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Saccades guided by somatosensory stimuli

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Abstract

The accuracy of somatosensory saccades defined by proprioceptive cues with and without an additional tactile stimulus was investigated over a wide range of stimulus amplitudes in 16 normal subjects. The present results confirm that somatosensory saccades are less accurate and more variable than visual saccades. Accuracy was minimal for saccades directed to hand distances of 40–50 deg and increased for larger stimulus amplitudes. The additional application of a tactile cue on the fingertip was not found to influence the accuracy of somatosensory saccades significantly. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Do the metrics of eye movements (EMs) guided by body-centered signals differ from those guided by eye-centered information? The comparison of saccades towards targets defined by somatosensory or visual cues may provide insights into the process of how sensory signals are transformed into oculomotor commands (Sparks, 1986; Milner & Goodale, 1995). Whereas visual saccades have been intensively investigated (i.e. Baloh, Sills, Kumley, & Honrubia, 1975; Collewijn, Erkelens, & Steinmann, 1988; for a review, see Becker, 1991), saccades towards somatosensory stimuli (Grüsser, 1982; Groh & Sparks, 1996) have received much less attention. Latter studies showed that somatosensory saccades are characterized by a lower accuracy, higher variability and higher rate of secondary saccades, as well as longer reaction times than visual saccades. However, only a few subjects were investigated and mode of stimulus presentation as well as saccade tasks differed between both studies. A more recent study reported on increased latency of somatosensory saccades if stimuli were applied at the knee, but did not investigate saccade metrics (Neggers & Bekkering, 1999).

The present study reinvestigates somatosensory saccades in 16 subjects over a large range of stimulus amplitudes with two principal questions in mind. One, does the application of an additional tactile cue on the fingertip improve the accuracy of somatosensory saccades? Two, how does the accuracy of somatosensory saccades depend on stimulus amplitude?

2. Methods

2.1. Subjects

Sixteen right-handed students (10 male) volunteered to participate in the study. In one subject, two saccade paradigms had to be excluded from analysis because of a bad signal-to-noise ratio. No ocular or neurological pathologies were noted. The average age was 23.5 years, and subjects were participating in an oculomotor study for the first time.

2.2. Apparatus

Subjects were seated comfortably in front of a half-circle with a diameter of 54.7 cm, which was mounted on a table at eye level (Fig. 1). The head was fixed with a bite-board adjusted at a comfortable height placed

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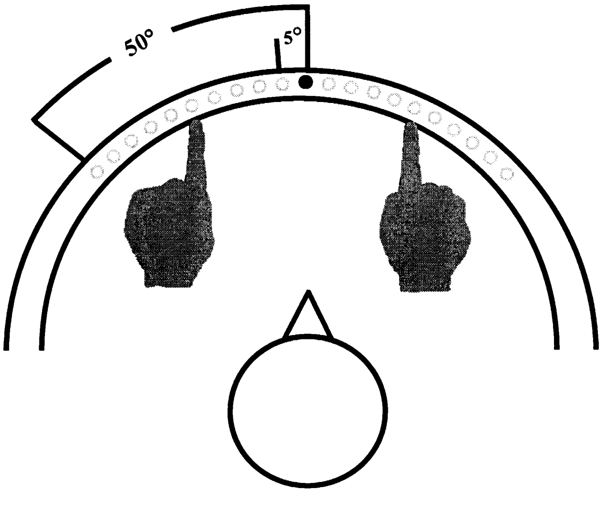

Fig. 1. Experimental set-up. For the somatosensory saccade paradigms, the index fingers of the subject were placed at symmetrical positions in indentations anterior to light-emitting diodes (LEDs). The LEDs (indicated by white circles) were placed on a halfperimeter over a stimulus range of ± 50° on each side of the central fixation LED. The interstimulus amplitude was 5°. The central fixation light was given as a red LED (black circle), target positions as green LEDs. Indentations and respective LEDs were located at identical angular distances. The height of the half circle was adjusted to the position of the eyes. For the somatosensory saccade paradigms, the subjects were instructed to perform alternating saccades between the tip of both index fingers, placed by the experimenter at symmetrical positions. The visually guided saccades were carried out between two symmetrically positioned LEDs.

31.5 cm from light-emitting diodes (LEDs). LEDs were placed on the halfcircle for stimulus amplitudes of ± 50° every 5° on each side of the central LED. The central fixation light was given as a red LED, peripheral target positions as green LEDs. Indentations in front of the LEDs allowed for the positioning of the index fingers at identical angular distances.

