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Cognitive control of saccadic eye movements

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ABSTRACT

The saccadic eye movement system provides researchers with a powerful tool with which to explore the cognitive control of behaviour. It is a behavioural system whose limited output can be measured with exceptional precision, and whose input can be controlled and manipulated in subtle ways. A range of cognitive processes (notably those involved in working memory and attention) have been shown to influence saccade parameters. Researchers interested in the relationship between cognitive function and psychiatric disorders have made extensive use of saccadic eye movement tasks to draw inferences as to the cognitive deficits associated with particular psychopathologies. The purpose of this review is to provide researchers with an overview of the research literature documenting cognitive involvement in saccadic tasks in healthy controls. An appreciation of this literature provides a solid background against which to interpret the deficits on saccadic tasks demonstrated in patient populations.

1. Introduction

In everyday life we typically make around three saccadic eye movements every second (e.g. Rayner, 1998). We are rarely conscious of these movements (in the sense that we are conscious of other movements we make such as reaching to grasp an object) and, subjectively at least, they appear to involve little or no cognitive effort on our part. Given these credentials saccadic eye movements would not appear to be a particularly promising tool with which to study cognition. In fact, over the last 30 years, researchers have demonstrated that saccadic eye movements are influenced by a wide range of cognitive processes, including those involved in attention, working memory, learning, long term memory and decision making. Moreover, as Carpenter (1994) argues, the oculomotor system provides researchers with "a microcosm of the brain"—one whose sensory input can be precisely controlled and manipulated, and whose limited motor output can be measured with exceptional accuracy with current eye tracking equipment.

It is now widely accepted that the patterns of cognitive dysfunction associated with psychiatric disorders are not simply unfortunate sequelae, but represent information processing deficits that lie at the very heart of the disorders. Furthermore, future pharmacological and psychological intervention strategies will be informed by a more sophisticated understanding of the aetiological role of neurocognitive dysfunction in psychiatric disorders. The combination of a close relationship with cognitive processes and considerable practical advantages in terms of ease of measurement and manipulation mean that the saccadic system will continue to provide researchers with a powerful tool with which to understand neurocognitive processes central to a variety of psychopathological disorders (see e.g. Hutton & Ettinger, 2006).

Studies using psychiatric and neurologically impaired populations and functional neuroimaging techniques have made considerable contributions to our understanding of the role of cognitive processes in saccadic eye movements, and this research is reviewed elsewhere in this special issue (McDowell et al. and Mueri & Nyffeler). This review will focus on studies using healthy human participants, and the cognitive processes involved in performing saccadic tasks that are typically used with psychiatric populations (see Fig. 1).

1.1. What is cognitive about saccades?

Electrophysiological studies in non-human primates have demonstrated that it takes around 40 ms for a signal to be transmitted from the retina to the superior colliculus (see glossary), and about 20 ms for stimulation of the same region of the superior colliculus to trigger a saccadic eye movement to a specific location in space (Carpenter, 1981). In reality, however, the typical latency of a "reflexive" saccade (one made towards a sudden onset target) in humans is around 200 ms, and the variability around this average is large. Why do saccades take more than three times longer than they could?

As Carpenter has so elegantly argued (Carpenter, 1981, 2001), saccadic eye movements have such long latencies because we need to work out not just where to look, but whether it is worth our looking there at all (given all the possible places we could be looking). A 15° saccade typically takes around 50 ms, during which much visual processing is suppressed (Ross, Burr, & Morrone, 1996). The more saccades made, the less time there is for fixations (see glossary)—during which the image remains stable enough on

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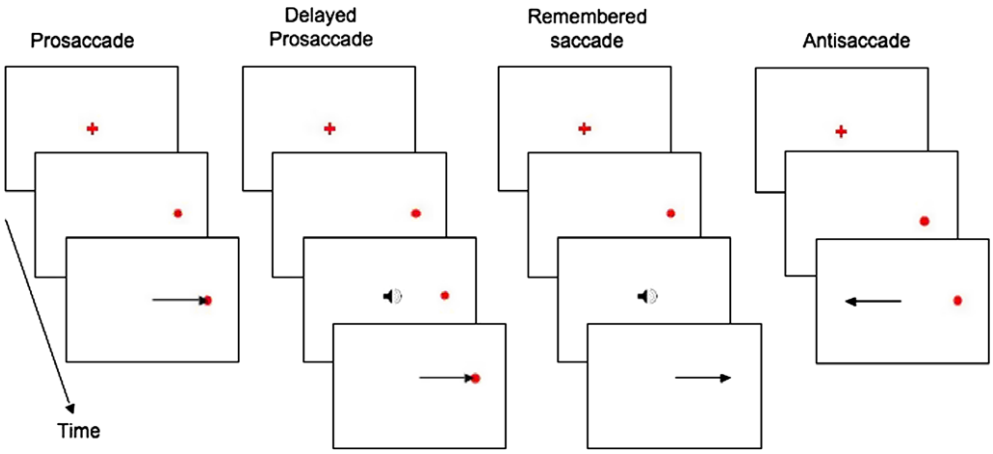


Fig. 1. Standard saccadic tasks used in psychiatric research. The arrow indicates the direction in which the eye moves in order to make a correct response. The speaker symbol indicates an auditory "go signal".

the retina for us to "see". We need, therefore, some means of determining whether the cost any given saccade is worth it given our current goals and limited processing resources (although certain saccadic eye movements such as square wave jerks (see glossary) and micro-saccades are probably not subject to such a cost-benefit analysis). In other words, in most instances saccadic latencies can be viewed as decision times, and, as with any decision process, the outcome can depend on a large number of influences, many of which could be termed "cognitive".

The LATER (Linear Approach to Threshold with Ergodic Rate) model of saccade generation (Carpenter, 1981; Carpenter & Williams, 1995) provides a useful starting point with which to consider the influences of cognitive processes on saccade generation. According to this model, a decision signal rises linearly from a baseline level (S_0) at a rate (r) until it reaches a threshold value (S_T) at which point the saccade is triggered. The baseline level (S_0) is considered to reflect expectation—the prior probability that a target is present and should be looked at. The rate of rise (r) reflects the supply of information, and the threshold at which the saccade is triggered (S_T) can be considered to reflect "urgency". Cognitive processes could potentially influence all three of these parameters and therefore mediate how quickly, or even whether, a saccade to a specific location is triggered.

The superior colliculus, in conjunction with other subcortical structures, is perfectly capable of determining the position of a target and generating an accurate saccade towards its location (Moschovakis, 1996; Schall, 1995). It does not, however, operate in isolation. It receives connections (typically inhibitory) from a wide range of cortical areas (including the parietal cortex and frontal regions such as the frontal eye fields (FEF) and supplementary eye fields (SEF) which themselves receive projections from V1 and other areas of visual cortex (see Johnston & Everling in this volume). This wider cortical network, and its interactions with other cortical areas such as the dorsolateral prefrontal cortex (DLPFC; see glossary), can therefore influence the "decision" as to whether a saccade should be made. In other words saccade generation involves a trade off between "bottom up" signals that concern basic stimulus properties such as position, size and luminance, and "top down" signals that reflect the current goals and intentions of the observer. In this sense the extent to which a saccade can ever be said to be truly "reflexive" is debateable, and for the remainder of this review, the term prosaccade (see glossary) will be used to refer to saccades made towards targets.

The review itself is divided into three main sections. The first considers cognitive factors that have been found to influence visually guided saccades made towards targets—most notably attentional processes. The second considers experimental tasks in which the saccades are triggered on the basis of more central cues (although, as argued above, a binary distinction between visually and centrally guided saccades is an over simplification). The final section considers antisaccades (see glossary)—a powerful and popular task in which the peripheral cue and task instructions compete for the control of behaviour.

