

Research Report

Interstimulus contingency facilitates saccadic responses in a bimodal go/no-go task

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Abstract

The saccadic response to a suddenly appearing visual target stimulus is faster when an accessory auditory stimulus is presented in its spatiotemporal proximity. This multisensory facilitation of reaction time is usually considered a mandatory bottom-up process. Here, we report that it can be modulated by the predictability of the target location provided by an accessory stimulus, thereby indicating a form of top-down processing. Subjects were asked to make a saccade in the direction of a visual target randomly appearing left or right from fixation. An accessory auditory stimulus was presented either at the same location or opposite to the target, with the probability varying over blocks of presentation. Thus, the auditory stimulus contained probabilistic information about the target location (interstimulus contingency). A certain percentage of the trials were catch trials in which the auditory accompanying stimulus (Experiment 1) or the visual target (Experiment 2) was presented alone and the subjects were asked to withhold their response. In particular with visual catch trials, varying the predictability of target location resulted in reaction time facilitation in the bimodal trials, with both high (80%) and low predictability (20%), but only when both stimuli were presented within a small time window (40 ms). As subjects could not possibly follow the task instructions in this short period explicitly, we conclude that they utilized the interstimulus contingency information implicitly, thus revealing an extremely fast involuntary top-down control on saccadic eye movements.

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1. Introduction

One of the key questions addressed in multisensory research is to what extent the presentation of an accessory stimulus from another sensory modality, such as audition, improves processing of a target stimulus in a given modality, such as vision. The ability to discover and utilize the co-occurrence of such events is an important part of an individual's capacity to adapt to ongoing changes in the

environment. Since the presence of different sensory modalities at the same time and place often indicates one and the same event (e.g., a rapidly approaching car), a speeded response to this event should have a certain survival value. Here, we ask whether the facilitation effects observed under multisensory stimulation are affected by regularities in the co-occurrence of these events. Such interstimulus contingencies (ISC) were introduced as follows. Subjects were asked to make a saccade in the direction of a visual target randomly appearing left or right from fixation. An auditory stimulus was presented either at the same location or opposite to the visual target, with the probability varying over blocks of presentation. Thus, the likelihood of the visual target to occur at a certain location was contingent

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upon the occurrence of the auditory accessory stimulus at the same or opposite location. In choice reaction time tasks, interstimulus contingency effects are well established [39,41,52]. However, it is not clear if, and at what stage, a cortical top–down influence of interstimulus contingencies can affect the very rapid time course of a saccadic eye movement toward a visual–auditory target. Saccadic eye movements are especially suited for studying spatial interstimulus contingencies because shifts of the eyes are spatially structured and in general have shorter reaction times than manual responses [33].

1.1. *The intersensory facilitation effect*

Saccadic reaction time to a visual target tends to be facilitated by the concurrent presentation of an auditory non-target. Specifically, this intersensory facilitation effect (IFE) is most prominent when the visual and auditory stimulus are presented in close spatial and temporal proximity, and it diminishes, or even reverses into inhibition, with increasing spatial or temporal distance between the stimuli [9,12,18,28,29].

On a physiological level, it was shown that multisensory cells in the deep layers of the superior colliculus (SC) and other cortical areas play an important role in multisensory processing [6,55,59]. The SC is a midbrain structure receiving converging afferents from a multitude of cortical and subcortical areas related to eye movement control (for a review, see [51]). It integrates information from different sensory modalities (visual, auditory, somatosensory) and relays this information to the brainstem premotor circuitry to trigger eye movements toward the source of stimulation. Electrophysiological recordings from the deep layers of the SC in the cat and monkey showed that multisensory cells exhibit substantially enhanced discharge rates if a visual and an auditory stimulus are presented within its receptive fields given the stimuli are presented close in time. However, if one of the stimuli is presented outside the neuron's receptive fields and/or the onsets of the stimuli are presented with large temporal disparity, the discharge rate of the cell is depressed [4,58]. Thus, the spatiotemporal rules of multisensory integration observed in the mammal SC largely parallel those observed in the oculomotor response.

In the domain of reaction time analysis, the classic explanation for the speed-up of responses to multisensory stimulation is that subjects are merely responding to the first stimulus detected. The observed reaction time to the combined visual–auditory stimulus would then be the response time to the faster signal in each trial causing a statistical facilitation effect [45]. However, as many subsequent studies have clearly shown, statistical facilitation alone is not sufficient to explain the speed-up of saccadic reaction times with multisensory stimulation, especially when the two stimuli are spatially aligned [12,28,29]. A recently proposed time-window-of-integration model for multisensory interaction in saccadic reaction times (TWIN,

[10]) assumes two serial, but dependent, stages of processing, the first being devoted to peripheral sensory transduction followed by the second stage which integrates the sensory inputs in time and space. In this framework, multisensory integration occurs only if the peripheral processes of the first stage all terminate within a given time interval (window of integration), and the amount of integration depends on the spatial proximity between the stimuli.

For the following, it is important to note that, since auditory transduction times are shorter than visual ones [55], intersensory facilitation can occur even if the auditory stimulus is presented (shortly) after the visual target because their internal representations would still arrive close in time on multisensory neurons.

1.2. *Top–down influences on early stimulus processing*

Interaction of bottom–up and top–down factors is a key element of theories of visual attention. With respect to bottom–up factors, considerable evidence suggests that salient stimulus events automatically “capture” the allocation of spatial attention [63]. Evidence for the modulation of attentional capture by top–down factors comes from spatial cuing experiments in which a cue presented prior to a target stimulus captured attention only if it contained the elementary target properties. Thus, abrupt onsets captured attention when participants were asked to process targets defined by an abrupt onset, but not when the target was defined as a color singleton. On the basis of these and similar results, Folk and colleagues [16,17] proposed the contingent involuntary orienting hypothesis stating that task goals condition attention by defining which stimulus features will elicit an involuntary attention shift.

