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Review

Eye movement trajectories and what they tell us

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Abstract

In the last two decades, research has shown that eye movement trajectories can be modified by situational determinants. These modifications can inform us about the mechanisms that control eye movements and they can yield information about the oculomotor, memory and attention system that is not easily obtained via other sources. Eye movement trajectories can deviate either towards or away from elements in the visual field. We review the conditions in which these deviations are found and the mechanisms underlying trajectory deviations. It is argued that deviations towards an element are caused by the unresolved competition in the oculomotor system between elements in a visual scene. Deviations away from an element are mainly observed in situations in which top-down preparation can influence the target selection process, but the exact cause of such deviations remains unclear.

Keywords: Eye movements; Trajectory; Saccades; Superior Colliculus; Attention

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1. Introduction

In everyday life, we are continuously faced with complex visual scenes that might contain important information. As visual acuity is best only in a small part of our retina, the fovea, we typically make rapid eye movements called saccades to examine different locations in our environment. It is commonly assumed that saccades are ballistic movements: once launched, their trajectories are fixed as that of a bullet. However, eye movement research has suggested that this is not the case (Robinson, 1975; Becker, 1989). A saccade can initially be executed to one location but mid-flight turn around and land on a second location (Van Gisbergen et al., 1987; Amador et al., 1998). This finding has been taken as evidence that saccades are not pre-programmed movements, but are dynamic in nature.

Also in a second way saccades are not comparable to bullets going straight to their target. Instead, eye movements can better be compared to the flight of an airplane. The trajectory of an airplane from the start location to its destination is rarely if ever straight, but deviates from a straight line under influence of a multitude of factors like airstreams, fixed air traffic corridors and the other airplane traffic. When looking at the trajectory of saccadic eye movements, one will also observe that the eyes are almost never moved in a straight line.

One of the first to report this finding was Yarbus (1967), who wrote that "saccades performed at an angle … are most frequently recorded as curved lines" (pp. 140). After this observation, many other researchers investigated this phenomenon and its origins (e.g. Viviani et al., 1977; Minken et al., 1993; Erkelens and Sloot, 1995). They found that there is substantial between-subjects variability, but the within-subject variability in the curvature in the trajectory of a simple eye movement is limited (Bahill and Stark, 1975). This led Smit and Van Gisbergen (1990) to describe dynamic properties of saccade curvature as a 'signature' (pp. 341): when saccading to the same location, idiosyncratic eye movement trajectories can be observed for each participant (Fig. 1). Although the exact cause of this phenomenon is not yet known, it has been suggested that saccade curvature is determined by mechanisms located in the final pathway of the eye movement production system (Smit and Van Gisbergen, 1990).

In addition to individual variation in trajectories, recent studies have revealed that environmental determinants can modify the idiosyncratic saccade trajectories. For instance, recent studies reported effects of the allocation of attention and the presence of an irrelevant distractor on saccade trajectories (i.e. Sheliga et al., 1994; Doyle and Walker, 2001; Van der Stigchel and Theeuwes, in press; Walker et al., in press). The current paper reviews these studies. We will claim that modifications observed in saccade trajectories are a measure of visual processing, and that they can inform us about the underlying mechanisms that control saccadic eye movements.

Two terms have been used to denote the environmental modifications of the baseline eye movement trajectory, namely 'curvature' and 'deviation'. Although this description does not fit for all studies, 'curvature' is generally used to describe differences in trajectories from saccadic fixation to the saccade endpoint (i.e. whether the saccade was a straight line or a curved one), whereas 'deviation' measures mainly compare the saccade trajectory with a straight line from saccadic fixation to the designated target position. This last measure includes possible changes in saccade endpoints relative to the target location (see Appendix for an overview of the different trajectory measures). In this review, we consistently will use the term 'deviation,' because our overview concerns the influence of environmental factors on the total change of the trajectory of the saccade, including the saccade endpoint.

The studies we will review typically use a paradigm in which a central fixation cross is presented at the start of the trial. Participants are required to saccade to the location of a target that appears abruptly in the visual display ('an abrupt onset'). The trajectory of this eye movement is the measure central to this review. Other important measures are saccade latencies (the time between target presentation and saccade initiation) and the correctness of the saccade. The experimental variations used to manipulate trajectories include the addition of distracting elements in the visual fields ('distractors') and manipulations of attentional allocation, expectancy, memory and inhibition of return. In these experiments participants are typically either humans or rhesus monkeys.

Saccade deviations can be divided into deviations *towards* or *away* from locations in the visual scene other than the target

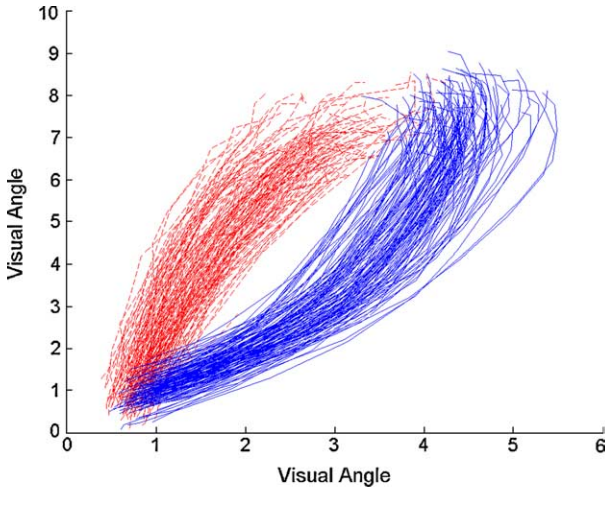

Fig. 1. Eye movement trajectories of two participants to a single target obtained in one of our experiments (Van der Stigchel and Theeuwes, in press). Saccade trajectories of the individual participants are quite idiosyncratic.

location. First, we will discuss conditions in which there is a deviation of the eye movement towards an element in the visual scene that is not the target. How these saccades come about is relatively well understood, and we will review both theoretical accounts of deviation towards and physiological evidence. In a later section, we review deviations away from non-target locations. It is much less clear how and why saccades deviate away from locations. We will review existing theories and discuss physiological evidence in line with each theory.

2. Deviation towards

In three situations deviation towards are observed: (1) in double step paradigms; (2) paradigms investigating the global effect and (3) in visual search paradigms. We discuss each in turn.

2.1. The double step paradigm

Among the first paradigms to reveal an influence of the environment on idiosyncratic eye movement was the double step paradigm (Westheimer, 1954; Wheeless et al., 1966; Levy-Schoen, 1969; Becker and Juergens, 1979; Findlay and Harris, 1984; Van Gisbergen et al., 1987; McPeek et al., 2000). In this experimental setup, observers are instructed to make an eye movement from the central fixation point to a target element in the visual field. After a variable delay the initial target disappears and a new target appears at a different location. When the time difference between the first and the second target is large, people correctly saccade to the second target. However, if the delay between the onset of the first and the second target is relatively short (i.e. 50 ms, Van Gisbergen et al., 1987) and the distance between the two targets is large (i.e. 40°, Van Gisbergen et al., 1987), the eye movement trajectory is influenced. Specifically, initially the saccade is executed to the first target location but changes its direction mid-flight and lands in the direction of the second target location (so-called 'turn-around saccades') (see also McPeek et al. (2000)).

