RESEARCH ARTICLE

Adele Diederich · Hans Colonius · Daniela Bockhorst ·
Sandra Tabeling

Visual-tactile spatial interaction in saccade generation

Abstract Saccadic reaction times to visual targets tend to be faster when non-visual stimuli are presented in close temporal or spatial proximity even if subjects are instructed to ignore the accessory input. The effect tends to decrease with increasing spatial distance between the stimuli. Multisensory interaction effects measured in neural structures involved in saccade generation have demonstrated a similar spatial dependence. The present study investigated visual-tactile interaction effects on saccadic reaction time using a focused attention paradigm. Compared to unimodal visual targets saccadic reaction time to bimodal stimuli was reduced by up to 30 ms. The effect was larger for ipsi- than for contralateral presentations, and it increased with the eccentricity of the visual target. The results are consistent with attributing part of the facilitation to a multisensory effect of bimodal neurons with overlapping visual and tactile receptive field structures in the deep layers of the superior colliculus.

Keywords Multisensory · Saccade · Crossmodal · Visual-tactile

Introduction

Adaptive behavior depends on the ability of the perceptual system to rapidly deliver information about ongoing events in the environment. This information typically arrives via different sensory channels and has to be integrated to produce a coherent internal representation of the outside world. Multisensory integration processes rely on multiple cues about the temporal and/or spatial coherence of the input. One important system where multisensory integration processes have been studied is the generation of saccadic eye movements. For example, it has been shown that saccadic reaction times to visual targets tend to be faster when auditory stimuli are presented in close temporal or spatial proximity even when subjects are instructed to ignore the auditory input (Colonius and Arndt 2001; Frens et al. 1995; Harrington and Peck 1998; Hughes et al. 1998). Specifically, it was observed that the amount of response facilitation tends to decrease with increasing spatial distance between visual and auditory stimuli.

These psychophysical observations are in line with neurophysiological evidence for multisensory integration in the deep layers of the superior colliculus (DLSC), an area clearly involved in saccade generation (Munoz and Wurtz 1995a, 1995b). A large majority of multisensory neurons in cat DLSC show an enhanced response to particular combinations of visual, auditory, and tactile stimuli relative to the best modality-specific responses (Meredith and Stein 1986a). Information about stimulus location is represented topographically within the structure by an orderly arrangement of neurons according to the location of their respective receptive fields (RFs). The spatial register among the different sensory maps is formed by the multisensory neurons whose different RFs are in register with one another (for a review, see Stein and Meredith 1993). In addition, the SC contains a motor map composed of output neurons coding appropriate eye movements (Sparks 1986), i.e., the locus of activity in the motor map encodes a movement command that reorients the eyes (and the head) a given distance in a particular direction. Thus, if the goal is to translate a sensory target into an appropriate motor command, the alignment of the visual, auditory, and tactile maps to each other and to the motor map is critical. The response enhancement observed in multisensory neurons could serve to facilitate orienting responses to a particular spatial location. This suggests that not only visual-auditory but also visual-*tactile* interactions occur in saccade generation. The goal

A. Diederich
School of Humanities and Social Sciences,
International University Bremen, Bremen, Germany

H. Colonius (✉) · D. Bockhorst · S. Tabeling
Institut für Kognitionsforschung, Universität Oldenburg,
PO Box 2503, 26111 Oldenburg, Germany
e-mail: hans.colonius@uni-oldenburg.de
Tel.: +49-441-7985158
Fax: +49-441-7985158

of this paper is to extend the study of multisensory integration effects in saccade generation to visual-somatosensory interaction.

While many rules governing the influence of accessory, i.e., task-irrelevant, auditory stimuli on saccades toward visual targets have been described in the literature, the effects of somatosensory stimuli on saccades have been examined in much less detail. Groh and Sparks (1996a) compared various properties of saccades to somatosensory and visual targets and found, for visual-somatosensory targets at the same spatial location, a tendency for saccade latency reduction (in monkey). In the first study with human participants Amlôt et al. (2003) observed (1) that accessory somatosensory stimuli reduced the latency of saccades, but only when presented before the visual target, and (2) that the facilitation effect was greatest for spatially coincident stimuli.

While the alignment of visual, auditory, and tactile topographical maps in DLSC suggests that, in analogy to visual-auditory interaction, visual-tactile interaction in saccade generation should depend on the spatial configuration of the stimuli, no detailed observations exist so far. Here we report results from three experiments examining the effect of a tactile stimulus (vibration applied to the palm) on response time for saccades toward a visual target as a function of the spatial visual-tactile stimulus configuration. Subjects were asked to make a saccade as quickly and as accurately as possible toward a visual stimulus appearing randomly left or right of the fixation point. They were instructed to ignore a tactile accessory stimulus that, in bimodal trials, was applied at different hand positions ipsi- or contralateral to the visual target. In the first experiment, the visual target was presented at a constant distance from fixation (left or right), while in the second experiment the tactile stimulus was presented at a constant distance from fixation (left or right) and the visual target positions varied. In the third experiment both stimuli were presented with a constant minimum distance to each other, while their distance to the fixation point was varied.

The main dependent variable of interest was a measure of multisensory response enhancement (defined below) that assesses the facilitation (or inhibition) of bimodal saccadic response time (RT) relative to unimodal responses over different stimulus configurations.