The latter studies determined the elementary target properties, as defined by the task goal, necessary for top–down influences on early stimulus processing to occur. However, what happens if these properties are held constant but the probability structure between the events is varied? In this study, we employed a bimodal go/no-go task to investigate spatial interstimulus contingencies between a visual target and an auditory non-target. Specifically, we were interested in the time limits for interstimulus contingencies to occur in bimodal saccadic reaction times. Our recent experiment showed that the predictiveness of a visual non-target modulates saccadic reaction times to auditory targets, but only if the visual stimulus is presented opposite to the auditory target [32]. This result led us to suggest a two-stage process for executing a saccade to an auditory target that is accompanied by a visual non-target in the opposite visual field. First, subjects have to inhibit an automatic saccadic response in the direction of the visual stimulus (ocular inhibition, OI). Then, the endpoint of the final saccadic response to the auditory target is encoded (covert attention allocation), and the saccade can be executed [32].

In the present study, we asked the participants to make a saccade in the direction of a visual target that was accompanied by an auditory stimulus. We introduced catch trials in which only the auditory (Experiment 1) or the visual (Experiment 2) stimulus was present, and the participants were instructed to withhold their response. Similar to our former experiment, these no-go trials should also introduce an ocular inhibition process into the task because subjects have to withhold their response in these trials, but here the ocular inhibition is separated in time from the interstimulus contingency manipulation. In so doing, we wanted to evaluate to what extent the processing of interstimulus contingencies depends on ocular inhibition during the task and whether these processes interact.

2. Bimodal go/no-go experiment with auditory catch trials

Participants were asked to make a saccade in the direction of a visual target. The auditory stimulus was a non-target that provided spatial contingency information with regard to the location of the visual target. When the auditory stimulus appeared alone, participants had to withhold their response (auditory catch trial).

We expected saccadic reaction time under bimodal stimulation to be shorter than under unimodal visual stimulation (intersensory facilitation effect). The auditory non-target appeared at the same location as the visual target or opposite to it, and its temporal onset relative to the visual target varied from 210 ms before to 40 ms after the target. Moreover, interstimulus contingency was varied on three levels (see below). We hypothesized that participants should show shorter saccadic reaction times in a high interstimulus contingency condition and longer reaction times in a low interstimulus contingency condition. Although participants tend to show greater effects of interstimulus contingency when they are not aware of them [8], our participants were explicitly instructed to use the contingencies to make sure that they would make an effort to use this kind of stimulus context.

2.1. Materials and methods

2.1.1. Experimental set-up

Participants were seated in a small, darkened, sound-attenuated booth with their head fixed by a dental impression plate. Visual stimuli were presented on a 37" monitor located outside the booth (viewing distance 57 cm). Auditory stimuli were presented via headphones by a high performance sound card. Stimulus presentation and data acquisition were synchronized with the onset of the visual stimulus determined by the monitor update rate to guarantee exact temporal presentation of the stimuli.

2.1.2. Protocol

White dots (diameter 0.1°) served as visual target and as fixation point. They had a luminance of 11 cd/m^2 and were

presented on a dark background. White noise auditory stimuli (5 ms rise time, 58 dB SPL) were convolved with head-related transfer functions of a dummy head resulting in virtual displays at 15° right or left of fixation. These auditory stimuli led to almost identical saccadic mean absolute angles of error, compared to free-field stimuli at 15° azimuth [25].

A trial started with a fixation point that, after a random time interval, was replaced by the target presented for 500 ms, 15° right or left of fixation. In bimodal trials, stimuli were presented with equal probability at each side of fixation, either at the same ('congruent') or at opposite ('incongruent') locations. Stimulus onset asynchrony (SOA) was varied on five levels with equal probability: The auditory stimulus was presented either simultaneously or 210, 110 or 40 ms before (–) or 40 ms after (+) the visual target. In different blocks of trials, interstimulus contingency (ISC) was applied on levels 20–80, 50–50, and 80–20. That is, in the 80–20 interstimulus contingency (respectively, in 20–80 ISC), the visual target was presented spatially congruent to the auditory stimulus in 80% (resp., 20%) of the trials, and it was presented spatially incongruent to the auditory stimulus in the remaining 20% (resp., 80%) of the trials. Thus, the auditory stimulus could be 80% predictive of the visual target location both in the congruent trials of 80–20 ISC and in the incongruent trials of 20–80 ISC.

The task was to make an eye movement as quickly and accurately as possible to the visual target and to use the auditory stimulus as a possible, albeit unreliable cue for the location of the visual target. Furthermore, participants were asked to withhold their response if only the auditory stimulus was present (catch trials). Feedback was given if the saccade did not fall within a region of 4° visual angle around the visual target, if the roughly estimated saccadic reaction time (first unit to fall in the 4° region) was longer than 250 ms, or if a saccade was made although no visual stimulus was present (catch-respond trials). The intertrial interval was 1 s, starting after the feedback display (presented for 500 ms) or, in trials without feedback, 1.5 s after the onset of the visual target. After each type of contingency level, participants were encouraged to take a break of about 2 min before restarting with the calibration procedure.

Interstimulus contingencies were employed in separate blocks of trials for a minimum of 200 trials per condition and participant. In order to familiarize them with the task, participants took three practice sessions with the 50–50 ISC. Before starting each block, they were informed about the interstimulus contingency to be presented next. In addition to the bimodal trials (50 trials in 20–80 and 80–20 ISC blocks and 40 trials in 50–50 blocks), each block contained 10 unimodal visual control trials plus 10 auditory catch trials (20 each in 50–50 ISC blocks). The order of blocks was counterbalanced between participants and sessions. Saccades to unimodal visual or auditory targets

were measured in separate blocks at the end of the sessions (Fig. 1).

2.1.3. Response recording and detection

Eye movements were recorded with an infrared light reflecting eye-tracker providing an analogue signal of the eye position that was digitized at a rate of 1 kHz and stored on a PC. Saccade onsets and offsets were identified automatically, using velocity criteria (50°/s for onsets and 20°/s for offsets). The experimenter verified the accuracy of

the computer-generated marks. Saccadic reaction time was defined as the time between the onset of the target and the onset of the saccade. The number of trials including blinks, direction errors, anticipations (reaction times <80 ms), and misses was small (each less than 1% of the bimodal trials) so that they were discarded from further analysis.

