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Control of voluntary and reflexive saccades

Received: 24 May 1999 / Accepted: 4 November 1999 / Published online: 28 December 1999
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Abstract The latency of ‘reflexive’ saccades (made in response to peripheral visual stimuli) was compared to that of ‘voluntary’ saccades performed in anti-saccade and symbolically cued paradigms. Manipulation of visual events at fixation was carefully controlled across all conditions. Reflexive saccade latency was significantly faster than the latency of all forms of voluntary saccades. Importantly, the latency of saccades made after presentation of a symbolic cue at central fixation (voluntary arrow-cue condition) was greater than that made in the anti-saccade paradigm that requires suppression of a reflexive response. It is suggested that the increase in latency of saccades made in the voluntary arrow-cue condition may reflect differences in programming a ‘When’ trigger signal for saccades made in the absence of a peripheral stimulus.

Key words Saccade · Anti-saccade · Voluntary · Endogenous · Exogenous

Introduction

Saccades are fast movements of the eyes made to bring the foveal high acuity region onto a visual target. Although all saccades can be regarded as being under voluntary control a distinction is made between so-called ‘reflexive’ (or ‘exogenous’) saccades which are made in response to a novel peripheral stimulus and ‘voluntary’ (or ‘endogenous’) saccades made on the basis of a symbolic cue or instruction. Furthermore, these two types of

saccades are thought to involve different neural structures for their control (Schiller 1998; Schall 1995; Guitton et al. 1985; Pierrot-Deseilligny et al. 1995; Rivaud et al. 1994; Henik et al. 1994; Doricchi et al. 1997; Sweeney et al. 1996).

Behavioural studies of voluntary saccades are uncommon and most have involved the so-called ‘anti-saccade’ paradigm in which subjects make saccades in the opposite direction to a peripheral stimulus (Hallett 1978, Hallett and Adams 1980). Anti-saccades are known to have longer latency, more variable amplitude and a lower peak velocity than reflexive saccades (see Everling and Fischer 1998 for review). In addition to anti-saccades some studies have examined voluntary saccades in delayed and memory-guided paradigms in which subjects must inhibit making a saccade to a peripheral stimulus until the offset of fixation (Funuhashi et al. 1991, 1993; Goldman-Rakic 1996). The anti-, delayed- and memory-guided saccade paradigms all require the additional process of response suppression, which is not a characteristic of the reflexive saccade paradigm. Although the latency of these forms of voluntary saccades is longer than for reflexive saccades it is not clear if this is due to the process of response suppression, or because voluntary saccades require the cognitive manipulation of spatial parameters of the saccade. Two studies of ‘inhibition of return’ have also included forms of voluntary saccades (Abrams and Dobkin 1994; Rafal et al. 1994) and latency was also found to be longer for voluntary saccades. However, direct comparison of reflexive and voluntary saccade latency was not the primary aim of these investigations and may not be appropriate, due to the use of different subject groups across studies.

There have been very few studies of voluntary saccades in tasks that do not require the suppression of a response, or which enable direct comparisons with reflexive saccades. One exception is a study by Henik et al. (1994) who compared voluntary saccades made after the onset of an arrow cue at fixation and reflexive saccades made to a peripheral target. The results for neurologically normal subjects revealed an increase in latency (by

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some 60 ms) for voluntary compared to reflexive saccades. A confounding factor, however, was the onset of the arrow cue in only the voluntary saccade condition. Visual onsets at fixation are well known to increase saccade latency (Ross and Ross 1980, 1981; Walker et al. 1997). It is important, therefore, to ensure that manipulations of visual events at fixation are comparable in voluntary and reflexive saccade paradigms.

The control of visual events at fixation was performed in a study by Forbes and Klein (1996) who examined the facilitatory effects of prior fixation offset – the ‘gap’ effect. Their study compared the latency of reflexive saccades to those of anti-saccades and included another endogenous condition in which saccades were made following a verbal instruction (e.g. “saccade left”). Most importantly, the manipulations of the fixation stimulus (gap paradigm) were comparable in the different conditions. Latency was found to be shorter in the reflexive condition than in the anti-saccade condition and longest in the verbal cue condition. A significant ‘gap’ latency facilitation effect was produced after fixation offset in all conditions, although the decrease was smallest for anti-saccades (cf. Reuter-Lorenz et al. 1991, 1995). The additional latency increase for verbally instructed saccades might be regarded as surprising, however, as the additional process of ‘response suppression’ is required in the anti-saccade task only. Thus, it appears that voluntary saccade latency may be greater when initiated by a symbolic cue than when made after the onset of a peripheral target as in the anti-saccade task. However, an alternative explanation is that auditory ‘cues’ may take longer to translate into a saccade programme than do visual cues.