Experiments

The goal of the following three experiments was to probe for the influence of a task-irrelevant tactile stimulus on saccadic RT to a visual target stimulus. In analogy with results from visual-auditory stimulation, we hypothesize that intersensory facilitation of saccadic RT should occur with tactile stimuli in close spatial proximity to the target, and the effect should decrease with increasing distance between visual and tactile stimulus.

Materials and methods

Subjects

Students served as paid voluntary participants in the experiments. All participants had normal vision. They were screened for their ability to follow the experimental instructions (proper fixation, few blinks during trial, saccades towards visual target). They gave their informed consent prior to their inclusion in the study. Local ethical approval was obtained for this study, and all experiments were conducted in accordance with the ethical standards described in the 1964 Declaration of Helsinki.

Apparatus and stimulus presentation

Red light-emitting diodes (LED, 5 mm, 3.7 mcd) served as visual targets presented against a black background. An additional LED (red, 5 mm, 0.4 mcd) served as fixation point. Tactile stimuli were vibrations (50 Hz, 0.6 V, 1–2 mm amplitude) transmitted through wooden balls applied to the center of the palm, generated by two silenced oscillation devices (Mini-shaker, Type 4810, B & K). The oscillation devices were such that a threaded bolt with the wooden ball (diameter 15 mm) on top of it could be mounted. All stimuli were positioned on top of a table (180×130×75 cm) with a recess to sit in (referred to as *vertex*). The fixation LED was 38.5 cm away from the lower edge of the table. Fifty-six LEDs and 56 holes for the vibrators were placed at various positions measured from the vertex. For each experimental condition the two vibrators were moved to the respective positions. Vibrators and LEDs were controlled by a PC multifunction card.

Experimental procedure

All experiments were carried out in a completely darkened room so that participants were unable to see their hands during the experiment. Every session began with 10 min of dark adaptation during which the measurement system was adjusted and calibrated. During this phase the participants put their hands at the position used during the entire experimental block. Thus, the participants were aware of the hand position and, thus, the position of the tactile stimulus. Participants were sitting at the longitudinal side (at the vertex) using a chin rest facing the calibrating screen and wearing a video camera frame. Each trial began with the appearance of the fixation point. After a variable fixation time (800–1,500 ms), the fixation point disappeared and, simultaneously, both a visual and a tactile stimulus were presented for 500 ms (no gap). In unimodal trials, only a visual stimulus was presented. Subjects were instructed to move their eyes to the visual target as quickly as possible, while the tactile stimulus could be ignored. The interval between stimulus offset and fixation onset for the next trial was 2 s. Each participant was first trained for 1,000 trials not included in the data analysis.

Data collection

Saccadic eye movements were recorded by an infrared video camera system (EyeLink system, Sensomotoric Instruments) with a temporal resolution of 250 Hz and a horizontal and vertical spatial resolution of 0.01°. Saccades were detected on a trial by trial basis using velocity (22°/s) and acceleration criteria (8,000°/s^2). Eye position data from each trial were inspected for proper fixation at the beginning of the trial, for blinks, and for correct detection of start and endpoint of the saccade. Saccadic reaction time (the time between the onset of the visual stimulus and the onset of the saccadic eye movement), start position of the eye, and end position after the saccade (vertical and horizontal positions in degree of visual angle relative to the straight ahead fixation point) were calculated from the controlled data samples.

Experiment 1

In the first experiment, visual target distance from the fixation point was kept constant, while the tactile stimulus position was varied. Visual stimuli were presented at positions 10° left and right from fixation, 50 cm from the vertex. Tactile stimuli were applied at positions 10°, 50°, 70°, or 110° left and right from fixation, 55 cm from the vertex (Fig. 1). Note that the 110° positions were not within the subject's visual field.

Subjects

Six students (five female) served as paid voluntary participants in the experiments. All participants had normal vision.

Stimulus arrangement and design

In each trial, a visual target was presented either on the left or on the right. With the visual stimulus appearing always at 10° (left or right) and the tactile stimulus appearing at 10°, 50°, 70°, or 110° (left or right), 16 different bimodal configurations (eight ipsi-, eight contralateral) and two unimodal (visual) conditions were possible, and a total of 100 trials per configuration were recorded. Collapsing over left/right hemispheres this results in four ipsi- and four contralateral configurations plus one unimodal (LED only) condition, with a total of 200 trials per condition. Since the participant was required to put the hands at a fixed position, tactile stimulus presentations were blocked for each position (10°, 50°, 70°, or 110°), but the order of the positions was randomized over subjects. Moreover, trials were randomized with respect to laterality (ipsi/contra) and modality (uni-/bimodal). One hundred and fifty trials were presented within each block, and a total of 12 blocks were performed by each participant.

For data analysis, we define a factor *laterality* with levels *ipsilateral, contralateral*, and *LED only*. The other factor, *eccentricity*, refers to the position of the tactile stimulus and includes four levels: 10°, 50°, 70°, and 110°.