2. Visually guided saccades

In the laboratory, prosaccades are generally elicited by instructing participants to look from a central fixation point towards a sudden onset peripheral target as quickly as possible. The latency with which the saccadic eye movement is initiated is usually the metric of most interest, although spatial accuracy (both of the primary saccade towards the target and any subsequent "corrective" saccades) is sometimes measured and reported. A distinction can be made between *peripherally (visually)* guided saccades, (such as those elicited by a sudden onset target), and *centrally* guided saccades, which are elicited by a central cue such as an arrow that indicates the location to which the saccade should be made (typically one of several place markers that remain visible throughout the trial). Visually guided saccades are often termed *prosaccades*, and in the present review this term will be used only to refer to saccades made towards a target on the basis of the target's appearance. Such saccades have been described as reflecting a "visual grasp reflex" (Theeuwes, Kramer, Hahn, & Irwin, 1998) although, as argued above, the extent to which saccades are ever truly reflexive is unclear. Developing a comprehensive understanding of the cognitive processes that underlie prosaccades is important because there is considerable evidence to suggest that prosaccade performance is largely unimpaired in psychiatric populations (see Rommelse & O'Driscoll in this volume).

The latencies of endogenously cued saccades are markedly longer than those of exogenously cued saccades (e.g. Walker, Walker, Husain, & Kennard, 2000). This difference is assumed to reflect the additional processing requirements of establishing the appropriate stimulus-response mapping given the symbolic cue. Endogenous saccades are generally considered to be more "volitional" in nature than exogenously cued saccades, but given the discussion above concerning the role of top down processes in the generation of exogenous saccades, the difference should be considered a quantitative rather than qualitative one. A wide variety of cognitive processes have been found to influence performance on both peripherally and centrally cued prosaccades, and these are reviewed below.

2.1. Attention

The relationship between saccadic eye movements and attention is clearly a close one—a typical natural scene contains far too much information for our limited capacity cognitive system to process simultaneously, and we must therefore focus our resources on those regions that contain the most relevant information given our current goals and intentions. Visual acuity drops extensively with increasing distance from the fovea, so we typically accomplish this by scanning the scene with a series of saccadic eye movements that foveate the area of interest, interspersed with fixations during which the visual information is sufficiently stable on the retina to be processed. In other words, what we are currently attending to and what we are currently looking at are generally one and the same thing (although, as is clear from research described below, attention and fixation are not always co-located). Indeed, the use of eye movements (in particular the location and duration of fixations) as an index of which aspects of a scene (or stimulus such as a face) receive most attention is the rationale behind a great many eye tracking studies, both in psychological research as well as commercial settings.

Despite this close coupling (see e.g. Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995), it has long been known that the locus of gaze and the locus of selective attention (see glossary) are not necessarily co-located. Helmholz (1894, cited in van der Heijden, 1992) observed that he was able to identify the letters present in a small portion of a briefly flashed array if he concentrated on that location whilst keeping his eyes fixated straight ahead. There have been many studies demonstrating that attention can be shifted covertly, resulting in performance enhancements at the attended locations, without requiring an overt shift of gaze (e.g. Posner, 1980).

Whilst there is a general acknowledgement that spatial attention and saccadic eye movements are closely linked, there is little consensus on how best to describe the relationship itself. Three broad positions can be identified (Clark, 1999). Some authors argue that *overt* shifts of attention (involving eye movements) are functionally independent of *covert* shifts (Hunt & Kingstone, 2003a; Klein, 1980; Remington, 1980). In other words saccades and attentional shifts are implemented in separate neural systems, but both of these systems respond to the same top down and bottom up signals, resulting in a correlational rather than functional relationship.

Other models of saccade generation propose a loose functional relationship between eye movements and attention. For example, Fischer and Weber (1993) proposed a model of saccade generation in which there is a disengaged attention phase, during which the target's location is computed in preparation for the upcoming saccade. In support of this position, Fischer and Weber (1993) cite evidence from studies in which the central fixation was removed prior to the target onset, resulting in a marked reduction in saccade latency. These studies are reviewed in more detail in Section 2.1.1 below.

Finally other authors have suggested a much more explicit functional relationship between attention and saccades. The premotor theory of attention (see glossary; e.g. Rizzolatti, Riggio, & Sheliga, 1994) and the Visual Attention Model (VAM; see glossary) proposed by Schneider (1995) are two examples of such a position. The premotor theory argues that the allocation of spatial attention to a specific location is equivalent to planning, but not executing a saccade to that location. According to this model the programming of an eye movement to a specific location facilitates activity in neurons that instantiate topographic oculomotor "pragmatic maps" which transform spatial information into eye movements. It is this increase in activation in specific regions of pragmatic maps that results in spatially selective attention to that location. In support of this position, Rizzolatti, Riggio, Dascola, and Umilta (1987) required participants to fixate a central box, surrounded by 12 peripheral boxes in a square configuration. When one of the peripheral boxes was cued, participants direct attention towards that location and pressed a key as soon as a target appeared. In invalid trials, the target appeared in a box that was not cued. A key finding, termed the "meridian effect" was that reactions times were slower when the cue appeared in the opposite hemifield to the target. According to the premotor theory this effect arises because the saccade program that was generated in response to a cue appearing in the opposite hemifield has to be modified in terms of its direction. This operation requires a new saccade program whereas when the cue appears in the same hemifield as the target an existing saccade program can be adjusted—a less time consuming exercise.

There are, however, some findings that question the strong claim made by the premotor theory that attention is consequent on movement planning. For example, some electrophysiological studies have found evidence for neurons in the frontal cortex of monkeys that are involved in the orienting of attention, but not saccade preparation (Juan, Shorter-Jacobi, & Schall, 2004). Similarly, Sato and Schall (2003) identified two types of neurons in the FEF of macaques performing pro or antisaccades to singletons in visual search arrays—those that first selected the target location (and subsequently the endpoint of the saccade) and those that selected the endpoint only. They argued that the responses of these neurons support the idea that visual selection and saccade selection are different processes. In humans, there is some evidence that saccade preparation does not necessarily invoke an attentional shift. For example Hunt and Kingstone (2003a) found that verbally pre-cuing a saccade target did not lead to an improvement in an unspeeded visual discrimination task at that location.

In contrast with the premotor theory, Schneider's Visual Attention Model suggests that targets are selected by a visual attention mechanism that is responsible for both "selection for action" and "selection for perception". Thus, a critical difference between the premotor theory and VAM is that the premotor theory suggests that programming a saccade causes a shift in attention whereas VAM argues that a saccade program may result as a consequence of a shift in attention. In support of this model, Deubel and Schneider (1996) required participants to saccade to locations within horizontal letter strings on the basis of a central cue. In the time period between the signal to initiate the saccade (the offset of the central cue) and the saccade itself, a discrimination target appeared at one of the locations in the letter string. They found that discrimination performance was close to chance levels unless the target appeared in the same location to which the saccade had been programmed. In a second experiment the discrimination target always appeared in the central location of the letter string. Despite knowing the location of the upcoming target, participants were unable to direct attention to this location (thus improve detection performance) if the saccade was directed to a nearby location. Similarly, Hoffman and Subramaniam (1995) found superior performance on a discrimination task when the location of the discrimination target matched that of an upcoming saccade. Further, they found that when participants were explicitly instructed to attend one location and saccade to another, discrimination performance was superior at the saccade location, not the attention location. Taken together, these findings (and similar findings by Kowler, Anderson, Dosher, & Blaser, 1995) provide strong support for an "obligatory" relationship between attention and saccade programming, such that saccades to a specific location are preceded by a shift in attention to that location.

It is worth noting that both the premotor theory and VAM assume that attentional processing is limited to the target of the upcoming saccade. There is, however, evidence that attention may well be distributed in parallel to several items in the visual field if they are the targets in a planned sequence of saccades (Baldauf & Deubel, 2007; Godijn & Theeuwes, 2003).

