionally demanding task is introduced that is to be performed simultaneously with the saccade, taxing the available attentional resources. In an attempt to answer this question, Pashler, Carrier & Hoffman (1993) found that a secondary *auditory* task requiring effort and thus taxing attentional resources, performed concurrently with a saccade task, resulted in slowed saccades to peripheral targets. They postulated that this would, in particular, be the case if the secondary task involved some interference with the saccade control generated by the frontal eye fields rather than lower level brain stem control of saccadic eye movements from, for example, the superior colliculus (with the implicit assumption that the part of the saccade preparation that involves the superior colliculus is more reflexive, and not modified by a secondary task; see the General discussion section for more discussion on the anatomy of saccade generation). Stuyven, Van der Goten, Vandierendonck, Claeys & Crevits (2000) also conducted a series of related studies of the interfering effects of dual-tasks on performance of various saccade types. Their observers were required to tap an unpredictable random sequence with their fingers on a key, a task that requires attention and working memory while also making saccades. They found that the secondary task had an interfering effect on both prosaccades and antisaccades (see below) and that this interference effect was larger upon antisaccades than prosaccades.

In what follows I will review a large number of experimental findings in the literature pertinent to the question of the involvement of visual attention in the generation of saccadic eye movements, as well as a series of experiments that my colleagues and I have undertaken in an attempt to shed light, from a number of different angles, on this issue of the involvement of attention in saccade generation (Kristjánsson, Chen & Nakayama, 2001a; Kristjánsson, Vandenbroucke & Driver, 2004; Edelman, Kristjánsson & Nakayama, 2001).

PROSACCADES AND ANTISACCADES

In our experiments aimed at looking at the role of attention in saccade generation, we contrasted performance on the regular saccade task involving shifting gaze to the peripheral target, and the so-called *antisaccade* task involving a saccadic eye movement in the direction opposite to where the saccade target appears (Hallett, 1978; Everling & Fischer, 1998; Amador, Schlag-Rey & Schlag, 1998; Funahashi, Chafee & Goldman-Rakic, 1993). We can contrast antisaccades with "regular" saccades (often called "prosaccades" in this context, see Fig. 1). The prosaccade entails a shift of gaze from the current center of fixation to the locus of a peripherally presented stimulus. In contrast, the antisaccade task requires a shift of gaze of the same size (or *amplitude*) in the exact opposite direction to the presented stimulus. Antisaccades tend to be less accurate (Krappmann, Everling & Flohr, 1998), have lower maximum velocities (often called "peak velocities") during the saccade (Leigh & Zee, 1999), and have higher response latencies than prosaccades (Hallett, 1978; Hallett & Adams, 1980; see e.g. Everling & Fischer, 1998, for a review of the basic findings of the antisaccade literature). Most, if not all, studies of antisaccade performance show that observers make many erroneous prosaccades when they are supposed to make antisaccades. These studies have also indicated that observers can compensate very quickly for these erroneous prosaccades. Interestingly, Mokler and Fischer (1999) noted that in approximately 50% of cases where an erroneous prosaccade is made and quickly corrected, observers are *not aware* of having made an erroneous prosaccade. Also, the fact that an erroneous prosaccade in the antisaccade task can be corrected very quickly, much faster than the latency of a regular prosaccade, suggests that the two types of saccade are processed in parallel in the antisaccade task (cf. Mokler & Fischer, 1999; Massen, 2004).

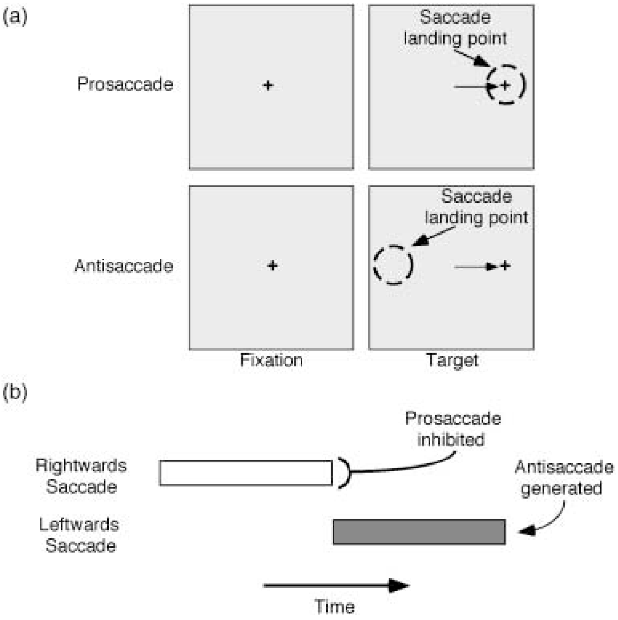

Fig. 1. The pro- and antisaccade experimental paradigms (Panel A) along with a schematic of the competition account of pro- and antisaccade performance.
Notes: Panel A: If the task is a prosaccade the saccade landing point should overlap with the displaced cross while in the antisaccade task the landing point should be in the opposite location in the visual field relative to the central fixation point. Panel B presents a functional schematic of how an antisaccade to the left, in response to a target displacement to the right, occurs under the competition scheme (see text for details). When a target is presented to the right the antisaccade task requires that the observer make an eye movement to the left of similar amplitude as the distance of the target. When observers are expecting to make a saccade they have a certain tendency to "follow the target" and this "visuo-motor grasp reflex" to make a rightwards saccade towards the target (the white bar) must be overcome or inhibited, and not until this has been accomplished can the leftwards antisaccade be generated (the grey bar). This scheme can explain why the latencies of antisaccades are higher than prosaccades, and also the higher number of errors (i.e. saccades in the wrong direction) in the antisaccade task, than in the prosaccade task.

When an antisaccade is made, a natural instinct to shift the eyes to the appearing stimulus (the so-called "visuo-motor grasp reflex") has to be overcome, to perform a saccade in the other direction successfully, in other words a "reflexive" saccade towards the stimulus must be suppressed (see e.g. Munoz & Everling, 2004; Kristjánsson *et al.*, 2001a; Forbes & Klein, 1996). One can perhaps then think of anti-versus prosaccade generation in terms of a "race towards threshold" for the two saccade types (see Fig. 1b). If the natural tendency to make a prosaccade towards the target stimulus can be overcome, the antisaccade can be subsequently generated; if not an erroneous prosaccade towards the target ensues. This is what is meant here with the *competition account* of prosaccade and antisaccade generation. Consistent with this, observers are, in general, slower at making antisaccades than they are at making prosaccades, and they make many more direction errors in the antisaccade than the prosaccade task (e.g. Hallett, 1978; Kristjánsson *et al.*, 2001a). Although this competition account is plausible and appealing, it seems often to be assumed true, without much evidence presented in its favor. Part of the aim of this review is to evaluate the competition account in light of the available evidence without assuming its truth *a priori*. Note that even though the competition account is often considered to involve *sequential* generation of the processes for prosaccades and antisaccades this need not be the case; in other words, that only after the prepotent prosaccade reflex has been suppressed can the process for the antisaccade begin. In fact, evidence suggests that the two proceed in parallel, as mentioned above (Mokler & Fisher, 1999; Massen, 2004).

The "gap effect"

Before proceeding further it is appropriate to say a few words on the so-called "*gap effect*", and the issue of *express saccades*. If the central fixation point in a saccade task is extinguished, shortly before a prosaccade is to be executed (e.g. by 200 ms), saccades tend to be faster than otherwise (Fischer & Boch, 1983, Saslow, 1967; Ross & Ross, 1980; 1981; Fischer & Weber, 1993). These speeded saccades have sometimes been called "express saccades" and there is controversy over whether they constitute a qualitatively distinct type of saccade from the "regular" prosaccade. They have sometimes been thought to manifest a "pure" version of the aforementioned visual grasp reflex (Munoz & Everling, 2004). The gap effect is thought to reflect that a tendency to keep the eye on the currently fixated stimulus, if it is still present, competes with the signal to generate a prosaccade. If the fixated stimulus is no longer present, there is no competition anymore so the saccade can be generated faster than otherwise (Edelman & Keller, 1996, 1998; Fischer & Weber, 1993; Munoz & Wurtz, 1995a, 1995b). One can conceive of the effects of the temporal gap between fixation offset and the target appearance in terms of competition between the activity of the saccade burst-neurons and fixation neurons in the superior colliculi of the midbrain and the frontal eye fields in the frontal lobes of the cerebral cortex (see e.g. Dorris & Munoz, 1995; Edelman & Keller, 1996; see Munoz & Everling, 2004 for a review, and further discussion below). The degree to which fixation is maintained (through the activity of the fixation neurons) dictates how quickly a saccade is generated under these conditions. If the fixated stimulus disappears, the activity of fixation neurons is assumed to be lessened allowing the saccade towards the stimulus to be executed with a shorter latency. It has also been suggested that the "express" saccades reflect that the gap before the target appears, speeds up an attentional disengagement from the stimulus (e.g. Fischer & Breitmeyer, 1987).

For the antisaccade in the gap paradigm the speeded saccades almost exclusively reflect erroneous prosaccades. It seems then that the "visual grasp-reflex" is particularly strong in the gap-task, reflected in the speeded prosaccades and the high error rates in the antisaccade task. This has been shown to be correlated with the activity of saccade-burst neurons in the superior colliculus in the monkey; the stronger the activity of these neurons, the higher the likelihood that an erroneous prosaccade will occur when an antisaccade should be performed (Everling, Dorris & Munoz, 1998; Everling & Munoz, 2000).

The evidence from research on the gap effect suggests that when a regular saccade is made (without the gap), disengagement from the fixated stimulus is required and that this disengagement is effortful – it results in increased saccade latencies. This disengagement is no longer required in the gap task, thus allowing faster saccades (no disengagement is required since the stimulus is no longer there, as discussed above). This means that one essential component of the antisaccade task may thus be disengagement from the current locus of fixation before the saccade can be generated (Funahashi *et al.*, 1993; Schlag-Rey *et al.* 1997; Forbes & Klein, 1996; Everling *et al.*, 1998). Disengagement from the currently fixated target is also often mentioned as an explanation for the slower prosaccades in the "overlap" than the "gap" paradigm. Related to this, Godijn and Pratt (2002) have argued that endogenous (or non-reflexive) saccades entail a similar shift of visual attention to the upcoming landing point as occurs for reflexive saccades as was reviewed above.

It seems, then, that for a saccade to be generated, disengagement from the current locus of fixation is required, and then if an antisaccade is required, competition between the incompatible responses occurs (leftwards or rightwards saccade, to or away from the target, see Fig. 1). In this review I summarize evidence from a series of experiments undertaken to shed light on this competition account of pro- and antisaccade generation and the involvement of attention and attentional disengagement in this process.