The aim of the present study was to examine the latency of reflexive and voluntary saccades under conditions in which manipulations at central fixation were carefully controlled to ensure that visual events at fixation were comparable across all conditions. Reflexive saccades were made in response to a peripheral target onset. Voluntary saccades were made in an anti-saccade paradigm and in two symbolically cued paradigms where saccade direction was indicated by an arrow at central fixation. The manipulation of visual events at central fixation was carefully controlled across conditions. In the arrow-cue condition the fixation manipulation produced an arrow which indicated saccade direction. In the arrow pre-cue condition saccade direction was known in advance of the fixation manipulation, thus removing the requirement of interpretation of the cue. All three forms of voluntary saccade required a voluntary movement programme, but the anti-saccade paradigm produces the additional demand of response suppression. Saccade direction was randomised and a single target eccentricity was used, thus avoiding the need for a complex symbolic cue that indicated both direction and eccentricity.

Materials and methods

Subjects

Four male and three female subjects aged from 21 to 35 years participated in the experiment. All had normal or corrected-to-normal vision.

Apparatus

Stimuli were generated by a Macintosh IICi computer using Superlab™ software and were displayed on a 14-inch colour monitor. Horizontal eye movements were recorded at a rate of 250 Hz using a video based eye tracker (SensoMotoric Instruments GmbH). The subject’s eye position was displayed in real time on a second VDU monitor (visible to the operator only) which enabled the experimenter to check that the subject was following the instructions on a trial by trial basis. Saccades were detected online using a velocity ($22^\circ/\text{s}$) and acceleration ($8000^\circ/\text{s}^2$) criterion and were written to disk for later analysis. A chin rest was used to restrain head movements.

Stimuli

The stimulus display sequence is shown in Fig. 1. The first frame for the reflexive, anti- and symbolic (or ‘arrow-cue’) saccade conditions all consisted of a solid central fixation box (sides 1°) and two outline peripheral boxes (sides 1°) positioned 8° left and right of the central fixation box. In a fourth symbolic (‘arrow pre-cue’) condition the first frame used a solid arrow, pointing left or right, in place of the solid fixation box. The second frame always appeared after a random fixation foreperiod of 1000 to 1400 ms. In the reflexive and anti-saccade conditions the fixation box changed from being a solid to outline square and one of the peripheral marker boxes (‘target’) changed simultaneously to being a filled square. In the arrow-cue condition the solid fixation box was replaced with an outline arrow pointing left or right. In the arrow pre-cue condition the solid fixation arrow changed to an outline arrow. In the arrow-cue and arrow pre-cue conditions there were no changes to the peripheral target boxes. The second frame was

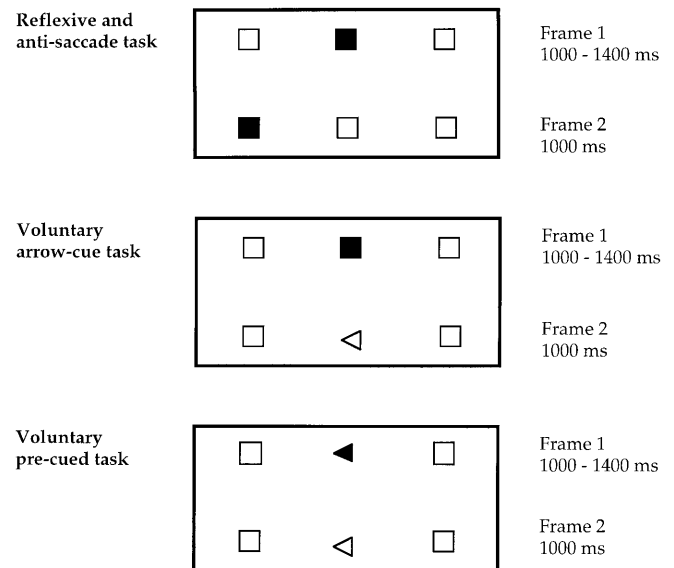


Fig. 1 The stimulus display sequence used in the reflexive saccade, anti-saccade, voluntary arrow-cue and arrow-precue conditions in Experiment 1

presented for 1 s and was then erased and an inter-trial delay of 1.5 s occurred before the next trial.