This arrangement of stimulus positions generates eight levels of visual-tactile stimulus distance: 0°, 20°, 40°, 60°, 60°, 80°, 100°, and 120° (ignoring laterality of bimodal stimulation.[1]

Results

Anticipatory saccades with reaction times shorter than 80 ms (e.g., Fischer and Ramsperger 1984), responses longer than 500 ms, saccades less than 5° and larger than 20° (target at 10°), and gaze direction errors (less than 1%) were excluded from the analysis in this and the following experiments. Since there were no systematic

[1] Note that a distance of 60° is obtained either by presenting the tactile stimulus at 70° ipsilaterally or at 50° contralaterally.
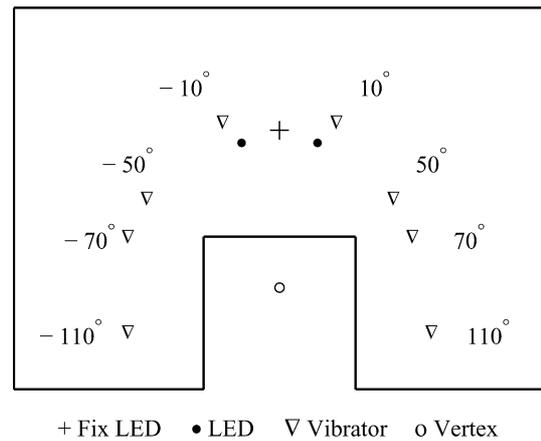
Fig. 1 Spatial configuration of visual and tactile stimuli on the table top for Experiment 1. Visual stimuli were presented only at 10° left or right from fixation. Within one block of trials tactile stimuli were presented at symmetrical positions left or right from fixation at either 10°, 50°, 70°, or 110°; eccentricity varied across blocks. The subject's head was positioned at the vertex
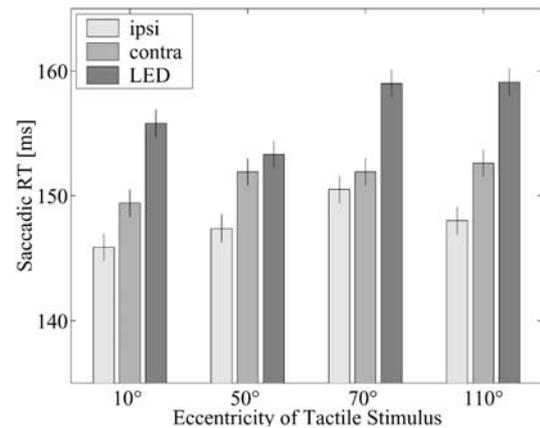
Fig. 2 Mean saccadic reaction time as a function of the eccentricity of the *tactile* stimulus for bimodal ipsi- and contralateral and unimodal visual presentations. The visual stimulus was always presented at 10° left or right from fixation

hemispheric differences, mean saccadic RTs were computed regardless of the specific side (left or right) of stimulus presentation.

Mean saccadic RTs and standard errors (over all subjects) as a function of eccentricity and laterality are shown in Fig. 2. If tactile stimulation had no effect on saccadic RT to the visual target, the 12 means should be about the same since the target LED was presented at 10° from fixation in all conditions. However, the means differ with respect to both eccentricity and laterality. In particular, the presence of a tactile "distractor" always had a facilitating effect on saccadic RT, whether presented ipsi- or contralateral to the visual target. The effect appears to be larger for ipsi- than for contralateral presentations. These observations were confirmed by the subsequent analysis of variance.

Table 1 Accuracy of saccade landing position. The target LED was presented at ±10° for all four eccentricity levels of the tactile stimuli. Mean amplitude (*Ampl.*) and standard deviation (*SD*) were determined for all conditions. "Accurate" saccades were defined as landing position within 1 SD around the mean. Mean saccadic RTs (*RT*) for "accurate" saccades were compared to RTs with saccades of shorter (<) or longer (>) amplitudes, i.e., more than 1 SD below or above the mean amplitude. In 20 out of 24 conditions "accurate" saccades were faster than "inaccurate" ones, giving no evidence for a speed-accuracy tradeoff

Eccentricity of tactile stimulus	Laterality					
	Ipsi		Contra		LED only	
	Ampl. (SD)	RT	Ampl. (SD)	RT	Ampl. (SD)	RT
10°	<	159.0	<	158.0	<	167.7
	11.5 (3.0)	145.0	11.4 (2.9)	150.3	11.4 (3.0)	158.3
	>	149.5	>	154.6	>	151.5
50°	<	156.2	<	156.0	<	155.3
	10.9 (2.8)	147.5	10.9 (2.8)	153.6	11.0 (2.9)	154.5
	>	154.2	>	164.2	>	162.5
70°	<	159.6	<	164.7	<	172.6
	11.0 (2.7)	152.0	11.2 (2.7)	154.0	10.9 (2.6)	160.9
	>	162.9	>	159.2	>	165.4
110°	<	151.1	<	152.3	<	159.2
	11.2 (2.9)	150.9	11.4 (2.9)	157.4	11.5 (2.9)	163.9
	>	157.8	>	160.4	>	158.1

A two-way (3×4) ANOVA of laterality and eccentricity revealed significant main effects of eccentricity and of laterality (*P*<0.01). The interaction *laterality × eccentricity* was not significant. Post hoc tests showed that the presence of a tactile stimulus had a significant effect (Tukey's, *P*<0.01) on mean saccadic RT. Further, the difference ipsi- vs. contralateral stimulation was also significant (*P*<0.01). Moreover, there were significant differences between eccentricity values. In particular, mean saccadic RT was significantly longer when the tactile stimulus was presented at position 110° compared to position 10° (*P*<0.01) or position 50° (*P*<0.05). In addition, mean saccadic RT was significantly shorter when the tactile stimulus was presented at position 10° compared to position 70° (*P*<0.01) or position 110° (*P*<0.01). Note that mean saccadic RTs at neighboring positions (i.e., 10–50° and 70–110°) were not significantly different.

