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Minireview

Recent advances in the study of saccade trajectory deviations

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ABSTRACT

In recent years, the number of studies that have used deviations of saccade trajectories as a measure has rapidly increased. This review discusses these recent studies and summarizes advances in this field. A division can be made into studies that have used saccade deviations to measure the amount of attention allocated in space and studies that have measured the strength of the activity of a distractor. Saccade deviations have also been used to measure target selection in special populations. Most importantly, recent studies have revealed novel knowledge concerning the spatial tuning and temporal dynamics of target selection in the oculomotor system. Deviations in saccade trajectories have shown to constitute a valuable measure of various processes that control and influence our behavior which can be applied to multiple domains.

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1. Introduction

One of the important advantages of using eye movements as a measure is that eye movements provide a multitude of information: not only the reaction time of the eye movement, but also its velocity, duration and endpoint can be measured. One of these measures, the trajectory of the saccade, has been shown to be informative of various processes that control or influence our behavior. In recent years, the number of studies that have used deviations of saccade trajectories as a measure has rapidly increased. Not only have saccade deviations been measured in normal vision, but also in special populations like hemianopic patients, elderly and patients with Huntington's disease. This review will discuss all studies published after 2005 that have used deviations of eye movement trajectories as a measure (for a review of earlier studies, see Van der Stigchel, Meeter, and Theeuwes (2006)). It will focus on recent advances in this rapidly growing field and on the lessons that have been learned about the underlying mechanisms of these deviations.

Because an eye movement brings the central focus of the eye from one point to another, each saccade has a starting point and an endpoint. When multiple elements are presented in a visual scene, one location has to be selected as the target for the subsequent eye movement. The location of the endpoint therefore informs us about the outcome of the process of target selection. While the eye changes fixation from the starting point to the endpoint, it generally does not take the shortest route in terms of a straight line between starting point and endpoint, but shows a trajectory which is slightly curved. This was already acknowledged by Yarbus (1967) in his classic recordings of eye movement scan patterns. Although this in itself is already an interesting phenomenon, work by Sheliga, Riggio, Rizzolatti (1994) was the first to inform us about deviations of these curved trajectories (1994). This measure refers to the deviation of the eye movement trajectory in response to an internal or an external event when compared to the trajectory when this event is absent. Because the event that influences the trajectory is generally spatial in nature, trajectories can either deviate towards or away from the location that is associated with this event. As will be discussed, the direction of the deviation has shown to be an indicator of the strength of this event.

The application of this measure seems to vary between studies, however: some studies use eye movement trajectories to measure the activity of distracting elements ('distractors'), whereas other studies focus on measuring the amount of attention allocated in space. Before these studies are discussed, the common underlying mechanism of deviations will be explained.

2. Common underlying mechanisms of saccade deviations

Classic theories of saccade deviations have explained deviations in terms of population coding (McSorley, Haggard, & Walker, 2004; Tipper, Howard, & Houghton, 2000; Tipper, Howard, & Jackson, 1997). These theories state that each neuron in a motor map codes an individual vector that encodes the movement towards the corresponding location. Eye movements are initiated in the direction of the average of the vectors present in the oculomotor system. It is assumed that a movement program results in activation of a broad population of vectors. When two elements are presented simultaneously that are not too far apart, the average movement

vector will therefore point to an intermediate location. Because participants are instructed to move their eyes to the target location (and not to an intermediate location), competition between the two active populations has to be resolved by inhibiting one of them. Due to the distributed nature of the population code, inhibitory selection of one population over the other will inhibit a subset of the vectors coding for the movement to the target. The vector average will therefore not include the inhibited vectors, resulting in a shift of the vector average away from the inhibited vector. In this situation, the eye movement will deviate away from the inhibited site. When the inhibition is weak, the average vector will still be directed to a location in between target and the inhibited site. Deviation towards a distractor has therefore been associated with weak inhibition.

According to the population coding theory, deviations of eye movement trajectories reflect the strength of the other oculomotor programs at the moment the eye movement is initiated ('residual oculomotor activity'). In this view, every external or internal event that influences an eye movement trajectory does this because it evoked the programming of an eye movement to the spatial location of the event. With respect to the deviations evoked by spatial shifts of attention, the population coding theory assumes that a shift of spatial attention results in the presence of a vector to the attended location. Support for this assumption can be obtained by combining the population coding theory with the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umilta, 1987). This theory claims that the mechanisms responsible for spatial attention and the mechanisms involved in programming eye movements are basically the same. A strict interpretation of the theory states that a shift of attention is nothing more than a by-product of the programming of an eye movement to a particular location in space. In this situation, there is a competition between the vector coding for the target location and the vector coding for the location to which attention is allocated. The vector to the attended location has to be inhibited when an eye movement has to be initiated to the target location. The deviation of the eye movement trajectory then reflect the strength of the oculomotor program to the attended location at the moment the eye movement is initiated.

Because saccade deviations in paradigms that measure the activity of a distractor and the allocation of attention in space reflect residual oculomotor activity, deviations in both paradigms are the result of a common underlying mechanism.