The role of working memory in antisaccade generation, and relation to the operation of the frontal lobes

Some lines of research, both from behavioral paradigms as well as from neurophysiology, suggest that working memory plays a key role in the generation of antisaccades. Mitchell, Macrae and Gilchrist (2002) had their observers execute antisaccades while also performing an "n-back" task where they had to remember letters presented auditorally, for differing amounts of time (0-back, 1-back or 2-back) which is widely considered to be a task that taxes working memory, to a differing degree depending on for how long a letter had to be remembered. They found that errors on the antisaccade task increased as a function of increased working memory load. Mitchell *et al.* concluded that working memory plays a key role in inhibiting prepotent responses (such as the visuo-motor grasp reflex in this case). This result falls in line with the results of Stuyven *et al*. (2000) who found that an ongoing tapping task with considerable working memory load interfered with pro- and antisaccade performance, as mentioned before.

Furthermore, Matsuda *et al.* (2004; see also DeSouza, Menon & Everling, 2003; Connolly, Goodale, Menon & Munoz, 2002) have shown that the dorsolateral prefrontal cortex (DLPFC) shows increased activity when an antisaccade is to be made than when prosaccades are to be made. DLPFC has long been considered to be a key cortical region for working memory (Goldman-Rakic & Leung, 2002; D'Esposito & Postle, 2002). Research with transcranial magnetic stimulation also shows that frontal TMS slows memory-guided saccades, where the landing point of the saccade disappears and must be kept in memory before the observer is allowed to execute the saccade (Müri *et al*., 2000). A similar result has also been found for TMS of the frontal eye fields in humans (Thickbroom, Stell & Mastaglia, 1996). This result corresponds well with the findings of Guitton, Buchtel and Douglas (1985) who found that patients with frontal lesions have great difficulty inhibiting reflexive saccades towards the stimulus onset in the antisaccade task (see also Henik, Rafal & Rhodes, 1994). Similar results have been observed in other patient groups that show prefrontal dysfunction such as schizophrenic patients (Sereno & Holzman, 1995; Fukushima, Fukushima, Chiba, Tanaka, Yamashita & Kato, 1988; Fukushima, Morita, Fukushima, Chiba, Tanaka & Yamashita, 1990); in Parkinson patients (Fukushima, Fukushima, Miyasaka & Yamashita, 1994; Crevits & De Ridder 1997); patients with Alzheimer's disease (Currie, Ramsden, McArthur & Maruff, 1991); and even patients suffering from obsessive-compulsive disorder (Maruff, Purcell, Tyler, Pantelis & Currie, 1999; Rosenberg, Averbach, O'Hearn, Seymour, Birmaher & Sweeney, 1997). Also, patients with attention-deficit hyperactivity disorder who exhibit many signs of frontal dysfunction show the classic signs of being unable to inhibit reflexive saccades (Munoz, Armstrong, Hampton & Moore, 2003; Cairny, Maruff, Vance, Barnett, Luk & Currie, 2001). The antisaccade task is, in fact, part of the diagnostic kit of health professionals trying to test for frontal lobe dysfunction. Note that the proposed involvement of working memory mechanisms in antisaccade generation suggests a role for neural mechanisms traditionally connected with working memory function, such as the dorsolateral prefrontal cortex in antisaccade generation in addition to mechanisms such as the supplementary eye fields (see further discussion of neural mechanisms below).

The effects of a secondary discrimination task on prosaccade and antisaccade performance.

Kristjánsson *et al.* (2001a) presented the results of a number of experiments which were designed to investigate the effects of a secondary attentionally demanding task on the saccade process, presented at various times before, after or simultaneously to the time when a prosaccade or antisaccade was to be made. In light of the proposed competition account of prosaccade versus antisaccade generation, and the demonstrated importance of attention and working memory for saccade production (see the above discussion) we wondered what the effect of a secondary attentionally demanding task would be on saccade performance, when the secondary task was presented concurrently with the saccade target at various times relative to the onset of the saccade target (prior to, simultaneous to and subsequent to the target onset, in other words different stimulus onset asynchronies, or "SOAs").

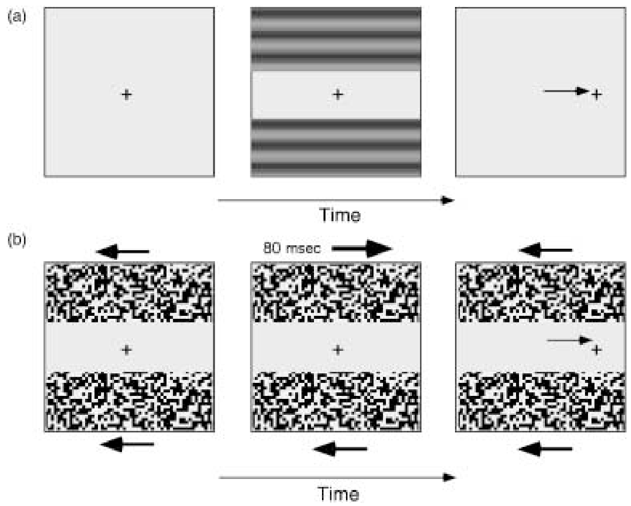

Fig. 2. Two examples of the stimuli used in the experiments in Kristjánsson *et al.* (2001a).
Notes: In the first task (panel A) the observers were required to indicate which of the two gratings was of higher spatial frequency (the upper or lower). In the task in panel B the task was to indicate which of two drifting random dot patterns briefly reversed direction (again the upper or lower). The secondary task occurred at various SOAs relative to the displacement of the saccade target (before, simultaneous to or after the displacement).

Figure 2 presents the stimuli for two of the secondary tasks used in Kristjánsson *et al.* (2001a), along with the primary saccade target stimulus. The observers' task was to make either a prosaccade towards the fixation cross as soon as it moved away from the centre of the display to the periphery, or make an antisaccade in the opposite direction to the target (on different blocks), to a location about as far away from the center of the display as the target (see Fig. 1). We ran the task under two conditions: In one case the observers were supposed to *ignore* the secondary task (even though it was still present on the screen), while in the other case they were supposed to perform the secondary task as well as possible while also trying to perform the saccade task as quickly and accurately as they could. We also measured performance for prosaccades and antisaccades *without* the presence of a secondary stimulus to establish a baseline for performance for each subject, for comparison. In the first of the two tasks shown in Fig. 2 the secondary task was a spatial frequency discrimination task, where two gratings were presented above and below the display for the saccade task and the observers' task was to indicate whether the grating above or below was of higher spatial frequency while also making prosaccades or antisaccades (on different blocks of trials). The secondary task was presented at different stimulus onset asynchronies relative to the saccade target displacement (from 300 ms before the target displacement to 200 ms after its displacement, in steps of 100 ms).

Few would probably need much persuading that performing two tasks simultaneously is harder than performing only one and this has been shown in many studies where dual-task performance is contrasted with performance on only one task (Treisman, 1964; Neisser & Becklen, 1975; Most, Simons, Scholl, Jimenez, Clifford & Chabris, 2001; Kristjánsson & Nakayama, 2002; see e.g. Pashler, 1998 for a thorough review) and such dual task slowing has been shown to occur for saccadic eye movements as discussed above (Mitchell *et al.*, 2002; Pashler *et al.*, 1993; Stuyven *et al.*, 2000).

The effect of this secondary task on antisaccade performance was quite unexpected however. For prosaccades, the secondary task interfered strongly with performance on the secondary task (see Fig. 3; the data show performance on the task shown in Fig. 2a), no matter at what time relative to the offset of the saccade target to the peripheral target the secondary task appeared. For comparison, the performance when the observers were instructed to ignore the task even though it was presented is shown as well, along with the baseline prosaccade performance (measured without any secondary stimulation at all being presented). This is, of course, not an unexpected result since such dual-task slowing is a common finding in the literature on dual-task performance, as discussed above.[1]

So far, the results are not particularly surprising. Performing another task while making saccades results in worse performance for the prosaccades. On the other hand, the effects of the secondary task on antisaccade performance were quite unexpected, to say the least (see the graphs on the right in Fig. 3, and Fig. 1 in Kristjánsson *et al.*, 2001a). While we did see the expected slowed performance when the secondary task was presented simultaneously to, or after the target for the antisaccade, the pattern was quite different when the secondary task was presented 200 to 300 ms *before* the target appeared. Then, antisaccade performance became *faster* than the baseline performance *measured without the secondary stimulus*. In other words, the presentation of the secondary task speeded up the antisaccade generation, over and above what these latencies were for these observers when no secondary stimulation at all occurred (compare the white disks and dashed line in Fig. 3 for the antisaccades). It is important to note that this effect was totally dependent upon performance of the task – saccade latencies were more or less unaffected when the secondary task was to be ignored (black disks in Fig. 3).

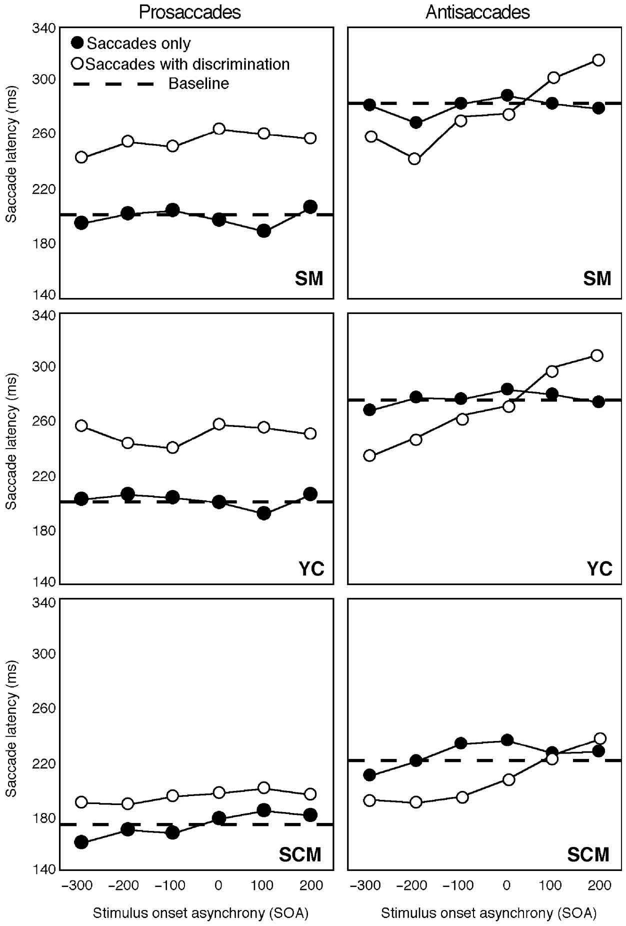

Fig. 3. Results from the dual-task experiments from Kristjánsson *et al.* (2001a) for three observers.

Notes: The task that the observers performed in this experiment is shown in Fig. 2a. The graphs on the left show performance for prosaccades and the ones on the right show performance for antisaccades. The black disks show performance when observers were supposed to ignore the secondary task although it was presented. The white disks show performance when both tasks were to be performed. The dashed line shows baseline performance for each subject for pro- and antisaccades *without presentation of any secondary task*. The data in the figure were collected at the same time as the data presented in Kristjánsson *et al.* (2001a), with the exact same experimental setup as in that paper, but the data were not presented there; other data showing more or less identical results were presented in that paper.