To test for the effect of distance a one-way ANOVA with respect to factor *distance* (the eight levels ranging from 0° to 120°) was performed. While the main effect was significant (*P*<0.01), a post hoc test (Tukey's) did not indicate a monotonic increase in saccadic RT with distance. For example, saccadic RT for a distance of 80° was significantly longer than for 0° distance, but saccadic RTs for 0° and 100° did not differ significantly.

Accuracy

Before these results can be interpreted in terms of visual-somatosensory integration, it must be ruled out that participants traded speed for accuracy in the saccade landing position. To this end, the saccade amplitude distributions for each stimulus configuration were subdivided into three subsets: "accurate" saccades (those within 1 SD above or below the mean amplitude) and two types of "inaccurate" saccades (those more than 1 SD above or below the mean amplitude). A speed-accuracy tradeoff would imply that "accurate" saccades have

Table 2 Multisensory response enhancement (see text) as (1) a function of laterality of bimodal stimulus pair and (2) of eccentricity of the tactile stimulus

Eccentricity of tactile stimulus	Laterality	
	Ipsi	Contra
10°	6.3	3.4
50°	3.8	0.9
70°	5.3	4.4
100°	6.9	4.0

longer mean reaction times than "inaccurate" saccades. However, no indication for a speed-accuracy tradeoff could be found. "Accurate" saccades were faster than "inaccurate" ones in 20 out of 24 stimulus configurations, in particular in all ipsilateral conditions, where facilitation was most conspicuous (see Table 1).

Measure of multisensory response enhancement (MRE)

A convenient way to quantify the amount of facilitation/inhibition by the task-irrelevant modality is to use a measure of response enhancement that relates saccadic reaction time in the bimodal condition to that in the unimodal condition. The following measure presents the percent enhancement in analogy to a measure proposed for multisensory enhancement in neuronal responses (cf. Meredith and Stein 1986b; Anastasio et al. 2000; Colonius and Diederich 2002):

$$\text{MRE} = \frac{\text{RT}_{\text{unimodal}} - \text{RT}_{\text{bimodal}}}{\text{RT}_{\text{unimodal}}} \times 100. \quad (1)$$

For example, an MRE value of 10 means that saccadic reaction time to the visual target is reduced by 10% when a tactile stimulus is present. MRE is meant as a descriptive measure only, reflecting the statistical results previously obtained by ANOVA. MRE values obtained are shown in Table 2.

Note that MRE was larger for stimuli presented ipsilateral than contralateral. In either case, the effect of eccentricity was non-monotonic, reflecting the behavior of the means observed before. The non-negativity of the MRE values indicates that saccades in the bimodal conditions were always performed faster than in the unimodal conditions.

Discussion

To summarize, a task-irrelevant tactile stimulus (a) had a significant facilitatory effect on saccadic response time to the visual target, and (b) this effect was larger when both stimuli were presented in the same hemisphere.

Unlike the observations in visual-auditory studies, in this experiment there was no clear tendency of the facilitation effect to decrease with increasing distance between the visual and the tactile stimulus. A possible explanation, suggested by one of the reviewers, is that the tactile stimuli were poorly localized in the dark. Assuming that the perceived position of a tactile stimulus is blurred around the true position, probably with a larger region of uncertainty for the more eccentric positions, would result in the perceived distance not necessarily increasing with the physical distance between the stimuli. Note that this cannot be ruled out since we could not check tactile localization for eccentricity values 50° and larger, and it would be consistent with the observed large MRE values for the higher eccentricity values. Nevertheless, the significant difference between ipsi- and contralateral presentations indicates that the effect of distance was not wiped out entirely.

The following experiments were designed to further investigate the effect of spatial stimulus configuration.

Experiment 2

The conditions of this experiment were identical to the first one, except for the following: while in the first experiment the position of the visual target was held constant (except for left/right presentation) and tactile stimulus position was changed over blocks, in Experiment 2 tactile stimulation was applied at a fixed position (left or right from fixation). Thus, the position of the limbs was held constant over the entire experiment. The visual stimulus was presented at various spatial locations, but in order to keep comparability with the first experiment, visual stimulus positions were blocked. Thus, within a block subjects could anticipate the visual target position except for the left/right presentation.

Subjects

Six students (five female) served as paid voluntary participants; four of them had participated in the first experiment. All participants had normal vision.

