

Vom Fachbereich 5
Philosophie/Psychologie/Sportwissenschaft
der Universität Oldenburg
zur Erlangung des Grades einer Doktorin der
Philosophie angenommene Dissertation.

Visual-auditory interstimulus contingency effects in saccade programming

Holle Kirchner

geb. am 6. Dezember 1971
in Hameln

Erstreferent: Prof. Dr. Hans Colonius
Koreferent: Prof. Dr. August Schick
Tag der Disputation: 20. Dezember 2001

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Overview

This thesis investigated the effects of visual-auditory interstimulus contingencies on the latencies and amplitudes of saccadic eye movements. In a new experimental procedure, the interstimulus contingencies were defined in the locations of a target and an accompanying stimulus rather than in the mere presence or absence of the stimuli. Human subjects were asked to make a saccade to a visual target and to use the location of an auditory accompanying stimulus as a possible, but unreliable cue for the location of the visual target.

We investigated several different types of saccades. The latencies of reflexive visual prosaccades did not show contingency effects. However, in a bimodal go/no-go task the contingency effects did reach significance indicating shorter latencies in the positively and negatively correlated conditions than in the control condition. It was concluded that these effects were specific to the go/no-go task, because in experimental tasks which involved the choice in saccade direction the saccade latencies in the unlikely condition were longer than in the control condition. This result was true for visual antisaccades, auditory prosaccades and visual prosaccades with outline boxes. We therefore conclude that the processing of interstimulus contingencies requires the choice in saccade direction and thus leads to shorter latencies to targets at the likely location and longer latencies to targets at the unlikely location.

The choice in saccade direction was implemented in a new, per interval linear approach to threshold (ILAT) model. Simulations of the model gave a good fit to the mean saccadic latencies of auditory prosaccades. The model parameters were in good accord with neurobiological evidence.

1

Introduction

The ability to discover and use the co-occurrence of perceptual events is an important part of an individual's capacity to adapt to ongoing changes in the environment. Specifically, if the probability was high that environmental events occurred closely together in time and space, preparing to respond to these events should be facilitated. Do humans use knowledge about such a predictive context?

Learning means to expand one's knowledge and repertory of behaviour through experience. Does the covariation, and thus association, of two simple stimuli induce implicit or explicit learning? Research on so-called interstimulus contingencies provides an appropriate framework to investigate this question. In the present thesis, subjects were instructed to make a saccade to a target which was accompanied by an accessory stimulus. This accompanying stimulus could either occur at the same spatial location or opposite to the target, with the probability varying over blocks of presentation. The probability of the target to occur at a certain location was thus contingent on the occurrence of the accompanying stimulus at the same or at the opposite location. The issue addressed with this paradigm is to which extent the knowledge about probabilistic context affects reaction times and kinematics of saccadic responses.

1.1 Historical background

Even before psychology became an experimental science in the 1890s, learning was already part of philosophical theory. David Hume (1739; see Wasserman, 1990) developed three principles which cause the association of two instances. These so-called cues to causality are the spatial and temporal proximity of two events (contiguity), their resemblance, and the probability of co-occurrence of these events (contingency). Even nowadays these three principles build the grounds for research on associative learning theory.

The principle of contiguity was reformulated by John B. Watson (1914) who founded the well-known stream of research called 'behaviorism'. Edwin Guthrie (1935), expressing the mechanistic view of his time, stated that just the co-occurrence of a stimulus and a response creates their connection, irrespective of the response being reinforced by an

environmental event. This statement was in clear opposition to Edward Thorndike (1911) who argued that there exist different degrees of strength of an association which grows with the frequency of a stimulus and a response being associated (law of exercise). Repetition of a response in a certain situation thus increases the probability of the response to occur in that very situation. Note that the law of exercise lends some similarity to the principle of contingency by David Hume (1739).

The idea that learning occurs due to reinforcement was developed even more firmly by Burrhus F. Skinner (1938) who stated that most of our behaviour is not elicited by stimulation, but is emitted for its operand consequences. Learning may be due to the effects of a response and not due to the association of an eliciting stimulus and a response. Skinner called the sequence of a response and its consequences 'contingency'. However, in order to take into account the significance of David Hume's work (1739), today it is common practice to define contingency as the probability that two events occur together.

The assumptions of behaviorism were criticised by the cognitivist theorists. One of their most prominent researchers was Edward C. Tolman (1932). He stressed the importance of motivation for learning. He maintained that animals learn the predictive significance and value of environmental events, sequences of events, and where things are located (cognitive map). This knowledge, Tolman argues, serves as a basis for the deliberate decision to exhibit a certain response and to develop expectancies about future events.

Nowadays associative learning theorists mainly examine under which conditions humans and animals detect response-outcome covariations (Alloy and Tabachnik, 1984) and how humans control voluntary actions by the anticipation of the action goals (Elsner and Hommel, 2001). During the last decades, a parallel stream of research has emerged investigating effects of interstimulus contingencies.

1.2 Interstimulus contingency effects

In this section we will first describe two paradigms used for the study of interstimulus contingencies (ISC) and then we will introduce the experimental paradigm used throughout the present thesis.

1.2.1 The flanker task

Eriksen & Eriksen (1974) were concerned about the effects of non-target (noise) letters on the processing of a visual target, in the common visual search paradigm. In order to control for the process of searching the display, they reduced the visual search paradigm to a simpler condition in which the visual target always appeared in the same known location while being surrounded by several noise letters. The latter paradigm has been termed the flanker task. Subjects were asked to press a response key if the centre letter belonged to one set of targets, and another response key if the centre letter came from another set of targets. They found that reaction times were the longest in the condition in which the noise was a letter of the opposite response set than the target (incongruent), while the fastest reaction times were obtained when the noise was identical to the target

(congruent). This difference in reaction times between the congruent and incongruent conditions is called congruency effect.

1.2.2 The correlational cueing task

Miller (1987) pointed to one problem of the flanker task. The flankers were sometimes taken from the same set of stimuli as the targets. Because the subjects expected the targets to appear, the presentation of the flankers may have attracted attention. To overcome this problem, he designed a somewhat different paradigm, the correlational cueing paradigm, in which the targets and flankers always belonged to different sets of stimuli. Furthermore, he correlated the identity of the flankers with the correct response. Given the presence of any particular flanker, one response was much more likely to be correct than was the other response.

Miller showed that the flanker identity can act as a cue to the correct response which indicates learning of covariation. Subjects responded faster in the high correlated condition, in which the target was presented with its more frequent flanker, than in the low correlated condition. Furthermore, this correlational cueing effect occurred even when the subjects were not aware of the flankers being correlated with the correct response, and the effect carried over to a test block in which the flanker letters became targets.

With respect to learning theory, Miller (1987) concluded that the correlational cueing effect reflects the build-up of a classical stimulus-response association (see Thorndike, 1911) with a stimulus that neither causes the response nor signals reinforcement. Whereas in Miller's study the target was arbitrarily defined for the subject, in the classical studies it was biologically meaningful like *e.g.* a food pill. Also, Miller argued, his correlational cueing effects showed that the build-up of stimulus-response associations did not require a causal connection between the stimulus and a response. These latter observations may be understood as the basis for research on interstimulus contingencies.