For the purposes of this review, it is sufficient to note that whilst the precise nature of the relationship between attention and eye movements remains a topic of lively debate, the fact that a relationship of some sort exists is not in dispute and there is now extensive neuroimaging evidence to suggest that the neural systems underlying saccadic eye movements (see Johnston & Everling in this volume) and attentional shifts overlap considerably (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Nobre, Gitelman, Dias, & Mesulam, 2000). The remainder of this section summarises a number of key manipulations that have been found to impact on prosaccade performance, and whose effects have been considered to be mediated (to some extent at least) by attentional processes.

2.1.1. Gap/overlap effects

One of the most common manipulations employed in prosaccade tasks concerns the relationship between the offset of the central fixation stimulus and the onset of the peripheral target stimulus. In standard "step" trials, the fixation offset coincides with the target onset (leading to the percept of a single object stepping from one location to another). In gap trials, the fixation offset precedes the target onset, whereas in overlap trials, the fixation stimulus remains visible after target onset. Studies have employed a variety of gap/overlap durations, but 200 ms for both is typical.

Box 1. Pro and antisaccade tasks

In the standard prosaccade task participants are instructed to direct their gaze towards a sudden onset target as quickly and as accurately as possible. The temporal relationship between the offset of the central fixation stimulus and the onset of the peripheral target can be varied—typically either gap, step or overlap conditions are used. The most common metric is latency but the peak velocity and amplitude of the primary saccade as well the final eye position (after any corrective saccades) can also be informative.

The antisaccade task uses exactly the same stimuli as the prosaccade task—only the task instructions are different. Participants are told to direct their gaze to the mirror image location of the sudden onset target. The metric of most interest is typically the proportion of antisaccade errors (prosaccades towards the target that are corrected), although correct antisaccade latency, error latency, and latency to correct (the time between the erroneous prosaccade and subsequent corrective antisaccade) are also informative, as are the amplitude and peak velocity of correct antisaccades.

Antisaccade error rate is typically around 20% in healthy adults—but the range both across participants and studies is enormous. Differences in task parameters such as the number of potential targets, their distance from central fixation, the precise instructions given and the extent of performance feedback provided may all have non-trivial impacts on antisaccade performance.

An interesting variant of the prosaccade task requires participants to delay making a saccade towards a sudden onset target until a go signal (typically a brief tone) is given. The delayed prosaccade task thus shares with the antisaccade task the requirement to avoid making an immediate saccade towards the target, but does not require the spatial transform needed to provide the co-ordinates for a correct antisaccade.

A large number of studies confirm the basic finding that prosaccade latencies are markedly reduced in gap trials, and increased in overlap trials compared to step trials (Fischer & Weber, 1992; Reuter-Lorenz, Hughes, & Fendrich, 1991; Saslow, 1967). Interestingly saccades also have higher peak velocities in gap conditions (Pratt, 1998) but the majority of studies report only latency data. According to one account, the disappearance of the fixation point in gap trials allows attention to be disengaged before the target appears (resulting in faster saccade latencies), whereas during overlap trials visual attention is engaged and saccades are inhibited, resulting in slower latencies (Fischer & Breitmeyer, 1987; Fischer & Weber, 1993).

Not all researchers have interpreted the gap effect in attentional terms. It has been argued that the offset of the fixation stimulus serves as a warning cue, which results in a reduction in saccade latencies through a general alerting process. For example, Reuter-Lorenz, Oonk, Barnes, and Hughes (1995) compared the gap effect with and without an acoustic warning signal delivered at the same time as fixation offset. They found that the warning signal significantly reduced, but did not eliminate the gap effect-prosaccades were still approximately 40 ms faster in the gap compared to no-gap conditions. The authors agree with Kingstone and Klein (1993) that the gap effect reflects both a warning component, and a "fixation release" component.

This fixation release component has been argued to be mediated by low-level neural mechanisms in the superior colliculus (e.g. Reuter-Lorenz et al., 1991). According to this account, the removal of the central stimulus causes fixation neuron (see glossary) in the superior colliculus to become less active, thus disinhibiting movement cells and facilitating the initiation of a subsequent saccade (see Johnston & Everling, this issue). A lack of difference in gap effects in saccades made towards attended or unattended stimuli (Walker, Kentridge, & Findlay, 1995), and a lack of difference in saccade latencies to targets made from attended or unattended offset stimuli (Kingstone & Klein, 1993) have both been taken as evidence for a minimal role of attention in the gap effect. More recent research has, however, challenged this position. Participants demonstrate a larger gap effect when the attended portion of a central stimulus is removed 200 ms prior to the target onset compared to when the unattended portion is removed (Pratt, Lajonchere, & Abrams, 2006). The authors suggest that attentional selection modulates the activity of the fixation neurons in the superior colliculus, with attended fixated objects producing greater activity than unattended fixated objects. Removing the attended portion of a fixated object results in a greater disinhibition of the movement cells then removing the unattended portion, thus resulting in a larger gap effect. In previous research the attended and unattended offset objects were not fixated.

Some researchers have found that, under certain conditions, introducing a temporal gap between fixation offset and target onset can result in a bimodal distribution of saccade latencies—in addition to the standard peak at around 200 ms an earlier peak is observed at around 120 ms (Fischer & Ramsperger, 1984). These low latency saccades were referred to as "express saccades" (see glossary) and it was argued that the reduction in saccade latency seen in gap trials reflects an increase in the production of these express saccades. Express saccades have been observed to be greater in children compared to adults (Klein & Foerster, 2001). Interestingly, Klein and Fischer (2005) have shown that they demonstrate similar developmental patterns and load on the same factor as erroneous prosaccades towards the target with express latencies in the antisaccade task (see Section 4).

The status of express saccades as a separate type of saccade, generated by a relatively simple neural circuit involving the superior colliculus and parietal cortex, has been challenged by several researchers. Bimodal distributions are not always observed (Reuter-Lorenz et al., 1991; Kingstone & Klein, 1993; Wenban-Smith & Findlay, 1991) and it has been suggested that express saccades may reflect preparatory processes that occur only in relatively spe-

cific and artificial situations (Carpenter, 2001; Dickov & Morrison, 2006; Pare & Munoz, 1996). Recently Edelman, Kristjánsson, and Nakayama (2007) demonstrated that the direction (but not latency) of express saccades can be influenced by higher level cognitive processes concerning task instructions. They showed that the endpoints of express saccades are biased in the direction of a central cue which indicated which of two stimuli should serve as the target. This finding highlights the interactive nature of top down and bottom up processes in saccade generation, and suggests that even the fastest and most "reflexive" of saccades are amenable to top down modulation.

For the purposes of this review it is sufficient to note that the introduction of a gap in prosaccade trials reliably results in a reduction in latency, and this effect may provide important insights into the cognitive and neural mechanisms underlying saccade generation. The extent to which this reduction in latency reflects an increase in the generation of express saccades, and the extent to which express saccades can be considered an independent saccade type remain controversial issues.

2.1.2. Effects of cueing

Just as cueing the location of an upcoming target enhances detection at that location in the absence of eye movements (e.g. Posner, 1980), studies have shown that cues also reduce the latencies of saccades made towards the cued location (e.g. Cavegn, 1996). As with the attentional literature, in which invalid cues decrease detection times at the target location, invalid cues have been found to increase the latencies of saccades towards the target (Walker et al., 1995). These findings can be accommodated by models that assume a functional relationship between saccades and spatial attention. The cue serves to direct attention towards the target location, thus facilitating the generation of a saccade to that location.

With longer delays between cue and target presentation, and if attention is removed from the cue back to a central stimulus, target detection at the cued location is delayed—a phenomenon known as inhibition (see glossary) of return (Klein, 2000; Posner & Cohen, 1984). It has been suggested that this property of the attentional system may facilitate foraging and other visual search behaviours (although see Hooge, Over, van Wezel, & Frens, 2005). The mechanisms underlying inhibition of return are still the focus of considerable research, but there is some evidence to suggest that they may be related to eye movement programming. Rafal, Calabresi, Brennan, and Sciolto (1989) found inhibition of return effects when a saccade had been prepared or directed to a location on the basis of a central cue. Other research has suggested that attentional and oculomotor influences on inhibition of return can be dissociated (Hunt & Kingstone, 2003b).