+ Fix LED   • LED   ∇ Vibrator   o Vertex
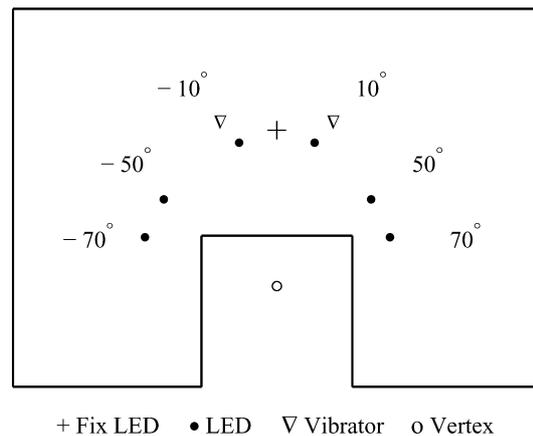
Fig. 3 Spatial configuration of visual and tactile stimuli on the table top for Experiment 2. Tactile stimuli were presented only at 10° left or right from fixation. Within one block of trials visual stimuli were presented at symmetrical positions left or right from fixation at either 10°, 50°, or 70°; eccentricity varied across blocks

Stimulus arrangement and design

The two vibrators were positioned at 10° left and right from the fixation point, 55 cm from the vertex. Visual stimulus positions were 10°, 50°, and 70° left and right from fixation, 50 cm from the vertex (Fig. 3).

As before, bimodal stimuli were presented ipsi- and contralateral. This results in 12 different bimodal configurations (6 ipsi-, 6 contralateral, left or right) and 6 unimodal (visual) conditions, with 100 trials per configuration. Collapsing over left/right hemispheres this amounts to 3 ipsi- and 3 contralateral configurations plus 3 unimodal (LED only) conditions, with a total of 200 trials per condition. Again, we have three levels of *laterality*: ipsilateral, contralateral, and LED only. The other factor, *eccentricity*, now refers to the eccentricity of the *visual* stimulus and includes the levels 10°, 50°, and 70°.

Results

Overall mean saccadic RTs and standard errors as a function of eccentricity and laterality are shown in Fig. 4.

Presentation of the tactile accessory stimulus had a facilitating effect on saccadic RT in all conditions, whether presented ipsi- or contralateral. The effect was larger for the ipsilateral presentation. A two-way (3×3) ANOVA with factors *laterality* and *eccentricity* yielded significant main effects ($P<0.01$). Moreover, the interaction was significant ($P<0.01$). Post hoc tests showed that the presence of the tactile stimulus had a significant effect ($P<0.01$) on mean saccadic RT. Further, ipsi- vs. contralateral stimulation was also significant ($P<0.01$) as were the differences between all eccentricity values ($P<0.01$). Again, there was no systematic decrease in facilitation with target-accessory distance.
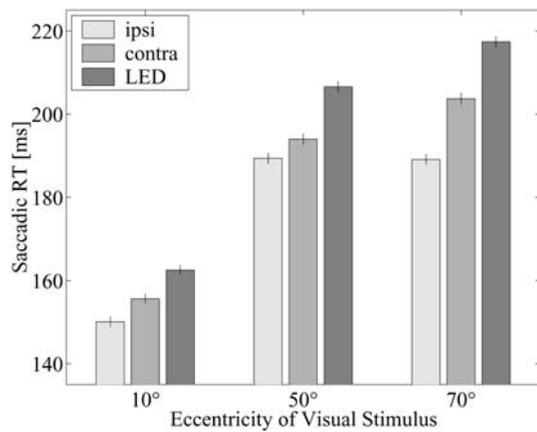
Fig. 4 Mean saccadic reaction time as a function of the eccentricity of the *visual* stimulus for bimodal ipsi- and contralateral and unimodal visual presentations. The tactile stimulus was always presented at 10° left or right from fixation

Table 3 Multisensory response enhancement (see text) as a function of laterality of the bimodal stimulus pair and of eccentricity of the visual target

Eccentricity of visual stimulus	Laterality	
	Ipsi	Contra
10°	7.2	4.2
50°	8.3	6.1
70°	13.7	6.3

The fact that saccadic RT typically increases with eccentricity of the visual target[2] (e.g., Findlay and Walker 1999) could be a confounding factor for the effect of eccentricity on facilitation. However, the relative enhancement as measured by the MRE introduced above would not be affected by this. Nonetheless, MRE *increases* with increasing eccentricity of the visual stimulus separately for the ipsi- and the contralateral condition (Table 3).

Accuracy was determined for the 10° condition only since amplitudes to targets at positions 50° and 70° could not be accurately registered by the recording system. As before, no speed-accuracy tradeoff could be observed (Table 4).

To summarize, Experiment 2 replicates the significant effect of a tactile accessory stimulus on saccadic reaction time to the visual target. Again, there was no systematic decrease in facilitation with increasing distance between visual and tactile stimulus. However, increasing the eccentricity of the visual target led to an increased facilitation effect of the tactile stimulus.

Experiment 3

The above result suggested that eccentricity of the visual target, rather than distance between tactile accessory stimulus and target, determines the amount of facilitation. Therefore, in the final experiment the distance between the visual and the tactile stimulus was kept at a constant minimal level but the positions of both stimuli and, thereby, the eccentricity of the target were varied simultaneously across blocks.
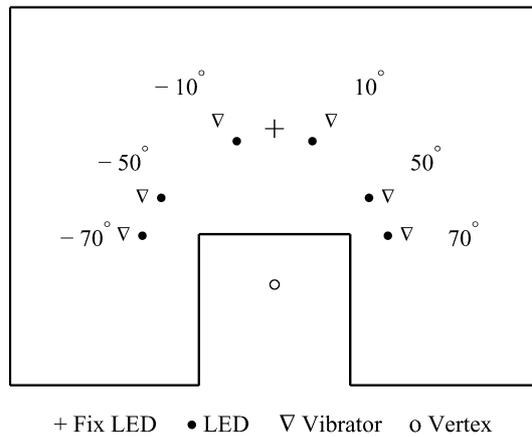
Subjects

Six students (four female) served as paid voluntary participants. Four of them had participated in the previous experiments.