This pattern of results held across the three different secondary tasks that we tried. We also used a task where two random dot patterns drifted in the same direction continuously, but one of them reversed its direction of drift for 80 ms and the observers task was to indicate by key press whether the upper or lower dot pattern had reversed its direction of drift (see Fig. 2b). The reason for testing saccade performance along with this secondary task, as well, was to rule out that the sudden stimulus onset on its own in the first version of the experiment that we tried (where we used the spatial frequency discrimination task, suddenly appearing for 80 ms) was responsible for the observed pattern of results rather than the performance of the task itself. It is well known that sudden luminance changes can grab attention, especially when the stimulus is task relevant (Kristjánsson & Nakayama, 2003; Kristjánsson *et al.*, 2001b; Nakayama & Mackeben, 1989; Folk & Remington, 1999; Yantis & Jonides, 1990; Theeuwes & Godijn, 2001). The same pattern of speeded antisaccades was observed, with this non-luminance onset secondary stimulus, however, ruling out the possibility that the pattern was the result of the stimulus per se, rather than task performance (see Fig. 2 in Kristjánsson *et al.*, 2001a), while we continued to see the slowed prosaccades at all SOAs.

The fact that the secondary attentionally demanding task actually speeded up antisaccade performance in some cases seems on the face of it to fly in the face of the proposal that attention is required for eye movements. In my view, however, this pattern is quite consistent with the competition account of pro- and antisaccade generation, and with the proposal that attention is required for saccade generation. In short, this result may reflect that the attentionally demanding task interfered with the generation of the prosaccade (the "reflexive prosaccade", or in other words the results indicate that the visuo-motor grasp reflex is in some sense inhibited). This, in turn, means that less effort is required to generate a voluntary antisaccade in the direction opposite to where the target moved. We reasoned, based on previous results on the antisaccade task, that when observers are expecting to make an antisaccade that is dependent upon the stimulus on the screen, the probability of an erroneous prosaccade is high (see e.g. Munoz & Everling, 2004). Thus, under normal conditions, much effort is required to suppress the "reflexive" prosaccade. If less effort is required for this suppression process, the antisaccade can be generated faster, faster even than when *no secondary task* is involved. This conception of pro- and antisaccade generation and the proposed effect of the secondary task is depicted in Fig. 4. Note, however, that this proposal is agnostic as to whether the programming of the two types of saccade occur in parallel or in sequence. Massen (2004) has, for example, argued from her findings where the involuntary reflex and voluntary attention were selectively interfered with that the two programs occur in parallel (see also Mokler & Fisher, 1999). The current proposal merely states that the prosaccade must be suppressed in order for the antisaccade to be made and that the time this takes does depend on the task configuration. There is more discussion of this issue below.

There were, however, some outstanding questions regarding the observed pattern of results. In a third experiment in Kristjánsson *et al.* (2001a) we asked whether the effect of the secondary task could simply be explained by the withdrawal of attention from the fixation point due to the secondary task. It is conceivable that the results simply reflect that the *withdrawal of attention* from the fixation stimulus results in the pattern of speeded antisaccades rather than the findings reflecting the dynamics of pro- and antisaccade generation. To investigate this we conducted an experiment where we now had the discrimination task confined to the saccade target itself, so that the secondary task was to indicate whether the fixation cross brightened or darkened (Kristjánsson *et al.*, 2001a, experiment 3). In short, the results were that the same pattern of speeded antisaccades was observed when the secondary task was presented shortly before the task (200 to 300 ms before the saccade target displacement) and as in the other experiments this pattern of results was not seen for the prosaccades. We could thus rule out that attentional disengagement from the saccade target itself could account for the pattern of speeded antisaccades when preceded by a secondary attentionally demanding task. Rather, the attentional load from the secondary task, per se, caused the observed speed-up.

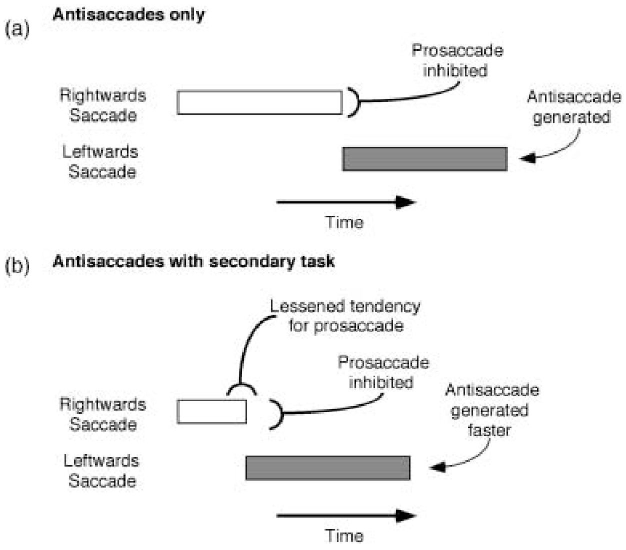

Fig. 4. A conception of how a secondary task can actually lead to speeded antisaccades when a secondary task is presented at the appropriate time as shown by Kristjánsson *et al.* (2001a).
Notes: If we assume that when the stimulus for the antisaccade is presented in the right visual hemifield (requiring a saccade into the left hemifield in the antisaccade task), a certain amount of time will pass before the antisaccade (grey bar) can be generated since a reflexive prosaccade to the right (white bar) must be inhibited. When the secondary task is presented at the appropriate time, however (approximately 200 to 300 ms before the saccade must be executed; see Panel B), the tendency for a prosaccade is lessened and the inhibition process for the prosaccade doesn't take as long, so that the antisaccade can be generated faster.

It is important to note that the speeded antisaccades *do not* simply reflect a "gap effect"-like pattern, where the disappearance of the fixation point about 200 ms before the target for the saccade appears speeds up saccades to a peripheral target (see discussion above), with the secondary task in our case serving a similar purpose as the disappearing fixation point. There are two reasons why this explanation can be ruled out: First, because our speed-up effect is *not* upon prosaccades as is the case with the regular gap effect (the prosaccades are actually *slowed* in our results), so in fact the effect upon the prosaccades is almost the exact opposite of the pattern that occurs in the gap-effect/express-saccade literature. Secondly, the error rates did not increase with the speed-up (see Kristjánsson *et al.*, 2001a) as is the case with antisaccades under the gap condition (see, e.g., Munoz & Everling, 2004).

Overall the studies in Kristjánsson *et al.* (2001a) show that antisaccades can be speeded up, to below baseline levels if a concurrent secondary discrimination task occurs at the appropriate time. This result can be relatively easily explained in light of the competition account of pro- and antisaccade generation explained above. Figure 4 shows how we hypothesized that the secondary task interfered with the reflexive prosaccade, decreasing the tendency for the visual grasp reflex, which in turn means that less resources are required for the suppression of the prosaccade. This then means that the antisaccade can be generated faster than otherwise, resulting in the observed speed-up when the secondary task appears at the appropriate time.

Furthermore the results are overall consistent with the competition account of pro and antisaccades, since they indicate how inhibition of one (the prosaccade) can aid performance on the other (the antisaccade), which is exactly what one would expect when competition between two processes occurs.

Further enquiries into the competition account of pro- and antisaccade generation

Following the demonstrations in the experiments explained above of how competition between pro- and antisaccade generation occurs when observers make an antisaccade, we conducted a set of experiments where we manipulated factors that were known or suspected to have an effect on prosaccade latency (Kristjánsson *et al.*, 2004). We reasoned that the stronger the prosaccade reflex, the more effort would be required to suppress it and that the antisaccades made in the same context would be slowed subsequently, while the converse would occur if the prosaccade tendency is lessened. Furthermore, we reasoned that this would in particular be the case if the manipulations would have an effect on neural pathways that involve the automatic generation of saccades, perhaps especially the phylogenetically old tectal pathway (so-called because in various organisms this is the pathway that projects to the optic tectum) projecting from the retina to the superior colliculus in the midbrain in primates (Goldberg, 2000; Sparks & Barton, 1993; Schall & Thompson, 1999; Sparks, 2002; Leigh & Zee, 1999). It is well known that the superior colliculus is a crucial component of the eye movement system containing similar burst and fixation neurons as were previously mentioned for the frontal eye fields (Everling & Munoz, 1999; Leigh & Zee, 1999).

It is well known from neuroanatomy that the projections from the nasal half of the retina (hemiretina) to the superior colliculus in humans are stronger than the ones from the temporal hemiretina. Rafal, Henik and Smith (1991) investigated the potential effects of this asymmetry in retinotectal connections on prosaccade performance. Their observers had one eye covered with an eye patch, while they performed a standard prosaccade task. The results were that the saccades were faster to targets in the temporal hemifield than to targets in the nasal hemifield (targets in the *nasal hemifield* are projected via the optics of the eye to the temporal half of the retina while targets in the *temporal hemifield* are projected to the nasal hemiretina). This means that the stronger projections from the nasal hemiretina (responsive to targets in the temporal hemifield) through the tectal pathway to the superior colliculus, result in faster prosaccades than targets in the nasal hemifield projecting to the temporal hemiretina (see also Shulman, 1984).

Taking this result of Rafal *et al.* as a starting point, we measured pro- and antisaccade performance while observers had one eye covered with an eye patch (Kristjánsson *et al.*, 2004; see Fig. 5a). We reasoned that if prosaccades are slower into the nasal hemifield, *antisaccades* might be faster into the temporal than the nasal hemifield, if the slowed prosaccades into the nasal hemifield reflect that the tendency for a reflexive prosaccade in response to the stimulus onset is lessened. When an antisaccade into the temporal hemifield is to be made, the target appears in the nasal hemifield. It was clear from the results of Rafal *et al.* that monocular prosaccades (performed with the view from one eye blocked) into the temporal hemifield are faster than prosaccades into the nasal hemifield, so if there is competition involved in antisaccade generation, the antisaccades should be faster into the temporal hemifield if the reflex for the prosaccade is lessened under those conditions, and if this effect exerts its influence on a pathway that involves competition between the two opposite responses.

The results are shown in Fig. 5b, and as predicted we found the reverse pattern of latencies for pro- and antisaccades. As reported previously by Rafal *et al.* (1991), prosaccades were faster into the temporal than the nasal hemifield, while our novel finding was that antisaccades were faster into the nasal hemifield than the temporal hemifield. Note that the target in the case of a temporal landing point for a prosaccade and a nasal landing point for an antisaccade, appears in the temporal hemifield in both cases – with the stimuli projected to the nasal hemiretina. The prosaccade reflex is stronger if the stimuli are projected to the nasal part of the retina (and the target appears in the temporal hemifield) – resulting in faster prosaccades but the antisaccades are slowed under these same conditions, since a stronger reflex for a prosaccade needs to be overcome. The converse then occurs for targets in the nasal hemifield.