2.2. The global effect

The 'global effect' occurs when a target and an irrelevant distractor element are placed close to each other, typically within 20 or 30° of angular distance (Coren and Hoenig, 1972; Walker et al., 1997; Van der Stigchel and Theeuwes, 2005b). In this situation, eye movements to the target generally land on an intermediate location between target and distractor. Behavioral findings show that the eyes typically land closer to the location where a target is most likely to appear (He and Kowler, 1989), and closer to the onset with the greatest luminance (Deubel et al., 1984) or largest size (Findlay, 1982). These findings support a 'center of gravity' account, which states that the saccade endpoint is based on the relative saliency of the elements in the saccade map (Coren and Hoenig, 1972). Furthermore, the global effect occurs more frequently in saccades with a short latency (Ottes et al., 1985).

2.3. Visual search

In visual search experiments, participants have to search for a target presented among multiple distractors. Although in most visual search paradigms the influence of individual distractors is intractable, in several studies one distractor had a special position that made it possible to investigate the effect of this distractor on saccade trajectories. The distractor may, for example, be the only one not placed on one line with the target (McPeek et al., 2000) or may be the only salient one among non-salient distractors (Godijn and Theeuwes, 2002b). Even if such a distractor is positioned far enough from the target to not elicit a global effect, deviations towards the distractor are observed for saccade trajectories to the target. This effect has been shown in both humans (McPeek et al., 2000; Godijn and Theeuwes, 2002b; Walker et al., in press) and monkeys (McPeek and Keller, 2001; McPeek et al., 2003; Port and Wurtz, 2003). For example, human observers had to make a saccade to an odd-colored target presented along homogenously colored multiple distractors (so-called 'color-oddity search task', McPeek et al., 2000). Target and distractor colors were switched from trial to trial, so on some trials a green target was presented along red distractors, while on other trials a red target was presented along green distractors. When a color switch occurred, observers were more likely to make erroneous saccades to a distractor and deviations towards a distractor were observed for correct saccades. This indicated that the target color of a previous trial primes the search process on the current trial.

In all visual search and double step studies, the dichotomy between deviations towards and turn-around saccades is ill defined. A saccade that turns around mid-flight can be seen as deviating towards the initial saccade goal. There is no clear definition of when a saccade is a turn-around saccade and when it is 'just' deviating towards a distractor. It is therefore likely that studies reporting either one of these two, are actually reporting both types of eye movement trajectories.

2.4. Theories of deviations towards

As reviewed above, deviations towards thus occur when the target and another element (target or distractor) are presented at the same time (global effect and visual search), or in close temporal proximity (double-step paradigm). A dominant explanation of these deviations is the one provided by Tipper's population coding theory (Tipper et al., 1997, 2000). This theory was first proposed to account for trajectory deviations in hand movements, which are beyond the scope of this review. Since similar dynamics are observed with reaching for an object are also found in saccades (Tipper et al., 1997), Tipper and colleagues extended their theory of manual responses to eye movements. The theory states that possible target objects are represented by a large population of neurons that encode the movement towards each target object as a vector. The strength of a population code is related to the saliency of the corresponding object. When two possible targets are positioned in close proximity, the populations corresponding to these targets will be combined to one mean population of which the vector will point to an intermediate location. Since participants are instructed to move their eyes to only one location, competition between the two active populations has to be resolved by inhibiting one of them. Inhibitory selection of one population over the other may shift the resulting movement vector in such a way that it affects the final response to the target.

According to this theory, inhibition can be achieved through two independent inhibitory mechanisms. The first mechanism makes use of lateral inhibition between direction-coding cells within a motor map (Georgopoulos, 1995). Direction-coding cells are positioned so that they are near cells coding for the same direction. Because each cell has excitatory connections to cells that are near and inhibitory connections to cells that are more distant (Munoz and Istvan, 1998), distractors can be inhibited by the enhancement of target cells. However, if the distractor activity is too high, this mechanism is not sufficient to resolve the response conflict. In that case, a second mechanism can suppress the distractor activity by ‘reactive feedback’ (Houghton and Tipper, 1994). This feedback is much stronger and is related to the saliency of the to-be-inhibited object. This mechanism is responsible for deviation away from the inhibited object. The population coding theory predicts that distractors that are highly salient will evoke a large amount of inhibition and therefore will cause the hand or eye movement to deviate away from the distractor. Distractors that are not so potent will not evoke reactive feedback, resulting in deviation towards the distractor.

This latter assumption can be questioned with respect to eye movements. Whereas the population coding theory claims that deviation towards will only be observed with distractors that are not potent, behavioral studies seem to indicate that the opposite is true: deviation towards seem to be present when the competition between the target and the distractor is very strong. The three types of experimental setups that typically show deviations towards are the ones that evoke either a very strong competition between target and distractor (in ‘double-step’ or ‘visual search’ setups) or in which target and distractor are closely aligned (the ‘global effect’).

A second interpretation of deviations towards can be seen as a simplified version of Tipper’s population coding theory. This simplified account shares with Tipper’s theory the claim that targets are represented as population codes, but states that saccade trajectories are initiated on the basis of the ‘weighted average’ of the corresponding vectors (Robinson, 1972; McPeek and Keller, 2001; McPeek et al., 2003; Port and Wurtz, 2003). This account claims that deviations towards is observed when the average vector points to a location between two elements. It does not assume that only less potent distractors result in deviation towards, but all distractors can evoke deviations towards as long as the average vector points to an intermediate location. This weighted average account is based on results from neurophysiological recordings, reviewed in the next section.

2.5. Neurophysiological investigations of deviation towards

To provide some background, we first shortly outline what is known about the neurophysiology of saccade target selection. Many models of saccade generation have assumed that target selection is the result of competitive interactions among groups of neurons coding for the possible target locations on a common motor map (Kopecz, 1995; Trappenberg et al., 2001; Godijn and Theeuwes, 2002b; McSorley et al., 2004; Van der Stigchel et al., submitted for publication). This motor map is often thought to be located in the intermediate layers of the superior colliculus (SC) (Sparks and Hartwich-Young, 1989; Schall, 1991). This mid-brain structure contains a retinotopically organized map in which neural activity is correlated with target selection (Wurtz et al., 1980; McPeek and Keller, 2004). Moreover, stimulation of cells in the SC results in a saccade to the coordinates corresponding to the stimulated location (Robinson, 1972). When multiple targets are present, activity at the site of the chosen target in the SC increases until saccade initiation, whereas it decreases at other sites (Basso and Wurtz, 1997) suggesting that the SC is involved in target selection. To accomplish this, the SC integrates input from many cortical areas such as the Frontal Eye Fields (FEF), the Supplementary Eye Fields (SEF), the posterior parietal cortex and occipital visual areas (Munoz, 2002). It sends the outcome of this integration process to the brainstem premotor circuitry where the eye movement is programmed (Moschovakis, 1996). Evidence suggests that the region of maximal activity in the SC determines which target is going to be foveated, but not how this is to be brought about (e.g. via a saccade, or a combined eye and head movement, or via smooth pursuit, Krauzlis et al., 2004).