Cohen, Fuchs, Bar-Sela, Brumberg & Magen (1999) questioned Miller's conclusion that correlational cueing effects implied any kind of learning. In several different experiments, they varied the stimulus properties of the target and flankers and they introduced a transfer test block at the end of each experimental series. The subjects were first trained with four regular correlated cueing blocks in which the flankers were correlated with the correct responses. Without telling the subjects, in the last transfer test block flankers and responses were no longer correlated. Cohen *et al.* found that only if the flankers and targets were similar colours or letters, transfer to tasks without correlation occurred. Although this latter finding was a strong indicator of (implicit) learning, Cohen *et al.* concluded that correlational cueing effects are not due to learning, but are rather caused by on-line processes that occur during the correlation manipulation. In their third experiment they identified repetition priming as one of these on-line processes. Although all target-flanker pairs were presented equally often, subjects responded faster when the target and flankers were repeated in a series of two trials, than when only the target was repeated. However, note that this response time difference was much smaller than the overall correlational cueing effect observed in their experiments. It might thus be concluded that repetition priming plays some role in correlational cueing effects, but that this observation does not exclude learning to occur at all.

1.2.3 The go/no-go task

Whereas the studies outlined in the former sections investigated manual response times, Hughes, Reuter-Lorenz, Nozawa & Fendrich (1994) studied saccadic eye movements in a visual-auditory interaction paradigm. Subjects were asked to make a saccade as soon as they detected a stimulus. Although the authors did not aim at investigating interstimulus contingency effects, the presence or absence of simple visual and auditory stimuli were correlated to different degrees. As the stimulus intensities were readjusted in each experiment in order to produce equivalent saccadic reaction times to both modalities, it is not possible to decide whether the subjects showed contingency effects across the different experiments.

Mordkoff & Yantis (1991) and Schwarz (1996) investigated a go/no-go task in which the presence of a non-target letter in one display location was correlated with the presence of a target letter in a second location. Subjects were instructed to press a button as soon as they detected a target in either location (divided attention). If no target was present, subjects were instructed to withhold their response (no-go trials). If the correlation between the target and non-target letters was positive, responses were made faster (Lambert, Naikar, McLachlan & Aitken, 1999; Mordkoff & Yantis, 1991). On the other hand, if the correlation was negative, the results of different studies diverged: Mordkoff (1995) reported that reaction times slowed down, whereas in Schwarz (1996) the reaction times with negative correlation were facilitated compared to no correlation.

Lambert, Norris, Naikar & Aitken (2000) examined the effects of peripheral information on the latency of saccadic eye movements. They presented a simple visual target in one out of two outline boxes. Prior to each target, a pair of cue letters was presented bilaterally outside the outline boxes. The relative location of the letters was correlated with the target location. In 9% of the trials, only the cue letters were presented, and the subjects were asked to withhold their response (no-go trials). After a brief practice period, the subjects showed shorter saccade latencies, if the target was presented at the likely, relative to the unlikely location. This was true whether or not they were aware of the cue-target contingency relation. Therefore, Lambert *et al.* (2000) concluded that this so-called derived peripheral cueing effect was due to implicit learning.

1.3 Experimental task of the present thesis

One purpose of the present study was to investigate the effect of positively and negatively correlated interstimulus contingencies in simple bimodal stimuli. As opposed to most of the former studies, in our paradigm interstimulus contingencies were defined over spatial locations rather than by the mere presence or absence of the stimuli.

In more technical terms, the interstimulus contingencies (ISC) were defined as the conditional probability that the target (T) was presented at the same location as the accompanying stimulus (A) or opposite to it:

$$\begin{cases} P(T^{left}|A^{left}) &= 20\%, 50\%, 80\% \\ P(T^{right}|A^{right}) &= 20\%, 50\%, 80\% \end{cases}$$

where superscripts denote the location at which the respective stimulus was presented.

If, for example, in one block of trials the target was presented at the same location as the accompanying stimulus in 80% of the trials, it was presented opposite to the accompanying stimulus in the remaining 20% of the trials.

We chose a similar paradigm to the go/no-go task by Mordkoff & Yantis (1991), because it has the advantage that the target can be presented with equal probability at either location preventing stimulus repetition accounts. In contrast to the correlational cueing paradigm, it allows to investigate separate spatial locations of the target and an accompanying stimulus. Contrary to Lambert *et al.* (2000), we used one auditory rather than two visual letter cues in order to establish the lower bound of the time course of interstimulus contingencies.

1.4 Saccade programming in spatial cueing tasks

Note that the spatial contingency task used in the present study is somewhat similar to the well-known spatial cueing task (Posner, 1980), in which a peripheral cue indicates, with some validity, either the location of the target (valid trials) or another location (invalid trials). Subjects are asked to shift their attention to the cue while maintaining fixation, but to make a saccade to the target as soon as it is presented. In contrast to the spatial contingency task, the cue is presented and extinguished prior to the target. The spatial cueing technique revealed some effects specifically related to saccade programming which will be further investigated in the present thesis.

1.4.1 Express saccades

Cavegn (1996) investigated the peripheral cueing technique in the gap paradigm, in which the initial fixation point is turned off before presentation of the peripheral cue. When the cue was valid, saccadic response times had latencies of about 100 ms or even less. These shortest possible latencies to a visual event are called express saccades (Fischer & Ramsperger, 1984). Although disputed by some research groups (*e.g.* Wenban-Smith & Findlay, 1991), express saccades may form a separate population in saccade-latency distributions. They have a mode latency of about 100 ms and are distinguished from anticipatory saccades (latencies below 70-80 ms), fast-regular saccades (at about 150 ms) and slow-regular (above 190 ms) saccades (Fischer & Boch, 1989; Fischer & Weber, 1993). In Cavegn's study (1996) the express saccades disappeared when the peripheral cue was invalid and the latencies corresponded to fast-regular saccades.

The present thesis will examine whether subjects exhibit express saccades in the spatial contingency task as well, specifically when responding to positively correlated stimuli. The findings by Cavegn (1996) suggest that subjects will be more ready to respond when the stimuli are correlated and that the enhanced response readiness will generate a higher rate of express saccades.

1.4.2 Saccade amplitudes

Sheliga, Riggio & Rizzolatti (1994) examined the effect of spatial cueing on saccade trajectory. The cue consisted of a short line presented centrally, the direction of the line indicating in which box the visual target was going to appear. In particular, when the cue was presented in the same hemifield as the target (right or left of fixation), the trajectory of vertical saccades deviated in the direction opposite to the target (Sheliga *et al.*, 1995a). Similarly, expecting a stimulus in the upper or lower hemifield resulted in a contralateral deviation of horizontal saccades (Sheliga *et al.*, 1995b). Although the authors surmised spatial cueing to affect saccade amplitudes, no such effects showed up in their data. The present study will probe whether interstimulus contingencies show an effect on the programming of saccade amplitudes.

1.5 The intersensory facilitation effect

Since the early studies on manual response times (Todd, 1912), it has been shown that reaction times to a visual target when accompanied by an auditory stimulus (bimodal stimulation) are shorter than both responses to the visual or auditory stimulus presented alone. This intersensory facilitation effect (IFE) has generally been attributed to some kind of multimodal integration (see Welch & Warren, 1986, for a review) and has more recently also been observed in studies measuring saccadic response times (Frens, van Opstal & van der Willigen, 1995; Hughes, Reuter-Lorenz, Nozawa, & Fendrich, 1994; Hughes, Nelson, & Aronchik, 1998; Corneil & Munoz, 1996; Colonius & Arndt, 2001).