Procedure

Subjects viewed the VDU monitor at a distance of 57 cm. Voluntary and reflexive saccades were recorded in four separate blocks of 40 trials (20 left and 20 right targets). The order of testing was counterbalanced across subjects. In the reflexive saccade condition subjects were instructed to move their eyes to the peripheral marker box where the visual onset had occurred. In the anti-saccade condition subjects were instructed to move their eyes to the marker box opposite to the visual onset. In the arrow-cue condition subjects were instructed to move their eyes to the marker box indicated by the arrow. In the arrow pre-cue condition subjects were instructed to move their eyes in the direction indicated by the arrow when it changed to being an outline arrow. In all conditions subjects were instructed to move their eyes as quickly and as accurately as possible in the required direction.

Results

Saccades with latency <80 ms were regarded as anticipations (1%) and those with latency >600 ms (4%) were also excluded. Any saccade that landed more than $\pm 2^\circ$ away from the target box (2%) were regarded as inaccurate and excluded from further analysis. In the anti-saccade condition subjects made erroneous 'pro-saccades' to the target on 4% of trials which were also not analysed. The overall mean latency of saccades in each condition, collapsed across direction, is shown in Fig. 2.

Mean saccade latency was compared in a two-factor repeated measures analysis of variance (with the factors condition and direction). The factor of saccade direction was not significant ($F < 1$), but the factor of condition was significant ($F_{3,18} = 29.9$, $P < 0.001$). Post-hoc analysis (Scheffé F -test) showed that reflexive saccade latency was significantly faster than in all other conditions ($P < 0.05$). Latency in the voluntary arrow-cue condition was significantly longer than for all conditions ($P < 0.05$), but there was no difference between latency in the arrow pre-cue and anti-saccade conditions ($P > 0.05$). A separate analysis showed that saccade amplitude was comparable for each condition ($F < 1$) and direction ($F < 1$).

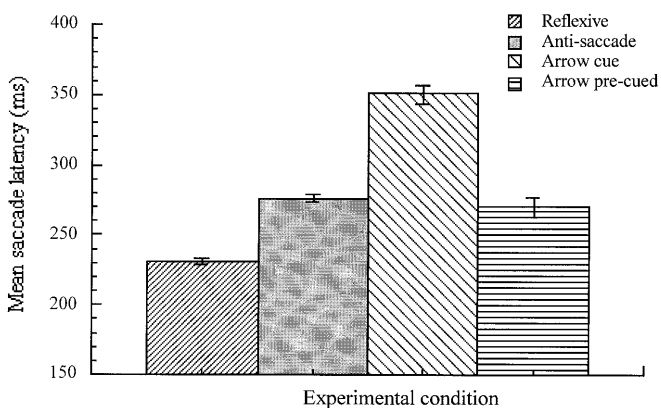


Fig. 2 Mean saccade latency (and SEM) obtained in Experiment 1

In Experiment 1 latency was much longer for saccades made in the voluntary arrow-cue condition than in the anti-saccade paradigm (by some 75 ms). This result may be regarded as surprising, as although both paradigms require some form of cognitive manipulation of a symbolic 'cue' the anti-saccade task also requires the additional process of response suppression. One possible interpretation of this result is that the additional latency increase observed in the arrow-cue condition arises because of the change of shape of the fixation stimulus (filled square to outline arrow) in this condition (we are grateful to an anonymous referee for highlighting this possible interpretation). For this reason we performed a second experiment with a modification to the fixation stimulus. The new fixation stimulus (see Fig. 3) used a central cross located inside a diamond shape. In the reflexive and anti-saccade conditions two lines were removed at the time of the peripheral target onset, forming the shape shown in a) in Fig. 3, while in the arrow-cue condition the removal of the two lines formed an arrow (pointing left or right) as shown in b) in Fig. 3. The arrow 'pre-cue' condition was not included (due to limitations of the new stimulus display) but all other conditions were identical to those used in Experiment 1.