A further control experiment also showed that the critical factor behind the asymmetries between temporal and nasal stimulation for the two saccade types, was not simply whether the saccade landing point was in the temporal or nasal

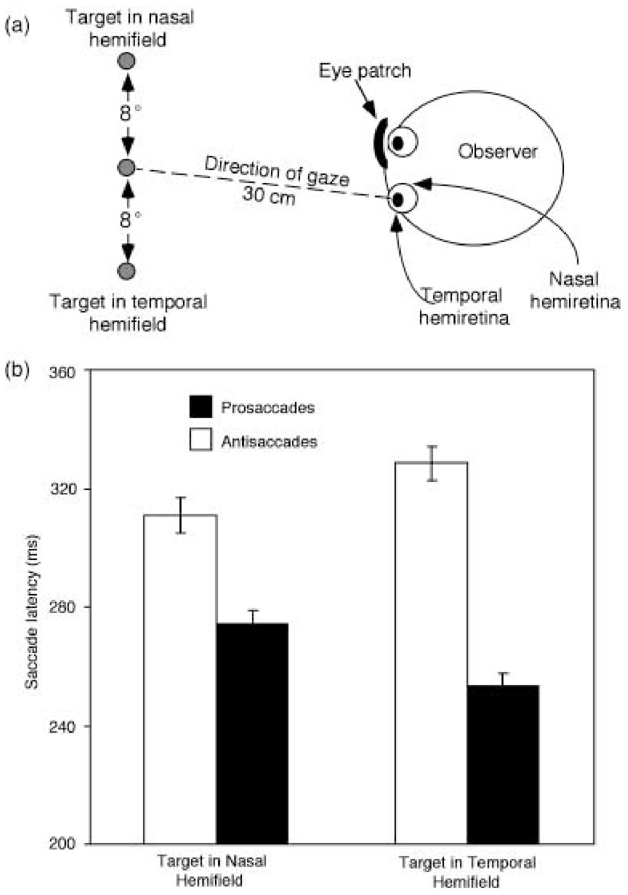

Fig. 5. The experimental setup and the results from the first experiment in Kristjánsson *et al.* (2004).
Notes: Panel A shows the experimental setup. The observers had one eye covered while they made either prosaccades or antisaccades to the peripheral LED targets. Panel B then shows the latencies for pro- and antisaccades depending on whether the target moved into the right or the left visual hemifield (the mean for the six observers, with the error bars showing the standard error of the mean between subjects).

hemifield which was a possible confound since in both cases we found faster performance when the correct response was to make a saccade into the temporal hemifield (see experiment 2 in Kristjánsson *et al.*, 2004).

Pro- and antisaccades triggered by somatosensory stimulation

There has not been a lot of research into eye movements triggered through somatosensory stimulation. It is clear, however that prosaccades triggered by haptic stimuli have slower latencies than their visually triggered counterparts. Groh and Sparks (1996) used either visual or tactile saccade triggers (vibration applied to posts grabbed by the subject) and observed firstly that the tactile saccades were less accurate than the visually triggered ones, and also had a higher latency. They also observed that the "main sequence" ratio (the relationship between the amplitude and velocity of the saccade) is different for visual and tactile saccades. Neggers & Beckering (1999) also found that the somatosensory saccades were slower than the visually triggered ones. These haptically triggered saccades also tend to be less accurate than visually triggered saccades (Groh & Sparks, 1996; Amlot, Walker, Driver & Spence, 2003; Blanke & Grüsser, 2001). In a further investigation into the competition account of pro- and antisaccades, we decided to contrast pro- and antisaccade performance triggered visually versus when triggered with stimulation through somatosensation. If haptically triggered saccades do not have the same "reflexive" property as visually triggered saccades, then we might not see the standard latency difference normally found between visual pro- and antisaccades for the haptically triggered saccades.

The saccades were either triggered by the appearance of a light (a light emitting diode), or vibration applied to the thumb of the observer (using a magnified sinusoidal signal to Oticon-A bone conductors; see Kristjánsson *et al.*, 2004, experiment 3, for further details). The observers had their thumbs placed right below the two possible landing points for the saccades (see Fig. 6a), so that which thumb was stimulated determined the direction of the saccade (from the center) when a

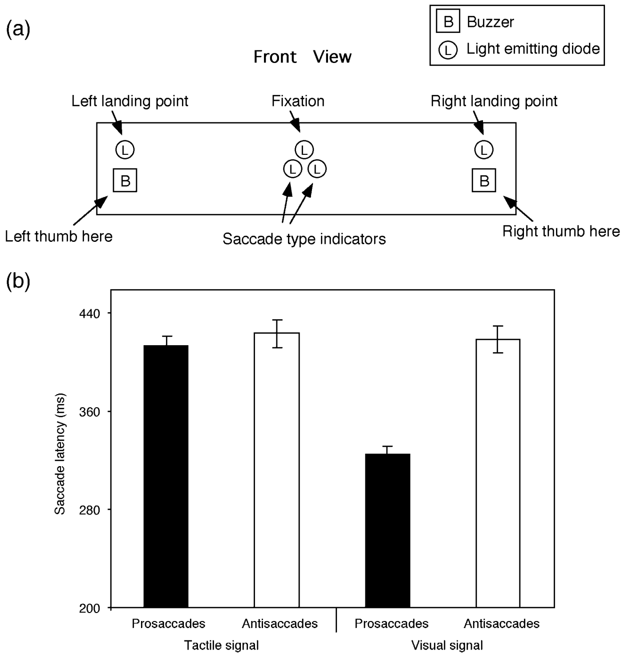

Fig. 6. Pro- and antisaccades triggered by somatosensory and visual stimulation.
Notes: Panel A shows the experimental set-up. There were three LEDs at the center of a panel – the top one was the fixation stimulus while the two right below it indicated whether the task on each trial was to make an antisaccade or prosaccade (depending on which one of them was lit). The saccades were triggered either by vibration applied to the thumb by the "buzzer" or by the lighting of an LED at the right or left of fixation simultaneously with the extinguishing of the fixation LED (see text). Panel B then shows the mean latencies for pro- and antisaccades for visually and haptically cued saccades. The error bars show the standard error of the mean for the six observers.
Source: Adapted from Kristjánsson *et al.* (2004).

haptically triggered saccade occurred (the peripheral LEDs indicated the desired landing point for the visually triggered saccades, see Fig. 6a). The results are presented in Fig. 6b, and show the usual pattern for *visually* triggered pro- and antisaccades. The pattern for the saccades triggered by *somatosensation* was quite unexpected, however. In this case the latencies for the two types of saccade were almost the same; the prosaccades were slightly faster but the difference was very small and not statistically significant.

While the pattern was similar to what we (and others) have seen before for the visually triggered saccades, there was, on the other hand, no difference between latencies for pro- and antisaccades for the somatosensory saccades. What this result suggests is that the antisaccades can be generated just as fast as the prosaccades when the tendency for a prosaccade is sufficiently weakened, as is the case for saccades triggered with tactile stimulation. This general pattern of results is, of course, consistent with there being competing pathways for pro- and antisaccade generation, and in general the competition account presented in Fig. 1. More generally, it also seems that haptically triggered prosaccades are simply not "reflexive" in the same sense as visually triggered saccades, which is in line with the studies mentioned above (Groh & Sparks, 1996; Neggers & Bekkering, 1999; Amlot *et al.*, 2003). This may be because a similar capture of attention doesn't occur as for visual target stimuli. There is simply no *haptic* counterpart to the *visuo*-motor grasp reflex.

The effect of the variation of contrast of target against background upon pro- and antisaccade performance

Prosaccades tend to be faster to higher contrast targets, other things being equal (Doma & Hallett 1988a, 1988b; Reuter-Lorenz, Hughes & Fendrich, 1991; Groh & Sparks 1996). Furthermore, Doma and Hallett (1988a) showed that under *photopic* luminance levels (under which both types of photoreceptors, rods and cones can operate) the well-known pattern of slower and less accurate antisaccades than prosaccades holds, while under *scotopic* luminance levels where light levels are so low that only rod vision is operative, this difference is not seen anymore. It seems, then, that under scotopic luminance levels, the prosaccade reflex may be nonexistent or severely disrupted. Related to this, it has been found that saccade latencies are shorter to achromatic targets than to chromatic targets (Satgunam & Fogt, 2005; Perron & Hallett, 1995). Satgunam & Fogt not only showed that saccade latencies are longer for isoluminant chromatic targets (differing only in *chromatic* contrast from the background), but they were also able to use a psychophysical procedure to ensure that the two contrasts (luminance and chromatic) were approximately equivalent, which gave the same result. This result suggests that the achromatic system has a superior temporal response compared with the achromatic system.

In Kristjánsson *et al.* (2004), we investigated what the latencies of pro- and antisaccades would be, in response to visual triggers of variable saliency in the visual field. More specifically, we measured pro- and antisaccade performance under different contrast levels of the target against the background. We reasoned that if prosaccades are overall faster to targets of higher contrast against the background we might see the opposite pattern for the antisaccades if a greater prosaccade reflex needs to be overcome. In our experiment, we varied the contrast of the visual trigger stimulus against the background and measured pro- and antisaccade performance of our observers. The results can be seen in Fig. 7. As can be seen in the figure, prosaccades are faster as the contrast of the target against the background is increased, while antisaccades are slower. This is consistent with the competition account – as the reflex is less strong (as the target/background contrast is decreased), antisaccades can occur faster. At the lowest contrast level, however, the pattern is different, in particular for the antisaccades. Here, both types of saccade are quite significantly slowed, compared to the other conditions. It seems that when the target is sufficiently difficult to register (or registers relatively slowly; in this case because of low contrast) latencies for both types of saccades are greatly affected. This may be because the contrast is too low to activate the achromatic system which is necessary for low saccade latencies as suggested by the results of the aforementioned studies (Doma & Hallett, 1988a; 1988b; Perron & Hallett, 1995; Satgunam & Fogt, 2005).

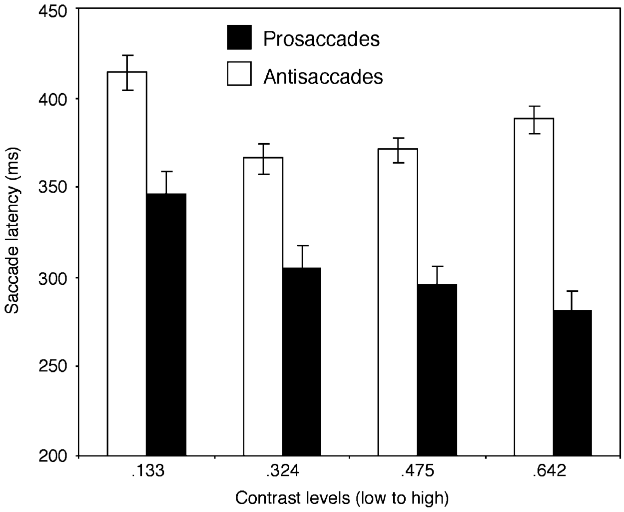

Fig. 7. Saccade latencies for pro- and antisaccades a function of the contrast of the saccade target against the background (see text, and Kristjánsson *et al.*, 2004 for details).
Notes: The figure shows the mean latencies for 6 observers and the error bars represent the standard error of the mean.