In this review, we focus on the SC when we discuss neurophysiological investigations of saccade deviations, as almost all studies in this area have been reports of recordings in the SC. However, it should be noted that other brain areas like the FEF or the SEF may also play a role in the determining of saccade deviations. It would not be surprising if similar results will be obtained when recording in the FEF or SEF as have been in the SC.

McSorley et al. (2004) proposed a model in which the initial saccade direction is controlled by the SC, while the cerebellum corrects possible deviations from the target direction (see also Quaia et al., 1998). The cerebellum monitors saccade progress and compensates for directional errors by adjusting the motor signal. So, when the initial direction of the saccade is programmed to a location that is not the target location, on-line cerebellum feedback takes care of the saccade the correct landing position.

Therefore, even though it is known that the SC does not determine the exact trajectory of a saccade (Quaia et al., 1998; Goossens and Van Opstal, 2000; Bergeron et al., 2003), its activity does seem to influence the trajectory beyond the initial direction. Three paradigms have been discussed in which deviations towards can be observed. All the three have been combined with cell recordings in the SC in at least one study.

These studies support the idea that deviations towards can be explained by competition between saccade goals in the SC, in line with the weighted average account.

McPeek et al. (2003) investigated deviation towards in a *visual search paradigm* using the color-oddity search task introduced earlier. If two saccade goals in the SC are activated, a saccade will be initiated to the goal with the highest activity, but will deviate towards the other location. McPeek and colleagues showed that this deviation was accompanied by increased pre-saccadic activity at the location the trajectory deviated towards. More important, the level of activity recorded at this location was correlated with the magnitude of this deviation. In the same study, further evidence was provided by micro-stimulation of the SC below the threshold for saccade generation. Eye movements that were initiated to a different location curved towards the stimulated location. The magnitude of this deviation was correlated with the induced activity at the stimulated location (McPeek et al., 2003).

In situations in which the *global effect* occurs, activity in the SC has been found to be highest at a location in between the two targets (Van Opstal and Van Gisbergen, 1990; Glimcher and Sparks, 1993). This seems to imply that activity at both target locations is summated and is therefore highest at an intermediate location. Whether eye movements are initiated to the weighted average or to the highest location in the saccade map (Findlay and Walker, 1999), they will land on an intermediate location between the two targets.

Port and Wurtz (2003) investigated saccade trajectories in a *double-step paradigm*. Trials in which turn-around saccades occurred were accompanied by initial high activity at the distractor location, with a later shift towards the target location. Such an effect was absent for straight saccades.

To summarize, deviation towards seems to be caused by unresolved competition between elements in a visual scene. It occurs when a target and a distractor both elicit activity in the motor map at the time of saccade initiation. These findings are in line with a weighted average account (see McPeek and Keller, 2001; McPeek et al., 2003; Port and Wurtz, 2003). According to this account, targets are represented as neural populations and saccade trajectories are initiated on the basis of the weighted average of the corresponding vectors, with activity in the SC being the physical instantiation of these vectors. The sole factor that seems to distinguish these three instances is the timing of the target selection process (see Fig. 2).

In case of the global effect in which two elements are presented in close proximity, the weighted average is located at an intermediate location because the vectors that encode the elements in the saccade map merge to one mean vector. The competition between the two elements is not resolved (or too late) and the saccade ends at the intermediate location. Evidence for this idea is the finding that the global effect is more frequent for short saccade latencies than for longer latencies (Ottes et al., 1985). Target selection is most likely not to be complete at shorter latencies. If, however, the competition is resolved shortly after saccade onset, a saccade is initially directed to an intermediate location but the movement is corrected and programmed to the target location ('deviation towards').

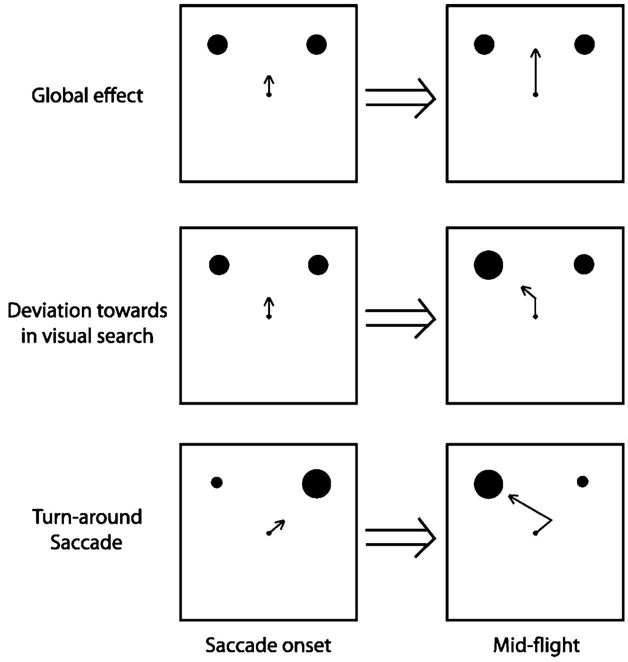

Fig. 2. Activity in the saccade map at two time points during saccadic target selection for the three instances of deviation towards. The arrows represent the weighted avqerage and the circles represent the height of activity at a certain location (large circle means high activity).

Turn-around saccades are explained by the change of saccade goal in mid-flight. In these situations, competition is at saccade onset biased towards one location, and the saccade is initiated towards it. However, mid-flight a different location than the original saccade target location wins the competition. In that case, the saccade will change direction to that location.

3. Deviation away

Paradigms in which deviation away occurs can be subdivided into two rough categories: those in which eye movements deviate away from irrelevant distractors and conditions in which saccades deviate away from a location to which attention is voluntary allocated. We will now discuss each in turn.