2.1.3. The effects of distractors

Research exploring the influence of task-irrelevant distractor stimuli on prosaccades has also provided useful insights into the relationship between attention and eye movements. Theeuwes et al. (1998) required participants to make saccades to one of six circular stimuli, arranged in a circle around a central fixation stimulus, in order to discriminate a small target contained within the circles. Saccades were made to a colour singleton that was revealed when all but one of the six peripheral circles changed from grey to red. On 50% of trials an additional red distractor stimulus appeared at one of four additional locations at the same time as the colour singleton was revealed. In about half of the distractor trials, a saccade was made first on or near the distractor location, then followed rapidly (25–150 ms) by an additional saccade that took the eye to the singleton. As a result, detection time at the colour singleton was significantly increased. These "capture errors" were eliminated by a condition in which the location of the colour singleton was precued. The authors argue that the precue allowed attention to be shifted to the location of the colour singleton in advance of the distractors appearance, thus facilitating a saccade towards its location as opposed to the location of the distractor.

In addition to provoking "capture errors" distractor stimuli can also result in deviations in saccade trajectories, even when the saccades themselves are ultimately spatially accurate, in that they deliver gaze to the target. For example, when participants make vertical saccades to a target below or above a central fixation point, the presentation of a distractor stimulus on either the left or right can result in marked curvature of the saccade path away from the side on which the distractor was presented (e.g. Doyle & Walker, 2001). Importantly, the direction of this curvature appears to be a function of the extent to which the saccade towards the target can be prepared prior to the distractor onset. If sufficient time is allowed for a saccade to be prepared to the target location, the distractor location is inhibited, resulting in curvature away from its location. If, on the other hand, there is insufficient time to prepare a saccade (for example when the target location is unpredictable), the activity in the oculomotor system caused by the distractor is not inhibited, and instead competes with the activity caused by the target, causing curvature towards the distractor (McSorley, Haggard, & Walker, 2006).

Competition between activities in topographic salience maps representing two different locations can also explain the global effect (also known as the centre of gravity effect). If a target and distractor are presented simultaneously, and are sufficiently close together, saccades are often made to a location in between the two (Findlay, 1982).

A recent experiment demonstrates the close relationship between working memory, attention and saccade trajectories. In a variation of the remembered saccade task (in which saccades are made to a previously cued location, see Section 3.2), Theeuwes, Olivers, and Chizk (2005) presented a peripheral target and, after a delay period required participants to make a forced choice decision as to whether a subsequent probe appeared in the same or different location. During the delay period, participants made a vertical saccade either upwards or downwards towards a marker that remained visible throughout the trial. They found that saccades deviated markedly away from the direction of the remembered target. The authors argued that in order for an accurate saccade to be generated toward the marker, activity in the oculomotor regions corresponding to the remembered target location needs to be inhibited. This inhibition, just as with the inhibition assigned to visible irrelevant distractors, leads to saccade curvature away from its location.

2.2. Learning

A number of studies have demonstrated a role for learning in mediating prosaccade performance. The most straightforward demonstration of learning effects is provided by studies that have manipulated the probability with which the target appears, either at all, or at a specific location. Prosaccade latencies are faster in blocks in which the target has a high probability of appearing (75%) than in blocks in which there is a low probability of target appearance (25%) (Dick, Kathmann, Ostendorf, & Ploner, 2005). Carpenter and Williams (1995) altered the probability of a target appearing on either the left or right of fixation, and again demonstrated decreases in reaction time for saccades made in the most probable direction. The effect of expectancy on prosaccade latencies was studied by Oswal, Ogden, and Carpenter (2007), who systematically varied the duration between the start of the trial and the appearance of the target. They found that an "aging foreperiod" (in which the probability of the target appearing increases as a function of foreperiod duration) led to reductions in saccade

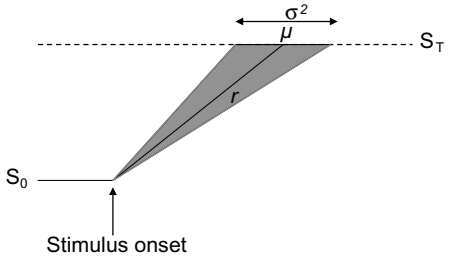
latencies as the length of the foreperiod increased. These results support the LATER model (see glossary) of saccade generation, which predicts that increasing expectation leads to an increase in the baseline level of activity (S_0) from which the decision signal rises.

Box 2. Carpenter's LATER model

Why is the typical latency of a prosaccade towards a sudden onset target around 100 ms longer than the minimum delay suggested by the shortest neural circuit between the retina and the oculomotor muscles? Carpenter suggests the delay reflects a deliberate "procrastination" strategy that allows a more sophisticated processing of potential saccade targets beyond simply determining their location. Such a strategy is required because a typical visual scene contains many objects/regions that might potentially be fixated. In other words some kind of decision process is needed to ensure that our limited processing resources are directed towards the most relevant part of the visual scene given our current goals.

A common theme of models of decision processes is that they involve a gradual accumulation of information concerning the different potential responses. A decision is reached when information concerning one response reaches some critical threshold before the others (or the decision not to respond is made if no threshold is reached). Electrophysiological research suggests that such accumulator models of decision making are plausible at a neural level. Carpenter's LATER (Linear Approach to Threshold with Ergodic Rate) model applies an accumulator model of decision making to saccade generation (see Fig. 1).

At the time of target onset a decision signal starting from a baseline level (S_0) begins to rise at a constant rate (r) until it reaches a threshold (S_T) at which point a saccade towards the target is initiated. The rate of rise is assumed to vary randomly from trial to trial, with a mean μ and variance σ^2. Manipulations that result in changes in the baseline level of activity, the rate of rise or the threshold could all result in changes in saccade latency. Factors such as expectancies and the level of activation of the intention would presumably influence baseline levels of activation.



More complex learning effects on prosaccade performance were recently demonstrated by Milstein and Dorris (2007). They varied the "expected value" (reward probability × reward magnitude) associated with prosaccades, and found that latency was negatively correlated with expected value. Importantly this correlation was stronger than correlations with either reward value or reward probability alone. The authors conclude that complex higher order information such as expected value can be used to influence activity in saccade preparation maps.

3. Endogenously guided saccades

The research described above highlights the point made at the beginning of the review that even in comparatively simple prosaccade tasks, "endogenous" factors such as expectation and learning can play a considerable role. The present section considers tasks in which the role of endogenous factors is made more explicit.

3.1. Predictive saccades

In the predictive saccade task participants are presented with a target that typically alternates between two spatial locations with a fixed temporal frequency (e.g. Stark, Vossius, & Young, 1962). Within three or four alternations, participants begin to make predictive saccades (see glossary) that are initiated before the target appears in the new location, and often result in the saccade arriving at the target location very close in time to the target onset (Hutton et al., 2001). As these saccades are not visually guided, the general assumption is that they are centrally guided saccades based on some internal model of the target movement (e.g. Simo, Krisky, & Sweeney, 2005). Despite several studies documenting impaired predictive saccade performance in psychiatric and neurological populations (e.g. Karoumi, Ventre-Dominey, Vighetto, Dalery, & d'Amato, 1998; O'Sullivan et al., 1997), there has been comparatively little research aimed at determining the mechanisms supporting unimpaired performance in healthy participants.

Ross and Ross (1987) confirmed the results of earlier studies that a "square wave tracking" task (in which a target alternated between two locations at a fixed temporal frequency) can produce markedly reduced (predictive) latencies provided the periodicity is neither too fast nor too slow. This effect on latency was further explored by Bronstein and Kennard (1987), who demonstrated that predictive saccades (which they defined as saccades occurring <100 ms before target onset) typically had lower peak velocities than saccades of equivalent amplitudes made towards non-predictable stimuli. In addition they found that predictive saccades were markedly hypometric compared to non-predictive saccades. The authors suggest that the decreased peak velocity and amplitude reflect the fact that in the predictive saccade task the saccade generating mechanisms in the brain stem are lacking the "optimised" input that is provided by visual information. They speculate that the signal for predictive saccades may originate in the frontal eye fields, but were not concerned with the cognitive mechanisms that may underlie predictive saccade performance.