Six subjects (four male and two female, age range 20–35 years) participated in Experiment 2. The mean latency of saccades, collapsed across direction, is shown in c) in Fig. 3. The pattern of results appears similar to that observed in Experiment 1. Importantly, saccade latency was again much longer in the arrow-cue condition than in the anti-saccade paradigm (by some 45 ms), thus confirming the finding of Experiment 1. A repeated-measures ANOVA confirmed an overall effect of saccade condition ($F_{2,10} = 26.9$, $P < 0.001$). Post-hoc analysis (Scheffé F -test) confirmed that reflexive saccades had

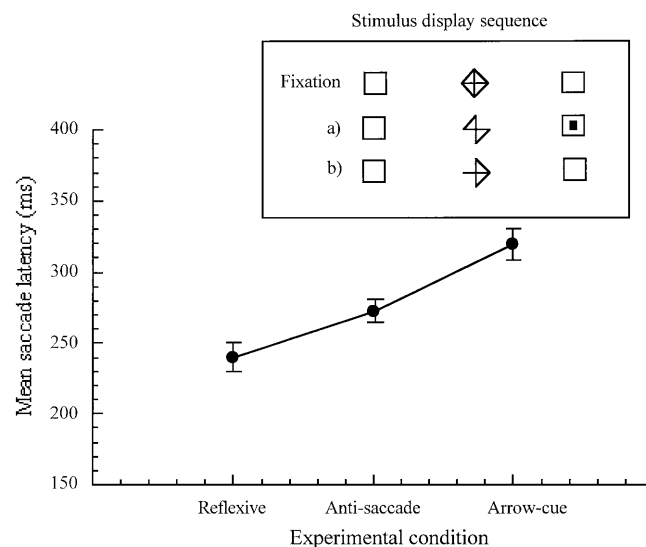


Fig. 3 The modified stimulus display sequence (timing and display otherwise identical to Experiment 1) used in Experiment 2. (a) Reflexive and anti-saccade conditions, (b) arrow-cue condition. The graph shows mean saccade latency (six subjects) observed under these conditions

shorter latency than saccades made in the anti-saccade ($P < 0.05$) or arrow-cue ($P < 0.05$) conditions. Latency was significantly longer in the arrow-cue condition than in the anti-saccade condition ($P < 0.05$). The difference in latency for saccades made in the anti-saccade and arrow-cue paradigms was not as large in the second experiment as was observed in Experiment 1 (45 ms and 75 ms respectively), showing that the change of shape at fixation in the first experiment may have contributed towards the latency increase in the arrow-cue condition. This explanation cannot, however, be applied to the second experiment, which has confirmed that voluntary saccades made after the onset of a peripheral stimulus in the anti-saccade task are faster than those made on the basis of a central symbolic cue.

Discussion

This study was performed to examine the latency of 'reflexive' and 'voluntary' saccades made under conditions in which manipulations of visual events at fixation were carefully controlled. Reflexive saccades were made to peripheral targets that appeared to the left or right of fixation. Voluntary saccades were made away from a peripheral target in the anti-saccade paradigm or were directed by an arrow cue or pre-cue presented at central fixation. All three types of voluntary saccades required voluntary movement programming in the desired direction; however, the anti-saccade task had the additional requirement of voluntary response suppression.

As expected, the fastest saccades were made to a peripheral visual onset in the reflexive saccade paradigm and a significant latency increase was observed for saccades made in all of the 'voluntary' saccade paradigms. A surprising finding of the first experiment was that anti-saccade latency (mean=275 ms) was significantly faster than for voluntary saccades made in the arrow-cue condition (mean=350 ms). Furthermore, in the arrow pre-cue condition, in which saccade direction was known in advance, latency remained greater than for reflexive saccades and comparable to that of anti-saccades. Thus, when subjects have time to process the meaning of the cue the difference between voluntary saccades initiated by a central cue is comparable to that of anti-saccades made after a peripheral onset. A second experiment confirmed that the increase in latency for saccades made in the voluntary arrow-cue condition could not be attributed entirely to the change of shape of the fixation stimulus. It appears, therefore, that in conditions in which direction is not predictable the latency of voluntary saccades initiated by a symbolic cue is much greater than that of anti-saccades (cf. Forbes and Klein 1996). This may be regarded as a surprising finding as the successful production of an anti-saccade requires the suppression of a reflexive saccade, which is a process not required in the symbolically cued saccade paradigms.