2.1.4. Participants

Four undergraduate students (aged 19–22) of the University of Oldenburg took part in the experiment. All

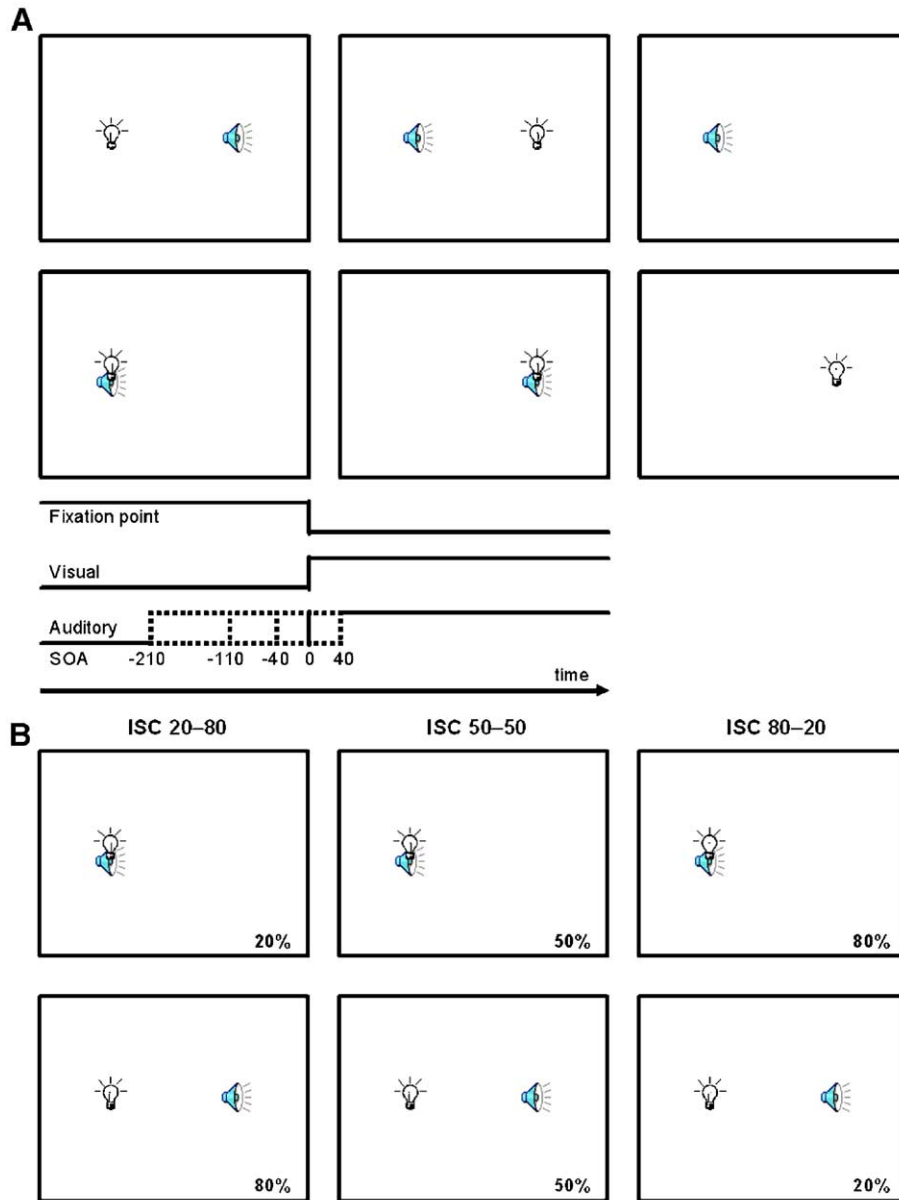


Fig. 1. Diagrams explaining the experimental protocols. The upper two lines and rows in panel (A) depict the spatial arrangement of the visual target (lightbulb) and the auditory accessory (loudspeaker) which could either be presented at opposite locations (upper line) or at the same location (lower line). The rightmost row illustrates the trials in which one of the stimuli was presented alone, such as in the catch and control trials. The lower part of panel (A) illustrates the stimulus timing: there was no gap between the offset of the fixation point and the onset of the visual target, whereas the auditory accessory could appear at different stimulus onset asynchronies (SOA) with respect to the visual target. Panel (B) illustrates the different interstimulus contingency (ISC) blocks. With varying probabilities (20%, 50%, or 80%), the visual target could appear either at the same or at the opposite location to the auditory accessory, while the overall probability for the visual target to be presented at either side from fixation was at chance level.

but one participant had right eye dominance. They had normal hearing and normal or corrected-to-normal vision². They either were paid or received partial course credit for participation. The experiment was undertaken with the understanding and written consent of each subject.

2.2. Results

2.2.1. Visual–auditory interaction effects

In the bimodal trials, the auditory stimulus facilitated the response to the visual target, replicating the intersensory facilitation effect. A one-way ANOVA compared the saccadic reaction times across all contingency conditions (for SOAs = −40 ms, 0 ms, and +40 ms) with the reaction times obtained in the control trials in which participants either responded to the visual or auditory stimulus when presented alone. This across-subjects analysis ($F_{2,6} = 7.6$, $P < 0.023$) indicated shorter saccadic reaction times to unimodal auditory and bimodal stimulation (200 ms and 210 ms) than to unimodal visual stimulation (231 ms).

2.2.2. Interstimulus contingency effects

Measuring the effect of spatial interstimulus contingencies requires separation of the effect of spatial congruence from the effect based on the predictability of the target location. To this end, we represent the data (1) as spatially congruent vs. incongruent in the respective contingency block and (2) across the different contingency blocks in terms of predictability of target location, irrespective of spatial congruence. In doing so, we are able to prevent confounding the more general effect of spatial congruence with the more specific effect of target predictability. In this sense, the rare trials of 80–20 ISC blocks in which the stimuli were spatially incongruent, as well as the rare trials of 20–80 ISC blocks in which the stimuli were spatially congruent will both be called “20% predictive” of the target location.