Stimulus arrangement and design

Both visual and tactile stimuli were presented at positions 10°, 50°, and 70° left and right from the fixation point, the tactile stimulus 55 cm and the visual stimulus 50 cm away from the vertex (Fig. 5).

As before, bimodal stimuli were presented ipsi- and contralateral, resulting in 12 different bimodal configurations (6 ipsi-, 6 contralateral, left or right) and 6 unimodal (visual) conditions, with 100 trials per configuration. Collapsing over left/right hemispheres this amounts to 3 ipsi- and 3 contralateral configurations plus 3 unimodal (LED only) conditions, with a total of 200 trials per condition. Again, we have three levels of *laterality*: ipsilateral, contralateral, and LED only. The other factor, *eccentricity*, now refers to the eccentricity of the *visual-tactile* stimulus pair with levels 10°, 50°, and 70°.

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[2] Up to 30° the increase is about 0.4 ms/1°.

Table 4 Accuracy of saccade landing position for the 10° target position (for explanation, see Table 2)

Eccentricity	Laterality					
	Ipsi		Contra		LED only	
	Ampl. (SD)	RT	Ampl. (SD)	RT	Ampl. (SD)	RT
10°	<	153.2	<	162.9	<	168.9
	10.9 (2.4)	149.6	11.1 (2.5)	153.4	11.4 (3.9)	160.9
	>	149.2	>	162.5	>	174.2

** Spatial configuration of visual and tactile stimuli on the
table top for Experiment 3. Within one block of trials visual and
tactile stimuli were presented at positions 10°, 50° or 70° ipsi- or
contralateral, unimodal visual stimuli at 10°, 50°, or 70° left and
right from fixation. Eccentricity varied across blocks

Fig. 6 Mean saccadic reaction time as a function of the eccentricity
of both stimuli for bimodal ipsi- and contralateral and unimodal
visual presentations

Table 5 Multisensory response enhancement (see text) as a
function of laterality and eccentricity of bimodal stimulus pair

Eccentricity of visual-tactile stimulus	Laterality	
	Ipsi	Contra
10°	4.9	1.8
50°	8.8	2.9
70°	12.7	4.8

The MRE measure reveals that facilitation increased
with increasing eccentricity of the visual-tactile stimulus
pair (Table 5).

As before, accuracy was determined for the 10°
condition only (Table 6). Again, no indication of a
speed-accuracy tradeoff could be observed.

To summarize, Experiment 3 shows that keeping
spatial distance between target and accessory stimulus
constant, the facilitation of saccadic response time, as
measured by MRE, increases monotonically with the
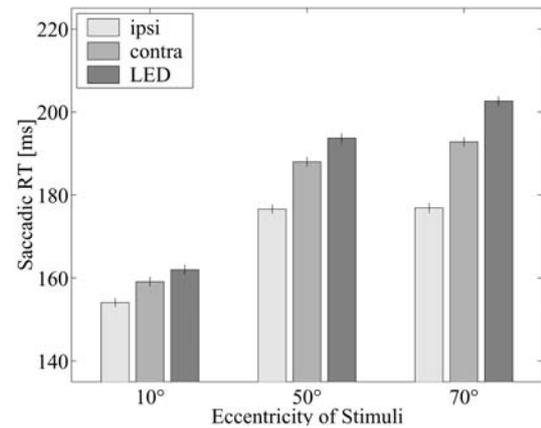eccentricity of the stimulus configuration.

Results

Overall mean saccadic RTs and standard errors as a
function of eccentricity and laterality are shown in Fig. 6.

Presentation of the tactile accessory stimulus had a
facilitating effect on saccadic RT in all conditions,
whether presented ipsi- or contralateral, as observed in
Experiment 2. Similarly, the facilitating effect is larger
for the ipsilateral presentation. A two-way (3×3) ANOVA
with factors Laterality and Eccentricity yielded signifi-
cant main effects ($P<0.01$). Moreover, the interaction was
significant ($P<0.01$). Post hoc tests showed that the
presence of a tactile accessory stimulus had a significant
effect (Tukey's, $P<0.01$). Ipsi- vs. contralateral bimodal
stimulation was significant ($P<0.01$) as well as the
differences between all eccentricity values ($P<0.01$).

Discussion

The three experiments reported here demonstrate the
effects of a task-irrelevant somatosensory (vibratory)
stimulus on saccadic reaction time to a visual target
appearing randomly left or right from fixation: (1)
average saccadic reaction time in the bimodal condi-
tion, compared to unimodal visual responses, is reduced
up to 30 ms depending on the spatial configuration of
the stimuli; (2) the effect is larger for ipsilateral
stimulus pairs than for contralateral pairs; and (3) the
effect increases with the eccentricity of the visual
target.