All trials were carried out in a totally darkened room, and subjects were instructed to perform alternating saccades between the tip of both index fingers (somatosensory saccades) or between two symmetrical LEDs (visual saccades) in both visual fields. The frequency of alternation was chosen at 1 Hz according to Grüsser (1982), who showed that at this frequency, subjects are able to easily perform saccades between the tips of their index fingers.

2.3. Saccade paradigms

2.3.1. Tactile saccades (TAC, TAC-X)

A vibratory stimulator was attached by a strap at the tip of each index finger. Its size was 3.6 cm^3 ($2 \times 1.2 \times 1.5$ cm). Stimulation resulted from vibration of a small pin (diameter: 1 mm) in contact with the skin (frequency of vibration: 50 Hz, duration: 200 ms, Dipl.-Ing. Nitert, Free University, Berlin, Germany). The stimulator was attached in such a way that stimulation resulted at the center of the palmar surface of the end phalanx. This ensured that mainly the rapidly adapting Meissner's corpuscles with small receptive fields (approximately 2–4 mm) were activated. Rapidly adapting pacinian corpuscles, which are localized in deeper parts of the skin, have much larger receptive fields and are more sensitive to high-frequency mechanical stimulation (approximately 300 Hz, Weinstein, 1968; Johansson & Vallbo, 1983). The experimenter placed the fingers prior to each run in such a way that the middle phalanx came to lay in the indentations with the stimulator above. The subject was instructed to look at the stimulated fingertip as quickly and precisely as possible. Vibratory stimulation was silent, which is important since humans are able to execute precise saccades to auditory targets (Zambarbieri, Schmid, Magenes, & Prablanc, 1982). We did not use electrocutaneous stimulation as used by Grüsser (1982) because the detection of tactile stimulation and the algesic thresholds are quite variable between subjects and known to overlap extensively (Rollman & Harris, 1987). Two tactile saccade paradigms were given. During the first, the right finger of the subject was placed in indentations to the right of the visual fixation light and the left finger in its symmetrical position to the left of the fixation light (TAC). In the second experiment, the same target positions were tested with both arms crossed in front of the subject (TAC-X). Thus, during TAC-X, a tactile stimulus given at the right fingertip was localized to the left of the fixation light and vice versa.

2.3.2. Proprioceptive saccades (PROP)

Here, the index fingers were placed without the vibrators in the symmetrical indentations. The saccade frequency was given by an auditory signal (same duration as the tactile stimulus) from a loudspeaker placed behind the subject. The subjects were instructed to look in an alternating fashion from one fingertip to the other as soon as they heard the auditory signal.

2.3.3. Visual saccades (VIS)

Visual stimuli were presented in an alternating fashion at symmetrical stimulus positions (LED). Each LED was illuminated for a duration of 1 s. Subjects were instructed to perform alternating saccades between both LEDs.

2.4. Data collection and analysis

Saccade paradigms were run in two separate blocks, which were given pseudo-randomly. In one block, a non-crossed condition (PROP, TAC) was given pseudo-randomly before and after the visual condition. TAC-X were given in the other block with VIS (calibration) and given either before or after VIS. Stimulus amplitudes

Table 1
Results from t-tests for α_{sys} between the visual and somatosensory saccade paradigms

α_{sys}	n	t	df	P
VIS-PROP	15	4.455	14	<0.001
VIS-TAC	16	4.519	15	<0.001
VIS-TAC-X	15	4.513	14	<0.001

were chosen pseudo-randomly between 10° and 80° and consisted of a sequence of 12–16 alternating saccadic EMs between the symmetrically presented stimuli. Thus, for each stimulus position and saccade paradigm, 12–16 saccades were carried out.

Eye position was measured by dc-electrooculography (EOG) allowing recording of EMs over a large range of stimulus amplitudes. Data were sampled at 100 Hz. The mean of 10 visual saccades at each target amplitude was used to calibrate the eye position and compared with the non-visual saccades. Saccade amplitude was defined as the overall saccade amplitude including secondary saccades (see Zambarbieri et al., 1982). However, if two secondary saccades occurred after the main saccade, the saccade amplitude was determined after the first secondary saccade. Saccades consisting of more than three eye displacements were rarely encountered and rejected from analysis as were all saccades that started prior to stimulus onset or anticipatory saccades with reaction times <80 ms (Fischer & Ramsperger, 1984; Becker, 1991).