Saccadic reaction times in the bimodal trials were submitted to a three-way ANOVA with SOA (−210 ms, −110 ms, −40 ms, 0 ms, +40 ms), spatial congruence (congruent vs. incongruent), and interstimulus contingency (20–80, 50–50, or 80–20) as repeated factors. The effect of SOA ($F_{4,12} = 25.4$, $P < 0.001$) indicated a u-shaped pattern of reaction times, as illustrated in Fig. 2. Post-hoc comparisons showed that saccades were fastest when the auditory stimulus was presented before the visual target

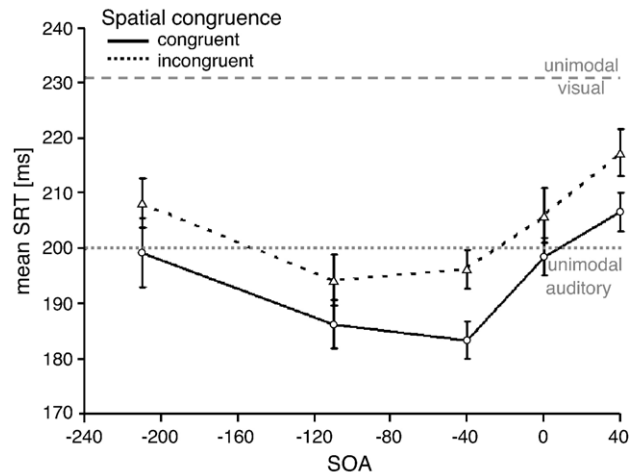


Fig. 2. Effects of stimulus onset asynchrony (SOA) and spatial congruence on mean saccadic reaction times (SRT) in a bimodal go/no-go task with auditory catch trials. The auditory stimulus was presented 210, 110, or 40 ms before (−), simultaneously, or 40 ms after (+) the visual target, either at the same (congruent) or at the opposite location (incongruent).

(SOA = −110 ms and −40 ms) compared to when the auditory stimulus was presented long before (SOA = −210 ms), simultaneously, or shortly after (SOA = +40 ms) the visual target.

Spatial congruence was the second effect on performance: average responses in the spatially congruent trials were 12 ms faster than in the spatially incongruent trials ($F_{1,3} = 20.9$, $P < 0.02$). Finally, the effect of interstimulus contingency revealed shorter reaction times in the 20–80 and 80–20 ISC blocks (199 ms and 196 ms) than in the 50–50 ISC blocks (204 ms) ($F_{2,6} = 6.7$, $P < 0.03$). This effect was also apparent in the individual data of all four participants.

2.2.3. Strategy effects

In order to determine whether participants used different response strategies in the respective interstimulus contingency conditions, we conducted two different types of analyses. First, we assessed the spatial congruence effect in each ISC block as a function of the event probabilities within that block. Separate ANOVAs on the regular saccadic reaction times across the short SOAs for each contingency condition, with spatial congruence (congruent vs. incongruent) as repeated factor, indicated shorter latencies in the spatially congruent than in the spatially incongruent trials of 50–50 and 80–20 ISC ($F_{1,3} = 20.1$, $P < 0.021$; $F_{1,3} = 24.4$, $P < 0.016$). The corresponding analysis in 20–80 ISC did not reach significance ($F_{1,3} = 5.4$, $P > 0.1$).

Separate ANOVAs on the regular saccades for each condition of spatial congruence (congruent vs. incongruent) with predictability as repeated factor revealed a significant effect of predictability in the incongruent trials only: post-hoc comparisons confirmed that reaction times in the 80% incongruent trials were shorter than in the 50% incongruent trials (7 ms, $F_{1,3} = 16.5$, $P < 0.027$). However, the

² Before starting the experiments, the participants were asked whether an ophthalmologist had controlled them during the former 6 months. If visibility was imperfect, the deficit was corrected by wearing appropriate glasses. Audition was assessed by a standard audiometer (Interacoustics, manual Audiometer AS208) conducted in a sound-attenuated room. If, across a large frequency range (125–8000 Hz), participants did not deviate more than 20 dB from the norm, they were considered hearing normally. After the first training session, they were further inquired where exactly they localized the sounds. They did not report any front/back confusions due to the auditory virtual display [61].

difference between 80% and 20% predictability as well as the difference between 50% and 20% predictability did not reach significance ($F_{1,3} = 4.8, P > 0.1$; $F_{1,3} = 6, P > 0.1$).

2.3. Discussion

Subjects were asked to make an eye movement in the direction of a visual target in the presence of an auditory stimulus. When both stimuli were presented at the same location, bimodal saccadic reaction times were about as short as in the unimodal auditory control condition. Thus, a spatially congruent auditory stimulus facilitated the response to the visual target, a case of intersensory facilitation [9,19]. In the SOA range of -110 to $+40$ ms, saccadic reaction times were the faster the earlier the auditory stimulus was presented [49]. When the auditory stimulus occurred rather long before the visual target (SOA = -210 ms), its average reaction time was comparable to that with simultaneous (SOA = 0) visual–auditory stimulation. This result may be due to our specific task demands because subjects were to withhold their response if only the auditory stimulus was presented (auditory catch trials). At the time point when they detected the auditory stimulus, they had to “wait” for the occurrence of the visual target in order to determine whether or not that trial was a catch trial. Fig. 2 further suggests that the effects of temporal and spatial proximity between the visual and the auditory stimulus were largely independent.

The analysis of strategy effects separated by spatial congruence (20%, 50%, and 80%) revealed that participants responded faster in the 80% incongruent trials of 20–80 contingency than in the incongruent trials of 50–50 contingency (see Fig. 3). This supports our hypothesis

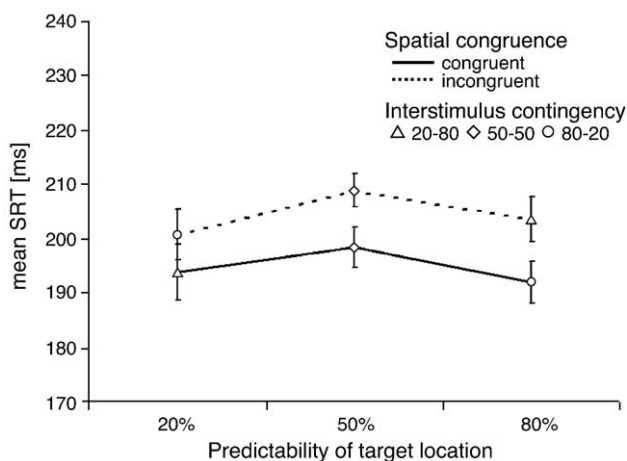


Fig. 3. Effects of predictability of target location on mean saccadic reaction times (SRT) in a bimodal go/no-go task with auditory catch trials. In 80–20 interstimulus contingency (ISC, circles) [respectively, in 20–80 ISC (triangles)], the visual target was presented spatially congruent to the auditory stimulus in 80% (resp., 20%) of the trials, and it was presented incongruent to the auditory stimulus in the remaining 20% (resp., 80%) of the trials. The 80% predictability level thus contains both congruent trials from 80–20 ISC and incongruent trials from 20–80 ISC.

that participants can learn to use the predictive context of interstimulus contingency in order to improve their performance.