Specifically, if the visual and auditory stimulus are presented in close spatial and temporal proximity, saccade latencies are shorter than if the stimuli are presented in opposite hemispheres and at long interstimulus intervals. Note that the latter observations are identical to the claims of the principle of contiguity (Hume, 1739, see 1.1) for associating the two events. It thus appears that the spatial and temporal proximity of a visual and auditory stimulus play an important role for their multimodal processing and for the association of the two events.

On a physiological level, it has been shown that multimodal cells in the deep layers of the superior colliculus and other, cortical areas play an important part in the processing of the IFE in saccadic responses (Stein & Meredith, 1993). The superior colliculus (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 Schall, 1991). It integrates information from different sensory modalities (*e.g.*, visual and auditory) and converges this information to the same brainstem premotor circuitry to trigger eye movements toward the source of stimulation or to the intended target (Stein & Meredith, 1993).

Electrophysiological recordings of multimodal cells in the cat's and monkey's deep SC layers have shown that the multimodal cells exhibit substantially enhanced discharge rates if a visual and auditory stimulus are presented onto its receptive fields (spatial proximity) and if they are presented close in time. However, if one of the stimuli is presented outside the receptive fields of the multimodal neuron and the onsets of the stimuli are presented with large temporal disparity, the discharge rate of the cell is depressed (see Sparks & Nelson, 1987, for a review). In other words, the effects of spatial and tempo-

ral proximity of visual-auditory stimulation can directly be observed in the behaviour of multimodal cells in the mammals SC. More recent studies, however, indicate that the multimodal integration in the mammal's SC crucially depends on cortical functioning (Stein, 1998) which in humans is characterised by a parallel distributed, highly adaptive system whereby crossmodal binding is achieved through feedback connections from higher-level heteromodal areas onto the primary sensory areas (Calvert, Brammer, Bullmore *et al.*, 1999; Giard & Peronnet, 1999).

The principal aim of the present thesis was to determine whether human subjects exhibit interstimulus contingency effects in saccadic responses to simple visual and auditory stimuli. As a consequence, we also wanted to determine whether the effects of interstimulus contingency superimpose on IFE, or whether these two processes interact.

1.6 The structure of this study

As interstimulus contingency effects have not yet been investigated systematically on different levels or this variation led to conflicting results (see 1.2), in the present thesis we investigated ISC on three different levels (20%, 50%, and 80% ISC). In analogy to the findings in spatial cueing paradigms, we hypothesised that human subjects show shorter saccadic reaction times and amplitudes in the positively correlated contingency (80%), and longer reaction times and amplitudes in the negatively correlated contingency (20%) compared to no correlation (50%). Several experiments using the identical stimulus paradigm were performed to determine the conditions under which visual-auditory contingency effects occur in saccade programming.

1.6.1 Visual prosaccades

In Chapter 2 we will describe a first experiment in which subjects were asked to make a saccade to a visual target (visual prosaccades) and to use an accompanying auditory stimulus as a possible, but unreliable, cue for the location of the visual target. We used a focused attention rather than a divided attention task, because the sudden onset of a light entails an automatic saccadic orienting response, so that subjects are biased against looking in the direction of an accompanying auditory stimulus in a divided attention task (Corneil, Hing, Bautista & Munoz, 1999, but see also Corneil & Munoz, 1996).

The analysis of saccade latencies and amplitudes did not show any interstimulus contingency effects in this experiment. We concluded that the automatic saccadic orienting response to the sudden onset of the visual target does not allow further stimulus information in the form of interstimulus contingencies to influence saccade programming.

1.6.2 Visual prosaccades in a bimodal go/no-go task

In the four experiments described in Chapter 3¹ we introduced a bimodal go/no-go task with visual or auditory catch trials in which the subjects were asked to withhold their

¹The content of Chapter 3 has been submitted for publication.

response if only the visual or auditory stimulus was present. We argued that the processing of catch trials slows saccade latencies down and thus would allow interstimulus contingencies to affect the saccade latencies.

With auditory catch trials some subjects exhibited shorter saccade latencies both in the positively correlated contingency and in the negatively correlated contingency. This observation was emphasised with visual catch trials with which all subjects exhibited shorter saccade latencies both in the positively correlated contingency and in the negatively correlated contingency. In two control experiments we further determined that these contingency effects did not depend on the contingency pre-information given at the start of each experimental block nor on the number of catch trials used. However, the systematic variation in the number of catch trials did show that the subjects have to be biased to prepare a response in order to exhibit contingency effects in the saccade amplitudes.

1.6.3 Visual antisaccades

At the end of the experimental series using the bimodal go/no-go task we still wondered why the subjects would exhibit shorter saccade latencies both in the positively correlated contingency and in the negatively correlated contingency. In order to determine whether this observation constitutes a specific effect of the bimodal go/no-go task, in our sixth experiment (Chapter 4) we asked three new subjects to make a saccade in the direction opposite to the visual target. This so-called antisaccade task induces longer saccade latencies than in the prosaccade task and thus should lead to even stronger interstimulus contingency effects.

All three subjects did exhibit contingency effects, but they also showed large interindividual differences. We thus concluded that the antisaccade task entails different response strategies.

1.6.4 Auditory prosaccades

In order to control for those trials in which the subjects made a saccade opposite to the visual target, but actually gazed in the direction of the auditory accompanying stimulus, we conducted a seventh experiment which will be described in Chapter 5. We asked subjects to make a saccade in the direction of the auditory target (auditory prosaccades) and to use the accompanying visual stimulus as a possible, but unreliable, cue for the location of the auditory target.

All subjects exhibited shorter saccade latencies in the positively correlated contingency than in the control condition which in turn was shorter than in the negatively correlated contingency. However, the latter observation only occurred in those trials in which the auditory target was presented opposite to the visual accompanying stimulus (disparate trials). Note that the overall mean latencies were as short or even shorter than in the visual prosaccade task (Chapter 2). We thus concluded that the knowledge about interstimulus contingencies can lead to improved performance even at very short saccade latencies.

1.6.5 Visual prosaccades with outline boxes

In a last experiment (Chapter 6) we addressed the question whether the contingency effects found in the disparate trials of Experiment 5 were due to intersensory inhibition effects, or whether the contingency effects were due to the subjects having to choose the proper direction of the saccade target. We introduced two outline boxes right and left of fixation which indicated the possible locations for the visual target. The outline boxes were presented throughout the whole trial. Subjects thus were reminded at the beginning of each trial that they had to choose between the two possible locations for the visual target.

All subjects exhibited similar contingency effects as in Experiment 5, but in all trials. We interpret this finding as evidence that visual-auditory interstimulus contingency effects in saccade programming only occur if the subjects have to choose the direction of the saccade target.

1.6.6 The ILAT model

In Chapter 7 we will outline the ILAT model. It is a variation of the LATER model (Linear Approach to Threshold with Ergodic Rate) by Carpenter (1981) which assumes that a response preparation signal initiated by a target rises in a linear fashion to a fixed activity threshold, with the rate of rise varying randomly from trial to trial.