Pro and antisaccades with, and without, a central warning sound

The effect of alerting observers before a particular response is made has been known for a long time. Posner (1978) showed that a warning sound can speed reaction times in various tasks (see also Posner & Petersen, 1990). Taylor, Klein and Munoz (1999) showed that a gap effect-like pattern could occur for "fixated" (in other words monitored) auditory stimuli presented concurrently with an eye movement task. The pattern of results was similar to that found for fixated visual stimuli (such as in the "gap effect" reviewed above) in that if the monitored sound was extinguished before the saccade target was presented, the saccades were faster.

In Kristjánsson *et al.* (2004), we examined what the effects of a non-spatial warning signal would be upon pro- and antisaccades. We asked what the effect of a non-spatial auditory warning signal on pro- and antisaccade performance would be (non-spatial in the sense that the sound was presented through a central speaker, and did not preferentially cue the location of either of the two possible landing points for the saccades). Our observers performed the traditional pro- and antisaccade task, under two conditions, either preceded by 200 ms by a relatively loud warning sound presented centrally through a speaker placed in front of the screen that the stimuli appeared on, or unaccompanied by a sound.

Our question was what the effect of a simple auditory warning sound would be on prosaccade and antisaccade performance. We compared performance with the auditory warning signal with performance when *no* warning signal was presented – in other words, when only the saccade trigger stimuli were presented on the screen.

The results for the task performed with the auditory warning signal were similar for both pro- and antisaccades (see Fig. 8). Both the pro- and antisaccades were speeded up relative to when no warning tone was presented. This, most likely, means that the central warning sound exerts its influence on a neural pathway that is *common* to the two types of saccade. A *general* speed-up of performance, common to the two types of saccade seems to occur with the non-spatial warning sound. In other words, the influence is exerted at a stage that probably does *not involve competition* between pro- and antisaccades, perhaps a more general alerting mechanism, and if so, the alerting mechanism does not produce a benefit for either type of saccade over the other, so that one or the other type is slowed.

This result indicates that a warning stimulus appears not to exert its effect at the level of competition between pro- and antisaccades – which is consistent with the results from the gap paradigm (if one can conceive of the gap as one form of a warning signal in this context) which results in rather similar effects for pro- and antisaccades (Munoz & Everling, 2004), although the pattern is not quite identical (cf. Fischer & Weber, 1997). Kirchner and Colonius (2004; 2005) have then recently shown that auditory cues can speed up prosaccades (Kirchner & Colonius, 2004) and antisaccades (Kirchner & Colonius, 2005) irrespective of whether they were opposite to, or coincident with the saccade landing point, which again suggests that the auditory sounds indeed serves as a *general* warning signal (see also Colonius & Arndt, 2001; Corneil & Munoz, 1996).

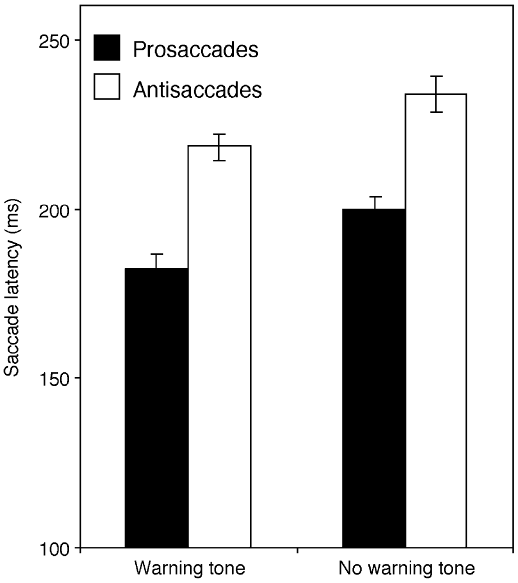

Fig. 8. Pro- and antisaccade performance along with a preceding warning sound (by 200 ms; bars to the left) and without a warning sound (bars to the right).
Notes: The bars show the mean latencies for six observers, and the error bars show the standard error of the mean (adapted from Kristjánsson *et al.*, 2004).

GENERAL DISCUSSION

We all know that it is often hard to look in the other direction when something interesting appears in our visual environment, or as in the case of the current studies, something behaviorally relevant appears. Research on such stimulus-response incompatibility has a long history. The general finding is indeed that when the required response is in conflict in some way with the stimulus triggering the response, performance is worse than otherwise. For example, we would expect observers to respond slower if they are asked to press a blue button in response to a red stimulus and a red button in response to a blue stimulus than if the stimulus and response mapping is more logical (red button press in response to a red stimulus and so on). Simon and Ruddell (1967; see also Simon & Small, 1969) presented a word (e.g. "right") to either ear of a subject and required subjects to press a response key located to the subjects left or right in congruence with the meaning of the word. Reaction times were shorter and accuracy greater when the mapping between stimulus and response was congruent (i.e. when the rightwards key should be pressed in response to the word "right") than when they were incongruent. Similarly it has often been found that with tasks that require spatial responses to spatial stimuli that a logical stimulus response mapping (e.g. a "right" response to a right target) is performed more easily and faster than one with a less logical, incongruent stimulus response mapping (Proctor & Vu, 2002). Similar results have been observed with congruent versus incongruent stimulus response mapping based on color by Hedge and Marsh (1975). Such effects have come under the blanket term of the "Simon" effect (see Hasbroucq & Guiard, 1991 and Valle-Inclán, Hackley & de Labra, 2002 for reviews). Another well-known example of effects involving stimulus response incongruence is the Stroop effect (Stroop, 1935) where naming the color of the ink of letters in a word is slowed if the word is the name of a different color, or the time taken to count how many digits are presented is slowed if the individual digits themselves represent a different number than the total number of digits presented. An automatic response like reading the presented word or registering the presented digit is simply extremely hard to overcome and ignore, and slows performance on the secondary task (naming the color of the ink). Related to this pattern is the finding that if observers need to perform the same task for a number of times in a row (like for example search for a target of a particular color among distractors of a different color) responses are greatly slowed if the distractors become the target (Maljkovic & Nakayama, 1994; Kristjánsson, Wang & Nakayama, 2002; see Kristjánsson, 2006 and Fecteau & Munoz, 2003, for reviews).

Similar logic, as has been reviewed above about how hard it can be to overcome a prepotent response, has indeed been used to explain the slowing of antisaccades relative to prosaccades. Observers simply find it very hard not to "follow" the target, rather than saccade away from it, when they are getting ready to make a saccade and the appearance of the target is the task defining event.

Such effects can provide important insights into how the human nervous system operates, and coupled with neurophysiological studies of humans and other animals on the neural processes and mechanisms that are involved, we can potentially learn much about how the brain handles contradictory and conflicting information, and how contradictory motor movements are encoded in the brain and produced by the motor areas of the nervous system (see, e.g., Kristjánsson, 2006; Nakayama, Maljkovic & Kristjánsson, 2004; Fecteau & Munoz, 2003), and ultimately achieve more general insights into how the brain and its visual system operate.

In this review I have presented evidence from a number of diverse paradigms for the competition account of pro- and antisaccade generation, showing how antisaccades are speeded up approximately to the extent that prosaccades are slowed down. This, however, does not occur under all conditions. In Kristjánsson *et al.* (2004) we put forth the conjecture that this will need to happen under conditions that influence the locus of competition – a pathway of competition, not a pathway that influences both processes similarly. In Kristjánsson *et al.* (2001) we also hypothesized that time can be a critical variable in this respect – if a secondary task (as used in that paper) is presented simultaneously to, or right after, the saccade trigger moves, this competition advantage for one or the other type does not apply and both saccade types are slowed relative to their baselines.

Perspectives from neurophysiology

Single cell studies of the monkey brain as well as neuroimaging on humans has provided important insights into what mechanisms are involved when an antisaccade is generated (Kustov & Robinson, 1996; Schlag-Rey *et al.*, 1997; Funahashi *et al.*, 1993; Everling, Dorris, Klein & Munoz, 1999; see, e.g., Munoz & Everling, 2004 for a review).

As mentioned in the introduction, evidence from many diverse paradigms indicates that when saccades are made, attention plays a key role in the process and that attention shifts to the location of an upcoming saccade before the saccade lands there (e.g. Deubel & Schneider, 1996; Kowler *et al.* 1996; Hoffman & Subramaniam, 1995; Shepherd *et al.*, 1986; Kristjánsson *et al.*, 2001). These studies, however, have not answered completely some of the details of how this might occur. For example, does the saccade plan precede the attention shift and cause it (the so-called "premotor" conception of attention; see, e.g., Rizzolatti *et al.*, 1987), or do observers simply shift their attention to saccade target locations (e.g. Posner, Snyder & Davidson, 1980) or are the two in essence unrelated, i.e. both covert attention and saccade plans can affect visual performance, but in separate ways and the observed pattern of results simply reflects correlation rather than causation.

In any case, evidence from neurophysiology indicates that the neural mechanisms for saccades and attention shifts overlap to a considerable extent (Kustov & Robinson, 1996) and that key regions in eye movement production also play a large role in attention shifts (Corbetta & Shulman, 2002; Hopfinger; Buonocore & Mangun, 2000; Yantis & Serences, 2003; Kristjánsson *et al.*, 2006; Labar, Gitelman, Parrish & Mesulam, 1999; Awh & Jonides, 2001; Culham, Cavanagh & Kanwisher, 2001; Jovicich, Peters, Koch, Braun, Chang & Ernst, 2001). Much evidence suggests that the neural activity triggered by visual stimuli corresponds to the allocation of visual attention as well as eye movements (Kustov & Robinson, 1996, but see Thompson, Bichot & Schall, 1997). The thesis that an attention shift *always* entails a plan for a saccadic eye movement towards the locus of attention (e.g. Schneider & Deubel, 2002; Rizzolatti *et al.*, 1987) has however, recently come under some criticism from single cell research on the macaque monkey that shows that neural mechanisms exist in the frontal eye fields for covert selection without that activity reflecting a plan for a saccade (Schall, 2004; Juan *et al.*, 2004).

As mentioned before, the frontal eye fields (FEF) in the prefrontal cortex are a key region in the cerebral cortex in the generation of saccadic eye movements. The FEF play a role in transferring visual information into an orienting response. The superior colliculi in the midbrain also play a key role in the generation of saccades. Both the FEF and the SC have projections to brainstem regions that control the generation of saccades (Sparks, 2002), and both contain so-called *fixation* neurons that show tonic activity throughout the fixation period and *saccade burst* neurons that give short bursts of activity when a saccade is generated, as was previously mentioned (see e.g. Edelman & Keller, 1996; 1998; Everling *et al.*, 1999; Everling & Munoz, 2000).

Furthermore, the supplementary eye fields (SEF) of the prefrontal cortex play a key role in antisaccade generation, and it has been shown that neurons in that region fire more before an antisaccade is generated than a prosaccade (Schlag-Rey *et al.*, 1997) and activity in the SEF is correlated with goal-directed and purposeful eye movements but not with spontaneous, or reflexive saccades (Schall, 1991).