3.1. Irrelevant distractors in the visual field

3.1.1. Visual search with one distractor

Doyle and Walker (2001) were the first to show that completely irrelevant distractors could evoke deviations away. Participants had to make a saccade either up or down from fixation in the presence of a completely irrelevant distractor. Two types of saccades were used: voluntary and reflexive saccades. Reflexive saccades were evoked by the onset of the target element, while voluntary saccades were initiated by a central cue. An irrelevant distractor was presented to the left or right of fixation. Both types of eye movements were

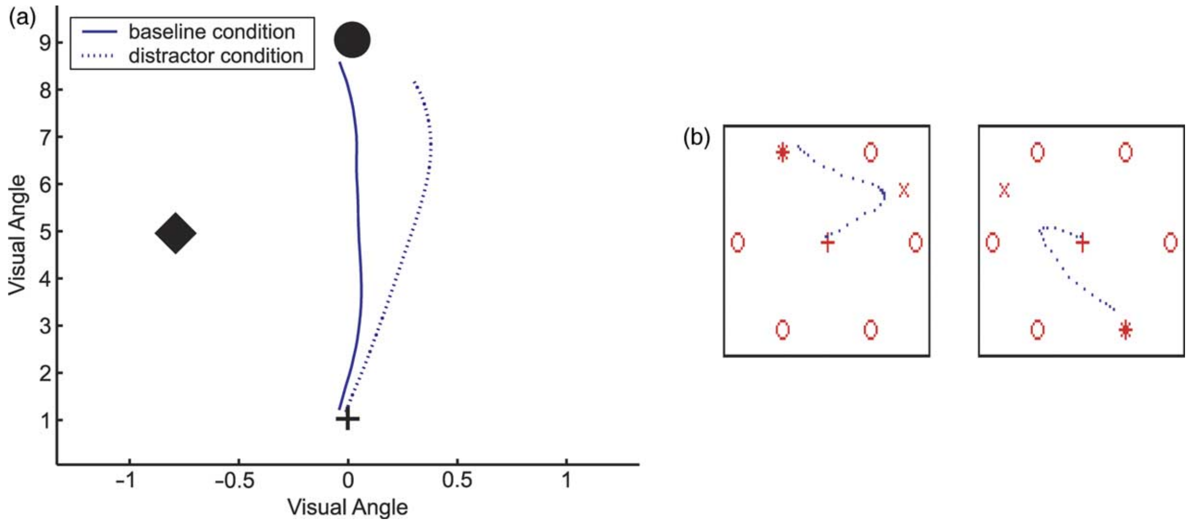

Fig. 3. (a) Mean eye movements of one participant in a cueing experiment. The target location was cued prior to target onset by a central arrow. Participants were instructed to make an eye movement to the target. In the baseline condition no distractor was presented, while in the distractor location a distractor was presented simultaneously with the target. The target is represented by the black circle, the distractor by the black triangle. Compared to the baseline condition, eye movements deviated away from the distractor in the distractor condition (Van der Stigchel and Theeuwes, unpublished data). (b) Two examples of turn-around saccades: eye movements that change direction during their flight (Godijn and Theeuwes, unpublished data). Participants were instructed to fixate on the central cross until the target ('*') was presented, to which had to make a saccade. In some cases, an irrelevant distractor ('x') was presented simultaneously with the target. In these cases, some turn-around saccades are elicited, saccades that are initiated to the distractor, but mid-flight change direction to the correct target location.

accompanied by deviation away from the distractor (see Fig. 3a).

3.1.2. Multiple irrelevant distractors

A recent paper examined eye movement trajectories to a target in the presence of multiple similar onset distractors (McSorley et al., 2004). The paradigm was similar to studies that have examined the influence of a single irrelevant distractor. Voluntary vertical saccade trajectories were shown to be straight when two distractors were presented at mirrored locations in both the left and right visual field. Also when the distractors were in opposite hemifields but not at mirrored locations there was no effect of the distractors on saccade trajectory. Therefore, the exact spatial location of a distractor does not seem to modulate saccade deviations. The only exception is that distractors induce more deviation when they are presented in the same hemifield as the target then when they are presented in a different hemifield (see also Doyle and Walker, 2001) and when a distractor is placed close enough to the target to elicit a global effect (i.e. Van der Stigchel and Theeuwes, 2005b).

3.1.3. Oculomotor capture tasks

When one of the distractors is highly salient, the eyes can be captured involuntarily (Theeuwes et al., 1998; Godijn and Theeuwes, 2002b). In 'oculomotor capture' tasks, observers view displays containing a number of gray circles positioned on an imaginary circle around a central fixation point. After a fixed period, all circles change color except one. This is the target circle. Upon the presentation of the target, on some trials an additional irrelevant red circle is presented with abrupt onset in the display. In 30 to 40% of trials in which the additional onset circle is presented, participants do not saccade to the target element, but erroneously make an eye movement to the onset distractor element: the eye is 'captured' by the onset distractor.

Saccade trajectories show two types of characteristics in the onset condition: when a saccade is correctly performed to the target element, saccade trajectories deviate away from the irrelevant distractor, as they do when only one distractor is present (Doyle and Walker, 2001). This shows that distractors do not uniformly influence saccade trajectories, but that their salience modulates how strongly saccades deviate away from a distractor.

In this paradigm, only in a small portion of trials turn-around saccades are observed: saccades initially go towards the distractor, but then turn to the target circle (see Fig. 3b). These cases seem related to the trials in which the eyes are captured by the onset distractor, with the difference that in trials with turn-around saccades the target location is activated in time to correct the saccade.

3.1.4. The role of target similarity

Distractor salience is a bottom-up characteristic, not influenced by task variables. Ludwig and Gilchrist (2003) showed that trajectories are also modulated by a task-related factor, namely the similarity of the distractor to the target. This research was based on the finding that oculomotor capture was more likely if the distractor has the same color as the target element relative to a condition in which the colors were different (Ludwig and Gilchrist, 2002b). The fact that goal-driven information can increase capture by a distractor indicates that stimulus-driven properties and goal-driven signals are integrated and jointly determine saccade goals. To find further evidence for the integration of these two signals Ludwig and Gilchrist (2003) used deviations in saccade trajectories as a measure. In their experiments, participants made saccades to one of two elements located either above or below the fixation point. Which element was the target was indicated by a color change. An abrupt onset distractor appeared either left or right of the horizontal meridian at the same time as the color change. The color of this distractor was either the same or different as that of the target. Deviations away were observed for both types of distractors. When target and distractor appeared simultaneously and the central fixation point was removed prior to target appearance, the deviation was unaffected by distractor color. This was not the case when either the onset appeared 78 ms before the target or when fixation point was not removed. In that case there was more deviation away when the target was similar to the distractor compared to when they were dissimilar. Not removing the fixation point delays saccade initiation (Saslow, 1967; Reuter-Lorenz et al., 1991), giving top-down signals more opportunity to manifest themselves in target-directed saccades.

The observed differences in saccade deviations led Ludwig and Gilchrist to conclude that the initial response is stimulus-driven, but that later in time the stimulus driven signal is combined with the influence of top-down input (see for a similar account Van Zoest et al., 2004).