LATER was modified in order to account for interstimulus contingency effects in auditory prosaccades (see Chapter 5). Specifically, we assumed two separate response preparation signals for the visual and auditory stimulus respectively. In those periods of time in which the two stimuli were presented and processed in parallel, they were assumed to coactivate a common process which was expressed as the sum of both response preparation signals. As we divided the time axis into separate intervals, we called our new model *per Interval Linear Approach to Threshold (ILAT)*.

The effects of interstimulus contingency were estimated as the prior probability that the locations of the visual and auditory stimulus were correlated. The response preparation signal of the stimulus to be presented first thus was assumed to start with more or less distance to the fixed activity threshold. The model parameters were estimated by Monte Carlo simulation. They provided a good fit to the mean saccadic reaction times of Experiment 5 and were in good accord with neurobiological evidence.

2

Visual prosaccades

In Experiment 1 subjects were asked to make a saccade in the direction of a visual target. Contingency information was provided by an accompanying auditory stimulus. The results of all experiments were analysed in four aspects: Express saccades, saccade latencies, saccade amplitudes, and visual-auditory facilitation in saccade latencies.

In analogy to the findings in spatial cueing tasks, we hypothesised that subjects should show shorter saccadic reaction times and amplitudes in the positively correlated contingency, and longer reaction times and amplitudes in the negatively correlated contingency (see Section 1.4.2). The second hypothesis was that subjects exhibit a large number of express saccades in the correlated conditions as these conditions should induce high response readiness (see Section 1.4.1). Finally, in analogy to earlier findings, we expected the reaction times to the visual target when accompanied by the auditory stimulus (bi-modal stimulation) to be shorter than either saccades to the visual or auditory stimulus presented alone (see Section 1.5).

In order to systematically investigate the temporal proximity of the visual target and the auditory accompanying stimulus we varied the stimulus onset asynchrony (SOA) of the stimuli over a large time scale. The spatial proximity was varied only on two levels, *i.e.* the auditory stimulus was presented either at the same or opposite location as the visual target.

Although subjects tend to show greater effects of interstimulus contingency when they are not aware of them (Carlson & Flowers, 1996), our subjects 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 Method

2.1.1 Participants

Seven students (mean age = 23 ± 3 years) of the University of Oldenburg took part in the experiment. All but one subject (TS) had right eye dominance. They had normal hearing

and normal or corrected-to-normal vision. They received partial course credit or were paid for participation. All subjects gave their informed consent prior to their inclusion in the study. They were not informed about the specific hypotheses under study.

2.1.2 Apparatus and stimulus materials

Subjects 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 (XP37, NEC) located outside the booth resulting in a viewing distance of 57 cm. Auditory stimuli were presented via headphones (AKG K1000) by a high performance sound card (Tahiti, Turtle Beach). Stimulus presentation and data acquisition were synchronised with the onset of the visual stimulus determined by the monitor update rate to guarantee exact temporal presentation of the stimuli.

White dots with a diameter of 0.1° served as visual stimulus and fixation point. They were presented with a luminance of 11 cd/m^2 on a dark background (less than 0.01 cd/m^2). Auditory stimuli consisted in white noise (5 ms rise time) convolved with head-related transfer functions of a dummy head (Oldenburger Kunstkopf) resulting in virtual displays at 15° right or left of fixation. These stimuli lead to almost equal saccade mean absolute angles of error compared to free-field stimuli at 15° azimuth (Heuermann & Colonius, 1998).

In a preliminary cross-modal matching experiment three subjects were asked to match the intensity of the auditory stimulus, presented with the visual stimulus at 15° eccentricity, to the brightness of the visual stimulus, and to hold their eyes on fixation. The mean of all judgements (58 dB SPL; SD = 2 dB) was taken as auditory intensity in the main experiment.

2.1.3 Design

Visual and auditory stimuli were presented for 500 ms at 15° right or left of fixation. The target appeared with equal probability at either eccentricity to prevent anticipatory responses. The SOA was varied on five levels with equal probability. For one group of subjects the auditory stimulus appeared either 210, 110 or 40 ms before (–), simultaneously, or 40 ms after (+) the visual target (negative SOAs). For a second group of subjects the SOAs were defined as –40, 0, +40, +80, or +120 ms (positive SOAs). The auditory stimulus was either presented at the same location as the visual target (coincident trials) or opposite to it (disparate trials) with varying probability (20%, 50%, or 80%). Interstimulus contingency (ISC) was defined as the conditional probability that the visual target (T) was presented at the same location as the auditory accompanying stimulus (A) or opposite to it:

$$\begin{cases} P(T^{left}|A^{left}) &= 20\%, 50\%, 80\% \\ P(T^{right}|A^{right}) &= 20\%, 50\%, 80\% \end{cases}$$

where superscripts denote the location at which the respective stimulus was presented.

The left panel of Figure 2.1 illustrates the relative frequencies of stimulus presentations in coincident or disparate trials in each contingency condition. That is, *e.g.*, in the

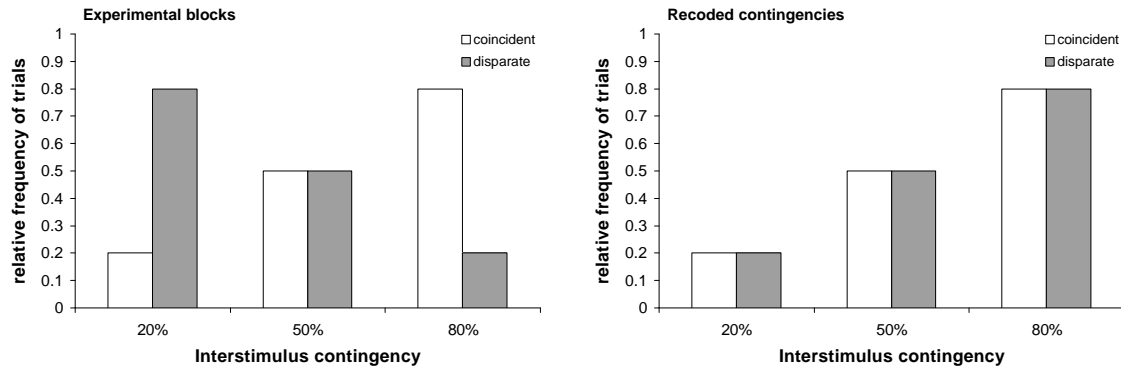


Figure 2.1: *Relative frequency of trials contained in each contingency condition. The left panel illustrates the relative frequency of trials as they were presented in the different experimental blocks. The right panel illustrates the relative frequency of trials after the contingencies had been recoded according to effective validity. coincident:= stimuli presented at the same location; disparate:= stimuli presented at opposite locations.*

20% ISC blocks the visual target was presented at the same location as the auditory accompanying stimulus in 20% of the trials, and in the remaining 80% of the trials the visual target was presented opposite to the auditory accompanying stimulus.