Neuroimaging in humans with PET and fMRI has also shown that the FEF and SEF are key regions in antisaccade generation and are in general more highly activated for antisaccades than for prosaccades (Connolly *et al.*, 2002; O'Driscoll, Alpert, Matthysse, Levy, Rauch & Holzman, 1995). It has, for example, been shown that activity as measured by fMRI shows a negative correlation with saccadic reaction times (increased FEF fMRI activity is correlated with decreased prosaccade latency; Connolly, Goodale, Goltz & Munoz, 2005). Dorsolateral prefrontal cortex in right hemisphere has been clearly indicated, as well, as a key region in the generation of antisaccades (Matsuda *et al.*, 2004; DeSouza *et al.*, 2002; see also Connolly *et al.*, 2002).

The FEF and SEF in the prefrontal cortex have been thought to play a major role (perhaps along with the lateral intraparietal area in parietal cortex) in the voluntary generation of saccades (Dorris, Pare & Munoz, 1997; Goldberg & Bushnell, 1981; Guitton *et al.*, 1985; Schiller, Sandell & Maunsell, 1987; Chen & Wise, 1995; Bruce & Goldberg, 1985; Schall, 1991; Munoz & Everling, 2004) while the SC may to a greater degree be responsible for reflexive saccades (Leigh & Zee, 1999; Edelman & Keller, 1996; Munoz & Everling, 2004). Activity in the SEF in particular seems *not* to be related to reflexive saccades, and SEF neurons seem to respond more vigorously before antisaccades than prosaccades (Schlag-Rey *et al.*, 1997) and show activity that is correlated with goal directed, purposeful eye movements (Schall, 1991), which has also been supported in fMRI studies of human observers (Connolly *et al.*, 2002).

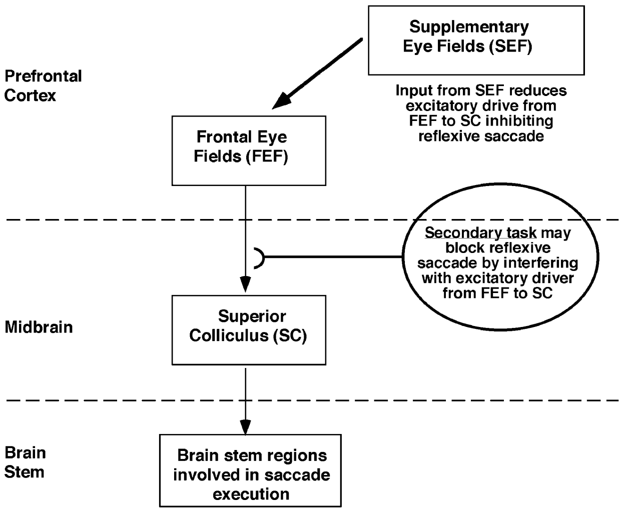

Fig. 9. A schematic of the key brain regions involved in pro- and antisaccade execution along with a proposal of how the speed-up of antisaccades may occur at the neural level, in the experimental paradigm used in Kristjánsson *et al.* (2001a) by attenuating excitatory input from the Frontal Eye Fields to the Superior Colliculus. *Note*: It is also thought that projections from the SEF contribute an inhibitory signal to the FEF when an antisaccade is generated. Neurons in the SEF show a higher rate of firing before antisaccades are generated than prosaccades (Schlag-Rey *et al.*, 1997).

A tentative proposal that I want to put forth here is that the SEF activity in the antisaccade task, revealed by the studies of Schlag-Rey *et al.* (and others) reflects the generation of a signal from the SEF that counteracts signals from the FEF for the generation of the prosaccade that would otherwise be generated. The inhibition of the prosaccade may be accomplished by the reduction of excitatory input from the FEF to the SC (Everling & Munoz, 2000; Everling *et al.*, 1999), along the lines that I have previously proposed (in Kristjánsson *et al.*, 2001a). Consistent with this, the activity of a set of neurons in SC differs according to whether a pro- or antisaccade is to be made (Everling *et al.*, 1999). If it is true that the stronger the reflex for prosaccade, the likelihood that the prosaccade will be successfully inhibited is lessened (and it becomes easier to "override" the inhibitory signal from the SEF) it is possible that as the reflex is inhibited (as I have argued occurs when a secondary task is presented along with the saccade stimulus, as in many of the experimental manipulations discussed in this review), this inhibitory signal from the SEF is more successful in inhibiting the reflex, allowing the antisaccade to be generated more quickly, since less resources are required for the suppression of the prepotent response to the saccade triggering event. Figure 9 presents this tentative conception of the relationship between pro- and antisaccades, especially as they relate to the manipulations in the paradigms used in this paper, in particular the dual-task experiments of Kristjánsson *et al.* (2001a; see also Mitchell *et al.*, 2002; Pashler *et al.*, 1993; Stuyven *et al.*, 2000). This conception could explain the speed-up of antisaccades in Kristjánsson *et al.* (2001a), as well as the fact that as the reflex for a prosaccade is attenuated, antisaccades tend to occur sooner, as shown in the experiments presented in Kristjánsson *et al.* (2004). My proposal entails that the processes for pro- and antisaccades are concurrently ongoing, in other words that the two are processed in parallel (see also Massen, 2004; Mokler & Fischer, 1999). Related to this is the "gap effect", since it involves disengagement from the fixation point. The early peak seen in the latency distributions of experiments on the gap effect may be indicative of the visual-grasp reflex. Research on antisaccades with the gap-effect has indeed revealed speeded saccades as in the prosaccade gap paradigm, but these tend to be in the wrong direction (e.g. Munoz & Everling, 2004). What this may mean is that if a strong visual grasp reflex occurs for one reason or another, prosaccades occur regardless of the observer's intentions, and this occurs because the two processes take place in parallel, although it should be noted that speed-accuracy trade-offs reflected in the observer's strategy in each case (whether the observer's goal in each case is to perform the task as accurately or as quickly as possible) can, most likely, have a decisive influence here.

CONCLUSIONS

When an antisaccade is generated one can conceive of two ongoing processes – a prosaccade process that is triggered automatically with the onset of the stimulus as well as a process for antisaccade generation. The evidence that I have presented here suggests that the two processes compete and has generally supported this competition model. The general pattern is that as prosaccades become faster, antisaccades are slowed, and as the prosaccades are slowed, antisaccades are speeded up, although this does not occur under all conditions as shown in the experiment where a non-spatial auditory warning signal preceded the saccade trigger. This seems, then, to be a classic trade-off situation. If conditions exist where the prosaccades are in general faster, a stronger reflex for making the prosaccade needs to be overcome, which may in turn slow the antisaccades (Kristjánsson *et al.*, 2001a; Munoz & Everling. 2004). In the converse situation where no strong reflex occurs, antisaccades can be generated faster on average.

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NOTE

[1] Note that the speed-ups observed in Kristjánsson *et al.* (2001) could not be explained in terms of a speed-accuracy trade-off. The speed-ups were not accompanied by an increase in error rates. This was also the case for the experiments presented here from Kristjánsson *et al.* (2004).

REFERENCES

Amador, N., Schlag-Rey, M. & Schlag, J. (1998). Primate antisaccades. I. Behavioral characteristics. *Journal of Neurophysiology*, *80*, 1775–1786.

Amlot, R., Walker, R., Driver, J. & Spence, C. (2003). Multimodal visual-somatosensory integration in saccade generation. *Neuropsychologia*, *41*, 1–15.

Awh, E. & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, *5*, 119–126.

Bahcall, D. O. & Kowler, E. (2000). The control of saccadic adaptation: Implications for the scanning of natural visual scenes. *Vision Research*, *40*, 2779–2796.

Bichot, N. P. & Schall, J. D. (1999). Effects of similarity and history on neural mechanisms of visual selection. *Nature Neuroscience*, *2*, 549–554.

Blanke, O. & Grüsser, O. (2001). Saccades guided by somatosensory stimuli. *Vision Research*, *41*, 2407–2412.

Bruce, C. J. & Goldberg, M. E. (1985). Primate frontal eye fields. I. Single neurons discharging before saccades. *Journal of Neurophysiology*, *53*, 603–635.

Cairney, S., Maruff, P., Vance, A., Barnett, R., Luk, E. & Currie J. (2001). Contextual abnormalities of saccadic inhibition in children with attention deficit hyperactivity disorder. *Experimental Brain Research*, *141*, 507–518.

Carrasco, M., Williams, P. E. & Yeshurun, Y. (2002). Covert attention increases spatial resolution with or without masks: Support for signal enhancement. *Journal of Vision*, *2*, 467–479.

Chen, Y., McPeek, R., Intriligator, J., Kristjánsson, A., Mednick, S. Holzman, P. & Nakayama, K. (1999). Attentional requirements for smooth pursuit. *Investigative Ophthalmology and visual Science*, *40*(suppl.), 2011.

Chen, L. L. & Wise, S. P. (1995). Neuronal activity in the supplementary eye field during acquisition of conditional oculomotor associations. *Journal of Physiology*, *73*, 1101–1121.

Colonius, H. & Arndt, P. (2001). A two-stage model for visual-auditory interaction in saccadic latencies. *Perception & Psychophysics*, *63*, 126–147.

Connolly, J. D., Goodale, M. A., Goltz, H. C. & Munoz D. P. (2005). fMRI activation in the human frontal eye field is correlated with saccadic reaction time. *Journal of Neurophysiology*, *94*, 605–611.

Connolly, J. D., Goodale, M. A., Menon, R. S. & Munoz, D. P. (2002). Human fMRI evidence for the neural correlates of preparatory set. *Nature Neuroscience*, *5*, 1345–1352.

Corbetta, M. & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.

Corneil, B. D. & Munoz, D. P. (1996). The influence of auditory and visual distractors on human orienting gaze shifts. *Journal of Neuroscience*, *16*, 8193–8207.

Crawford, T. J. & Muller, H. J. (1992). Spatial and temporal effects of spatial attention on human saccadic eye movements. *Vision Research*, *32*, 293–304.

Crevits, L. & De Ridder, K. (1997). Disturbed striatoprefrontal mediated visual behaviour in moderate to severe parkinsonian patients. *Journal of Neurology, Neurosurgery & Psychiatry*, *63*, 296–299.

Culham, J. C., Cavanagh, P. & Kanwisher, N. G. (2001). Attention response functions: Characterizing brain areas using fMRI activation during parametric variations of attentional load. *Neuron*, *32*, 737–745.

Currie, J., Ramsden, B., McArthur, C. & Maruff, P. (1991). Validation of a clinical antisaccadic eye movement test in the assessment of dementia. *Archives of Neurology*, *48*, 644–648.

DeSouza, J. F., Menon, R. S. & Everling, S. (2003). Preparatory set associated with pro-saccades and anti-saccades in humans investigated with event-related FMRI. *Journal of Neurophysiology*, *89*, 1016–1023.