As a measure of saccade accuracy, we determined the systematic error (α_{sys}) and the variable error (α_{var}) Means were used to describe each subject's α_{sys} and α_{var} for each somatosensory saccade condition and stimulus amplitude. α_{sys} was defined as: $\alpha_{sys} = \text{mean } [A_x \text{ (non-vis)} - A_{mean} \text{ (vis)}]$,where A_x (non-vis) represents the amplitude of non-visual saccades including secondary saccades (see above) and A_{mean} (vis) the mean of the visual saccades for a given stimulus position. α_{var} was calculated for all four saccade paradigms (VIS, PROP, TAC, TAC-X) following the equation: $\alpha_{var} = \text{mean } |A_x - A_{mean}|$. A_x is the amplitude of each saccade, and A_{mean} is the mean saccade amplitude in the respective saccade condition for a given stimulus amplitude. (Note that for VIS, α_{var} can differ from 0, whereas α_{sys} cannot). T-tests were applied to carry out a statistical analysis of the mean α_{sys} and the mean α_{var} between the different saccade paradigms. Subsequently, we used a two-way ANOVA to search for the effect of saccade paradigm (PROP, TAC, TAC-X) and stimulus amplitude on α_{sys} and α_{var}. We could not apply the latter variance analysis directly on all saccade paradigms, including VIS, since the saccade amplitude of VIS was used for calibration ($\alpha_{sys} = 0°$).

3. Results

The mean alpha sys was significantly greater for all somatosensory saccades when compared with VIS (one

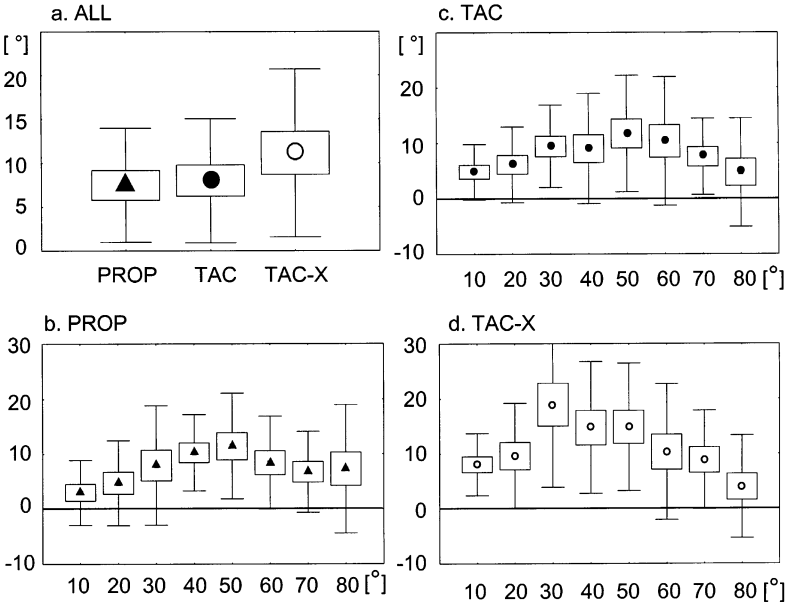

Fig. 2. Mean saccade accuracy. (a) Mean systematic error (α_{sys}, degrees) for PROP (triangle), TAC (filled circle) and TAC-X (empty circle). Visual saccades were used to calibrate eye position and are not shown since they had—per definitionem—an α_{sys} of 0. Mean, standard error (boxes) and standard deviation (whiskers) are indicated. All somatosensory saccades have a significantly larger α_{sys} than VIS. (b–d) Saccade accuracy (α_{sys}) for each tested stimulus amplitude (10°–80°) for PROP (b), TAC (c) and TAC-X (d). Note maximal errors for medium-size stimulus amplitudes (30°–60°).

sample t-test against 0, t-value: 4.5 and $P < 0.001$ for all paradigms; see Table 1, Fig. 2a). PROP showed a mean α_{sys} of 7.5° (S.D.: 6.5°) with maximal differences for saccades of 40°–60° (Fig. 2b). For TAC, a mean α_{sys} of 8.0° (S.D.: 7.1°) was found, and maximally inaccurate saccades were aimed at stimulus amplitudes of 40°–70° (Fig. 2c). The largest α_{sys} was observed for TAC-X (mean: 11.1°, S.D.: 9.6°, Fig. 2d). Hand distances of 30°–50° led to maximal errors of 14.9–18.9° for EMs towards the fingertips with crossed hands. A significant effect of the factors (saccade paradigm: F value: 4.72, $P < 0.05$; stimulus amplitude: F value: 8.79, $P < 0.001$) on the mean as well as a significant interaction between them (F value: 1.78, $P < 0.05$) was found for the somatosensory saccade paradigms (two-way ANOVA, see Table 2). A post-hoc LSD test for the saccade paradigm revealed no significant differences between PROP and TAC, but significant differences between both somatosensory conditions with uncrossed arms (TAC, PROP) and the crossed condition (TAC-X; TAC/TAC-X: $P < 0.01$, PROP/TAC-X: $P < 0.05$). A post-hoc LSD test for the stimulus amplitude revealed significant differences between small and large saccade amplitudes when compared with medium size stimulus amplitudes (30°–60°, P values between 0.02 and $<$ 0.001).