The ISCs were given in separate blocks in each session: Two subsequent blocks of the 20% and 80% ISC, and one block of the 50% ISC. The 20% and 80% ISC blocks contained 50 bimodal and 20 unimodal visual trials, and the 50% ISC blocks contained 40 bimodal and 20 unimodal visual trials. One block of trials lasted about 6 minutes, a session about 1h. Combination of two visual eccentricities * 3 ISCs * 5 SOAs * 6 sessions resulted in a total of 2160 trials per subject. In order to familiarise them with the task subjects took three practice sessions with the 50% ISC.

2.1.4 Procedure

Before starting each block the subject was informed about which contingency was going to be presented (see left panel of Figure reffig1). Each trial started with the onset of a fixation point. After a random time interval between 800 and 1300 ms the fixation point disappeared and, simultaneously (no gap), the target was presented. The task was to make an eye movement as quickly and as accurately as possible to the visual target and to use the auditory accompanying stimulus as a possible, but unreliable, cue for the location of the visual target. Feedback was given if the saccades did not fall within a region of 4° visual angle around the target or if the roughly estimated saccadic reaction times (first unit to fall in the 4° region) were longer than 250 ms. 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 target. Saccades to unimodal auditory stimuli were measured in a separate blocks at the end of the first session.

The order of ISCs was counterbalanced across sessions and subjects. After each type of ISC subjects were encouraged to take a break of about two minutes before restarting with the calibration procedure.

2.1.5 Response recording and detection

Eye movements were measured with an infrared light reflecting system (IRIS, Skalar Medical). This system provides an analogue signal of the eye position that was digitised at a rate of 1 kHz and stored on a PC. Spatial resolution after calibration and digitisation was 0.2° maximally. Saccade onsets and offsets were identified automatically, using velocity criteria ($50^\circ/\text{s}$ for onsets and $20^\circ/\text{s}$ for offsets). The accuracy of the computer generated marks was verified by the experimenter. Saccadic reaction time (SRT) 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 (SRTs < 80 ms; cf. Kalesnykas & Hallett, 1987), or misses was so small (less than 1% of the bimodal trials each) that they were discarded from further analysis. For the analysis of saccade amplitudes only trials in which the saccade amplitude started at less than 1° off the fixation point were used.

2.2 Results

2.2.1 Saccadic reaction times

Trials in the 20% and 80% ISC blocks were recoded according to their effective validity. The right panel of Figure 2.1 illustrates the results of this recoding procedure. That is, in the 80% ISC blocks (left panel), those trials in which the auditory stimulus was presented coincident to the visual target were defined as 80% valid (right panel), whereas the trials in which the auditory stimulus was presented disparate to the visual target were defined as 20% valid (right panel). Similarly, in the 20% ISC blocks (left panel), those trials in which the auditory stimulus was presented coincident to the visual target were defined as 20% valid (right panel), whereas the trials in which the auditory stimulus was presented disparate to the visual target were defined as 80% valid (right panel).

2.2.1.1 Express saccades

Graphical inspection of SRTs revealed that the four subjects having performed under the negative SOAs showed a large number of anticipatory and express saccades. For three subjects, these saccades formed separate populations in their saccade latency distributions. Also, both types of saccades were characterised by a large scatter in saccade amplitudes. An analysis of the relative frequencies of gaze direction showed that all four subjects gazed more often in the direction of the stimuli presented coincidentally than in direction of the auditory stimulus when presented disparate to the visual target. However, sometimes the subjects even gazed opposite to both stimuli.

To examine the effect of contingencies on express saccade behaviour, the number of express saccades in each ISC condition was divided by the total number of bimodal trials measured in the respective ISC condition in order to account for the different numbers of

Table 2.1: *Relative frequency of correct express saccades sorted by effective contingency validity for each subject.*

| Subject | Contingency validity | | |
|---------|----------------------|---------------|----------------|
| | 20% | 50% | 80% |
| CR | 15/237 = 0.06 | 11/216 = 0.05 | 37/926 = 0.04 |
| EN | 4/217 = 0.02 | 07/220 = 0.03 | 19/894 = 0.02 |
| MA | 15/352 = 0.04 | 10/219 = 0.05 | 42/910 = 0.05 |
| MW | — | 01/248 = 0.01 | 05/978 = 0.01 |
| SN | 3/239 = 0.01 | 05/259 = 0.02 | 12/963 = 0.01 |
| ST | 1/261 = 0.01* | 1/257 = 0.01* | 1/1018 = 0.01* |
| TS | 3/216 = 0.01 | 06/198 = 0.03 | 09/860 = 0.01 |

* If the relative frequency was too small, a procedure for the correction of ties was applied.

trials obtained especially in 20% and 80% ISC. The relative frequency of express gaze is summarised in Table 2.1 separately for each subject.

Chi-square tests on the relative frequencies shown in Table 2.1 did not reach significance in any subject. Finally, the saccade amplitudes of the correct express saccades were submitted to separate t-tests for each subject, direction of gaze (rightward or leftward), and for each comparison of ISC validity. These t-tests reached significance in subject TS indicating marginally longer amplitudes in 20% than in 50% ISC ($t_{1,8} = 2.1, p < 0.07, 1.9^\circ$), and significantly longer amplitudes in 80% ISC than in 50% ISC ($t_{1,11} = 2.4, p < 0.04, 2.3^\circ$) in the rightward saccades.

As the subjects performed under different combinations of SOAs, the remaining regular SRTs were analysed separately for each SOA.

2.2.1.2 SOA = -210 ms

The SRTs were analysed separately for each subject, because all but subject TS produced saccades mainly before the presentation of the visual target or with latencies less than 80 ms. These anticipations (Kalesnykas & Hallett, 1987) were sorted by gaze direction (coincident, visual disparate, auditory disparate, and opposite to coincident). The anticipations were also separated for ISC validity, but this time ISC validity was defined in terms of the trials as they were presented together in one experimental block of ISC (see left panel of Figure 2.1). Thus, in Figure 2.2 each main column of ISC contains all anticipatory saccades measured under that type of ISC. Note however that the relative trial frequency in each ISC condition should not be directly compared with the relative frequency subjects gazed at those stimuli, because the columns of Figure 2.2 only contain anticipatory saccades. Regular saccades, express saccades, blinks, or other errors were not included in this analysis.

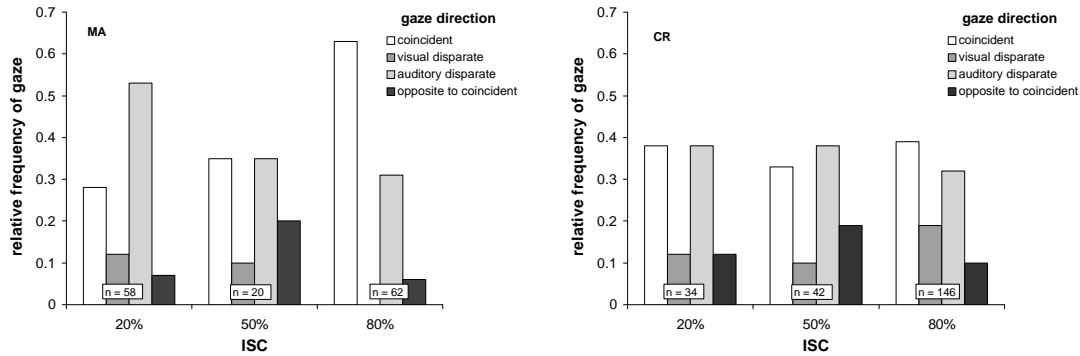


Figure 2.2: *Relative frequency of anticipatory saccades separated by gaze direction and interstimulus contingency (ISC) for two subjects (CR and MA). ISC validity is defined in terms of the trials as they were presented during the experiment. Note that the relative trial frequency in each ISC condition should not be directly compared with the relative frequency subjects gazed at these stimuli, because the graph does not include express or regular saccades obtained in the same conditions. coincident:= stimuli presented at the same location; disparate:= stimuli presented at opposing locations.*

Separate Chi-square tests were conducted for each subject comparing the number of anticipatory saccades in the different contingency conditions with the number of all correct saccades in the same conditions. None of these tests reached significance.