3. Saccade trajectories as a measure of the amount of attention in space

Studies that have used eye movement trajectories to measure the allocation of attention in space (spatial attention) have been inspired by experiments by Sheliga and colleagues (Sheliga, Riggio, Craighero, & Rizzolatti, 1995; Sheliga et al., 1994; Sheliga, Riggio, & Rizzolatti, 1995). These studies were the first to show that directing covert attention to a spatial location influences eye movement trajectories. In a recent study, these earlier findings by Sheliga and colleagues were extended in a series of experiments that showed that the oculomotor system is activated wherever spatial attention is allocated (Van der Stigchel & Theeuwes, 2007). In a standard Posner paradigm, participants were endogenously cued by an arrow cue to covertly attend to a peripheral location (i.e. without making an eye movement). They responded faster to target letters presented at cued than at uncued locations. On a subset of trials (20%), instead of a manual response, participants had to move their eyes to a location straight above or below the fixation point. These eye movement trials were indicated by the presentation of a specific letter ('go-signal') at either the cued or uncued location. On

trials in which the go-signal was presented at the cued location, eye movements deviated away from the cued location. When the arrow cue was invalid and the go-signal was presented at the uncued location, eye movements also deviated away from the uncued location but less strong compared to when the go-signal was presented at the cued location. The extent to which the eyes deviated away from cued and uncued locations was therefore related to the dynamics of the allocation of attention. With respect to the classic view of interpreting visual attention as a 'spotlight' that travels through space (Posner, 1980), it was concluded that activation in the oculomotor system elegantly travels along with the spotlight of attention: wherever attention is allocated, you will find activation in the oculomotor system.

One of the additional conclusions that could be drawn from these experiments was that the strength of saccade deviation is a measure of the *amount of attention* allocated to any particular location in space. Because reaction times to targets presented at validly cued locations were shorter than to targets presented at uncued locations, it could be inferred that the amount of attention allocated to the cued location was higher than to the uncued location. In line with these findings, the strength of the deviation was higher from the validly cued location when compared to the uncued location.

The direction of the saccade deviation, away from an attended location, is consistently observed across eye movement studies. This is in contrast to a study that measured the effect of attentional allocation on trajectories of hand movements which observed trajectory deviations towards an attended location (Lee, 1999). To investigate this inconsistency, a recent study measured eye movements in the same paradigm as which was used to measure hand movements (Van der Stigchel, Meeter, & Theeuwes, 2007b). In this experiment, a central cue indicated the likely target location of an upcoming eye movement. When the target was presented at a location different from that indicated by the cue, eye movements deviated away from the cued location. This study shows that the effects observed when executing eye movements can be different from those obtained when hand movements are executed. The consistently observed deviation away from attended locations seems therefore restricted to eye movements.

Deviations of saccade trajectories are not only observed when attention is allocated voluntary. A study by Nummenmaa and Hietanen (2006) elegantly showed that saccade deviations are also observed for reflexive shifts of visual attention without the presentation of a peripheral cue. Participants executed eye movements to a target presented on the vertical meridian while a gaze cue (consisting of a schematic face that either looked to the left or the right) was presented at fixation. Saccade trajectories deviated away from the direction towards which the gaze was oriented. Because it is known that visual attention is reflexively oriented towards the direction of the gaze cue (e.g. Friesen & Kingstone, 1998), this indicates that deviations of saccade trajectories can also be elicited by cues that reflexively direct attention in space.

Along similar lines of reasoning, Nummenmaa, Hyönä, and Calvo (2009) used saccade trajectories to measure to what extend the attentional system is influenced by picture content. This was the first study to use the trajectory measure in the context of higher level representation of complex scenes. Paired emotional and neutral scenes were presented in the periphery (e.g. an emotional scene to the left and a neutral scene to the right) while participants executed vertical saccades. Results showed that saccade trajectories deviated away from the visual field in which the emotional scene was presented. This way, saccade trajectories were used to reveal that attentional allocation is influenced by picture content; even when the pictures are irrelevant to the task, emotional pictures automatically attract attention.

4. Saccade trajectories as a measure of the activity of a distractor

Many studies have used saccade trajectories to measure the effect of a distractor on target selection. These studies were inspired by a study of Doyle and Walker (2001) in which a task-irrelevant distractor (a cross) was presented simultaneously with a target (a square). The task of the participant was to make an eye movement to the target as fast as possible. Results showed that eye movement trajectories to the target deviated away from the distractor. As discussed earlier, these deviations away from a distractor are assumed to result from the rejection of the distractor ('oculomotor inhibition', Doyle & Walker, 2001; Tipper et al., 1997). The deviation of the trajectory reflects *the activity of the distractor* on the moment that the saccade is initiated. Strong inhibition of a distractor results in deviation away, whereas weak inhibition leads to deviation towards the distractor. The strength of the inhibition is determined by various factors which will be discussed in this section.