The variability (mean α_{var}) of somatosensory saccades was found to be significantly larger than of VIS (paired t-test, t-values between -5.22 and -6.79, $P < 0.001$ for all paradigms, Fig. 3a, Table 3). The

Table 2
Results from two-way ANOVA for α_{sys}

α_{sys}	df effect	MS effect	df error	MS error	F	P
Saccade paradigm	2	0.277	26	145.6	4.72	<0.05
Amplitude	7	475.9	91	54.5	8.79	<0.001
Interaction (12)	14	55.2	182	47.9	1.78	<0.05

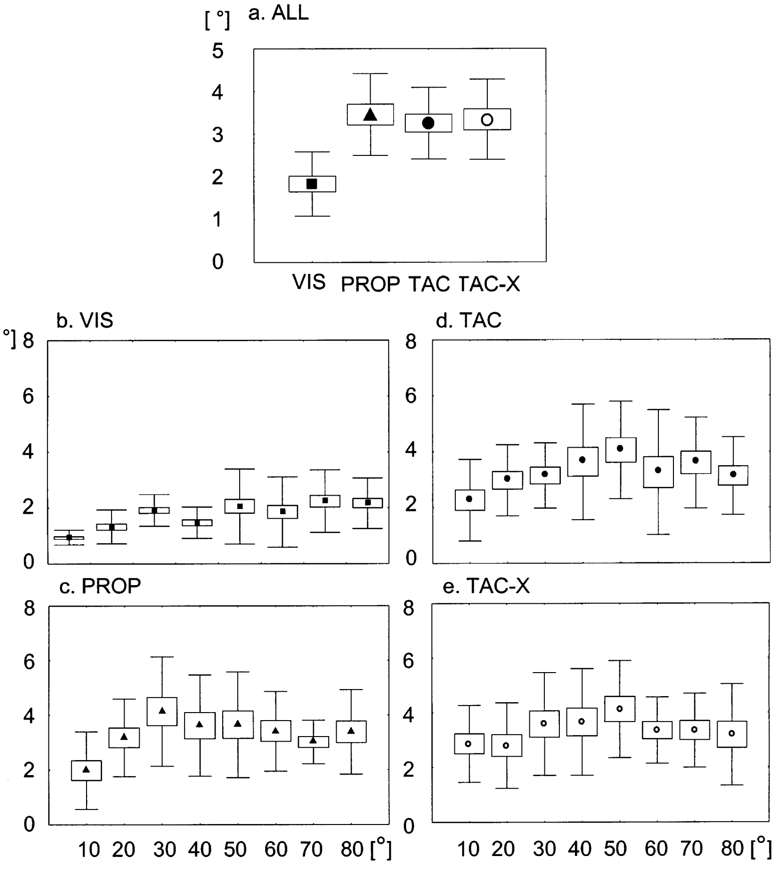

Fig. 3. Mean saccade variability. (a) Mean variable error (α_{var}, degrees) for VIS (square), PROP (triangle), TAC (filled circle) and TAC-X (empty circle). The mean, standard error (boxes) and standard deviation (whiskers) are indicated. All somatosensory saccades have a significantly larger α_{var} than VIS. (b–e) Saccade variability for all tested stimulus amplitudes, as a function of stimulus amplitude for VIS (b), PROP (c), TAC (d) and TAC-X (e), in degrees.

mean α_{var} for PROP was 3.5° (S.D.: 1.0°), for TAC at 3.3° (S.D.: 0.8°) and for TAC-X at 3.3° (S.D.: 0.9°, Fig. 3c, d, and e). VIS were characterized by a lower variability of 1.80 (S.D.: 0.8°, Fig. 3b). A significant effect of the stimulus amplitude on the α_{var} was found (F value: 4.59, $P < 0.001$). No effect of the saccade paradigm and no significant interaction was found (two-way ANOVA, Table 4). The post-hoc LSD test only revealed significant differences for saccades of 10°.