A separate ANOVA on the regular SRTs of subject TS with spatial congruence (coincident vs. disparate) and ISC validity as unrepeatable factors did not reach significance.

2.2.1.3 SOA = -110 ms

The regular saccades in SOA = -110 ms were submitted to a two-way ANOVA with spatial congruence (coincident vs. disparate) and ISC (20%, 50% or 80%) as repeated factors. The analysis revealed a significant main effect of spatial congruence ($F_{1,3} = 19.9, p < 0.021$). When the SRTs were analysed separately for each subject, three of the four subjects (EN, MA, and TS) showed a significant effect of spatial congruence with responses in the coincident trials being 14 ms faster on average than responses in the disparate trials. No other effects reached significance.

2.2.1.4 SOA = -40, 0, and +40 ms

The SRTs of all seven subjects were submitted to an ANOVAs with SOA, spatial congruence (coincident vs. disparate) and ISC (20%, 50% or 80%) as repeated factors. This analysis revealed two significant main and interaction effects. The main effect of SOA ($F_{1,3} = 19.9, p < 0.021$) indicated shorter latencies the earlier the auditory accompanying stimulus was presented before the visual target (see left panel of Figure 2.3). The main effect of spatial congruence ($F_{1,3} = 19.9, p < 0.021$) was due to shorter latencies in the coincident trials than in the disparate trials (see left panel of Figure 2.3). The interaction effect of SOA * spatial congruence indicated that the latency difference of spatial

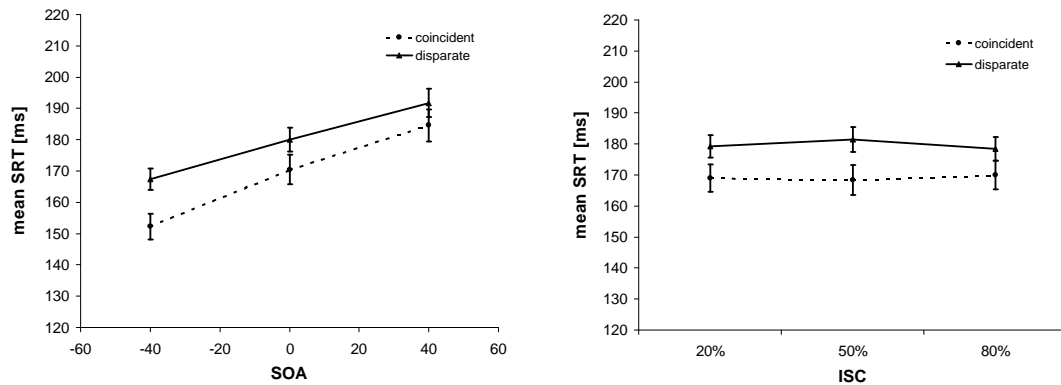


Figure 2.3: Mean saccadic reaction times (SRT) in the bimodal trials. The left panel illustrates the effects of stimulus onset asynchrony (SOA) and spatial congruence (coincident vs. disparate). The auditory accompanying stimulus was presented 40 ms before (–), simultaneously, or 40 ms after (+) the visual target. The right panel illustrates interstimulus contingency effects. They did not reach significance.

congruence was accentuated in the $SOA = -40$ ms (see left panel of Figure 2.3). Finally, the interaction effect of spatial congruence * ISC validity was due to marginally different ISC patterns in the coincident and disparate trials (see right panel of Figure 2.3).

When the SRTs were analysed separately for each subject, the main effects of SOA and spatial congruence were confirmed for all subjects. Also, four subjects exhibited significant interaction effects of $SOA * \text{spatial congruence}$. Two subjects exhibited significant main effects of ISC validity in the $SOA = +40$ ms (see Figure 2.4). Subject MA exhibited shorter latencies in 20% ISC than in 50% and 80% ISC (mean difference = 11 ms), and subject ST showed shorter latencies in 20% and 80% ISC than in 50% ISC (mean difference = 10 ms and 11 ms).

2.2.1.5 $SOA = +80$ and $+120$ ms

Separate two-way ANOVAs for each SOA were conducted with spatial congruence (coincident vs. disparate) and ISC validity (20%, 50% or 80%) as repeated factors. None of these factors reached significance. However, in separate ANOVAs for each subject and SOA, subjects SN and ST showed significant main effects of spatial congruence in $SOA = +80$ ms. Furthermore, subject ST exhibited significant main effects of spatial congruence and ISC validity in $SOA = +120$ ms. The main effect of ISC validity indicated shorter latencies in 80% ISC than in 50% ISC (see Figure 2.5). The same subject also showed a significant interaction effect of spatial congruence * ISC validity in $SOA = +120$ ms (see Figure 2.5).

2.2.2 Saccade amplitudes

Separate ANOVAs were conducted for each subject and rightward vs. leftward saccades with ISC validity and spatial congruence (coincident vs. disparate) as unreplicated factors.

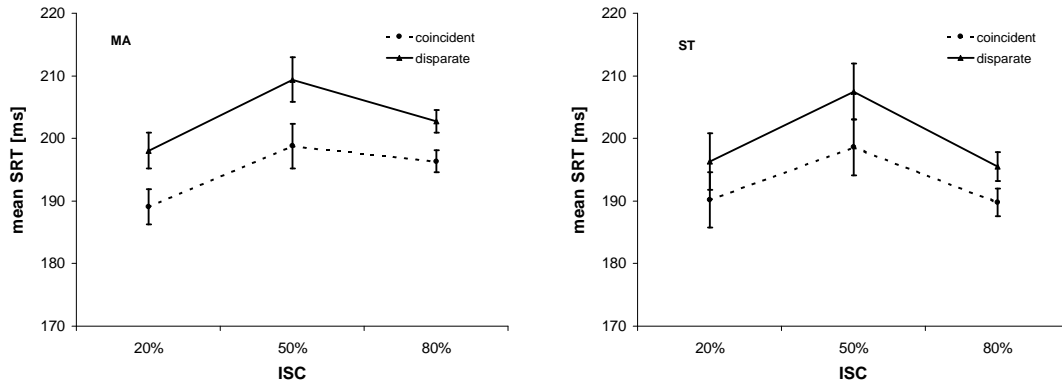


Figure 2.4: *Interstimulus contingency effects (ISC) on the saccadic reaction times (SRT) in SOA = + 40 ms. Subject MA exhibited shorter latencies in 20% ISC than in 50% and 80% ISC, and subject ST showed shorter latencies in 20% and 80% ISC than in 50% ISC. coincident:= stimuli presented at the same location; disparate:= stimuli presented at opposite locations.*