One possible explanation for the difference in latency observed in the anti-saccade and arrow-cue paradigms is that the decision process to initiate a saccade may be

quicker after a peripheral visual onset than when indicated by a central symbolic cue. In common with reflexive saccades, the anti-saccade programme is initiated by the onset of a peripheral stimulus. By contrast, voluntary saccades in the arrow-cue conditions are made in the absence of a peripheral stimulus onset. The importance of visual onsets in the triggering of saccades has been illustrated in a study by Todd and Van Gelder (1979) who found that saccades made in response to peripheral visual onsets had much shorter latency than saccades made to targets defined by the offset of non-target distractors. This difference in latency was thought to be consistent with differences in conduction rates of transient and sustained retinal ganglion cells, as seen in the cat retina (Enroth-Cugell and Robinson 1966). A similar distinction has been made between parasol and midget cells in the primate retina which project to different layers of the lateral geniculate nucleus and ultimately form the basis of the so-called M and P visual pathways (see Schiller 1998). Parasol cells, like the cat Y-cells, respond transiently to visual stimulation and have rapidly conducting axons. Parasol cells are scarce in the foveal region and increase in number in the periphery, and form the predominant input to the superior colliculus and parietal lobe. Although peripheral visual stimuli should have privileged access to the cortical and subcortical structures involved in oculomotor generation the known differences in neural conduction rates for peripheral and central visual events are unlikely to account for all of the latency difference observed in the present study.

Models of saccade generation have proposed separate 'When' (go signal) and 'Where' (metrics) channels for saccade programming (Findlay and Walker 1999; Schall 1995). Thus, a peripheral visual onset may have direct access to initiating a saccade 'When' programme, while saccades made after a symbolic cue would require an additional indirect (higher-level) input to this process. Saccade generation is thought to be subject to inhibition until a decision 'When' to initiate a saccade is made after the outcome of processes of response competition (see: Findlay and Walker 1999; Schall 1995). The decision 'When' to trigger a reflexive saccade is regarded as the final outcome of processes of competitive inhibition within the neural network which forms a spatial representation (or map) of potential target locations (e.g. Munoz and Wurtz 1995a, b). Multiple inhibitory links are assumed to result in the selection of a single saccade target after the suppression of activity in other regions of the neural network. Thus, the programming of the 'go' signal for both reflexive and anti-saccades may be initiated by the onset of a peripheral visual stimulus. In addition, anti-saccades may require a higher-level input to this network to voluntarily suppress a reflexive saccade and for the voluntary control of saccade metrics. One suggestion is that a higher-level 'search' process may control anti-saccade generation whereby the search 'target' is defined as the region of absence of activity within this neural network (Findlay and Walker 1999). In the arrow-cue condition where there was no peripheral visual onset the level of activity within

this neural network will remain unchanged and the decision to trigger a saccade would depend entirely on higher-level inputs. In the arrow pre-cue condition, where saccade metrics could be fully programmed in advance of the 'go' signal, latency remained much greater than for reflexive saccades. It appears therefore that an increase in the time required for programming the trigger signal could account for the increase in latency observed in paradigms which use central symbolic cues. In conclusion, our results have demonstrated that the latency of voluntary saccades can be dramatically influenced by the mode of saccade triggering and indicate that the onset of peripheral visual stimuli can produce shorter latency voluntary saccades than those initiated on the basis of a central symbolic cue alone.

Acknowledgements This work was supported by a grant from the Wellcome Trust. The authors would like to thank Melanie Doyle for her help with the development of the second experiment and two anonymous referees for their helpful comments and suggestions.