D'Esposito, M. & Postle, B. R. (2002). The organization of working memory function in lateral prefrontal cortex: Evidence from event-related functional MRI. In D. T. Stuss & R. T. Knight, *Principles of frontal lobe function* (pp. 168–187). New York: Oxford University Press.

Deubel, H. & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*, 1827–1837.

Doma, H. & Hallett, P. E. (1988a). Rod-cone dependence of saccadic eye movement latency in a foveating task. *Vision Research*, *28*, 899–913.

Doma, H. & Hallett, P. E. (1988b). Dependence of saccadic eye movements on stimulus luminance, and an effect of task. *Vision Research*, *28*, 915–924.

Dorris, M. C., Munoz, D. P. (1995). A neural correlate for the gap effect on saccadic reaction times in monkey. *Journal of Neurophysiology*; *73*, 2558–2562.

Dorris, M. C., Pare, M. & Munoz, D. P. (1997). Neuronal activity in monkey superior colliculus related to the initiation of saccadic eye movements. *Journal of Neuroscience*, *17*, 8566–8579.

Edelman, J. A. & Keller, E. L. (1996). Activity of visuomotor burst neurons in the superior colliculus accompanying express saccades. *Journal of Neurophysiology*, *76*, 908–926.

Edelman, J. A. & Keller, E. L. (1998). Dependence on target configuration of express saccade-related activity in the primate superior colliculus. *Journal of Neurophysiology*, *80*, 1407–1426.

Edelman, J., Kristjánsson, Á. and Nakayama, K. (2001). Facilitation of saccade target selection by object-centered priming. *Journal of Vision*, *1*(Suppl.), 238.

Everling, S., Dorris, M. C., Klein, R. M. & Munoz, D. P. (1999). Role of primate superior colliculus in preparation and execution of anti-saccades and pro-saccades. *Journal of Neuroscience*, *19*, 2740–2754.

Everling, S., Dorris, M. C. & Munoz, D. P. (1998). Reflex suppression in the antisaccade task is dependent on prestimulus neural processes. *Journal of Neurophysiology*, *80*, 1584–1589

Everling, S. & Fischer, B. (1998). The antisaccade: A review of basic research and clinical studies. *Neuropsychologia*, *36*, 885–899.

Everling, S. & Munoz, D. P. (2000). Neuronal correlates for preparatory set associated with pro-saccades and anti-saccades in the primate frontal eye field. *Journal of Neuroscience*, *20*, 387–400.

Fecteau, J. H. & Munoz, D. P. (2003). Exploring the consequences of the previous trial. *Nature Reviews Neuroscience*, *4*, 435–443.

Fischer, B. & Boch, R. (1983). Saccadic eye movements after extremely short reaction times in the monkey. *Brain Research*, *260*, 21–26.

Fischer, B. & Breitmeyer, B. (1987). Mechanisms of visual attention revealed by saccadic eye movements. *Neuropsychologia*, *25*, 73–83.

Fischer, B. & Weber, H. (1993). Express saccades and visual attention. *Behavioral & Brain Sciences*, *16*, 553–567.

Fischer, B. & Weber, H. (1997). Effects of stimulus conditions on the performance of antisaccades in man. *Experimental Brain Research*, *116*, 191–200.

Fischer, B. & Weber, H. (1998). Effects of pre-cues on voluntary and reflexive saccade generation. I. Anti-cues for pro-saccades. *Experimental Brain Research*, *120*, 403–416.

Folk, C. L. & Remington, R. (1999). Can new objects override attentional control settings? *Perception & Psychophysics*, *61*, 727–739.

Forbes, K. & Klein, R. M. (1996). The magnitude of the fixation offset effect with endogenously and exogenously controlled saccades. *Journal of Cognitive Neuroscience*, *8*, 344–352.

Fukushima, J., Fukushima, K., Chiba, T., Tanaka, S., Yamashita, I. & Kato, M. (1988). Disturbances of voluntary control of saccadic eye movements in schizophrenic patients. *Biological Psychiatry*, *23*, 670–677.

Fukushima, J., Morita, N., Fukushima, K., Chiba, T., Tanaka, S. & Yamashita, I., (1990). Voluntary control of saccadic eye movements in patients with schizophrenic and affective disorders. *Journal of Psychiatric Research*, *24*, 9–24.

Fukushima, J., Fukushima, K., Miyasaka, K. & Yamashita I. (1994). Voluntary control of saccadic eye movement in patients with frontal cortical lesions and Parkinsonian patients in comparison with that in schizophrenics. *Biological Psychiatry*, *36*, 21–30.

Funahashi, S., Chafee, M. V. & Goldman-Rakic, P. S. (1993). Prefrontal neuronal activity in rhesus monkeys performing a delayed antisaccade task. *Nature*, *365*, 753–756.

Godijn, R. & Pratt, J. (2002). Endogenous saccades are preceded by shifts of visual attention: Evidence from cross-saccadic priming effects. *Acta Psychologica (Amsterdam)*, *110*, 83–102.

Goldberg, M. E. (2000). The control of gaze. In E. Kandel, J. H. Schwartz & T. M. Jessel (Eds.) *Principles of neural science* (4th edn, pp. 782–800), New York: McGraw-Hill.

Goldberg, M. E. & Bushnell, M. C. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. *Journal of Neurophysiology*, *46*, 773–787.

Goldman-Rakic, P. S. & Leung, H. (2002). Functional architecture of the dorsolateral prefrontal cortex in monkeys and humans. In D. T. Stuss & R. T. Knight, *Principles of frontal lobe function* (pp. 85–95). New York: Oxford University Press.

Groh, J. M. & Sparks, D. L. (1996). Saccades to somatosensory targets. I. Behavioral characteristics. *Journal of Neurophysiology*, *75*, 412–427.

Guitton, D., Buchtel, H. A. & Douglas, R. M. (1985). Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal directed saccades. *Experimental Brain Research*, *58*, 455–472.

Hallett, P. E. (1978). Primary and secondary saccades to goals defined by instructions. *Vision Research*, *18*, 1279–1296.

Hallett, P. E. & Adams, B. D. (1980). The predictability of saccadic latency in a novel voluntary oculomotor task. *Vision Research*, *20*, 329–339.

Hasbroucq, T. & Guiard, Y. (1991). Stimulus response compatibility and the Simon effect: Toward a conceptual clarification. *Journal of Experimental Psychology: Human Perception & Performance*, *17*, 246–266.

He, P. Y. & Kowler, E. (1989). The role of location probability in the programming of saccades: implications for "center-of-gravity" tendencies. *Vision Research*, *29*, 1165–1181.

Henik, A., Rafal, R. & Rhodes, D. (1994). Endogenously generated and visually guided saccades after lesions of the human frontal eye fields. *Journal of Cognitive Neuroscience*, *6*, 400–411.

Hedge, A. & Marsh, N. W. A. (1975). The effects of irrelevant spatial correspondences on two-choice response time. *Acta Psychologica*, *39*, 427–439.

Hoffman, J. E. & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, *57*, 787–795.

Hopfinger, J. B., Buonocore, M. H. & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*, 284–291.

Jovicich, J., Peters, R. J., Koch, C., Braun, J., Chang, L. & Ernst, T. (2001). Brain areas specific for attentional load in a motion-tracking task. *Journal of Cognitive Neuroscience*, *15*, 1048–1058.

Juan, C. H., Shorter-Jacobi, S. M. & Schall, J. D. (2004). Dissociation of spatial attention and saccade preparation. *Proceedings of the National Academy of Sciences*, *101*, 15541–15544.

Khurana, B. & Kowler, E. (1987). Shared attentional control of smooth eye movement and perception. *Vision Research*, *27*, 1603–1618.

Kirchner, H. & Colonius, H. (2004). Predictiveness of a visual distractor modulates saccadic responses to auditory targets. *Experimental Brain Research*, *155*, 257–260.

Kirchner, H. & Colonius, H. (2005). Cognitive control can modulate intersensory facilitation: Speeding up visual antisaccades with an auditory distractor. *Experimental Brain Research*, *166*, 440–444.

Kowler, E., Anderson, E., Dosher B. & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*, 1897–1916.

Krappmann, P., Everling, S. & Flohr, H. (1998). Accuracy of visually and memory-guided antisaccades in man. *Vision Research*, *38*, 2979–2985.

Krauzlis, R. J. (2004). Recasting the smooth pursuit eye movement system. *Journal of Neurophysiology*, *91*, 591–603.

Kristjánsson, Á. (2006). Rapid learning in attention shifts – a review. *Visual Cognition*, *13*, 324–362.

Kristjánsson, Á., Chen, Y. & Nakayama, K. (2001a). Less attention is more in the preparation of antisaccades, but not prosaccades. *Nature Neuroscience*, *4*, 1037–1042.

Kristjánsson, Á., Mackeben, M. & Nakayama, K. (2001b). Rapid, object-based learning in the deployment of transient attention. *Perception*, *30*, 1375–1387.

Kristjánsson Á. & Nakayama, K. (2002). The attentional blink in space and time. *Vision Research*, *42*, 2039–2050.

Kristjánsson, Á. & Nakayama, K. (2003). A primitive memory system for the deployment of transient attention. *Perception & Psychophysics*, *65*, 711–724.

Kristjánsson, Á., Vandenbroucke, M. W. & Driver, J. (2004). When pros become cons for anti-versus prosaccades: Factors with opposite or common effects on different saccade types. *Experimental Brain Research*, *155*, 231–244.

Kristjánsson, Á., Vuilleumier, P., Schwarz, S., Macaluso, E. & Driver, J. (2006). Neural basis for priming of pop-out during visual search revealed with fMR1. *Cerebral Cortex*, doi: 10.1093/cercor/bhl072

Kristjánsson, Á., Wang, D. & Nakayama, K. (2002). The role of priming in conjunctive visual search. *Cognition*, *85*, 37–52.

Kustov, A. A. & Robinson, D. L. (1996). Shared neural control of attentional shifts and eye movements. *Nature*, *384*, 74–77.

LaBar, K. S., Gitelman, D. R., Parrish, T. B. & Mesulam, M. (1999). Neuroanatomic overlap of working memory and spatial attention networks: A functional MRI comparison within subjects. *Neuroimage*, *10*, 695–704.

Leigh, R. J. & Zee, D. S. (1999). *The neurology of eye movements* (3rd edn). Oxford: Oxford University Press.

Maljkovic, V. & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition*, *22*, 657–672.

Maruff, P., Purcell, R., Tyler, P., Pantelis, C. & Currie, J. (1999). Abnormalities of internally generated saccades in obsessive-compulsive disorder. *Psychological Medicine*, *9*, 1377–1385.

Massen, C. (2004). Parallel programming of exogenous and endogenous components in the antisaccade task. *Quarterly Journal of Experimental Psychology A*, *57*, 475–498.

Matsuda, T., Matsuura, M., Ohkubo, T., Ohkubo, H., Matsushima, E., Inoue, K., Taira, M. & Kojima, T. (2004). Functional MRI mapping of brain activation during visually guided saccades and antisaccades: Cortical and subcortical networks. *Psychiatry Research*, *131*, 147–155.