Note that the auditory stimulus, on the one hand, contained the spatial contingency information and, on the other hand, constituted the catch stimulus. In order to control for this twofold function of the auditory stimulus, we ran a second experiment employing visual catch trials.

3. Bimodal go/no-go experiment with visual catch trials

In Experiment 2, participants were asked to make an eye movement to the visual target only if an auditory go-stimulus was present. If only the visual stimulus appeared, participants had to withhold their response (visual catch trial). Thus, participants had to detect the auditory stimulus in order to decide whether to make a saccade. We hypothesized that in this way contingency effects should show up stronger than in Experiment 1 because participants would pay more attention to the auditory stimulus and, thereby, to the contingency information it contained.

3.1. Materials and methods

3.1.1. Participants

Seven students (mean age 23 ± 4 years) of the University of Oldenburg took part in the experiment. Three of them already participated in Experiment 1. The remaining four participants had never participated in a psychophysical experiment before. All but one participant had right eye dominance. All had normal hearing and normal or corrected-to-normal vision. They were either paid or received partial course credit for participation. The experiment took place with the subjects' understanding and written consent.

3.1.2. Task and procedure

Experiment 2 was identical to Experiment 1, except for the following: first, the task was to make an eye movement as quickly and as accurately as possible to the visual target and to use the auditory stimulus as a possible, albeit unreliable cue for the location of the visual target. Participants were asked to withhold their response if only the visual target was present (visual catch trials). Second, the 20–80 and 80–20 ISC blocks contained 50 bimodal and 20 catch trials, and the 50–50 ISC blocks contained 40 bimodal and 40 catch trials. Third, four participants, of whom two already had participated in Experiment 1, were presented, with equal probability, the following (negative) SOAs: the auditory stimulus appeared either 210, 110, or 40 ms before ($-$), simultaneously, or 40 ms after ($+$) the visual target (same SOAs as in Experiment 1). For the other three participants, the SOAs were $-40, 0, +40, +80, \text{ or } +120$ ms (positive SOAs), presented with equal probability.

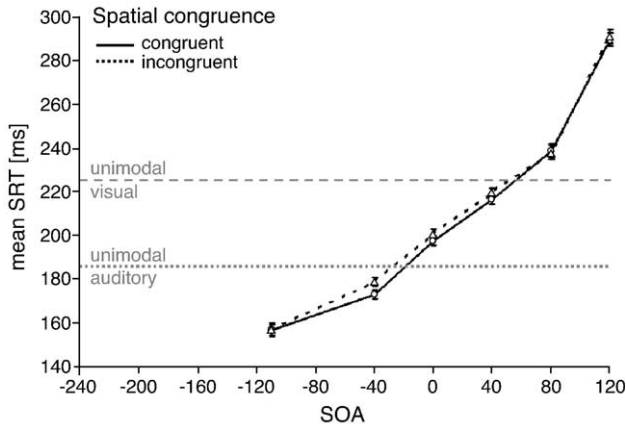


Fig. 4. Effects of stimulus onset asynchrony (SOA) and spatial congruence on mean saccadic reaction times (SRT) in a bimodal go/no-go task with visual catch trials. Reported are the conditions in which the auditory stimulus was presented 110, or 40 ms before (–), simultaneously, or 40, 80, or 120 ms after (+) the visual target, either at the same (congruent) or at the opposite location (incongruent).

3.2. Results

3.2.1. Visual–auditory interaction effects

Again, the auditory stimulus in the bimodal trials facilitated the response to the visual target (intersensory facilitation effect). A one-way ANOVA compared the saccadic reaction times across all contingency conditions (for SOAs = –40 ms, 0 ms, and +40 ms) with the reaction times obtained in the control trials, in which participants either responded to the visual or auditory stimulus when presented alone ($F_{2,12} = 23.8, P < 0.001$). This analysis indicated shorter reaction times to unimodal auditory stimuli than to bimodal stimulation (187 ms vs. 198 ms), which in turn had shorter latencies than unimodal visual targets (226 ms).

3.2.2. Interstimulus contingency effects

Saccadic reaction times in the bimodal trials were analyzed by a three-way ANOVA with SOA (–210 ms, –110 ms, –40 ms, 0 ms, 40 ms, 80 ms, 120 ms), spatial congruence (congruent vs. incongruent), and interstimulus contingency (20–80, 50–50, or 80–20) as unreplicated factors. The effect of SOA ($F_{6,7263} = 340.3, P < 0.001$) indicated that reaction times were the shorter the earlier the auditory stimulus was presented before the visual target (see Fig. 4). The effect of spatial congruence did not reach significance ($F_{1,7263} = 1.9, P > 0.1$), that is, saccadic responses in the spatially congruent and incongruent trials had about the same latencies. The variation of ISC did reach significance ($F_{2,7263} = 29.2, P < 0.001$), indicating shorter reaction times with 20–80 and 80–20 ISC than with 50–50 ISC (201 ms and 203 ms vs. 217 ms: $F_{2,7263} = 29.4, P < 0.001$). Finally, an interaction effect between spatial congruence and ISC indicated shorter reaction times in the spatially congruent trials than in the spatially incongruent trials, but only with 20–80 ISC ($F_{2,7263} = 5.8, P < 0.003$).

3.2.3. Short SOAs (SOA = –40, 0, and 40 ms)

Saccadic reaction times in the bimodal trials were submitted to separate two-way ANOVAs for each SOA with spatial congruence (congruent vs. incongruent) and ISC (20–80, 50–50, and 80–20) as repeated factors. For all three SOAs, the effect of ISC was significant, indicating faster reaction times in the 20–80 and 80–20 ISC blocks than in the 50–50 ISC blocks (195 ms and 196 ms vs. 207 ms; $F_{2,12} = 15.1, P < 0.004$). For SOA = –40 and 40, the effect of spatial congruence reached significance as well but was very small (4 ms on average, $F_{1,6} = 7.1, P < 0.038$, partial $\epsilon^2 = 0.5$). The interaction term between spatial congruence and ISC did not reach significance ($F_{2,12} = 1.9, P > 0.1$).