Subsequent studies have extended this basic paradigm to further explore the dynamics of target selection. For instance, the activity of a distractor was compared across different types of saccades, like prosaccades, antisaccades and memory-guided saccades (van Zoest, Van der Stigchel, & Barton, 2008). In all conditions, the distractor was presented along the path of the required eye movement. The prosaccade condition was a replication of the basic paradigm by Doyle and Walker (2001). In the antisaccade condition, however, no visual element was presented at the location towards the saccade was executed, because the task was to make an eye movement in the opposite direction of the target. In the memory-guided condition, the task was to hold fixation until the fixation point was removed. After this, an eye movement had to be made to the location at which the target had previously been presented. Simultaneously with the fixation offset, the distractor was presented. In this condition, there was no visual signal, except the distractor. The absence of a visual stimulus at the goal location increased the strength of the oculomotor inhibition of the distractor as revealed by an increase in deviation away from the distractor. Deviation away from the distractor was strongest in the memory-guided condition and weakest in the prosaccade condition. The antisaccade condition was in between these two conditions. The results of this study suggest that oculomotor inhibition of a distractor is dependent on the strength of the stimulus presented at the target location: when no stimulus is presented at the target location, the interference evoked by the distractor is strong, resulting in stronger oculomotor inhibition.

Important insights regarding the mechanisms underlying the rejection of a distractor were provided by a study of Cardoso-Leite and Gorea (2009). Distractors with low contrast were presented along with a target. After the saccade was executed to the target, participants had to indicate whether they had detected the distractor on that particular trial. This way, it could be investigated whether the interference of the distractor is dependent on the perceptual detection of the distractor. The results showed that saccades deviated away from the distractor only when participants reported to have seen the distractor. Saccade deviation was correlated with the inferred internal response associated with the perceptual report: the stronger the perceptual response evoked by the distractor, the more saccades deviated away from the distractor. In the condition in which two distractors were presented, the deviation was strongest from the distractor that was perceived to be present by the participant. This seems to indicate that saccade deviations follows the same non-linearity as the internal perceptual response. The perceptual threshold needs to be exceeded in order for the distractor to affect the trajectory.

In the study of Cardoso-Leite and Gorea (2009), the distractor was presented with low contrast and did not influence the eye movement trajectory when it was unseen. A different study showed that an unseen distractor can influence the saccade trajectory when presented with high-contrast (Van der Stigchel, Mulckhuyse, & Theeuwes, 2009). One of four circles in each trial was presented 17 ms earlier than the other three circles. Because the other three circles followed immediately after onset of the first circle, participants were unaware of this earlier onset. Although the effect was smaller than when a supraliminal distractor was presented, saccade trajectories deviated in the presence of the first circle, indicating that it evoked oculomotor competition. The crucial difference between the two studies seems to be the level of contrast with which the distractor was presented.

5. The temporal dynamics of oculomotor inhibition

One of the most important findings in the domain of oculomotor inhibition concerns its *temporal* dynamics. It was discovered that the direction of the deviation depends on the speed of responding (McSorley, Haggard, & Walker, 2006). In this experiment, a broad range of saccade latencies was elicited by offsetting the fixation point at different time points relative to target onset. This enabled the researchers to examine the strength of oculomotor inhibition throughout the distribution of saccade latencies. Trajectory deviations away from a distractor were only observed for the longest latencies in the saccade latency distribution. For the shorter latencies (less than 200 ms), the saccade trajectory deviated towards the distractor. Similar results were observed by Mulckhuyse, Van der Stigchel, and Theeuwes (2009) and McSorley, Haggard, and Walker (2009). The latter study confirmed that the temporal dynamics described above are observed for a large variety of distances between target and distractor. These converging results reveal that oculomotor inhibition has its strongest influence late in the selection process and that early in the selection processes, responses are less strongly driven by inhibitory processes (see Fig. 1).

The finding that oculomotor inhibition varies in time should be taken into account when interpreting results from studies on saccade deviations. When the deviation away is strongest in the experimental condition in which saccade latency is the highest, the deviation away might not be explained by the strength of the distractor activity, but by the slowing of the response. This explanation does not hold for the differences between the effect of the distractor on prosaccades, antisaccades and memory-guided saccades (van Zoest et al., 2008). While antisaccades had the longest latencies, they did not have the greatest distractor-induced deviations.