McLaughlin, S. C. (1967). Parametric adjustment in saccadic eye movements. *Perception and Psychophysics*, *2*, 359–361.

Mitchell, J. P., Macrae, C. N. & Gilchrist I. D. (2002). Working memory and the suppression of reflexive saccades. *Journal of Cognitive Neuroscience*, *14*, 95–103.

Mokler, A. & Fischer, B. (1999). The recognition and correction of involuntary prosaccades in an antisaccade task. *Experimental Brain Research*, *125*, 511–516.

Most, S. B., Simons, D. J., Scholl, B. J., Jimenez, R., Clifford, E. & Chabris, C. F. (2001). How not to be seen: The contribution of similarity and selective ignoring to sustained inattentional blindness. *Psychological Science*, *12*, 9–17.

Munoz, D. P., Armstrong, I. T., Hampton, K. A., Moore, K. D. (2003). Altered control of visual fixation and saccadic eye movements in attention-deficit hyperactivity disorder. *Journal of Neurophysiology*, *90*, 503–514.

Munoz, D. P. & Everling, S. (2004). Look away: The anti-saccade task and the voluntary control of eye movement. *Nature Reviews Neuroscience*, *5*, 218–228.

Munoz, D. P. & Wurtz, R. H. (1995a). Saccade-related activity in monkey superior colliculus. I. Characteristics of burst and build-up cells. *Journal of Neurophysiology*, *73*, 2313–2333.

Munoz, D. P. & Wurtz, R. H, (1995b). Saccade-related activity in monkey superior colliculus. II. Spread of activity during saccades. *Journal of Neurophysiology*, *73*, 2334–2348.

Müri, R., Gaymard, B., Rivaud, S., Vermersch, A. I., Hess, C. W. & Pierrot-Deseilligny, C. (2000). Hemispheric asymmetry in cortical control of memory-guided saccades: A transcranial magnetic stimulation study. *Neuropsychologia*, *38*, 1105–1111.

Nakayama, K. and Mackeben, M. (1989). Sustained and transient components of visual attention. *Vision Research*, *29*, 1631–1647.

Nakayama, K., Maljkovic, V. & Kristjánsson, Á. (2004). Short term memory for the rapid deployment of visual attention. In M. Gazzaniga (Ed.), *The cognitive neurosciences*, III (pp. 397–406). Cambridge, MA: MIT Press.

Neggers, S. W. F. & Bekkering, H. (1999). Integration of visual and somatosensory target information in goal-directed eye and arm movements. *Experimental Brain Research*, *125*, 97–107.

Neisser, U. (1967). *Cognitive psychology*. New York: Appleton-Century-Crofts.

Neisser, U. & Becklen, R. (1975). Selective looking: Attending to visually specified events. *Cognitive Psychology*, *7*, 480–494.

O'Driscoll, G. A., Alpert, N. M., Matthysse, S. W., Levy, D. L., Rauch, S. L. & Holzman, P. S. (1995). Functional neuroanatomy of antisaccade eye movements investigated with positron emission tomography. *Proceedings of the National Academy of Sciences*, *92*, 925–929.

Pashler, H. (1998). *The psychology of attention*. Cambridge, MA: The MIT Press.

Pashler, H., Carrier, M. & Hoffman, J. (1993). Saccadic eye movements and dual-task interference. *Quarterly Journal of Experimental Psychology A*, *46*, 51–82.

Perron, C. & Hallett, P. E. (1995). Saccades to large coloured targets stepping in open fields. *Vision Research*, *35*, 263–74.

Posner, M. I. (1978). *Chronometric explorations of mind*. Hillsdale: Erlbaum.

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.

Posner, M. I. & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.

Posner, M. I., Snyder, C. R. R. & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, *109*, 160–174.

Proctor, R. W. & Vu, K. L. (2002). Eliminating, magnifying and reversing spatial compatibility effects with mixed location-relevant and irrelevant trials. In W. Prinz & B. Hommel (Eds.), *Common Mechanisms in Perception and Action: Attention and Performance* XIX (pp. 443–473). New York: Oxford University Press.

Rafal, R., Henik, A. & Smith, J. (1991). Extrageniculate contributions to reflex visual orienting in normal humans: A temporal hemifield advantage. *Journal of Cognitive Neuroscience*, *3*, 322–328.

Rashbass, C. (1961). The relationship between saccadic and smooth tracking eye movements. *Journal of Physiology*, *159*, 326–338.

Reuter-Lorenz, P. A. & Fendrich, R. (1992). Oculomotor readiness and covert orienting: differences between central and peripheral precues. *Perception & Psychophysics*, *52*, 336–344.

Reuter-Lorenz, P. A., Hughes, H. C. & Fendrich, R. (1991). The reduction of saccadic latency by prior offset of the fixation point: an analysis of the gap effect. *Perception & Psychophysics*, *49*, 167–175.

Rizzolatti, G., Riggio, L., Pascola, I. & Umilta, C. (1987). Reorienting attention across the horizontal and vertical medians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*, 31–40.

Rosenberg, D. R., Averbach, D. H., O'Hearn, K. M., Seymour, A. B., Birmaher, B. & Sweeney, J. A. (1997). Oculomotor response inhibition abnormalities in pediatric obsessive-compulsive disorder. *Archives of General Psychiatry*, *54*, 831–838.

Ross, L. E. & Ross, S. M. (1980). Saccade latency and warning signals: Stimulus onset, offset, and change as warning events. *Perception & Psychophysics*, *27*, 251–257.

Ross, L. E. & Ross, S. M. (1981). Saccade latency and warning signals: Effects of auditory and visual stimulus onset and offset. *Perception & Psychophysics*, *29*, 429–437.

Saslow, M. G. (1967). Effects of components of displacement-step upon latency for saccadic eye movements. *Journal of the Optical Society of America A*, *57*, 1024–1029.

Satgunam, P. & Fogt, N. (2005). Saccadic latencies for achromatic and chromatic targets. *Vision Research*, *45*, 3356–3364.

Schall, J. D. (1991). Neuronal activity related to visually guided saccadic eye movements in the supplementary motor area of rhesus monkeys. *Journal of Neurophysiology*, *66*, 530–558.

Schall, J. D. (2004). On the role of frontal eye field in guiding attention and saccades. *Vision Research*, *44*, 1453–1467.

Schall, J. D. & Thompson, K. G. (1999). Neural selection and control of visually guided eye movements. *Annual Review of Neuroscience*, *22*, 241–259.

Schiller, P. H., Sandell, J. H. & Maunsell, J. H. (1987). The effect of frontal eye field and superior colliculus lesions on saccadic latencies in the rhesus monkey. *Journal of Neurophysiology*, *57*, 1033–1049.

Schlag-Rey, M., Amador, N., Sanchez, H. & Schlag, J. (1997). Antisaccade performance predicted by neuronal activity in the supplementary eye field. *Nature*, *390*, 398–401.

Schneider, W. X. (1995). VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition and space based motor action. *Visual Cognition*, *2*, 331–375.

Schneider, W. X. & Deubel, H. (2002). Selection-for-perception and selection-for-spatial-motor-action are coupled by visual attention: A review of recent findings and new evidence for stimulus driven saccade control. In W. Prinz & B. Hommel (Eds.), *Common Mechanisms in Perception and Action: Attention and Performance* XIX, (pp. 609–627). New York: Oxford University Press.

Seidlits, S. K., Reza, T., Briand, K. A. & Sereno A. B. (2003). Voluntary spatial attention has different effects on voluntary and reflexive saccades. *Scientific World Journal*, *3*, 881–902.

Sereno, A. B. & Holzman, P. S. (1995). Antisaccades and smooth pursuit eye movements in schizophrenia. *Biological Psychiatry*, *37*, 394–401.

Shepherd, M., Findlay, J. M. & Hockey, R. J. (1986). The relationship between eye movements and spatial attention. *Quarterly Journal of Experimental Psychology Section A–Human Experimental Psychology*, *38*, 475–491.

Shulman, G. L. (1984). An asymmetry in the control of eye movements and shifts of attention. *Acta Psychologica (Amsterdam)*, *55*, 53–69.

Simon, J. R. & Ruddell, A. P. (1967). Auditory S-R compatibility: The effect of an irrelevant cue on information processing. *Journal of Applied Psychology*, *51*, 300–304.

Simon, J. R. & Small, A. M. (1969). Processing auditory information: Interference from an irrelevant cue. *Journal of Applied Psychology*, *53*, 433–435.

Sparks, D. L. (2002). The brainstem control of saccadic eye movements. *Nature Reviews Neuroscience*, *3*, 952–964.

Sparks, D. L. & Barton, E. J. (1993). Neural control of saccadic eye movements. *Current Opinion in Neurobiology*, *3*, 966–972.

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*, 643–662.

Stuyven, E., Van der Goten, K., Vandierendonck, A., Claeys, K. & Crevits, L. (2000). The effect of cognitive load on saccadic eye movements. *Acta Psychologica (Amsterdam)*, *104*, 69–85.

Taylor, T. L., Klein, R. M. & Munoz, D. P. (1999). Saccadic performance as a function of the presence and disappearance of auditory and visual fixation stimuli. *Journal of Cognitive Neuroscience*, *11*, 206–213.

Theeuwes, J. & Godijn, R. J. (2001). Attentional and oculomotor capture. In C. L. Folk & B. S. Gibson (Eds.), *Attraction, distraction and action: Multiple perspectives on attentional capture* (pp. 121–149). Amsterdam: Elsevier.

Thickbroom, G. W., Stell, R. & Mastaglia, F. L. (1996). Transcranial magnetic stimulation of the human frontal eye field. *Journal of Neurological Sciences*, *144*, 114–118.

Thompson, K. G., Bichot, N. P. & Schall, J. D. (1997). Dissociation of visual discrimination from saccade programming in macaque frontal eye field. *Journal of Neurophysiology*, *77*, 1046–1050.

Treisman, A. (1964). The effect of irrelevant material on the efficiency of selective listening. *American Journal of Psychology*, *77*, 533–546.

Treisman, A. & Sato, S. (1990). Conjunction search revisited. *Journal of Experimental Psychology: Human Perception & Performance*, *16*, 459–478.

Valle-Inclan, F., Hackley, S. A. & de Labra, C., (2002). Does stimulus driven response activation underlie the Simon effect? In W. Prinz & B. Hommel (Eds.), *Common mechanisms in perception and action: Attention and performance* XIX, (pp. 474–493). New York: Oxford University Press.

Wang, D., Kristjánsson, Á. & Nakayama, K. (2005). Efficient visual search without top-down or bottom-up guidance. *Perception & Psychophysics*, *67*, 239–253.

Yantis, S. & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception & Performance*, *16*, 121–134.

Yantis, S. & Serences, J. T. (2003). Cortical mechanisms of space-based and object-based attentional control. *Current Opinion in Neurobiology*, *13*, 187–193.

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