3.2.4. Anticipations

For SOA = –210 ms, two of the participants (MA and MW) produced saccades before the presentation of the visual target or with latencies shorter than 80 ms. In Fig. 5, these anticipations [31] were sorted by gaze direction (congruent, visual incongruent, auditory incongruent, and

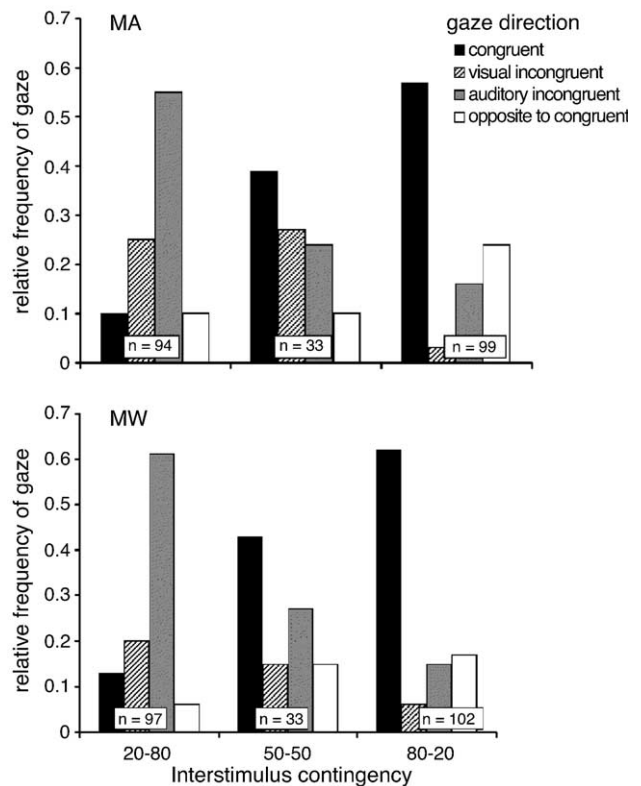


Fig. 5. Relative frequency of anticipatory saccades in SOA = –210 ms, separated by gaze direction (congruent, visual incongruent, auditory incongruent, and opposite to congruent) and interstimulus contingency in two participants (MA and MW) in a bimodal go/no-go task with visual catch trials. Note that the relative trial frequency in each contingency condition as defined by the experiment should not be directly compared with the relative frequency participants actually gazed at those stimuli. Regular saccades, express saccades, and blinks were not included in this analysis.

opposite to congruent) and ISC (20–80, 50–50, and 80–20). It is important to note, however, that the relative trial frequency in each contingency condition as defined by the experiment should not be directly compared with the relative frequency participants actually gazed at those stimuli because the bars of Fig. 5 only contain anticipatory saccades. Regular saccades, express saccades, and blinks were not included in this analysis.

Separate Chi-square tests compared the effects of contingency level in each direction of gaze: both participants more often made a saccade to the spatially congruent stimuli in the 80–20 ISC blocks than in the 20–80 ISC blocks. Furthermore, they more often made a saccade in the direction of the auditory incongruent stimulus in the 20–80 ISC blocks than in the 80–20 ISC blocks, and one participant more often made a saccade in the direction of the incongruent visual target in the 20–80 and 50–50 ISC blocks than in the 80–20 ISC blocks. Both participants sometimes made a saccade opposite to the spatially congruent stimuli, but these errors did not depend on ISC. In summary, these results clearly show that the participants anticipated the relative frequency of stimulus events in the different contingency conditions.

3.2.5. Strategy effects

In a first analysis, we assessed the spatial congruence effect in each ISC block as a function of the event probabilities within that block. Separate ANOVAs for each contingency condition were conducted on the regular saccadic reaction times across the short SOAs, with spatial congruence (congruent vs. incongruent) as repeated factor. This analysis only reached significance in the 20–80 ISC blocks, indicating shorter latencies in the 20% congruent than in the 80% incongruent trials (see Fig. 6; $F_{1,6} = 36.5$, $P < 0.001$).

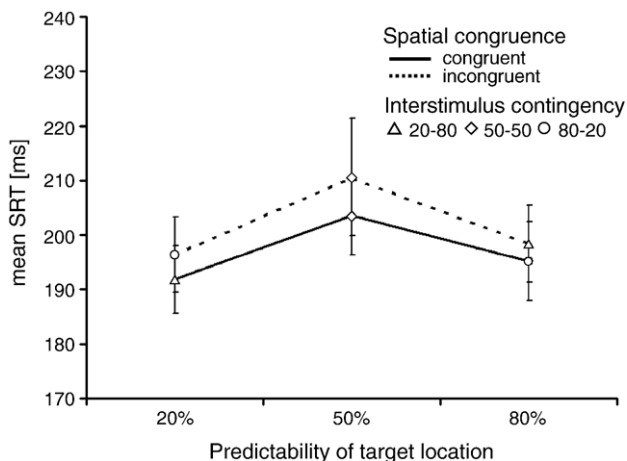


Fig. 6. Effects of predictability of target location on mean saccadic reaction times (SRT) in a bimodal go/no-go task with visual catch trials. For a detailed description of predictability and ISC, see Fig. 3. Reported are the means across all seven participants in the small SOAs (SOA = –40 ms, 0 ms, and 40 ms).

In a second analysis, we separated the reaction time data by spatial congruence in order to control for the more general effect of spatial proximity with respect to the more specific effect of predictability of the target location (20%, 50%, and 80%). Separate ANOVAs for each condition of spatial congruence with predictability as repeated factor indicated that saccadic reaction times in the 20% and 80% predictability conditions were about equal but significantly shorter than in the respective control conditions (50%) (see Fig. 6; congruent: $F_{2,12} = 16.9$, $P < 0.001$; incongruent: $F_{2,12} = 8.8$, $P < 0.021$).

3.2.6. Summary

Experiment 2 again replicated an intersensory facilitation effect in that saccadic reaction times in the bimodal trials were shorter than unimodal visual reaction times. Variation of SOA revealed a particular effect of the auditory go-signal in the bimodal trials: when it was presented before the visual target, reaction times could be extremely short (160 ms in SOA = –110 ms), whereas when it was presented after the visual target, bimodal reaction times were prolonged compared to unimodal visual reaction times (see Fig. 4). The effects of spatial and temporal proximity were independent, in accord with Experiment 1. However, spatial congruence did interact with ISC in the 20–80 condition, indicating shorter reaction times in the 20% spatially congruent trials than in the 80% spatially incongruent trials.