3.1.5. Eye movements and multi-modal interactions

Not only visual distractors or the allocation of attention can influence saccade trajectories, but distractors in other modalities evoke similar deviations. It is known that multi-modal information about an object's location can reduce response latencies to this target. For example, saccade latencies to a target are lower when target onset is accompanied by an auditory signal at its location (Lee et al., 1991; Corneil et al., 2002). Frens et al. (1995) showed that when visual and auditory stimuli were presented vertically aligned, saccades typically started in a direction in between the two stimuli. The presence of a localized auditory stimulus can thus influence the trajectory of saccades to a visual target when they are placed close enough, in a similar way as in the case of two visual targets (global effect).

Doyle and Walker (2002) examined the relation between non-visual modalities and saccade trajectories. Participants made eye movements to locations above or below central fixation. During these eye movements, visual, auditory, or somatosensory stimuli were present on the left or the right side. These distractors provided task-relevant information about which target to saccade to. In line with earlier studies, these voluntary eye movements deviated away from visual distractors. Although smaller, this effect was also observed for auditory and somatosensory stimuli. This was replicated for reflexive saccades when task-irrelevant distractors preceded the onset of the target by 100 ms.

The observation that stimuli of modalities other than the visual modality can influence saccade trajectories gives rise to the idea that stimuli of all modalities are represented on a common motor map. Indeed, neurons in the SC are also responsive to auditory and tactile stimuli (Stein and Meredith, 1993), although fewer neurons in the SC respond to auditory and tactile stimuli than to visual stimuli (Stein and Meredith, 1993). The finding that fewer neurons respond to auditory and tactile stimuli might also explain why deviation away was smaller for auditory and somatosensory stimuli. These stimuli have less pronounced representations in the SC and therefore evoke less competition than visual stimuli.

3.2. Eye movements and manipulations of voluntary attention

In the previous section, studies were reviewed in which saccades deviated away from irrelevant distractors. In this section, we discuss studies involving endogenous (or top-down, voluntary, goal-directed) covert orienting. Covert orienting is achieved by a shift of spatial attention without making an eye movement (overt orienting refers to an eye movement).

The first to study the influence of voluntary attention on eye movement trajectories were Sheliga et al. (1994, 1995a,b). Their findings were considered evidence for the premotor theory of attention (Rizzolatti et al., 1987; Rizzolatti et al., 1994). This theory claims that the mechanisms involved in programming saccades are the same as those involved in spatial attention. In particular, according to the theory directing attention to a location is nothing more or less than preparing a saccade to that location.

In their experiments, Sheliga and colleagues examined whether directing attention to a spatial location influences the trajectory of a predetermined eye movement. Observers had to make vertical saccades to a target below or above the fixation point (Sheliga et al., 1995b). An imperative stimulus indicated whether an upward or downward saccade had to be made. This imperative stimulus was presented within one of four peripheral boxes positioned in the upper and the lower hemifield to the left and right of the target locations. The eyes deviated away from the imperative stimulus. This deviation was greater when the saccade target and the imperative stimulus were both in the upper or lower hemifield. In another study, deviations were observed for horizontal as well as vertical saccades (Sheliga et al., 1995a), and were observed when attention was oriented reflexively to a transiently presented imperative stimulus and when attention was oriented voluntary by a central directional cue (Sheliga et al., 1995b). These studies indicate that spatial attention, as directed to the imperative stimulus, leads to activation within the oculomotor system. This supports the premotor theory's assumption that a covert shift of attention involves the same mechanisms as those involved in saccade programming.

In a dual task study, Van der Stigchel and Theeuwes (2005a) recently investigated whether the premotor theory also holds for conditions in which attention is allocated to multiple locations. Two locations were endogenously cued as possible target locations, while only one eye movement had to be executed. After a cue period this eye movement had to be executed to one of the two cued locations. The saccade goal was indicated by removing one of the two cues. During the cue period letters were briefly presented at both the saccade and no-saccade goal. Performance was better for the letters presented at the saccade goal, showing that attention was allocated to the possible target locations. This is consistent with recent findings that covert spatial attention precedes the eyes to the saccade goal (e.g. Shepherd et al., 1986; Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996; Godijn and Pratt, 2002; Godijn and Theeuwes, 2003). Furthermore, in line with the premotor theory, eye movements deviated away from the target location to which no saccade was executed. These results indicate that the allocation of attention to multiple locations may result in saccade deviation away from either one of these locations.

3.3. Eye movements and spatial working memory

An interaction between spatial working memory and visual attention was established by Awh and Jonides (2001), who showed that when a location is kept in memory, visual processing at this location is better than at other locations. In a recent study, a direct link between spatial working memory and the eye movement system was established by looking at saccade trajectories (Theeuwes et al., 2005). Participants in the study had to remember the location of a dot during a particular time interval. When in this interval a voluntary eye movement to a designated target was made, trajectories deviated away from the remembered location. This provided evidence for a strong overlap between spatial working memory and the eye movement system, because it shows that locations that are kept in memory generate activity in the motor map of the oculomotor system.

3.4. Eye movements and IOR

Inhibition of return (Posner and Cohen, 1984) refers to the finding that response times are longer when a target is presented at a previously cued location than when it is presented at an uncued location. Saccades to cued locations are also found to have longer latencies than to non-cued locations (Posner and Cohen, 1984; Abrams and Dobkin, 1994). Rafal et al. (1989) revealed the crucial role of oculomotor programming in manual IOR by showing that IOR only occurred after saccade preparation or execution, but not after endogenous allocation of attention. It was therefore proposed that IOR is tied to motor programming (Klein and Taylor, 1994). However, the exact operating mechanisms are still unclear.

The source of the inhibition in IOR can be investigated by examining saccade trajectories. In an experiment by Godijn and Theeuwes (2004) one of four locations was cued (both voluntarily and reflexively). Subsequently, participants executed a saccade to one of these four locations. IOR was observed at the cued location, as revealed by increased saccade latencies. Interestingly, saccades trajectories also deviated away from the cued location. Both saccade latencies and deviations were stronger with an onset cue than with a color singleton cue, suggesting that the inhibition presumed to underlie IOR and saccade trajectories are related. However, the time course of IOR and saccade deviations was different. Saccade deviations were only found at short delays between cue and saccade, whereas IOR lasted longer. This suggests that the possible inhibition underlying IOR and saccade deviations is not applied within the same system and must therefore have different neurophysiological correlates.

Theeuwes and Godijn (2004) further investigated the relation of irrelevant distractors on IOR and saccade trajectories. They presented irrelevant distractors either at the inhibited (by IOR) or the non-inhibited location. As observed in the oculomotor capture paradigm, saccades with short latencies deviated towards the irrelevant distractor. When the distractor was presented at the inhibited location this deviation towards was reduced. At longer latencies, deviations away were observed, which were identical for both distractor locations.