Joiner and Shelhamer (2006) found that some participants were able to generate temporally accurate predictive eye movements after only 3 saccades at a given stimulus periodicity, and also that participants typically continued to generate 2–3 predictive saccades at the original periodicity when the stimulus was abruptly switched to a lower periodicity. They argued that these data suggest predictive eye movements are based on a neural clock—an internal timing device that has evolved to support prolonged rhythmic behaviour.

The internal representation on which predictive saccades are based must include information concerning both the time at which a stimulus is due to appear, and also location in which it is due to appear. Whilst Joiner & Shelhamer's concept of a neural clock speaks to the first of these, it does not address the second. If participants are required to generate predictive saccades in time to a combined visual/acoustic signal in the dark, they demonstrate hypometric primary saccades initially, but if the visual signal is removed their primary saccades and final eye position typically become increasingly hypermetric (Hutton et al., 2001; O'Sullivan et al., 1997). It has been suggested that working memory may play a role in supporting predictive saccade performance, and working memory would certainly be able to generate a model of target

behaviour that included both temporal and spatial information, but there is little direct evidence in support of this hypothesis (Hutton et al., 2001).

Isotalo, Lasker, and Zee (2005) demonstrated a clear role for top down cognitive processes in predictive saccade performance. They manipulated the effect of task instructions, requiring participants to either "follow the lights"—a passive reflexive instruction, or "move your eyes in time with the lights"—an active volitional instruction. They found increased numbers of predictive (latency < −200 ms) and anticipatory (latency > −200, <100 ms) saccades with the active instruction compared to the passive instruction. The passive instructions presumably reduced the likelihood of participants instantiating an internal model of the target's movement and using this to generate predictive saccades.

The predictive saccade task provides a simple means of eliciting internally guided saccadic eye movements. Its utility as a tool with which to explore cognitive dysfunction in patient populations would be greatly increased by systematic studies of the cognitive mechanisms that support its performance in healthy participants.

Box 3. The predictive saccade task

In the predictive saccade task participants typically direct their gaze to a target that alternates between two locations with a fixed temporal frequency. Such a "square wave" target pattern rapidly (within 2–3 target steps) induces predictive saccades that are initiated before the next target step, and result in the eye arriving at the target location very close to the time at which the target itself appears.

The task is of interest because predictive saccades are clearly endogenously generated. That is they are not visually guided in the traditional sense, but rather depend on an internal model of the target's movement. As such the task has potentially informative links with cognitive processes involved in building and maintaining internal representations of the external world, including those involved in spatial working memory.

The most obvious metric derived from predictive saccade tasks is the latency. Saccades with latencies less than 80 ms after the target with which they are associated are generally considered to be predictive. The number of target steps before predictive latencies are reached is also a potentially informative metric. The amplitude of predictive saccades is also occasionally reported. Predictive saccades, like other endogenously guided saccades, can be markedly hypometric.

3.2. Memory guided saccades

In the remembered saccade task participants fixate a central stimulus, and a peripheral target is flashed briefly, cueing the location for a subsequent saccade that must be delayed until a "go signal" is given. In some studies the target can appear in one of several locations on a horizontal line to the left or right of the central stimulus, but in others the target may appear in one of several locations arranged in a circle around the central stimulus. Participants are instructed to refrain from saccading towards the target when it appears until a "go signal" (for example a tone) is given. They then make a saccade towards the location they remember the target appeared in. The task thus combines the potential to investigate "distractibility" (the number of anticipatory or reflexive glances made towards the sudden onset target) as well as the ability to maintain a spatial location in mind over extended periods of time.

One of the key findings using this paradigm is that remembered saccades tend to be spatially less accurate than visually guided saccades. This inaccuracy is reflected both as an increase in spatial variability (e.g. White, Sparks, & Stanford, 1994) and as a general hypometria (see glossary; e.g. Becker & Fuchs, 1969). Ohtsuka, Sawa, and Takeda (1989) found that memory guided saccades (see glossary) made in the dark tended to overshoot the target positions, although this study used exceptionally large amplitudes (20–80°). However, Crawford, Haeger, Kennard, Reveley, and Henderson (1995) measured spatial accuracy in terms of both the amplitude of the primary saccade and the final eye position (after any corrective saccades) and apparently found no changes in either measure compared to a standard prosaccade condition. Factors such as whether the remembered saccades were performed in the dark or not are likely to have considerable bearing on their spatial accuracy.

Saccades made to remembered locations tend to be slightly hypometric, and have increased latencies and decreased peak velocities compared to visually guided saccades (e.g. Krappmann, Everling, & Flohr, 1998; Smit, Van Gisbergen, & Cools, 1987; White et al., 1994). Whilst most experiments exploring memory guided saccades have used comparatively short intervals during which the target location must be remembered, some researchers have used delays of 30 s or more, demonstrating that saccades can be guided on the basis of representations of spatial locations stored in long term memory, as well as those maintained in short term or working memory (Ploner, Gaymard, Rivaud, Agid, & Pierrot-Deseilligny, 1998). Comparatively few studies have reported inhibition error rates on the remembered saccade task, but Crawford et al. (1995) found rates that appear to be similar to those observed in the antisaccade task.

A number of studies have combined the remembered saccade paradigm with other cognitive tasks. Akdal, Hodgson, Hill, Mannan, and Kennard (2002) for example found that requiring participants to remember the form of a character written in kanji script during the delay period resulted in memory guided saccades becoming markedly hypermetric, but not in fluent kanji readers. Ostendorf, Finke, and Ploner (2004) found that reaction times to an interpolated discrimination task increased with the discrimination target appeared in the same hemifield as the target to be remembered. This finding supports other research (e.g. Theeuwes et al., 2005) demonstrating close links between spatial working memory, attention and saccadic eye movements.

An interesting variant of the standard prosaccade task is the delayed prosaccade task. As with the remembered saccade task, participants are instructed to saccade towards the location of a peripheral target only when a go signal is given. The critical difference between this task and the remembered saccade task is that the target remains visible during the delay before the go signal. As such it provides a useful control condition.

3.3. Other cognitive influences

Further evidence for top down control over prosaccades is provided by a study demonstrating that simply altering the verbal instructions participants receive can have dramatic effects on prosaccade parameters (Mosimann, Felblinger, Colloby, & Muri, 2004). Using a standard prosaccade gap paradigm, participants were given three different verbal instructions. In the standard instructions condition they were asked to look to the target "as precisely and as fast as possible". In a delay condition they were asked to "delay looking at targets, but be as precise as possible". Finally in an inaccuracy condition they were asked to "look as fast as possible, but inaccurately towards the targets". Compared to the standard

instructions the delay condition resulted in an increase in latency and a decrease in amplitude. The inaccuracy condition resulted in an increase latency and variability in amplitude. These results are important, as they demonstrate that basic prosaccade metrics such as latency and amplitude are readily modifiable by high level factors such as verbal instructions, and do not simply reflect stimulus properties.

3.4. Summary of cognitive effects on visually and centrally guided prosaccades

Taken together, the results outlined above demonstrate that prosaccades made towards sudden onset targets can be influenced by a wide range of cognitive processes. The link between saccades and spatial attention is clearly close, but the precise nature of the relationship remains unclear. Converging evidence suggests that attention invariably precedes a saccade towards a target, and a variety of manipulations impact on prosaccade performance in a way that supports models of saccade generation that make reference to topographic salience maps (e.g. Findlay & Walker, 1999; Godijn & Theeuwes, 2002; Trappenberg, Dorris, Munoz, & Klein, 2001). Activation in these maps can be influenced by bottom up and top down sources of information, and may guide saccadic eye movements as well as mediate effects that are generally considered to reflect the operation of spatial attention.