Our results are in line with the observations reported in
the recent study by Amlôt et al. (2003) where visual and
somatosensory stimuli were employed both as targets and

Table 6 Accuracy of saccade
landing position for the 10°
target position (for explanation,
see Table 2)

Eccentricity	Laterality					
	Ipsi		Contra		LED only	
	Ampl. (SD)	RT	Ampl. (SD)	RT	Ampl. (SD)	RT
10°	<	165.2	<	170.1	<	166.0
	11.2 (2.8)	151.1	11.3 (2.7)	156.1	11.3 (2.6)	159.9
	>	158.4	>	158.3	>	166.8

as distractors (over different blocks of trials). These authors also found facilitation for spatially coincident and disparate visual and tactile stimuli, but only when the tactile stimulus preceded the visual target.[3] The question then arises as to whether this speed-up of saccadic responses is a genuine integration effect presumably based on multisensory neurons in structures participating in the generation and control of eye movements.

A common alternative explanation is that the tactile stimulus acts as a warning signal about the forthcoming visual target onset. Although the tactile stimulus was not predictive with respect to the location of the target, the appearance of the accessory stimulus could lead to a decrease in activity of the fixation neurons in SC, thereby facilitating saccade generation, in analogy to the "gap effect" when a central visual fixation point is removed before the onset of the target stimulus (cf. Frens et al. 1995). This parallel programming of spatial ("Where") and temporal ("When") channels has been suggested in the recent model of saccade generation by Findlay and Walker (1999). In the Amlôt et al. study this warning signal effect has been probed further by introducing, in addition to the tactile distractor, an auditory warning signal in some of the trials. Their results indicate that part, but not all, of the saccadic RT reduction could be attributed to the temporal warning signal effect.

Our finding that contralateral distractors had a facilitating effect on saccadic RT seems to be at odds with certain empirical findings and models of saccade target selection (see Findlay and Walker 1999). The "remote distractor" effect consists in an observed increase in RT when the target and a distractor are presented at remote positions (Walker et al. 1997). According to the model by Trappenberg et al. (2001), each stimulus produces an increase in collicular neuronal activity in separate populations in the collicular salience map. Target selection is accomplished by the existence of a single salience peak in the collicular map. This requires an inhibitory process taking a certain amount of time that is not needed in the single target case, contrary to the facilitation observed in our contralateral distractor conditions. A possible way to reconcile this with our results is to assume that the "remote distractor" effect is confined to the visual modality. For example, both Frens et al. (1995) and Colonius and Arndt (2001) did find a facilitating effect of remote auditory distractors as well. While the size of these effects obviously depends on the relative intensity of target and distractor, it could be that visual distractors generate a more salient representation on the collicular activity map. This may be due in part to a more spread-out representation of auditory or tactile stimuli relative to visual stimuli, possibly resulting from differences in the corresponding receptive field sizes (for recent results on the effect of auditory and somatosensory distractors on saccade trajectories to visual targets see Doyle and Walker 2002).

Alternatively, it is quite plausible that the relatively small facilitation observed with contralateral distractors both here and in the other studies with auditory distractors is largely due to the above mentioned non-spatial warning effect in agreement with the parallel programming of spatial and temporal channels. Nevertheless, there is converging evidence both from the Amlôt et al. study and from our data that part of the spatially coincident facilitation effect cannot be attributed to the warning signal function. First, both studies found larger effects with spatially coincident stimuli and, second, the differential effect of eccentricity would not be compatible with an invariant warning signal influence.

Yet another account for the speed-up with spatially coincident stimuli would be that subjects are merely responding to the stimulus which is detected first. Formally, the observed saccadic RT would be the minimum of the response time to the visual and to the tactile signal causing a *statistical facilitation* effect (Raab 1962; Miller 1982; Gielen et al. 1983; Diederich and Colonius 1987; Hughes et al. 1998). Since in our experiments we did not collect unimodal saccadic responses to tactile targets, it is not possible to rule out such an effect entirely. Moreover, as conduction rates for visual stimuli are typically faster than for somatosensory stimuli under conditions similar to the present study (Groh and Sparks 1996c), statistical facilitation would be predicted to be greatest when the tactile stimulus is presented before the visual target, just as observed by Amlôt et al. (2003). Nonetheless, statistical facilitation may not be a sufficient explanation for the speed-up. If subjects had responded to the first stimulus detected, a sizable number of gaze direction errors (much more than the 1% actually registered) should have occurred for contralateral stimulus pairs. Moreover, experiments collecting manual response times to bimodal visual-tactile stimuli did find facilitation effects above the level that could be attributed to statistical facilitation alone (Diederich 1995; Forster et al. 2002).

Thus, we are led back to consider a possible contribution in terms of a crossmodal enhancement caused by activity in multisensory neuronal areas. Note, first, that this interpretation is in line with results from the exogenous spatial cuing paradigm (Spence et al. 1998). In a recent study by Kennett et al. (2001), a spatially non-predictive (tactile) cue was presented either at the left or right index finger shortly (200 or 350 ms) before a visual target appeared close to the hand position either ipsi- or contralateral to the stimulated hand. The task was an up/down visual judgment, i.e., a speeded discrimination whether the visual target came from an upper or lower position. Response times (using foot pedals) were significantly shorter for "cued" targets, i.e., for those targets on the same side of external space as the tactile cue, and this effect was larger for the short (200 ms) than the long (350 ms) cue-target interval. While both observations seem to speak against a simple warning or preparatory effect of the (spatially non-predictive) cue as the sole cause of the facilitation, it should be noted the mean RTs

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[3] This discrepancy may be due to intensity differences between the somatosensory stimuli used in the different laboratories.

in this paradigm were more than double in magnitude (around 400 ms) compared to the saccadic response times observed here. Thus, the underlying neural circuitry could be different. Nonetheless, based on a corresponding event related potential (ERP) study showing larger ERP amplitudes for visual events for "cued" targets, Kennett et al. (2001) suggested that multimodal neurons in subcortical structures and also in parietal and premotor cortical structures might be involved in the observed tactile-visual links (p. 473, ibid).