3.5. Preparation for upcoming targets and distractors

Two recent studies have investigated the role of preparation on eye movement trajectories. These studies have conducted experiments in which either the distractor or the target location was made known in advance to the participant. Van der Stigchel and Theeuwes (in press) designed experiments in which knowledge of the location of an upcoming *distractor* was provided to the participant. Observers expected a distractor to be presented on a designated location along with the target. In 80% of trials a distractor was indeed presented, in the remaining 20% of trials it was not. Both the locations of the target and the distractor were known in advance. In one experiment, the distractor location was constant and the target location cued by a central arrow, while in another experiment both the target and the distractor locations were cued. The two experiments showed that saccade trajectories deviated away from the distractor location when the distractor was present, but also when the distractor was only expected but not presented. This reveals that the mere expectation that a distractor will appear at a specific location is enough to generate saccade deviations away from that location.

Expectancy of a distractor is not the only factor involved in generating deviation away from a distractor. In the experiments of Van der Stigchel and Theeuwes (in press), deviation away was stronger when a distractor was presented, showing that distractor presence adds to the competition caused by mere expectancy. Moreover, in other experiments (Doyle and Walker, 2001; Godijn and Theeuwes, 2002b; Ludwig and Gilchrist, 2003), participants did not know in advance at what location a distractor would occur. Deviation away from a location observed in those experiments can thus not be explained by expectancy of the distractor.

Walker et al. (in press) showed that prior knowledge of an upcoming *target* also influences saccade deviations. Knowledge of the target location resulted in deviation away from a distractor, while when the target appeared at an unpredictable location, deviation towards the distractor was observed. In the predictable condition, the target location was indicated by a central arrow. In the unpredictable condition no such cue was presented, and the task essentially became a visual search task: participants searched the visual display for the target. Saccades curved towards distractors in the unpredictable condition, but away from distractors the predictable condition.

These findings highlight the contribution of preparation in determining the direction of saccade trajectories (Van der Stigchel and Theeuwes, in press; Walker et al., in press): when the relevant locations are known in advance, preparation for the upcoming saccade can already begin. In visual search tasks, in which prior knowledge of the relevant spatial locations is not available, prior preparation is impossible, resulting in an unprepared saccade program at the beginning of the target selection process.

3.6. Neurophysiological investigations of deviation away

In the case of deviation towards, a wealth of studies provide insights into the brain mechanisms underlying the deviation. This is not the case for deviation away. In fact, there has been no monkey study in which the eye movement trajectories deviate away from a distractor location. It has been shown in monkeys that after deactivating of a location by an injection of a GABA agonist, muscimol, the eyes deviate away from this location (Aizawa and Wurtz, 1998), but no such behavior has been observed in monkeys without pharmacological deactivation.

It has been argued that McPeek et al. (2003) did show neurophysiological correlates of deviation away in their visual search experiment with monkeys (e.g. Walker et al., in press). The evidence was inferred from activity measures of a SC location which revealed little or no activity. Eye movements deviated away from this location. However, in their experiment there was always another distractor located opposite of the location at which activity was recorded. No neuronal responses were recorded at that other distractor location. Therefore, it is unclear whether they observed deviation away from the recorded distractor location or deviation towards the other distractor present in the search display.

3.7. Theories of deviations away

To account for deviations away, two hypotheses were originally proposed by Sheliga et al. (1994): the suppression and the remapping hypothesis. The remapping hypothesis was based on evidence from neurophysiological studies indicating that the receptive fields of neurons in the lateral intraparietal area (LIP) shift before an eye movement to the endpoint of that eye movement (Duhamel et al., 1992). These neurons anticipate the programmed eye movement. The premotor theory states that when attention is shifted, an eye movement will be programmed to that location. According to this hypothesis, this should then cause the representation of the responsible neurons to shift to the location to which attention is shifted. The subsequent eye movement to the target location is then initiated from the remapped location, although the eyes are physically at the fixation point. This error is then responsible for the deviation.

This hypothesis was questioned by Doyle and Walker (2001), who cited evidence suggesting that remapping does not occur following covert attention: remapping in LIP is dependent on the intention to make a saccade and it is absent when only orienting covertly to a location (Colby et al., 1996). In the Sheliga et al. experiments, attention was covertly shifted to the location the eye movement trajectory deviated away from. If such shifts indeed do not result in remapping (Colby et al., 1996), the remapping hypothesis cannot explain the deviation away from the intended location.

The suppression (or inhibition) account states that the occurrence of the imperative stimulus is accompanied by an inhibition of the orienting response. This inhibition is the result of instructions not to make an eye movement to that location. The eye movement programmed when attention shifts should not be executed, and this is achieved through the use of inhibition. This inhibitory field then influences the subsequent voluntary eye movement, resulting in a saccade trajectory that deviates away from the inhibited saccade program.

Tipper's population coding theory also refers to inhibition to account for deviations away (Tipper et al., 1997, 2001). As mentioned before, when two possible targets are positioned in close proximity, the two populations will be combined to one mean population of which the corresponding vector points to an intermediate position. Competition between the two active responses has to be resolved by inhibiting one of the populations. Inhibitory selection of one target over the other may shift the mean vector in such a way that it affects the final response to the target. The amount of deviation is related to the inhibition applied to the cancelled vector: the stronger the inhibition, the greater the deviation will be.

Other models of saccadic target selection have also included inhibitory mechanisms to account for deviations away (Godijn and Theeuwes, 2002b; McSorley et al., 2004). In these accounts distractors get inhibited, which then alters the field of activity within the SC in such way that a deviating saccade results. Although such an inhibitory mechanism is able to account for the behavioral data, there is no direct neurophysiological evidence for such a process. Models of saccadic target selection have incorporated the FEF as a possible source of top-down inhibition of distractor locations (Godijn and Theeuwes, 2002b; McSorley et al., 2004; Van der Stigchel et al., submitted for publication). The FEF are known to send inhibitory connections to the SC via the substantia nigra of the basal ganglia (Basso and Wurtz, 1997, 2002; Munoz and Schall, 2003). Because no neurophysiological study has recorded SC activity during deviations away, it remains unknown whether the FEF can inhibit the SC such that it results in deviation away. Although Aizawa and Wurtz, 1998 have observed deviations away in monkeys after local deactivation, it is unknown whether such an effect can occur under normal circumstances.

An alternative account for deviations away that cannot be ruled out is the idea of 'overcompensation'. It is possible that an eye movement is 'overcompensated' to not reflexively saccade to a distractor location or location to which attention is directed. Because it is important not to land on these latter locations, the system could be set to compensate via the initialization of an eye movement in the direction away of the cancelled program. The underlying neurophysiological correlate could be similar to that proposed by inhibition accounts. The FEF does have direct excitatory connections to the SC and might activate the 'anti-saccade' location on the basis of top-down processes (Munoz and Schall, 2003).