6. The spatial tuning of oculomotor inhibition

Besides the temporal dynamics, a number of recent studies have examined the *spatial* tuning of oculomotor inhibition. The main manipulation in these studies was the location at which the distractor was presented. It was already established that the distance of the distractor to the target is a crucial factor in determining the *endpoint* deviation: when target and distractor are closely aligned (within 20°), the endpoint of the saccade is positioned in between the target and distractor (the global effect, Coren & Hoenig, 1972; Walker, Deubel, Schneider, & Findlay, 1997). Recent studies have extended these findings to the direction of the trajectory deviation (McSorley, Cruickshank, & Inman, 2009; Van der Stigchel & Theeuwes, 2005). In these studies, participants made eye movements to a target which could be accompanied by a distractor shown at
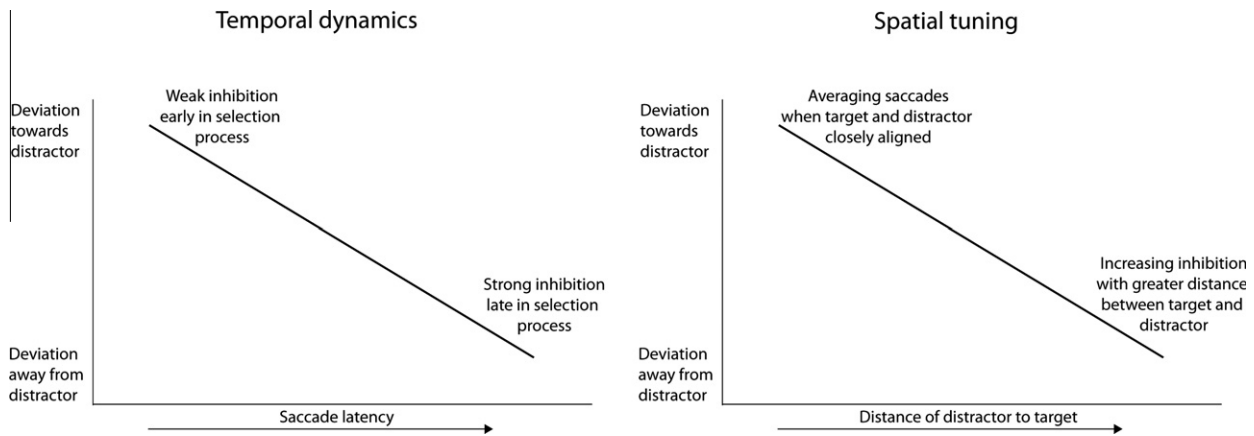
Temporal dynamics

Spatial tuning

Fig. 1. Temporal dynamics and spatial tuning as described in the review. Temporal dynamics: early in the selection process between target and distractor, oculomotor inhibition is weak, resulting in deviation towards the distractor. Later in the selection process, top-down inhibition increases resulting in deviations away from the distractor. Spatial tuning: when target and distractor are closely aligned, averaging saccades will lead to deviation towards the distractor. With increasing distance between target and distractor, the deviation away from the distractor will increase.

various distances from the target. When distractors were presented close to the target, saccade trajectories deviated towards the distractor, while at greater separations trajectories deviated away from the distractor (McSorley, Cruickshank, et al., 2009).

Saccade deviations can be used to determine whether the inhibition applied to the distractor is coarsely coded or not. More explicitly, the question can be answered whether the exact location of the distractor influences the strength of oculomotor inhibition. Although it was already revealed that the effect of the location of the distractor is weak (McSorley, Haggard, & Walker, 2005; McSorley et al., 2004), systematically manipulating the location of the distractor determined that the vertical distance of the distractor from fixation is an important factor (Van der Stigchel, Meeter, & Theeuwes, 2007a). Consistent differences were observed in saccade trajectories to a target for different spatial distractor locations: locations vertically closer to fixation evoked more inhibition than locations further away from fixation. A recent study of McSorley and colleagues also concluded that the exact location of the distractor influences the strength of oculomotor inhibition, although they focused on the distance of the distractor from the target (McSorley, Haggard et al., 2009). According to their results, inhibition decreased as the distractor distance from the target decreased (see Fig. 1).

When the inhibition of a distractor depends on the location of the distractor, the question emerges what happens when the target has to be selected in the presence of multiple distractors. In an earlier study, it was already discovered that two distractors presented at mirrored locations result in a straight trajectory to a target presented on the vertical meridian (McSorley et al., 2004). In this situation, the inhibition of both distractors 'cancels out'. When two distractors are presented at locations which are *not* mirrored, the straight trajectory should not be observed, because different strengths of inhibition should be evoked by the two distractors. This was exactly what was observed (Sogo & Takeda, 2007). Both distractors had a similar distance to the vertical meridian, but the distance from the horizontal meridian was manipulated. Results showed that the effect of inhibiting two locations on the trajectory was a linear summation of the effect of inhibiting each distractor when presented in isolation.

The strength of the inhibition not only depends on the location of the distractor, but also on the location of the target. The majority of the studies described above have focused on vertical saccades. When eye movements have to be made to a target presented on the horizontal meridian, the deviation away from a distractor is

less strong when compared to eye movements to a target on the vertical meridian (Van der Stigchel & Theeuwes, 2008). In case of a target on the horizontal meridian, target and distractor are both presented in the same (left or right) visual field. In terms of the neurophysiology, this means that both elements are presented in the same motor map. The finding that saccades deviate away from the distractor when both are presented in the same motor map suggests that the deviation is not only due to differences in activity between the two motor maps, but can also be evoked by local application of inhibitory processes in the same map as the target.