4. Discussion

The present study confirms that saccades directed to targets defined by proprioceptive and tactile signals are more inaccurate and more variable than saccades to visual stimuli (Grüsser, 1982; Groh & Sparks, 1996). Groh and Sparks (1996) examined the accuracy of primary saccades that were directed from five different visual fixation points (20°–40°) towards the index fingers (placed on two fixed hand posts) in two experienced subjects. The present study included secondary saccades in the determination of accuracy, examined saccades between symmetrical stimulus positions in naïve subjects and considered a much larger range of amplitudes. Despite these methodological differences, systematic and variable errors obtained by Groh and Sparks (systematic: 3.3°–8.0°, variable: 4°) and the errors reported in the present study are remarkably similar (systematic: 7.5°–8.0°, variable: 3.3°–3.5°). In both studies, the largest errors were found if the hands were crossed in front of the subject.

A main goal of the present study was to investigate the possible effects of an additional tactile cue upon the generation of somatosensory saccades. Given that localization and discrimination of tactile stimuli on the human body surface are extremely precise on the finger tip (Weinstein, 1968; Johansson & Vallbo, 1983), we hypothesized that the application of an additional tactile stimulus might increase the accuracy of somatosensory saccades. This increase was expected based on parallel processing via the addition of a precise tactile cue. Enhanced proprioceptive information processing related to an improvement of proprioception per se or via a tactile correction of proprioceptive information processing would be a second possibility. However, no metrical differences were detected between the two uncrossed somatosensory saccade paradigms. This result suggests that the localization of tactile cues on the finger does not influence saccade accuracy significantly. It is also conceivable that tactile cues do contribute to saccade accuracy but are not sufficient to influence proprioceptive signals significantly. In other words, large errors related to proprioceptive signal processing are present in both somatosensory saccade conditions and might not be correctable by the high precision of tactile cues of the finger (Weinstein, 1968; Johansson & Vallbo, 1983). Two further conditions might have diminished the potential difference between both uncrossed somatosensory conditions. First, since PROP were not purely proprioceptive as the fingers were in contact with the indentations of the halfcircle, cutaneous somatosensory receptors were stimulated in both conditions. Second, the presentation of the alternating frequency was indicated for PROP by an auditory cue and during TAC by a cutaneous cue.

It is generally assumed that saccadic EMs have a systematic error of approximately 10% of the angular target distance. For visual saccades, this pattern was found up to target distances of 90° (Becker & Fuchs, 1969; Collewijn et al., 1988; Becker, 1991). The present study shows that for somatosensory saccades, this positive correlation is only true for stimulus amplitudes of 10°–50°. Somatosensory saccades induced by larger angular hand distances were significantly more accurate—but equally variable—than saccades directed to smaller target distances (30°–50°). Although lower systematic errors for large somatosensory saccades could

Table 3
Results from t-tests for α_{var} between the visual and somatosensory saccade paradigms

α_{var}	n	Diff	S.D.-Diff	t	df	P
VIS-PROP	15	−1.76	1.16	−5.57	14	<0.001
VIS-TAC	16	−1.42	0.84	−6.79	15	<0.001
VIS-TAC-X	15	−1.50	1.11	−5.22	14	<0.001

Table 4
Results from two-way ANOVA for α_{var} between the different somatosensory saccade paradigms

α_{var}	df effect	MS effect	df error	MS error	F	P
Saccade Paradigm	2	0.27	26	2.8	0.08	0.92
Amplitude	7	10.19	91	2.2	4.59	<0.001
Interaction (12)	14	1.4	182	2.1	0.68	0.79

be based on more accurate determination of the finger position at more lateral hand positions, this seems rather unlikely. A more probable explanation is related to mechanical and/or neuronal mechanisms, which prevent the eyes (during non-visual saccades) from overshooting the stimulus position by an increasing resistance at the approach of the ocular motility range (Warabi, 1977; Zangemeister & Stark, 1982). This latter mechanism would especially influence the amplitude of somatosensory saccades, which systematically overshot the target positions (as calibrated by VIS).

We do not think that the alternating and predictable nature of the experimental paradigm—leading to the induction of saccades with shorter reaction times—provides an explanation for the observed metrical differences between visual and somatosensory saccades. Although saccades with shorter reaction times (i.e. express saccades, Fischer & Ramsperger, 1984) have been extensively studied, little is known about their accuracy in comparison to saccades with regular reaction times (see Becker, 1991; Fischer & Weber, 1993). Fischer and Weber (1993) have reported that express saccades are more inaccurate than saccades with regular reaction times. However, this has only been shown for saccades of 4° eccentricity and might differ for larger saccades, as examined in our study. Moreover, Lemij and Collewijn (1989) have reported an increase in saccade accuracy of saccades towards stationary targets when compared with saccades to jumping targets. Finally, the fact that our experimental set-up was similar for visual saccades and non-visual saccades suggests that the modality-specific differences were responsible for the observed metric differences.

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