4. Antisaccades

The prosaccade tasks described above involve saccades made towards targets whose latencies may be determined to a greater or lesser extent by "top down" influences. In some, such as the standard prosaccade task with sudden onset targets, these influences may be comparatively weak compared those involved in generating a memory guided saccade. Another task which emphasises top down control is the antisaccade task (Hallett, 1978). In this deceptively simple variation of the standard prosaccade task, participants fixate a central stimulus which is replaced by a sudden onset target that appears at some distance to the left or right. Participants are told to refrain from looking at the peripheral target, and direct their gaze instead to its mirror image location. The task thus contrasts controlled behaviour—a volitional saccade in the opposite direction to a sudden onset target—with the powerful urge to make a prepotent response—a prosaccade towards the target. Healthy participants typically fail to achieve this on a significant number of trials and instead make prosaccades towards the target (errors). These glances are followed rapidly by a correct antisaccade towards the mirror image location on the vast majority of trials (e.g. Tatler & Hutton, 2007). In comparison with prosaccades, the latencies of correct antisaccades are markedly increased—typically around 100 ms longer than prosaccades made to the same stimuli (e.g. Evdokimidis et al., 2002; Hutton et al., 1998). Importantly, the latencies of erroneous prosaccades towards the target are generally in the range of standard prosaccades (e.g. the average error latency in the very large sample of Evdokimidis et al. (2002) was 208 ms).

Despite the considerable number of studies that have used the antisaccade task to explore cognitive deficits in psychiatric disorders, there is surprisingly little consensus as to which cognitive processes healthy participants use when performing the task. Furthermore, a considerable variation in error rate and correct antisaccade latency can be readily observed in healthy populations, and the sources of this variation remain unclear.

4.1. Inhibitory processes in antisaccade performance

It is generally assumed that the sudden appearance of the target in an antisaccade task automatically triggers a motor program for a prosaccade in its direction, and that errors occur when certain endogenous (volitional) processes fail to inhibit or cancel this program (e.g. Everling & Fischer, 1998; Guitton, Buchtel, & Douglas, 1985). It is argued that correct antisaccade latencies are increased compared to prosaccade latencies because the application of the inhibitory processes is time consuming (Olk & Kingstone, 2003). This view is articulated clearly by Everling and Fischer (1998) in their review of the antisaccade task. They argued that antisaccade performance requires two intact subprocceses—the ability to suppress a reflexive saccade (see glossary) towards the visual stimulus, and the ability to generate a voluntary saccade in the opposite direction. This view is also prevalent in the psychiatric and neurological literature, where increased antisaccade errors are often interpreted as reflecting failures in inhibitory processing in the population studied (Crawford, Bennett, Lekwuwa, Shaunak, & Deakin, 2002; Hutton et al., 1998).

The extent to which the erroneous prosaccade towards the target should be considered "reflexive" is debateable. As argued earlier, with the possible exception of express saccades, average prosaccade (and average antisaccade error) latencies suggest the involvement of considerable top down processes. Godijn and Kramer (2006) provide compelling evidence suggesting that erroneous prosaccades should not be considered "reflexive"—participants made significantly more erroneous prosaccades towards targets when they were task relevant. More recent accounts of antisaccade performance have emphasised the parallel nature of saccade programming in the antisaccade task (Hutton & Ettinger, 2006; Massen, 2004; Munoz & Everling, 2004; Reuter & Kathmann, 2004) and argue that at stimulus onset a "competition" ensues between the exogenously triggered prosaccade and the endogenously initiated antisaccade—the co-ordinates for the antisaccade being computed as soon as the stimulus location is determined. Massen (2004), for example, argues that if the endogenously triggered antisaccade can be programmed fast enough (e.g. reaches some threshold for activation), it "wins" the competition, and the reflexive saccade is cancelled. Alternatively, if the exogenously triggered prosaccade is programmed fast enough (or the computation for the antisaccade is too slow) an erroneous prosaccade is made first, and the correct antisaccade follows (possibly even curtailing the erroneous saccade if it follows fast enough). In support of this model, Massen showed that manipulations resulting in increased latencies for correct antisaccades (such as reducing the probability of antisaccade trials) also result in increased errors—if the endogenous antisaccade is slow, there is a greater probability of the exogenously triggered prosaccade winning the competition. The parallel programming of the erroneous and correct response is also suggested by the finding that the average time to correct antisaccade errors is typically short—around 130 ms (Tatler & Hutton, 2007) and can be as low as 0 ms (Mokler & Fischer, 1999)—well below the latency that would be expected if the correct antisaccade were initiated as a response to the error.

According to one competitive race account of antisaccade performance, errors occur when processes related to the initiation of the prosaccade towards the target are inadequately "handicapped", resulting in an increased likelihood of it reaching the threshold for saccade triggering (Munoz & Everling, 2004). This account thus maintains the concept of an active inhibitory mechanism as being critical to antisaccade performance. The concept of a competitive race between decision signals for the erroneous reflexive saccade and correct antisaccade does, however, allow an alternative interpretation—that antisaccade errors result from a failure to sufficiently activate the correct response, as opposed to a failure to inhibit the incorrect response (Eenshuistra, Ridderinkhof, & van der Molen, 2004; Hutton, Joyce, Barnes, & Kennard, 2002; Nieuwenhuis, Broerse, Nielen, & de Jong, 2004; Reuter, Rakusan, & Kathmann, 2005; Roberts, Hager, & Heron, 1994). In other words,

rather than two separate processes (reflexive saccade suppression and antisaccade generation) being critical for antisaccade performance (as argued by Everling & Fischer, 1998), only one process really matters—the ability to generate the antisaccade itself. If this process is successful (e.g. implemented quickly enough), the inhibition of the reflexive prosaccade occurs by default.

A detailed formulation of this view is provided by Cutsuridis, Smyrnis, Evdokimidis, and Perantonis (2007), in their neural network implementation of a competitive race account of antisaccade performance. Drawing on Carpenter's LATER model, they propose that the decision signals for the volitional antisaccade and reactive prosaccade are integrated in a competitive manner in the intermediate layer of the SC. Cutsuridis et al. are quite clear that this competitive integration of the two decision signals means that "there is no need of a top down inhibitory signal that prevents the error prosaccade from being expressed" (p. 701). Within their model, the activity in the build-up neurons implementing the antisaccade begins to rise 50 ms after the activity build-up neurons mediating the prosaccade (on the grounds that the signal for the correct antisaccade must be derived from some temporally demanding vector transformation). The model also ensures that activity in antisaccade build-up neurons is always greater than activity in the prosaccade build-up neurons, and always eventually exceeds the threshold for saccade triggering (a reasonable assumption, they argue, given that it reflects the participants actual goal in the task). Given these parameters, and the competitive integration of the two decision signals (as activity in one pathway rises, it decreases in the other), their model accurately reproduced the error rate and correct antisaccade latency distribution of a large cohort of antisaccade data, and was also able to replicate the finding that whilst erroneous prosaccades towards the target are nearly always followed by a correct antisaccade, the opposite never occurs.

4.2. Working memory, goal activation and antisaccade performance

Goal directed behaviour relies on our ability to maintain and manipulate task relevant information in mind (working memory), whilst simultaneously ignoring task-irrelevant information and over-riding prepotent responses (inhibition). Converging evidence suggests that these two functions are highly interdependent (e.g. Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001) and several influential models consider them to be two sides of the same coin (e.g. Kimberg & Farah, 2001; Miller & Cohen, 2001; O'Reilly et al., 1999). Within Miller & Cohen's model of cognitive control, for example, the ability to ignore distractors does not involve an active suppression of irrelevant information, but rather reflects the frontally mediated biasing of information processing in posterior cortex in the favour of task relevant information. In other words, as with Cutsuridis et al's neural network implementation of the antisaccade task, current models of working memory and cognitive control have no need for a separate inhibitory mechanism. The interpretation of antisaccade errors as reflecting a failure to sufficiently activate the correct response (e.g. Eenshuistra et al., 2004; Nieuwenhuis et al., 2004; Reuter et al., 2005) suggests that working memory may play an important role in antisaccade performance.