7. The role of top-down processes in oculomotor inhibition

When target and distractor are presented simultaneously, the distractor has to be rejected and the target has to be activated. This selection process is performed on the basis of knowledge about the task. By task definitions, a certain element can be labeled as the target or the distractor. It is therefore very likely that the oculomotor inhibition of a distractor is top-down in nature. Behavioral evidence for this claim comes from a number of studies which have investigated the contribution of top-down processes to saccade deviations. For instance, prior knowledge of the target location has shown to be one of the top-down factors that influence the selection process (Walker, McSorley, & Haggard, 2006): when the target location was unpredictable, saccade trajectories deviated towards the distractor. When the target location was predictable, however, the direction of the deviation reversed and saccades deviated away from the distractor. Consistent with these results, Al-Aidroos and Pratt (2010) also observed a strong deviation away from a distractor when the target location was known in advance. The deviation away was less strong when this information was not provided. Also the mere expectation that a distractor will appear at a specific location already generates a saccade trajectory that deviates away from this location (Van der Stigchel & Theeuwes, 2006).

Additional evidence for the role of top-down processes on oculomotor competition was provided by a study in which the similarity between target and distractor was manipulated (Mulckhuyse et al., 2009). The distractor was either similar or dissimilar to the target (a similar distractor shared the color of the target). When the color of the distractor was the same as the target, the distractor evoked strong oculomotor competition (Ludwig & Gilchrist, 2002, 2003). Results showed that the strength of the saccade deviation was modulated by target-distractor similarity for both short and

long saccade latencies. When saccade latencies were short, less saccade deviation away from a similar distractor was observed than from a dissimilar distractor. When saccade latencies were long, the opposite pattern was found: more saccade deviation away from a similar than from a dissimilar distractor. Because the similarity between target and distractor modulated saccade deviation already for short saccade latencies, this indicates that top-down information can already influence the oculomotor system early in time. The priority of the location of the distractor might have been enhanced because of its similarity to the target color, resulting in the necessity of stronger inhibition to resolve the competition between target and distractor. Later in the selection process, the top-down inhibition becomes more dominant resulting in a stronger deviation away from the distractor which color matches the target (as was also revealed in an earlier study Ludwig and Gilchrist (2003)). These results were confirmed by an additional study which also showed more deviation away from a distractor that matched the target in terms of color when compared to a non-matching distractor (Al-Aidroos & Pratt, 2010).

A final piece of evidence that oculomotor inhibition has a top-down origin comes from a study on one of the hallmarks of higher-order processes, namely decision making (McSorley & McCloy, 2009). Participants had to make an eye movement to one of two possible peripheral markers. The location of the saccade was indicated by a cloud of moving dots presented at fixation. Evidence for a specific choice was manipulated by the proportion of dots moving in the same direction (i.e. more dots moving in a certain direction provided more evidence that a saccade had to be made in that direction). Saccades deviated away from the non-saccaded marker and this deviation was found to be stronger as evidence supporting the decision increased. The accumulation of evidence for a certain decision resulted in stronger oculomotor inhibition of the eye movement program to the non-saccaded marker. This elegantly reveals the link between higher-order decision making and oculomotor inhibition.

8. The relation between oculomotor inhibition and IOR

As mentioned, saccade deviations away from a distractor are generally attributed to the inhibition of the distractor, because the distractor has to be rejected in favor of the selection of the target. This inhibitory mechanism is reminiscent of the mechanisms underlying the inhibition of a previously attended location, resulting in delayed responses to targets presented at recently cued or recently fixated locations (a phenomenon called inhibition-of-return (IOR), Klein, 2000; Posner & Cohen, 1984). It is therefore perhaps not surprising that various studies have investigated whether both phenomena are caused by the same inhibitory mechanism. Sogo and Takeda (2006) examined eye movement trajectories during a visual search task in which multiple eye movements had to be made to find the target. This is different from previous studies which have only examined trials with a single eye movement to a designated target. The results showed that saccade trajectories deviated away from the side where more previously fixated locations were positioned, which suggests that the inhibition of saccades to previously fixations influenced the saccade trajectory. Further analyses revealed that saccade trajectories were affected by at least three previous fixations. Interestingly, the time course of the inhibition underlying saccade trajectories seems to be much faster from that generally associated with IOR. A previous study already showed that saccade deviations away from a distractor disappear at 800 ms after onset of the distractor, in contrast to the time course of IOR which became optimal only after a delay of about 800 ms after abrupt onset (Godijn & Theeuwes, 2004). This seems to imply that IOR and saccade deviations are caused by different inhibitory mechanisms.

This dissociation between the two inhibitory mechanisms was extended to the inhibition applied to a location that is kept in working memory (Theeuwes, Van der Stigchel, & Olivers, 2006). In an earlier study, it was already established that the maintenance of a location in spatial working memory influenced saccade trajectories, because saccades deviated away from the remembered location (Theeuwes, Chizk, & Olivers, 2005). This was assumed to be caused by the fact that spatial attention is allocated to a location which has to be remembered and the attended location has to be inhibited in order to execute an eye movement to the target location. In this new study, participants were required to hold a location in memory. The to-be-memorized location was indicated by an abrupt onset which is known to elicit IOR (Posner & Cohen, 1984). To measure IOR, on some trials observers were required to execute an additional saccade to either the memorized location or to an equidistant location on the opposite side of space. Results showed that the size of IOR to a location was not affected by whether or not the location was kept in working memory, but the size of the saccade trajectory was affected by the memory manipulation. This again confirms that the inhibitory mechanisms underlying saccade deviations differ from those associated with IOR and that there must be at least two different inhibitory processes.