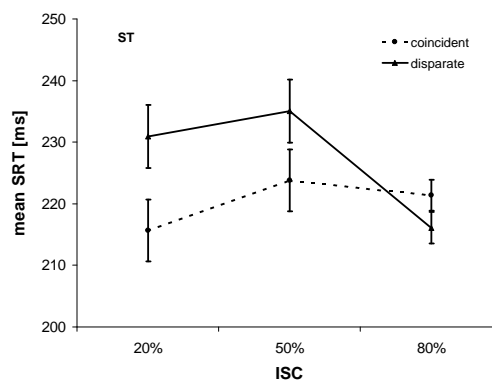


Figure 2.5: *Interstimulus contingency effect (ISC) on the saccadic reaction times (SRT) in SOA = + 120 ms. Subject ST exhibited shorter latencies in 80% ISC than in 50% and a significant interaction effect of contingency validity with spatial congruence (coincident vs. disparate).*

Only those effects are reported which were accompanied by equivalent effects in the peak velocities. Three subjects exhibited significant main effects of ISC validity in one direction of gaze. Subjects MA and SN exhibited shorter amplitudes in 20% and/or 80% ISC than in 50% ISC in the leftward saccades (mean difference = 0.8° and 0.7°). Subject ST showed 0.7° shorter amplitudes 20% and 80% ISC than in 50% ISC in the rightward saccades. A significant interaction effect of spatial congruence * ISC validity only showed up for subject MA.

2.2.3 Visual-auditory facilitation in saccadic reaction times

A one-way ANOVA with stimulus modality (visual, auditory, or bimodal) as unreplicated factor was highly significant ($F_{2,2504} = 120.1, p < 0.001$) indicating shorter saccade latencies to bimodal stimulation than to the unimodal auditory stimulus (177 ms, bimodal, 185 ms, auditory) which in turn were shorter than saccades to the unimodal visual stimulus (205 ms).

2.2.4 Summary

All but one subject having performed under the negative SOAs exhibited separate populations of anticipatory and express saccades in their saccade-latency distributions. The express saccades further were characterised by a large scatter in saccade amplitudes. Subjects gazed more often in the direction of the stimuli presented coincidentally than in direction of the auditory stimulus when presented disparate to the visual target. However, sometimes the subjects even gazed opposite to both stimuli. The subjects exhibited about the same number of express saccades in each contingency condition.

The saccadic reaction times were characterised by significant main effects of SOA and spatial congruence. Latencies were the shorter the earlier the auditory accompanying stimulus was presented before the visual target, and when the stimuli were presented coincidentally. In the SOA = -40 ms the latency difference in spatial congruence was bigger than in the SOA = 0 ms, and $+40$ ms, leading to a significant interaction effect of SOA and spatial congruence. One subject exhibited significant main effects of ISC validity in the SOAs = $+40$ ms and $+120$ ms indicating shorter latencies in 80% ISC than in 50% ISC. She also showed a significant interaction effect of spatial congruence and ISC in the SOA = $+120$ ms. A second subject showed a significant main effect of ISC in the SOA = $+40$ ms indicating shorter latencies in 20% ISC than in 50% ISC.

Three of the subjects exhibited significant ISC effects in the saccade amplitudes. They showed shorter amplitudes in 20% and 80% ISC than in 50% ISC in one direction of gaze.

Finally, the saccade latencies showed a significant intersensory facilitation effect with the latencies to bimodal stimulation being shorter than saccades to the unimodal auditory stimulus which in turn were shorter than latencies to the unimodal visual stimulus.

2.3 Discussion

Experiment 1 was designed to systematically investigate different levels of interstimulus contingencies. However, only two of seven subjects showed shorter saccade latencies in the negatively and/or positively correlated conditions than without correlation. There are two possibilities to explain this lack of significant contingency effects.

First, if subjects are seated in the dark, the sudden onset of a light entails an automatic saccadic orienting response. This automaticity of the response may preclude any voluntary (top-down) effort in form of interstimulus contingencies to influence the programming of a saccade. Second, most of the subjects told us in informal reports at the end of the experiment that they had tried to ignore as much as possible the auditory accompanying stimulus which contained the contingency information, because they were asked to make a saccade to the visual target. These reports thus further support the first explanation of an automatic orienting response.

Note, however, that the auditory accompanying stimulus did influence the saccade latencies on a pre-attentional level. Even when the subjects tried to ignore the auditory accompanying stimulus, they exhibited shorter overall latencies to bimodal stimulation than to the visual stimulus when presented alone. This replication of the intersensory facilitation effect (see Section 1.5) thus indicates that the processing of interstimulus contingencies is independent of multimodal processing as the contingencies did not alter or preclude the IFE. Also, the replication of IFE testifies to the validity of our experimental paradigm.

The observation that at least those participants showing a contingency effect in their saccadic latencies also exhibited contingency effects in their saccade amplitudes is most interesting, since it suggests a tight coupling of the processing of contingency information with the programming of saccade metrics. To our knowledge, this is the first result suggesting that the processing of interstimulus contingencies affects motor processing. Previous studies showed that the predictability of target location increases saccade accuracy (Coeffé & O'Regan, 1987; Bronstein & Kennard, 1987; Viviani & Swensson, 1982). Our results extend the latter finding in that the participants in our task exhibited more hypometric saccades in the correlated contingencies than in the control condition in one direction of gaze.

Three of the four participants who performed under the negative SOAs showed a considerable number of express and anticipatory saccades when the auditory stimulus was presented before the visual target. Interestingly however, the analysis of contingency effects in these saccades did not reach significance. As mentioned in the introduction, Cavegn (1996) investigated express saccades in a cueing (gap) paradigm (see Section 1.4.1). He only found express saccades when the cue was valid. While his results seem inconsistent with the present findings it should be noted, however, that in most cueing experiments the cue is presented and extinguished prior to target presentation. Cavegn (1996) used a cue-lead time of 100 ms. In the present study the 'cue', that is, the auditory stimulus, was always present at least for 300 ms while the visual target was present as well. This difference in paradigm may explain why we found express saccades in all contingency conditions.

In fact, Maruff, Yucel, Danckert, Stuart & Currie (1999) demonstrated that the temporal overlap of a cue and target plays a crucial role in facilitating manual reaction times at short SOAs. In a covert orienting of visual attention task (COVAT) participants were instructed to maintain central fixation throughout the entire experiment, but to respond as quickly as possible to the visual target by using a hand held microswitch. If the target was presented at the same location and temporally overlapped with the cue, reaction times were faster than if the cue did not temporally overlap with the target. These results thus suggested that the temporal overlap between the 'cue' and the target might have led to a general facilitation of reaction times eliciting equal numbers of express saccades in all contingency conditions. The latter conclusion was supported by the observation that Maruff *et al.* (1999) did not find any reaction time differences between cued and uncued locations, when the cue was not temporally overlapping with the target. Thus, the express saccades in Cavegn (1996) may have been a specific effect of cue validity rather than a general facilitation effect, as in the present study. Note that the interpretation in terms of a general facilitation effect is further supported by the fact that the subjects in the present study exhibited a large number of anticipatory saccades which were not affected by interstimulus contingency effects either.