Both the inhibition and overcompensation accounts can be integrated with the weighted average account (see Fig. 4). Inhibiting the distractor location would evoke a decreased activity in the left saccade map, resulting in a weighted average that is directed away from the inhibited location. The overcompensation account would assume activation of a location that, relative to the target, is opposite of the distractor. This activation process can be seen as a sort of 'anti-saccade' programmed away from the location that should be avoided, resulting in deviation away. For both accounts, on-line cerebellar feedback creates the deviation back towards the target location (Quaia et al., 1998; McSorley et al., 2004).

If deviation away would be found in monkey studies, neurophysiological recordings could provide evidence for or against both alternatives. The inhibition account would be supported when activity at the distractor location is below baseline during deviations away. Evidence for the overcompensation account would consist of increased activity at a location placed, relative to a straight saccade to the target, opposite of the distractor.

The recent finding that deviation away is stronger when the distractor is not only expected, but also presented (Van der Stigchel and Theeuwes, in press) should also be accounted for by an appropriate theory. This particular study showed that the mechanism underlying deviation away may have two components: one on the basis of the top-down expectancy of the distractor and one on the basis of the activity evoked by the onset of the distractor itself. Evidence for this last component originates from the discussed visual search experiments in which late saccades deviate away from a distractor presented on an unexpected location (Godijn and Theeuwes, 2002b; Walker et al., in press). The influence of these two components summates and results in a mean vector that is directed more away than when the distractor is only expected, but not presented.

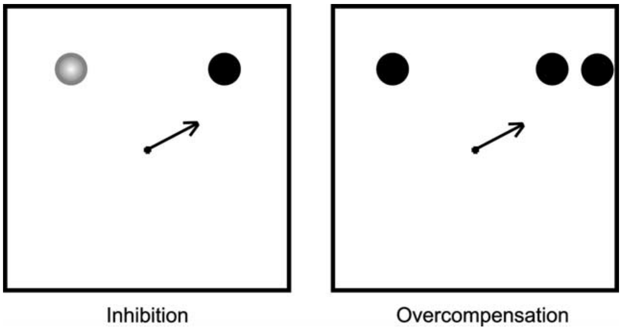

Fig. 4. Illustration of how both alternative accounts of deviation away can be integrated with the weighted average account. The distractor is positioned on the left and the target on the right side in the visual field. The inhibition account states that when the target is selected, the distractor will be inhibited (illustrated by the gray circle). As a result of this selection process, the weighted average vector will point away from the target location. The overcompensation account states that a location on the right side of the target will be activated in order to rule out the possibility that the weighted average will be directed to the distractor location. This, however, causes the weighted average to be pointed to a location away from the distractor.

4. When do saccades curve towards and when away?

It may seem inconsistent that eye movements sometimes deviate towards, but in other cases deviate away from a location. For instance, what determines whether saccade trajectories deviate towards a distractor, as in visual search, or away from it as in many other reported studies? We have suggested that deviation towards results from the averaging of populations coding the target and the distractor, but that deviation away occurs when a distractor is either inhibited or when a compensating saccade is planned. Why does such inhibition or compensating of saccades not occur in situations of deviation towards? The current review suggests that deviation away is observed in situations in which top-down preparation can influence the target selection process. The effects of two factors provide evidence for that idea: timing and prior knowledge. When observers know where to expect either the target or the distractor and have the time to top-down prepare for the saccade or correct an erroneous saccade, distractors will result in deviation away. If observers either do not have the knowledge or the time to prepare for the saccade or to correct an erroneous saccade, distractors will elicit deviation towards.

With respect to prior knowledge, it has been shown that prior knowledge about the location of an upcoming target influences whether the saccade will deviate away or towards that location (Walker et al., in press). The studies in which the target location was predictable have reported deviation away (Sheliga et al., 1994, 1995a,b; Theeuwes et al., 2005; Van der Stigchel and Theeuwes, 2005a, in press), whereas in paradigms in which the target location is less predictable (e.g. visual search experiments) both saccade deviations away and towards were observed (Godijn and Theeuwes, 2002b; Walker et al., in press). When the relevant locations are known in advance, preparation for the upcoming saccade can already begin. Based on advance expectancy of the target or distractor location, the relevant locations can already be selected or deselected. When prior knowledge is not available, as in visual search tasks, such prior preparation is impossible.

The second factor that determines the direction of deviation is timing of the target selection process. Two findings suggest the importance of timing:

- In some visual search experiments, fast saccades deviate towards, while slow ones deviate away from distractors (Theeuwes and Godijn, 2004; Walker et al., in press).
- The deviation away from a distractor is modulated by target similarity when the saccade is delayed, but this effect is absent when it is not delayed (Ludwig and Gilchrist, 2003).

These findings suggest that saccades deviations away from a distractor are more frequent for slow saccades than for fast saccades, whereas the opposite is true for deviations towards a distractor. For shorter latencies, the target selection process is unprepared and based more on stimulus-driven features (Ludwig and Gilchrist, 2003; Van Zoest et al., 2004). If competition between possible target locations is not yet resolved at the time of the saccade, deviation towards is frequently observed. For longer latencies top-down signals can manifest themselves in the selection process. Target selection is then more prepared and less based on saliency but on top-down processes like task variables, leaving its marks on saccade trajectories in the form of deviations away.

The relationship between timing and top-down preparation can explain why in visual search experiments early saccades deviate towards the distractor, while later saccades deviate towards such an element (Theeuwes and Godijn, 2004; Walker et al., in press). In visual search tasks, prior knowledge of the appropriate target location is not available and prior preparation is therefore impossible. Early saccades will therefore deviate towards the distractor, whereas later saccades will deviate away from the distractor.

In voluntary attention shifts, participants know that they will not have to make a saccade to the attended location. They thus have time to stop saccades to the attended location—whether this is through inhibition or compensating saccades. A similar explanation can account for deviation away in the memory experiments.

Deviations towards can be explained by the absence of dominant top-down preparation. In visual search experiments (where the relevant locations are unknown), in case of a global effect (where a decision is based on the relative saliency in the saccade map), in double step paradigms (where the target location switches), top-down preparation cannot influence the target selection process in an effective way.

5. Conclusion

Because vision is impaired during an eye movement, it is important that the flight is executed with the greatest possible speed to minimize the period of poor vision. The exact trajectory is therefore irrelevant to the observer, provided it is fast enough. Indeed, trajectories are seldom straight. On top of idiosyncratic, individually set deviations in normal saccade trajectories, trajectories have been found to deviate away or towards locations depending on the behavioral paradigm. Here, we reviewed the conditions in which deviation towards or away are found, and what is known about mechanisms underlying saccade trajectory deviations.