The dissociation between the inhibitory mechanisms underlying saccade deviation and IOR seem to be inconsistent with the findings of a study that investigated whether the strength of the deviation is related to the amount of *reflexive* attention (Theeuwes & Van der Stigchel, 2009). As discussed earlier, previous experiments already established such a link between the strength of the deviation and the amount of *voluntary* attention (Van der Stigchel & Theeuwes, 2007). In this new study, attention was summoned to a location using an abrupt onset cue which indicated the target location at chance level. When there was a delay between the cue and the target, participants responded slower to the target presented at the cued than at the uncued location (IOR). It could therefore be concluded that the amount of attention at the cued location was less than at the uncued location. When an eye movement had to be made on a subset of trials, the deviation away from the uncued location was stronger than deviation away from the cued location. Because IOR has been claimed to be a good indicator of exogenous capture of attention (Pratt, Hillis, & Gold, 2001; Pratt, Kingstone, & Khoe, 1997), this shows that deviations are also a measure of the amount of exogenous attention at a certain location. However, the observation that saccades deviated away from the location at which IOR was observed seems to be inconsistent with the findings discussed in this section. As the authors also argued, this apparent inconsistency can be explained by differences between the various tasks. In the studies that observed a dissociation between both types of inhibition (Godijn & Theeuwes, 2004; Theeuwes et al., 2006), participants did not have to perform a discrimination task at the cued or uncued locations. In the study by Theeuwes and Van der Stigchel (2009) participants had to perform a letter discrimination task after the presentation of the cue. In order to discriminate the target letter, attention needed to go back to the inhibited location. This return of attention then caused a small, yet reliable, saccade deviation away from this location. The authors concluded that their results were therefore not inconsistent with the idea that inhibitory mechanisms underlying saccade deviations and those associated with IOR differ.

9. Saccade deviations in special populations

With the increasing number of studies using deviations of saccade trajectories as a measure, a number of recent studies have adopted this measure to investigate target selection in special

populations. Besides elucidating the specific behavioral characteristics of these special populations, these studies have also been informative of the underlying neurological mechanisms influencing saccade trajectory deviations.

The first study of saccade trajectories in a special population focused on patients with Huntington's Disease (HD, Fielding, Georgiou-Karistianis, Millist, Fahey, & White, 2006), a disorder primarily affecting the basal ganglia (BG). The BG is strongly connected with the superior colliculus (SC, Munoz, 2002), a motor map in the midbrain in which the competition between possible saccade goals is assumed to be resolved (Schall, 1995; Sparks & Hartwich-Young, 1989). Because of the strong connection between these two areas, it was hypothesized that trajectory deviations would be modulated in patients with HD. A distractor was presented simultaneously with the target. The results of the patients with HD were different from those of healthy controls. Whereas healthy controls deviated away from the peripheral distractor, the deviations of the patients with HD did not show this pattern. Moreover, the participants' trajectory mainly showed leftward deviation compared to the baseline condition, irrespective of the location of the distractor. Saccade generation in the baseline condition was normal. These somewhat puzzling results suggest that correct functioning of the BG is important to observe the typical deviation away from distractors.

In a completely different domain, eye movement deviations induced by a distractor were investigated in patients with acquired visual field defects (Van der Stigchel, van Zoest, Theeuwes, & Barton, 2008). By presenting the distractor in the blind field of patients with field defects, it could be investigated whether visual information presented in the blind field is still processed and can influence saccade trajectories to a target presented in the intact part of the visual field. More explicitly, the hypothesis was tested that, in the absence of retinogeniculostriate processing, residual visual processing ('blindsight') may still be detected by measuring saccade trajectories. Whereas deviations in response to distractors in the intact field were present in all patients, the results for distractors in the blind field were mixed, with two of the five patients showing significant deviations away from a distractor presented in the blind field. In a second experiment, the influence of a distractor in the blind field was investigated when target and distractor were closely aligned. Careful mapping of the visual field defects and strict fixation control ensured that the distractor was presented in the blind part of the visual field, whereas the target was presented in the intact field. In the second experiment, two of the participants of the first experiment participated: one participant who did not show the effect in the first experiment and one who did show the effect. Both of them showed a deviation towards a distractor in their blind field, but the effect was larger for the participant who showed the effect in the first experiment. This experiment therefore replicated the modulating effects of a distractor in the blind field. So, in absence of an intact retinogeniculostriate pathway, projecting from the retina to the lateral geniculate nucleus to the primary visual cortex, trajectory modulations can still be observed. One possible neurological explanation for this effect is residual processing in the retinotectal pathway, which projects from the retina to the SC (Cowey, 2004), although it can not be excluded that these effects are due to spared islands of residual vision in the striate cortex. Despite thorough testing of awareness in the visual field, differences between the experimental task and the visual field test might lead to differences in the participant's criterion for awareness of a stimulus presented in the blind field. It is currently unclear what determines whether these effects of residual visual processing manifest themselves in a given patient.