Our behavioral data are consistent with the notion that the observed saccadic RT reduction results at least in part from genuine visual-tactile integration most likely taking place in multisensory brain areas involved in eye movement control. The SC is a prominent but certainly not the only area where multisensory interaction takes place. Moreover, multisensory integration properties of most SC neurons are mediated by influences from two cortical areas, the anterior ectosylvian sulcus (AES) and the rostral aspect of the lateral suprasylvian sulcus (rLS) (Jiang et al. 2001). In the focused attention paradigm studied here, where target and non-target modalities must be distinguished to accomplish the task, the contribution of other areas like the frontal eye fields (FEF) cannot be ruled out.

In order to understand the observed effects of spatial configuration the existence of different frames of reference for the modalities must be taken into account. Visual space is coded in retinal coordinates, auditory space is coded with respect to the head, and tactile/somatosensory space is referred to the body surface. Since these reference frames can move independently from one another (e.g., when the eyes or the hand move with the head fixed), in order to keep up receptive field register there is a need for a dynamic remapping of the modality-specific coordinate systems into a common frame of reference which is most likely closely aligned with the motor representation in SC (Sparks 1986; Sparks and Nelson 1987). For primates Groh and Sparks (1996b) have shown that saccades to somatosensory and visual targets are represented by the same population of neurons in SC. The somatosensory signals are not represented in body-centered coordinates but clearly depend on the position of the eyes with respect to the somatosensory target (Groh and Sparks 1996c). Moreover, the RFs of bimodal visual-tactile neurons are organized in close spatial register across the modalities, so that closely related regions of space are responded to in both vision and touch by a given cell.

Spatially coincident visual-tactile stimuli fall within a given neuron's overlapping RFs producing a response enhancement that typically exceeds the individual modality-specific responses by far (Meredith and Stein 1986b). However, RF field sizes of SC neurons are large and heterogeneous, and two stimuli with a substantial spatial disparity could still fall within the visual and tactile RF overlap. Recently, Kadunce et al. (2001) found no systematic relationship between the spatial disparity of visual and auditory stimuli and the magnitude of multi-sensory response enhancement, although the area of cross-modal RF overlap appears to be the major site of multisensory enhancement. As these authors suggest, however, the spatial resolution at the level of a population of neurons should be much higher: increasing spatial disparity decreases the likelihood of both stimuli falling in the RF overlap of a given neuron and, moreover, increases the incidence of multisensory inhibition (Kadunce et al. 1997). Although a generalization of these results to the human brain is not automatic, a participation of visual-tactile neurons in human DLSC in generating the saccadic speed-up is a plausible working hypothesis.

This interpretation agrees with previous eye movement studies with auditory stimuli (e.g., Frens et al. 1995; Harrington and Peck 1998; Hughes et al. 1998; Colonius and Arndt 2001) where visual-auditory facilitation was a decreasing function of the physical distance between target and accessory stimulus. Note, however, that there is an obvious discrepancy between these results and the findings from visual-auditory eye movement experiments: in Experiments 2 and 3, visual-tactile facilitation was shown to increase monotonically with the *eccentricity* of the visual stimulus position, but not with the *physical distance* between visual and tactile stimulus. While, as mentioned above, this lack of a distance effect could be attributed to a poor localization of the tactile stimuli in Experiment 1, the monotonic effect of eccentricity, even when physical distance was kept constant (Experiment 3), calls for further explanation.

A somewhat similar observation has been made in a behavioral study with cats trained to orient towards a visual stimulus always presented at center target (fixation point) (Stein et al. 1989). An auditory stimulus presented randomly at various positions enhanced responses to the visual stimulus when they were coincident, but also when it was lateral (temporal) to the visual stimulus. Depression occurred only when the auditory was nasal to the visual. Thus, in both studies enhancement was not a function of physical disparity but of the absolute position (eccentricity, temporal/nasal) of the stimuli. Stein et al. could explain their results with the asymmetry of the posterior borders of many auditory RFs with respect to the midline in cat SC. Similarly, studying the relationship between visual and somatosensory RFs, Stein et al. (1976) observed that, as visual RFs moved temporally, the underlying tactile RFs were displaced caudal and distal and were getting much larger. Thus, the correspondence between visual and somatosensory space becomes far poorer with eccentricity, i.e., in regions of large saccade generation. It remains for further study whether such an RF organization might also be involved in producing the eccentricity effects in humans.

Note that the increase in multisensory response enhancement with visual target eccentricity makes sense from a functional point of view as well. Orienting the eyes toward more eccentric targets takes more time and, thus, a facilitating effect of the tactile accessory stimulus would be more important for more eccentric targets. This differential contribution of multisensory neurons would

be an instantiation of the principle of inverse effectiveness (Wallace and Stein 1994) according to which smaller unimodal responses are associated with larger multisensory enhancement. For a discussion of this principle from a modeling perspective we refer to Anastasio et al. (2000) and Colonius and Diederich (2002).

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