In a direct test of the working memory hypothesis, Roberts et al. (1994) found that performing concurrent mental arithmetic tasks led to significant increases in antisaccade errors and correct antisaccade latencies in healthy participants. Presaging current competitive race models of antisaccade performance, they argued that successful "inhibition" of the erroneous prosaccade was an "associated by-product" of increased working memory activation underlying the production of the alternative, correct, response. Similar arguments have been used to explain the increase in antisaccade errors observed in elderly participants (Eenshuistra et al., 2004). More recently Mitchell, Macrae, and Gilchrist (2002) demonstrated that impairments in antisaccade performance vary as a function of working memory load. They used three variants of the *n*-back task, in which participants are presented with a sequence of letters (deliverd auditorially at the rate of one every 3 s) and required to indicate whether any given letter matches the letter that preceded it by *n* places. In the 0-back condition participants simply indicate whether the letter matches a prespecified target. They found that when performed simultaneously with a standard antisaccade task, a 2-back condition increased antisaccade errors and correct antisaccade latency compared to 1-back and 0-back conditions.

Further support for a role for working memory is provided by a study that compared antisaccade performance in participants with high or low working memory spans. Unsworth, Schrock, and Engle (2004) pre-screened individuals with the operation span task (OSPAN) which requires participants to solve a set of simple maths problems whilst simultaneously attempting to remember a set of unrelated words. Low span individuals made more antisaccade errors and had increased correct antisaccade latencies compared to controls. Finally, indirect supporting evidence is provided by studies (reviewed elsewhere in this volume) demonstrating increased antisaccade errors in psychiatric patients with established working memory dysfunction.

Whilst the studies cited above provide support for models suggesting working memory plays some role in antisaccade performance, the role itself and its relative importance remain ill defined. For example, Roberts et al. (1994) observed weak correlations between measures of working memory and correct antisaccade latency, and no correlation between working memory measures and antisaccade error rate. Other studies have failed to find clear cut relationships between measures of working memory capacity and antisaccade performance in healthy controls. For example Hutton et al. (2004) found no significant correlations between three measures of spatial working memory and antisaccade errors in a large sample of healthy participants (although these measures did correlate in patients with schizophrenia). According to goal activation accounts of antisaccade performance, the comparatively weak relationship between antisaccade performance and measures of working memory capacity is perhaps not surprising.

4.3. Attention and antisaccade performance

The nature of the relationship between attention and working memory is currently an active area of research within psychology (e.g. Awh & Jonides, 2001). According to one dominant model, working memory is comprised of a central executive component that controls three "slave" systems—the articulatory loop, the visuo-spatial scratch-pad and the episodic buffer (Baddeley, 2007). The central executive component of Baddeley's model is comparatively poorly specified compared to the articulatory loop component, but one of its functions is akin to attentional control—e.g. the selective activation and inhibition of information that is either more or less relevant to ongoing behaviour (Baddeley, 2007; Baddeley & Della Sala, 1996). Compelling support for a close link between working memory and attention is provided by Awh, Jonides, and Reuter-Lorenz (1998) who demonstrated that holding a specific spatial location within working memory facilitates processing at that location compared to other locations. Thus the extent to which attentional influences on antisaccade performance can be separated from working memory influences is not clear.

Fischer and Weber (1997) explored the influence of a number of stimulus conditions on antisaccade performance. They found that introducing a gap between the central fixation offset and the peripheral target onset results in an increase in antisaccade

errors. This finding is predicted by race accounts of antisaccade performance, because the effect of a gap on prosaccades is to decrease latency, thus increasing the probability of the prosaccade reaching threshold first. Interestingly, correct antisaccade latencies were approximately 25 ms faster when there was a 200 ms gap between fixation offset and target onset compared to overlap trials. This replication of the standard prosaccade gap effect in the antisaccade task has also been observed in other studies (e.g. Craig, Stelmach, & Tam, 1999; Klein, Bruegner, Foerster, Mueller, & Schweickhardt, 2000; Smyrnis et al., 2004). Importantly, it appears that the gap effect is attenuated in the antisaccade task compared to the prosaccade task (Reuter-Lorenz et al., 1991, 1995), a finding these authors attribute to the fact that the gap allows for a "fixation release" process (see Section 2.1.1) mediated by low-level neural mechanisms in the superior colliculus which is not involved to the same extent in more volitional, non-visually guided antisaccade responses.

In an extension of the cueing studies performed on prosaccade tasks, Weber, Durr, and Fischer (1998) sought to determine the effect of peripheral cues on antisaccades. In their task the cue (which occurred at one of two square markers placed either side of fixation) always signalled the position to which a correct antisaccade should be made (e.g. the location opposite to the one in which the target subsequently appeared). Despite the fact that the cue always correctly indicated the correct location for a saccade, antisaccade errors and correct antisaccade latencies were both increased. The authors suggest that under antisaccade instructions, the cue acts as a trigger for an antisaccade, resulting in an attentional shift in the opposite direction. As attention is now shifted towards the location in which the target subsequently appears, capture errors are more likely, and, even in the absence of an error there is a time cost associated with shifting attention back to the correct location, resulting in the increase in correct latencies. These results are in accord with the explanations of antisaccade performance based on goal activation described above.

Kristjánsson, Chen, and Nakayama (2001) explored the role of attention in antisaccade performance by requiring participants to perform a concurrent discrimination task. They found that when the discrimination event occurred shortly before (100–300 ms) the peripheral target appeared, correct antisaccade latencies were dramatically reduced compared to a baseline condition in which there was no concurrent task. They argue that the attentionally demanding discrimination task interferes with the reflexive prosaccade towards the target, thus negating the need for a time consuming disengagement from the target and allowing the correct antisaccade to be initiated more quickly. Interestingly there was no reduction in antisaccade errors, although error rates were very low, and only a small number of highly trained participants performed the task. Further evidence in support of this interpretation is provided by Kristjánsson, Vandenbroucke, and Driver (2004), who demonstrated that somatosensory stimulation slowed prosaccades and speeded antisaccades, removing the substantial latency difference that is typically observed between pro and antisaccades. Indeed, the competition model of antisaccade generation put forward by Kristjánsson et al., 2001; Kristjánsson, 2007) could be considered as another example of a "parallel processing" or "race" account in that it clearly predicts that processes that result in increases in prosaccade speed will result in decreases in correct antisaccade latency (and hence an increase in error rate).

4.4. Cognitive control and error monitoring in the antisaccade task

A great advantage of saccadic tasks, one which is only just beginning to be exploited by researchers interested in cognitive processes, is that they allow the ongoing control of behaviour to be studied. Complex behaviour requires that its progress be continually monitored in order to prevent, detect and (if necessary) correct any erroneous responses that are made (e.g. Mayr, 2004; Mayr, Awh, & Laurey, 2003; Miller & Cohen, 2001). Current models of cognitive control suggest that this ongoing "conflict monitoring" should result in trial by trial contingency effects in the antisaccade task. In other words the outcome of any given trial (correct or error) should have some impact on performance in the subsequent trial (Botvinick, Braver, Barch, Carter, & Cohen, 2001). An example from reaction time tasks is "post-error slowing"—a shift in the trade off between speed and accuracy to a more cautious response mode which occurs on the trial following an erroneous response (Botvinick et al., 2001; Hodgson, Golding, Molyva, Rosenthal, & Kennard, 2004; Rabbitt, 1966).

In a contingency analysis of a large number of antisaccade trials, Tatler and Hutton (2007) found some evidence for post-error slowing of correct antisaccade on trials following errors with long correction latencies, but also, contrary to conflict monitoring accounts of cognitive control, no corresponding reduction in error rate. In fact, there was a significantly increased probability of making an error if an error had been made on the preceding trial and the probability of making an error increased as a function on the number of preceding errors. The authors concluded that the time course of goal neglect (a failure to sufficiently activate the correct antisaccade response) can often span several trials in the antisaccade task.