Finally, saccade deviations have recently been used to compare target selection in elderly in a distractor paradigm (Campbell, Al-Aidroos, Fatt, Pratt, & Hasher, 2010; Campbell, Al-Aidroos, Pratt, & Hasher, 2009). Due to the variable fixation offset, a distribution of short and long saccade latencies was obtained. The results in the control group with younger adults replicated earlier findings (McSorley et al., 2006): saccades with short latencies deviated towards the distractor, whereas saccades with long latencies deviated away from the distractor (Campbell et al., 2009). Interestingly, older adults did show a decrease of deviation towards with increasing saccade latency, but deviation away from the distractor was not observed. The authors concluded that the inhibition causing the deviation away from a distractor decreases with age. This is in line with the idea that the inhibition causing the deviation away has a frontal origin, as aging leads to a decline in frontal inhibitory mechanisms (e.g. Nieuwenhuis, Ridderinkhof, de Jong, Kok, & van der Molen, 2000). The differences in saccade deviations between younger and older adults were recently further investigated in a distractor paradigm with multisensory targets (Campbell et al., 2010). Visual targets were presented with an auditory signal, allowing for multisensory integration. Because multisensory targets are processed more quickly than unisensory targets, this allows for a faster discrimination between target and distractor, resulting in greater top-down inhibition of the distractor location at the time the saccade is initiated. In line with the idea that older adults benefit more from multisensory integration than younger adults (Laurienti, Burdette, Maldjian, & Wallace, 2006), deviation away from distractor was similar for both groups when a multisensory target was presented.

10. Neural correlates of saccade deviations

Many models of oculomotor selection have focused on the role of the frontal eye fields (FEF) and the SC in selecting the target and rejecting the distractor (Godijn & Theeuwes, 2002; McSorley et al., 2004; Meeter, Van der Stigchel, & Theeuwes, 2010; Trappenberg, Dorris, Munoz, & Klein, 2001). The SC receives both visual (bottom-up) and task related (top-down) signals and integrates those signals on a common motor map. Task related signals are projected from the FEF to the SC (Munoz, 2002; Sommer & Wurtz, 2001), as the FEF is known to respond differently to targets and distractors (Bichot & Schall, 2002). McPeek, Han, and Keller (2003) showed using neurophysiological recordings that deviation towards a distractor location was accompanied by increased activity in the neurons of the SC coding for the distractor location. It was therefore concluded that deviations in saccade trajectories reflect activity in the SC.

In contrast to the numerous behavioral studies that have used saccade trajectories in the last few years, the number of studies investigating its neural correlates has been low. The two studies that were published on this topic have focused on the role of the FEF in the generation of saccade deviations, one using neurophysiological recordings in monkeys (McPeek, 2006) and one using transcranial magnetic stimulation (TMS) in humans (Walker, Techawachirakul, & Haggard, 2009). With respect to neurophysiological recordings in the FEF, similar results were recently reported as described for the SC (McPeek, 2006). Monkeys performed a visual search task in which distractors were presented. Saccades that deviated towards a distractor were associated with increased activity at the distractor location in FEF. By applying micro-stimulation to sites in the FEF before saccades were executed to targets without distractors, eye movements to a target deviated towards the location coded by the stimulation site. These results are in line with the idea that the FEF plays an important role in target selection. In visual search, the FEF has been shown to select one population of activity as the target and inhibit the distractor location (Schlag-Rey, Schlag, & Dassonville, 1992).

There has been one study in humans in which TMS was applied and saccade trajectories were measured (Walker et al., 2009). Participants made eye movements to a target presented on the horizontal meridian in the presence or absence of a distractor. By applying single-pulse TMS to the right FEF, it could be investigated whether the FEF plays a role in oculomotor target selection. Saccades deviated away from the distractor, but the deviation was increased when TMS was applied. The effect of the TMS pulse could have been caused by two reasons (Walker et al., 2009). On the one hand, the TMS pulse might have increased the oculomotor inhibition of the distractor. This would be in line with the idea that top-down inhibition originates from the FEF. On the other hand, FEF stimulation might have increased the competition between target and distractor by enhancing the saliency of the distractor, thereby enlarging the need for oculomotor inhibition to resolve the competition between these two elements.

Additional studies are necessary to better understand the underlying neurological mechanisms of the oculomotor inhibition associated with deviations away from a location. One of the reasons for the absence of this knowledge is the fact that deviations away have never been observed in monkeys (without pharmacological intervention), in contrast to humans. This inconsistency between humans and monkeys seems in line with the results of the discussed studies on FEF: micro-stimulation of the FEF in monkeys results in stronger deviation *towards*, whereas TMS-stimulation in the FEF in humans results in stronger deviation *away*.