Deviation towards is found when competition between two possible targets is unresolved by the time of saccade initiation. This occurs in paradigms in which two targets are presented in close succession or in visual search when a saccade is initiated before the target is differentiated from distractors. At the physiological level, such situations result in multiple activation spots on the SC motor map. These spots seem to be integrated into a weighted average that then determines to which location saccades are directed.

What causes deviations away is less clear. Behaviorally, it is found when observers know where they will have to make a saccade to, and have the time to top-down inhibit tendencies to saccade to attended locations or distractor locations. Two hypotheses remain viable accounts of how saccades deviate away from such locations. Both follow logically from the weighted averaging account that provided the best explanation for physiological studies of deviation towards. One is that observers inhibit locations on the SC motor map they attend to, expect a distractor to appear, or see a distractor appear. This inhibition then skews the activation field in such a way that saccades deviate away from the inhibited location. The other is that observers, to prevent deviation towards the location, plan a saccade in the opposite direction, which generally overcompensates and leads to deviation away from the attended or distractor location.

Although the exact mechanisms thus remain unclear, it can be concluded that top-down preparation is responsible for deviations away. When top-down preparation can influence the target selection processes, deviation away can be observed. Examples of situations in which this occurs are paradigms in which the target location is known in advance or in which observers voluntarily attend to a location or keep one in spatial working memory.

Eye movement trajectories can yield information about the oculomotor and attention systems that are not easily obtained via other sources. We have reviewed various findings that support this idea. For example, the study of trajectories suggests that IOR is not a unitary phenomenon, as it occurs on different time scales in different measures in the same experiment. Furthermore, evidence is provided for the idea that spatial working memory involves attending to the location where the stored stimulus was presented. Also evident from eye movement trajectories is the surprising extent to which multimodal sources of input are integrated into one single map guiding overt and covert orienting.

Future aspects to explore are the correlation between the size and the time course of saccade deviations with dynamic behavioral processes. Furthermore, individual differences between participants are still unexplored, and it might be very interesting to look at the influences of neurophysiological disorders like ADHD and Alzheimer's disease on saccade deviation. Their decreased oculomotor control might be further investigated by saccade deviations.

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Appendix A. How to measure saccade trajectories?

Different methods have been used throughout the literature to quantify saccade trajectories. A recent paper has compared

Table 1
The different measures to quantify saccade trajectories

Name (letters refer to Fig. 5)	Definition	References
Overall direction (B)	Angular difference between saccade landing point and the correct target location	Coren and Hoenig (1972), Findlay, (1982) and Ottes et al. (1985)
Initial direction (A)	Angular difference between initial direction and overall direction of saccade. Initial direction computed at a fixed point in the saccade (e.g. 20 ms after initiation).	Findlay and Harris (1984) and Van Gisbergen et al. (1987)
Initial average (mean(A))	Mean angular deviation of sample points in the initial 10 ms of the saccade relative to the overall direction of the saccade	Sheliga et al. (1995a,b)
Maximum curvature (max(C))	Largest absolute perpendicular deviation of the sample points between start and end of the eye movement	Smit and Van Gisbergen (1990), Doyle and Walker (2001), Doyle and Walker (2002) and McPeek and Keller (2001)
Area curvature $\int C * d(x)$	For each sample point n, distance traveled along straight path between onset and endpoint since previous sample ($n-1$) multiplied by the perpendicular deviation of sample point n. Sum divided by saccade amplitude	McSorley et al. (2004), Walker et al. (in press)
Quadratic curvature	Second-order polynomial is fitted to normalized saccade. Measure used is the quadratic parameter of polynomial	Ludwig and Gilchrist (2003)
Saccade deviation (mean(A+B))	Average angle between the saccade sample points and the straight path from saccade start to the correct target location	Godijn and Theeuwes (2002a,b, 2004), Theeuwes et al. (2005), Theeuwes and Godijn (2004) and Van der Stigchel and Theeuwes (2005a)
Overall initial direction (A+B)	Angular difference between initial direction and the straight path from saccade start to the correct target location	Van der Stigchel and Theeuwes (2005b)

many of these methods (Ludwig and Gilchrist, 2002a). Table 1 and Fig. 5 give a short description of each method.

The different measures can be divided on the basis of two criteria. First, some measures include all sample points on the trajectory of the saccade (Area curvature, Quadratic curvature and Saccade deviation), while others focus on one specific sample (Initial direction, Maximum deviation and Saccade endpoint). Second, some measures use as a reference a straight line to a predefined target (Saccade deviation, Saccade endpoint, Overall initial direction), while others use as reference a straight line to the saccade endpoint (all other measures). The first are often said to measure *deviation* of the saccade, the latter the *curvature* of the saccade.

To minimize the influence of sample noise, it may be preferable to include all sample points in the computation of saccade trajectories. This consideration led Ludwig and Gilchrist (2002a) to recommend Quadratic curvature as measure. As there may be valid reasons to focus on some aspects of trajectories over the others, however, it may not be possible to blankly favor one method over the other. It should be noted that many are highly correlated (Ludwig and Gilchrist, 2002a), so that conclusions usually do not hinge on the exact measure chosen (e.g. Van der Stigchel and Theeuwes, in press).

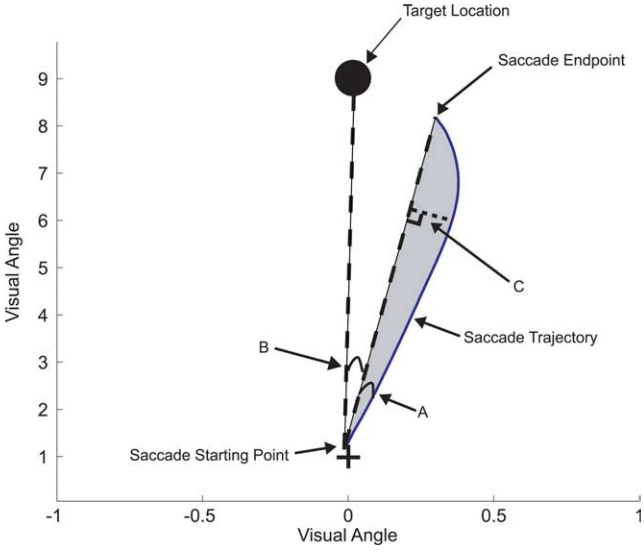

Fig. 5. The different possible measurements of a saccade trajectory.

In the main text, it was discussed that activation on the SC motor map at saccade initiation seems to determine the initial direction of the saccade, while cerebellar mechanisms then correct the saccade to target locations that later in time win the competition. This suggests reporting a measure of initial direction relative to the target to investigate processing at saccade initiation (Overall initial direction), and a measure of curvature to investigate later processing (e.g. Maximum curvature, Area curvature, or Quadratic curvature).

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