Interstimulus contingencies affected average saccadic reaction times in each short SOA irrespective of spatial congruence: 20% and 80% predictability resulted in shorter reaction times than 50% predictability of target location (see Fig. 6).

Two of the participants exhibited a large number of anticipatory saccades in SOA = –210 ms. An analysis of gaze direction showed that they anticipated the relative frequency of stimulus events in the respective contingency conditions (see Fig. 5).

4. General discussion

In two experiments, multisensory stimulation facilitated saccadic reaction times when an auditory stimulus appeared in spatiotemporal proximity to a visual target [9,18]. This intersensory facilitation effect was modulated by the inclusion of catch trials in the task: if the catch stimulus was auditory (Experiment 1), saccadic reaction times in the bimodal trials showed an effect of spatial proximity, but this facilitatory effect of the auditory stimulus reached a plateau when it was presented 100–200 ms before the visual target. On the other hand, the visual catch stimulus (Experiment 2) had a strong effect on the time course of the saccadic response by reinforcing the importance of the auditory stimulus: if the auditory signal was presented before the visual target, it had a strong warning effect (cue) so that bimodal reaction times were even shorter than unimodal

auditory reaction times [23]. Whereas, when the auditory signal appeared after the visual target, we observed a prolongation of response times. This suggests an ocular inhibition effect, similar to the one observed in our study with auditory prosaccades and a spatially incongruent visual non-target [32].

Note that with visual catch trials the effect of spatial congruence vanished, in contrast to auditory catch trials (Experiment 1). While it certainly is difficult to suppress an automatic orienting response toward a visual stimulus [56], especially when seated in the dark, our results further show that this ocular inhibition is spatially unspecific. Indeed, in a countermanding task in which the subjects are asked to withhold a response when an auditory stop signal is occasionally presented after the visual target, bimodal reaction times in the stop-respond trials are independent of the spatial congruence between the visual and auditory stimulus [11]. Our results indicate that this spatially unspecific ocular inhibition process has a sustained component as it can affect reaction times in the remaining bimodal go-trials, such as in a go/no-go task with visual catch trials [1,30]. Finally, the difference between our first and second experiment with respect to the processing of auditory and visual catch trials shows that saccadic eye movements critically depend on the catch modality, in contrast to manual responses [34]. While an auditory cue can automatically attract spatial attention and initiate a saccade program in its direction [53], this attention shift is less effective and can therefore be inhibited more easily than with a visual (catch) stimulus [56]. This would explain why saccadic responses in bimodal trials, when randomly interleaved with auditory catch trials, are less inhibited than with visual catch trials, thereby allowing spatial congruence to affect the reaction times. In case of visual catch trials, however, any oculomotor program seems to be inhibited so much that in the remaining bimodal trials spatial proximity of the auditory go-signal no longer facilitates a response to the visual target.

4.1. Interstimulus contingency effects

Varying the probability of spatial congruence between a visual target and an auditory non-target resulted in saccadic reaction time facilitation, at least with 80% predictability of the target location. This is in line with go/no-go experiments and manual reaction time facilitation when the presence of a non-target letter in one display location was correlated with the presence of a target letter in a second location [35,41,52]. Our results support studies investigating the effect of conditional probabilities between an attended and an unattended stimulus. For example, in a Stroop task, participants had to report the meaning of a word (ABOVE or BELOW) while the position of the word was either congruent or incongruent with the meaning, with different probabilities [38]. In these conditions, the processing of predictability critically depended on the spatial congruence

between the position and meaning of the words, whereas in the present study we observed reaction time facilitation not only with 80%, but also with 20% predictability of the target location, but irrespective of the spatial congruence between the visual target and auditory go-signal (Experiment 2). Essentially, this result corroborates that interstimulus contingencies can facilitate performance even in the particular case of extremely fast saccadic responses to a visual–auditory target.

Nevertheless, it seems difficult to explain why subjects should be faster with only 20% predictability of target location compared to the control condition (50%). In particular, in our previous study on ISC in auditory prosaccades, we obtained a significant increase in saccadic reaction times with 20% compared to 80% predictability when the auditory target occurred opposite to the visual non-target [32]. Thus, it seems that the inclusion of catch trials in the present study, not only had a sustained inhibition effect on the remaining bimodal trials, but also that this catch mode had a specific effect on ISC processing. These results suggest that ocular inhibition and interstimulus contingency processing in a go/no-go task are not independent, and this should be considered in the interpretation of earlier results [41,52]. In an unpublished control experiment, we took care to equalize the number and percentage of catch trials in each ISC condition, but we replicated the facilitation effect in both predictability conditions (20% and 80%).

A second main finding was the short time window (SOA = ± 40 ms) in which ISC effects occurred. This indicates that ISC is used very early in the programming of a saccadic eye movement, that is, when both stimulus modalities are being processed simultaneously [55]. When Lambert and colleagues investigated contingency effects in the locations of bilateral letter cues and a simple visual target, they obtained rather long average saccadic reaction times of 250–300 ms [36]. Our observation of much shorter reaction times (217 ms, Experiment 2), in combination with a short time window for ISC to occur, thus establishes a lower bound on the time course of interstimulus contingency processing. Although the saccadic responses were already facilitated by the temporal proximity of the visual target and the auditory non-target, subjects were able to use interstimulus contingencies in order to improve performance, a case of top–down control. Note that we varied the spatial proximity of the visual target and auditory non-target on two levels only (congruent vs. incongruent). It would be interesting to see in future investigations to what extent the effect of intersensory facilitation and interstimulus contingency differ if more than two locations for the stimuli are used.³

Note that observing interstimulus contingency effects in crossmodal processing has implications for the interpretation of top–down influences in peripheral cuing experiments. According to the contingent involuntary orienting

³ We thank an anonymous reviewer for this interesting suggestion.