As mentioned above, the SC is assumed to be the location where the competition between multiple saccade goals is resolved, resulting in deviations of saccade trajectories. In recent years, neurophysiological recordings in the SC have elucidated the mechanisms underlying this process of target selection. It is now known that the output of the SC represents the intended saccade trajectory, rather than the actual trajectory. Each spike from a neuron in the SC adds a fixed, site-specific contribution to the intended eye movement command (Goossens & van Opstal, 2006). During target selection, there is no single locus of activity in the SC, but there is activity at all sites in the SC that compete for target selection (Arai & Keller, 2005; McPeek et al., 2003). Although the saccade is initiated to the weighted average of activity at the SC, the activity remains localized at the locations of the visual stimuli. Little activity appears at the location between stimuli that represents the vector of the actual averaging saccade that is made (which seems to be in contrast with the spread of activity assumed by the population coding theories). Saccade trajectories indicate that strong lateral inhibitory connections are unlikely to exist, because these mechanisms tend to produce one locus of activity by the time of saccade onset. To account for the multiple sites of activity in the SC, the model of Arai and Keller (2005) proposes an absence of intrinsic long-range inhibitory connections, in contrast to previous claims (Munoz & Istvan, 1998).

The assumption that the trajectory of the saccade is fully determined by the weighted average of the normalized activity of two locations is problematic, because it does not account for the final direction of the movement (Port & Wurtz, 2003; Walton, Sparks, & Gandhi, 2005). Although the weighted average nicely codes for the initial direction of the saccade, the initial 'motor error' directed by the average vector has to be corrected on-line in order for the eye movement to land correctly on the target location. In a recent computational model by Walton and colleagues (2005), the final direction of the saccade could be predicted by assuming that the collicular output is interpreted by the brain stem saccade generator as desired displacement. While the saccade is executed, the desired eye displacement vector is updated by collicular output on every time step for as long as the saccade lasts. A possible area for this process is the cerebellum, which monitors the saccade progress and adjusts the motor signal (Quaia, Lefevre, & Optican, 1999; Quaia, Optican, & Goldberg, 1998).

11. Summary

A number of important conclusions can be drawn on the basis of the reviewed studies. As discussed, deviations of saccade trajectories constitute a measure of the amount of attention allocated in space. It has been revealed that this holds for exogenous and endogenous attention, but also for exogenous attention triggered by a central cue, like a gaze cue. One of the appealing aspects of the use of this measure is that no response or motor action has to be performed to the location at which attention is allocated: simply observing the bending of the trajectory of an eye movement to a peripheral location can index the amount of attention allocated to a certain location.

With respect to distractor paradigms, saccade trajectory deviations have been shown to measure the strength of the activity of a distractor. Deviation towards the distractor indicates that the activity of the distractor is not fully inhibited once the saccade is initiated, whereas the activity of the distractor is fully inhibited when a saccade deviates away from a location. Also here, no action has to be performed to the location of the distractor to measure the strength of the rejection. This rejection, or oculomotor inhibition, is influenced by various factors like the strength of the stimulus presented at the target and the distractor location. A weak stimulus presented at the target location results in strong competition between target and distractor which requires strong inhibition of the distractor to resolve this competition. When the distractor is weak, no inhibition has to be applied to the distractor, because the perceptual threshold is not exceeded.

Insight has been obtained on both the spatial tuning and the temporal dynamics of the oculomotor competition involved in selecting a target and rejecting a distractor. With respect to the spatial tuning, the location of a distractor influences the amount of inhibition applied to the distractor. This inhibition is a linear summation of the effect of inhibiting each distractor when presented in isolation. With respect to the temporal domain, oculomotor inhibition is mostly dominant in the later responses, whereas the faster responses are less influenced by top-down inhibition.

Manipulations of top-down influences strongly point to a determining role of higher-order processes in the strength of oculomotor inhibition. Knowing the location of the target in advance increases the amount of inhibition applied to the distractor. The influence of higher-order processes was also revealed in the context of decision making, as oculomotor inhibition increases when evidence for a certain decision increased. The origin of the higher-order signals is likely to be the frontal eye fields, although the present knowledge on the underlying neurophysiological underpinnings of saccade deviations is still somewhat limited. Many of the assumptions concerning the underlying mechanisms are still assumptions that are not yet thoroughly tested. For instance, the origin of oculomotor inhibition has not yet been revealed in neurophysiological recordings. Dissociations between the inhibition observed in IOR and saccade deviations have been observed in visual search tasks in which multiple eye movements need to be executed to find the target. These results expose that both types of inhibition do not have the same origin.

The application of this measure to studies on special populations provides an additional domain in which saccade deviations can be useful to measure processes that are not easily obtained via other sources. For instance, by measuring abnormal saccade deviations in Huntington's Disease, the crucial role of the basal ganglia to observe the typical deviation away from a distractor was highlighted. Results in special populations like elderly and patients with visual field defects provide fruitful sources for further

research to elucidate the process of target selection in these and other special populations.

In recent years, it has been shown that saccade deviations constitute a valuable measure in multiple domains, like visual attention, distractor interference, emotional scene context, visual search and spatial memory. As mentioned in the beginning, one of the important advantages of using eye movements as a measure is the multitude of information that can be obtained. Part of this information is the trajectory which can be measured concurrently with saccade latency and saccadic endpoint. This measure therefore adds to the many benefits the recording of eye movement have.

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