References

- Abrams RA, Dobkin RS (1994) Inhibition of return: effects of attentional cuing on eye movement latencies. *J Exp Psychol Hum Percept Perform* 20:467–477
- Doricchi F, Perani D, Incoccia C, Grassi F, Cappa SF, Bettinardi V, Galati G, Pizzamiglio L, Fazio F (1997) Neural control of fast-regular saccades and antisaccades: an investigation using positron emission tomography. *Exp Brain Res* 116:50–62
- Enroth-Cugell C, Robson JG (1966) The contrast sensitivity of retinal ganglion cells of the cat. *J Physiol* 187:517–552
- Everling S, Fischer B (1998) The antisaccade: a review of basic research and clinical studies. *Neuropsychology* 36:885–900
- Findlay JM, Walker R (1999) A framework of saccade generation based on parallel processing and competitive inhibition. *Behav Brain Sci* 22:661–721
- Forbes K, Klein RM (1996) The magnitude of the fixation offset effect with endogenously and exogenously controlled saccades. *J Cogn Neurosci* 8:344–352
- Funahashi S, Bruce CJ, Goldman-Rakic PS (1991) Neuronal-activity related to saccadic eye-movements in the monkey dorso-lateral prefrontal cortex. *J Neurophysiol* 65:1464–1483
- Funahashi S, Bruce CJ, Goldman-Rakic PS (1993) Dorsolateral prefrontal lesions and oculomotor delayed-response performance – evidence for mnemonic scotomas. *J Neurosci* 13:1479–1497
- Goldman-Rakic P (1996) The prefrontal landscape – Implications of functional architecture for understanding human mentation and the central executive. *Phil Trans R Soc B* 351:1445–1453
- Guietton D, Buchtel HA, Douglas RM (1985) Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generation of goal directed saccades. *Exp Brain Res* 58:455–472
- Hallett PE (1978) Primary and secondary saccades to goals defined by instructions. *Vis Res* 18:1279–1296
- Hallett PE, Adams WD (1980) The predictability of saccadic latency in a novel oculomotor task. *Vis Res* 20:329–339
- Henik A, Rafal R, Rhodes D (1994) Endogenously generated and visually guided saccades after lesions of the human frontal eye fields. *J Cogn Neurosci* 6:400–411
- Munoz DP, Wurtz RH (1995a) Saccade-related activity in monkey superior colliculus 1. Characteristics of burst and buildup cells. *J Neurophysiol* 73:2313–2333
- Munoz DP, Wurtz RH (1995b) Saccade-related activity in monkey superior colliculus 2. Spread of activity during saccades. *J Neurophysiol* 73:2334–2348
- Pierrot-Deseilligny C, Rivaud S, Gaymard B, Muri R, Vermersch A (1995) Cortical control of saccades. *Ann Neurol* 37:557–567
- Rafal R, Egly R, Rhodes D (1994) Effects of inhibition of return on voluntary and visually guided saccades. *Can J Exp Psychol* 48:284–300
- Reuter-Lorenz PA, Hughes HC, Fendrich R (1991) The reduction of saccadic latency by prior offset of the fixation point: An analysis of the gap effect. *Percept Psychophys* 49:167–175
- Reuter-Lorenz PA, Oonk HM, Barnes LL, Hughes HC (1995) Effects of warning signals and fixation point offsets on the latencies of pro versus anti-saccades: Implications for an interpretation of the gap effect. *Exp Brain Res* 103:287–293
- Rivaud S, Müri RM, Gaymard B, Vermersch AI, Pierrot-Deseilligny C (1994) Eye movement disorders after frontal eye field lesions in humans. *Exp Brain Res* 102:110–120
- Ross LE, Ross SM (1980) Saccade latency and warning signals: Stimulus onset, offset, and change as warning events. *Percept Psychophys* 27:251–257
- Ross SM, Ross LE (1981) Saccade latency and warning signals: Effects of auditory and visual stimulus onset and offset. *Percept Psychophys* 29:429–437
- Schall JD (1995) Neural basis of saccade target selection. *Rev Neurosci* 6:63–85
- Schiller PH (1998) The neural control of visually guided eye movements. In: Richards JE (ed) *Cognitive neuroscience of attention: a developmental perspective*. Erlbaum, Hillsdale, NJ, pp 3–50
- Sweeney JA, Mintun MA, Kwee S, Wiseman MB, Brown DL, Rosenberg DR, Carl JR (1996) Positron Emission Tomography study of voluntary saccadic eye movements and spatial working memory. *J Neurophysiol* 75:454–468
- Todd JT, Van Gelder P (1979) Implications of a transient-sustained dichotomy for the measurement of human performance. *J Exp Psychol Hum Percept Perform* 5:625–638
- Walker R, Deubel H, Schneider WX, Findlay JM (1997) Effect of remote distractors on saccade programming: evidence for an extended fixation zone. *J Neurophysiol* 78:1108–1119