hypothesis, a cue (auditory non-target) influences performance (only) if it contains information that matches an intentionally searched-for attribute of the (visual) target—that is, if it matches the target–search criterion [16]. Specifically, stronger cuing effects result if abrupt-onset cues also share the color or location of the visual target, whereas in conditions in which the cues are dissimilar to the target and do not match the top–down control settings of the task, no cuing effects are observed [2]. However, it is a well-established fact that multisensory stimulation results in facilitation even if the stimuli are dissimilar (i.e., of different modalities) and do not share the target–search criterion (e.g., location). Thus, at least some bottom–up processes, such as intersensory facilitation, are mandatory. On the other hand, our results show that IFE can be modulated by top–down control from ISC, albeit in a very short time window. This facilitation by predictability also occurred in a condition in which the visual target was presented 80% of the times opposite to the auditory ‘cue’ [60]. As the subjects were instructed to make a saccade to the visual target, the auditory ‘cue’ thus did not share any target–search criterion. Given the very short time interval for ISC effects to occur, it seems plausible that subjects did not have time, first, to attend to the ‘cue’ and then to re-orient their attention to the target. Rather, they seem to have implicitly learned the contingency rule in order to improve performance [8,35]. We conclude that contingent-capture and interstimulus contingency are different phenomena, yet both implying top–down control over early stimulus processing.

4.2. Possible neural underpinnings of interstimulus contingency effects in saccadic eye movements

The deep layers of the superior colliculus (SC), a midbrain structure containing both uni- and multisensory neurons responsive to visual, auditory, and somatosensory stimulation and converging onto a common motor map for triggering the response in the brainstem saccade generator [51], is a prime area for representing the multisensory integration processes in saccade generation as postulated, e.g., in the second stage of the time-window-of-integration model [10].

At rest, the SC is tonically inhibited by the substantia nigra pars reticulata (SNr) which in turn is inhibited by the caudate nucleus [26,27]. Rizzolatti and colleagues proposed that this tonic circuit controlling the excitability of the SC might mediate the expectancy of a stimulus. In particular, when a stimulus is expected in a given location, a cortical motor program is set that disinhibits, via caudate nucleus and SNr, the SC neurons of the intermediate and deep layers related to the expected space position. The increase in firing of these neurons facilitates the collicular superficial neurons [40]. As a consequence, the superficial neurons allow a better detection of the stimulus, while the deeper premotor collicular neurons provide an increase in the readiness to respond when the expected stimulus occurs [47,53,54].

Dorris and Munoz [14] directly investigated this increase in the firing of SC neurons in advance of eye movements by recording the extracellular activity of neurons in the intermediate layers of the SC. They showed that the build-up activity of certain neurons increased with increasing probability of saccades being directed into their response fields. Moreover, this build-up activity was negatively correlated with the saccadic reaction times, indicating that the shorter reaction times the stronger the neuronal activity (50% vs. 100% probability), especially in the epoch preceding saccade initiation (50–60 ms after target presentation). These results have been implemented in a neural field model of saccade initiation in the superior colliculus, assuming a weak pre-target input at the more likely target location [57]. Simulations of the model reflected well the facilitation of human saccadic reaction times with high stimulus probability. Note that the weight matrix of the model, representing the effective interaction structure within the SC, was set constant throughout the simulations precluding any learning effects. It would be interesting to examine whether the interstimulus contingency effects found in the present study could be captured by assuming a non-constant interaction matrix in the model representing some kind of adaptation or learning process within the SC neurons [62].

But who tells the caudate and SNr what to expect? A possible cortical circuit in this framework are the frontal eye fields (FEF), the lateral intraparietal area (LIP) of the posterior parietal cortex, and the dorsolateral prefrontal cortex (DLPFC) which all are involved in the programming of voluntary, visually, and aurally guided eye movements [21,37,50]. These cortical structures are known to mediate the selection of the saccade target (FEF, [5]), the coding of the target location (LIP, [22]), and learning of stimulus–response associations (DLPFC, [3]). Single-cell activity in the FEF allows predicting the form of saccade latency distributions when used as parameter estimates of a simple accumulator model for the decision to initiate a saccade [24], while the neural activity in area LIP directly reflects the probability of saccade instruction [44]. Interestingly, both areas directly project onto the deep layers of the superior colliculus (SC), they are strongly interconnected, and they both receive input from the thalamus ([20], for a review). This might be one possible neural circuit underlying the extremely fast saccadic responses of this study, even when varying the expectancy of the target location in the form of interstimulus contingencies. Indeed, given that interstimulus contingency effects only occurred in a tight time window of ± 40 ms of stimulus onset asynchrony, our results corroborate the idea of a shortly leaking tonic cortical control via the caudate and SNr on the SC in order to optimize even extremely fast multisensory responses.

With respect to the cognitive control over saccadic eye movements, converging evidence in blood-flow neuroimaging studies indicates that voluntary saccades are mediated by the FEFs, the supplementary eye fields (SEFs), the

dorsolateral prefrontal cortex (DLPFC), the parietal cortex, and the anterior cingulate [7,13]. Recent neuromagnetic investigations with visual and auditory targets show that the instruction to withhold a response (go/no-go tasks) results in a negative going event-related component that peaks 250–300 ms after target onset (N2), with a frontal maximum (close to the anterior cingulate) that is smaller or totally absent in go trials [15,43]. While there is a debate over whether this N2 component reflects the inhibition of the prepotent (go) response [15,48] and/or the detection of response conflict [42], there appears to be consensus that the N2 is a marker of a general control process in the medial frontal cortex [46]. It may convey a feedback signal to the brain areas involved in the actual execution of the control, such as the (dorsolateral) prefrontal cortex, informing these areas that executive control processes (via the FEFs, LIPs, and SNr onto the SC) must be activated more strongly. Note, however, that the saccadic responses in the present study already occurred even before this N2 component generally reaches its maximum at around 300 ms after target onset. While it seems implausible that cognitive control processes reflected in the N2 component might have been involved in the present task, this clearly is an interesting question for future investigation.

4.2.1. Conclusion

Interstimulus contingencies facilitate saccadic responses. While intersensory facilitation was observed in a time window of about 100 ms of temporal separation between the visual and auditory stimulus, interstimulus contingency effects occurred only in a much tighter window of ± 40 ms of stimulus onset asynchrony. Clearly, during this short period of time, subjects could not explicitly follow the task instructions. This suggests a form of unconscious top–down processing, in contrast to the contingent involuntary orienting hypothesis. Interstimulus contingency effects thus reveal an extremely fast time course of top–down control on multisensory interaction in saccadic eye movements.

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