These findings extend earlier research by Mokler and Fischer (1999) that demonstrated that participants are typically unaware of around 50% of the errors that they make. Importantly, these "unaware" errors tended to have smaller amplitudes and faster correction times than errors of which the participant was aware. These results were replicated by Nieuwenhuis, Ridderinkhof, Blom, Band, and Kok (2001). This research suggests the possibility that there may be more than one "type" of antisaccade error. Rapidly corrected errors, typically of small amplitude and of which the participant is unaware, may occur when the correct response is sufficiently activated, and generated in parallel with the erroneous response, but a very fast prosaccade towards the target reaches threshold first. The correct saccade follows very shortly afterwards, possibly even curtailing the prosaccade, and thus resulting in the reduced amplitude. As Tatler and Hutton (2007) point out, these "errors" can occasionally be corrected so rapidly that a significant proportion of them actually result in the eye reaching the mirror image location faster than on the average correct trial. In this sense there may be something adaptive about having sufficient noise in the system to allow for occasional errors. More slowly corrected errors, (which include trials on which errors are "compounded" by one or more further saccades towards the target) may reflect genuine goal neglect, and suggest that the correct response is not always programmed in parallel, and may occasionally be made in response to awareness that an error has been made. An important goal for future research will be to establish the extent to which different "types" of antisaccade errors reflect the same or different underlying cognitive operations.

4.5. Learning effects in the antisaccade task

A number of studies have demonstrated that participants can demonstrate significant improvements in antisaccade performance when performance is measured over time. For example, antisaccade error rates and correct antisaccade latencies decreased significantly in a group of participants who practiced the antisaccade for 8 days over a 2 week period (Dyckman & McDowell, 2005). Interestingly, participants in this study who practiced a fixation task demonstrated no reduction in error rates, whereas participants who practiced a prosaccade task made more errors when subsequently tested on the antisaccade task. These findings support parallel "race" models, in that practicing the prosaccade task presumably increased the likelihood of activity underlying the pro-

saccade response reaching threshold first. Ettinger et al. (2003a) observed a reduction in antisaccade error rate and increase in spatial accuracy in a group of healthy participants tested an average of two months apart, and with no intervening practice. Research suggests that learning effects can also operate over much shorter timescales, and with considerably less rehearsal than occurred in the Dyckman and McDowell (2005) study. Smyrnis et al. (2002) in a very large sample found that antisaccade error rate and correct latencies decreased significantly from the first block of 10 trials to the second block of 10 trials. Similar within-session practice effects have been observed in studies using pre-post experimental designs (Ettinger et al., 2003b; Klein, Raschke, & Brandenbusch, 2003; Rycroft, Hutton, & Rusted, 2006). These latter findings are of particular relevance in the context of longitudinal research, or other studies that involve repeat testing. These practice effects are not seen in prosaccades (Ettinger et al., 2003a) and are thus likely to reflect the learning of strategies that support correct antisaccade performance.

Further evidence for learning effects is provided by the demonstration that antisaccade errors to targets appearing on the left or right increase with increasing probability of saccades being made in that direction (Koval, Ford, & Everling, 2004). The authors interpret this finding as reflecting increased preparatory activity in neurons implementing saccades in the most likely direction that increases the likelihood of stimuli appearing in that location triggering a saccade.

4.6. The effects of incentive

A more complex influence of learning on antisaccade performance is revealed in studies that manipulate reward or incentive associated with saccade targets. Blaukopf and DiGirolamo (2006), for example, found that both high reward and high punishment conditions resulted in increased correct antisaccade latencies. In this study the target form determined the nature of the reward or punishment. In other studies, in which the value of the incentive was indicated prior to the targets onset, increased incentives have been found to reduce antisaccade errors in healthy adults (Duka & Lupp, 1997; Hardin, Schroth, Pine, & Ernst, 2007; Jazbec et al., 2006). These latter findings are readily explained within the working memory activation model outlined above on the assumption that high reward trials result in an increased activation of the task goal.

4.7. Other cognitive influences on antisaccade performance

Other top down effects on antisaccade performance have been observed in studies that have manipulated the instructions that participants are given. In a recent study Taylor and Hutton (in preparation) examined antisaccade performance under four different conditions, each of which differed only in the instructions given. In the standard condition participants were asked to make saccades to the mirror image location as quickly and as accurately as possible. In the speed condition participants were asked to make saccades to the mirror image location as quickly as possible, and in the accuracy condition the participants were instructed to take as much time as they needed to make a saccade to the precise mirror image location of the target. Finally, in a "hold" condition, participants were instructed to try and maintain fixation centrally until they were sure they had identified the target's location, and then initiate a saccade to the mirror image location. Compared to the standard condition, the "hold" instructions led to a significant reduction in the number of antisaccade errors, despite dramatically increasing the average correct antisaccade latency. According to race models increasing the amount of time taken to produce a correct response should result in an increase in errors. The "hold" instructions encourage sequential (as opposed to parallel) processing, suggesting that race models may not account for antisaccade performance under all circumstances.

Mosimann et al. (2004) instructed participants to make brief glances towards a sudden onset target and then "correct" this eye movement by looking towards the mirror image location as quickly as possible. They found that the latency of such "deliberate errors" was significantly higher than the latency of true antisaccade errors. In addition, the time between the "error" and the "correction" was significantly greater when genuine antisaccade errors are made, a finding that supports parallel race models of antisaccade performance.

5. Conclusions and future directions

Despite their ubiquity and apparent effortlessness, saccadic eye movements can involve a wide variety of different cognitive processes. Even the generation of a simple prosaccade towards a sudden onset target can be seen as a decision process, involving a complex weighting of both bottom up information concerning basic stimulus properties, and top down information concerning current goals and intentions. Whilst attention appears intimately linked to saccadic eye movements made under varying degrees of bottom up and top down control, the precise nature of the relationship remains unclear. Techniques such as transcranial magnetic stimulation (see glossary) have the potential to generate important data allowing the causal links between attention and saccades to be elucidated.

The antisaccade task remains a popular tool with which to explore the cognitive processes involved in the ongoing control of purposeful behaviour, and current competitive race models of antisaccade performance are allowing new insights into the processes underlying successful performance on this task. This understanding will inevitably provide important insights into why certain psychiatric populations perform more poorly than healthy controls, but several important questions remain to be resolved. In particular, researchers need to develop a more refined understanding of what exactly constitutes an antisaccade error—and be open to the possibility that there are different types of error that may have different types of causes and consequences on subsequent behaviour. Developing race models to incorporate these findings will be a challenging, but by no means impossible task.

Another important focus for future antsiaccade research must be identifying the source (or sources) of the enormous individual differences in both error rate and correct antisacade latency that are routinely observed in healthy participants. With a few exceptions, most attempts to identify individual differences (for example in working memory capacity) that correlate with antisaccade performance have found weak only relationships at best (see Hutton & Ettinger, 2006). Correlational research has tended to focus on individual differences in working memory such as capacity that are not necessarily the most relevant to antisaccade performance. Future research employing measures of goal activation may help clarify the role of working memory in antisaccade performance. As Reuter and Kathmann (2004) point out, the term "working memory" is often used in a rather vague sense, and accounts of antisaccade performance that make reference to it need to ensure that the precise mechanisms involved are well specified. A systematic programme of research is required in order to establish the extent to which a wide range of individual differences mediate antisaccade performance. These individual differences should include personality traits such as impulsivity and schizotypy and also measures of basic information processesing efficiency such as processing speed.

In conclusion, research in healthy participants into the cognitive processes involved in saccadic eye movements has been, and will continue to be critical in developing sophisticated models of the

neurocognitive processes underlying goal directed behaviour, and how these processes may become dysfunctional in psychiatric disorders.

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