In summary, the analysis of anticipatory and express saccades pointed to a general facilitation effect irrespective of contingency validity. However, two of the seven subjects exhibited contingency effects in the latencies and amplitudes of regular saccades. In particular, the contingency effects occurred in those SOAs in which the regular saccades had latencies of about 200 ms or more. Therefore, we suggest that the processing of interstimulus contingencies needs some time before they can be used for improving performance.

3

Visual prosaccades in a bimodal go/no-go task

3.1 Introduction

The results of the first experiment indicated that interstimulus contingencies can be used for better performance only if the saccades had latencies of about 200 ms or longer. In order to investigate this hypothesis, we introduced a bimodal go/no-go task in which the subjects were asked to withhold their response to a 'catch' stimulus, while in the go trials they were instructed to make a saccade to the visual target. Contingency information was provided in the location of the auditory accompanying stimulus.

Studies investigating the effects of catch trial frequency on manual and saccadic reaction times showed a direct relationship between catch trial probability and reaction times (Alegria, 1978; Jüttner & Wolf, 1992), *i.e.*, the more catch trials were included in the experiment, the longer were the reaction times. Furthermore, these studies also showed a strong effect of trial history on reaction times. Responses in trials following a catch trial had longer latencies than those following a target trial.

In analogy to these findings, we expected the subjects to exhibit significantly longer saccadic reaction times than in Experiment 1. Also, we expected them to pay more attention to the auditory stimulus, because they had to identify the modality of the first stimulus present in order to decide whether to make a saccade (go trial) or to withhold their response (catch trial).

In this chapter, we will describe four experiments investigating interstimulus contingency effects on visual prosaccades in a bimodal go/no-go task. In Experiment 2, the catch stimulus consisted in a unimodal auditory stimulus, while in the following three experiments it was visual. In Experiment 4, the subjects were misled about the contingency condition to be investigated in the next block of trials in order to investigate the effects of pre-information in our experimental set-up. Finally, in Experiment 5, we systematically varied the catch trial frequency in each block of trials in order to demonstrate that this variable did not alter the contingency effects.

3.2 Experiment 2: Auditory catch trials

In a bimodal go/no-go task, subjects were asked to make a saccade in the direction of a visual target. Contingency information was provided by an accompanying auditory stimulus that also served as catch stimulus when presented alone. In analogy to the findings in spatial cueing paradigms, the hypothesis was that subjects show shorter saccadic reaction times and amplitudes in the positively correlated contingency, and longer reaction times and amplitudes in the negatively correlated contingency.

In analogy to Jüttner and Wolf (1992), we further hypothesised that the overall mean saccade latencies should be longer than in Experiment 1 without catch trials. Consequently, subjects should have some more time to use the contingency information for improving performance. Furthermore, as the contingency information was contained in the auditory stimulus and it also served as the catch stimulus, the subjects should be more motivated than in Experiment 1 to consider the information it contained. Finally, the subjects should show longer saccade latencies in trials following a catch trial than in trials following a bimodal trial (see Jüttner & Wolf, 1992).

3.2.1 Method

3.2.1.1 Participants

Four undergraduate students (aged 19-22) of the University of Oldenburg took part in the experiment. All but one subject (TS) had right eye dominance. All subjects had normal hearing and normal or corrected-to-normal vision. They were either paid or received partial course credit for participation. All subjects gave their informed consent prior to their inclusion in the study. They were not informed about the specific hypothesis under study.

3.2.1.2 Task and procedure

Experiment 2 was identical to Experiment 1, except for the following: The task was to make an eye movement as quickly and as accurately as possible to the visual target (both in bimodal and in unimodal visual trials), but to withhold a response if only the auditory target was present (catch trials). For experimental parsimony the SOAs were varied only on five levels with equal probability: The auditory stimulus appeared either 210, 110 or 40 ms before (–), simultaneously, or 40 ms after (+) the visual target. The 20% and 80% ISC blocks contained 50 bimodal and 10 unimodal visual and auditory trials, and the 50% ISC blocks contained 40 bimodal and 20 unimodal visual and auditory trials. Saccades to unimodal auditory stimuli were measured in a separate block at the end of the first session.

3.2.2 Results

Trials in the 20% and 80% ISC blocks were recoded according to their effective validity (see Figure 2.1). For better comparability, the SRTs of each subject were normalised by subtracting their overall mean SRT.

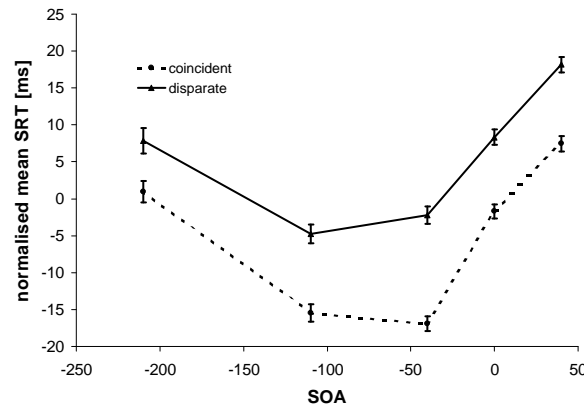


Figure 3.1: *Time course of saccadic reaction times (SRT) of all subjects to bimodal stimuli in auditory catch trials. The SRTs were normalised by subtracting the overall mean SRT for each subject separately. The auditory stimulus was presented 210, 110, or 40 ms before (–), simultaneously, or 40 ms after (+) the visual target. coincident:= stimuli presented at the same location; disparate:= stimuli presented at opposite locations.*

3.2.2.1 Saccadic reaction times

Each subject showed less than 0.1% express saccades. The regular SRTs were submitted to a three-way ANOVA with SOA, spatial congruence (coincident vs. disparate), and ISC validity (20%, 50%, or 80%) as repeated factors. Three main effects but no significant interaction effect emerged. The main effect of SOA ($F_{4,3} = 26.65, p < 0.001$) was highly significant indicating a u-shaped pattern of SRTs as illustrated in Figure 3.1: Subjects reacted the fastest when the auditory stimulus was presented 40 to 110 ms before the visual target. Latencies increased when the auditory stimulus was presented 210 ms before, simultaneously, or 40 ms after the visual target.

Spatial congruence was the second main effect on performance ($F_{1,3} = 20.8, p < 0.02$). When the SRTs were analysed for each subject separately, three of the four subjects showed a significant effect of spatial congruence: Responses in coincident trials were 12 ms faster on average than responses in disparate trials (also see Figure 3.1). The main effect of ISC was significant ($F_{2,3} = 7.97, p < 0.02$) indicating shorter SRTs to 20% and 80% ISCs than to the 50% ISC.

Note that this effect only reached significance in two subjects (CR and EN) when the SRTs were analysed for each subject separately. The effects of ISC validity in combination with spatial congruence are illustrated in Figure 3.2 for each subject separately. Separate post-hoc analyses (Newman-Keuls tests) for each SOA revealed that subject CR showed shorter SRTs in 20% ISC than in 50% ISC in SOA = –210 ms, and also shorter SRTs in 80% ISC than in 50% ISC in SOA = –40 ms. Subject EN showed the same effect of shorter SRTs in 20% and 80% ISC than in 50% ISC, but only in SOA = +40 ms.

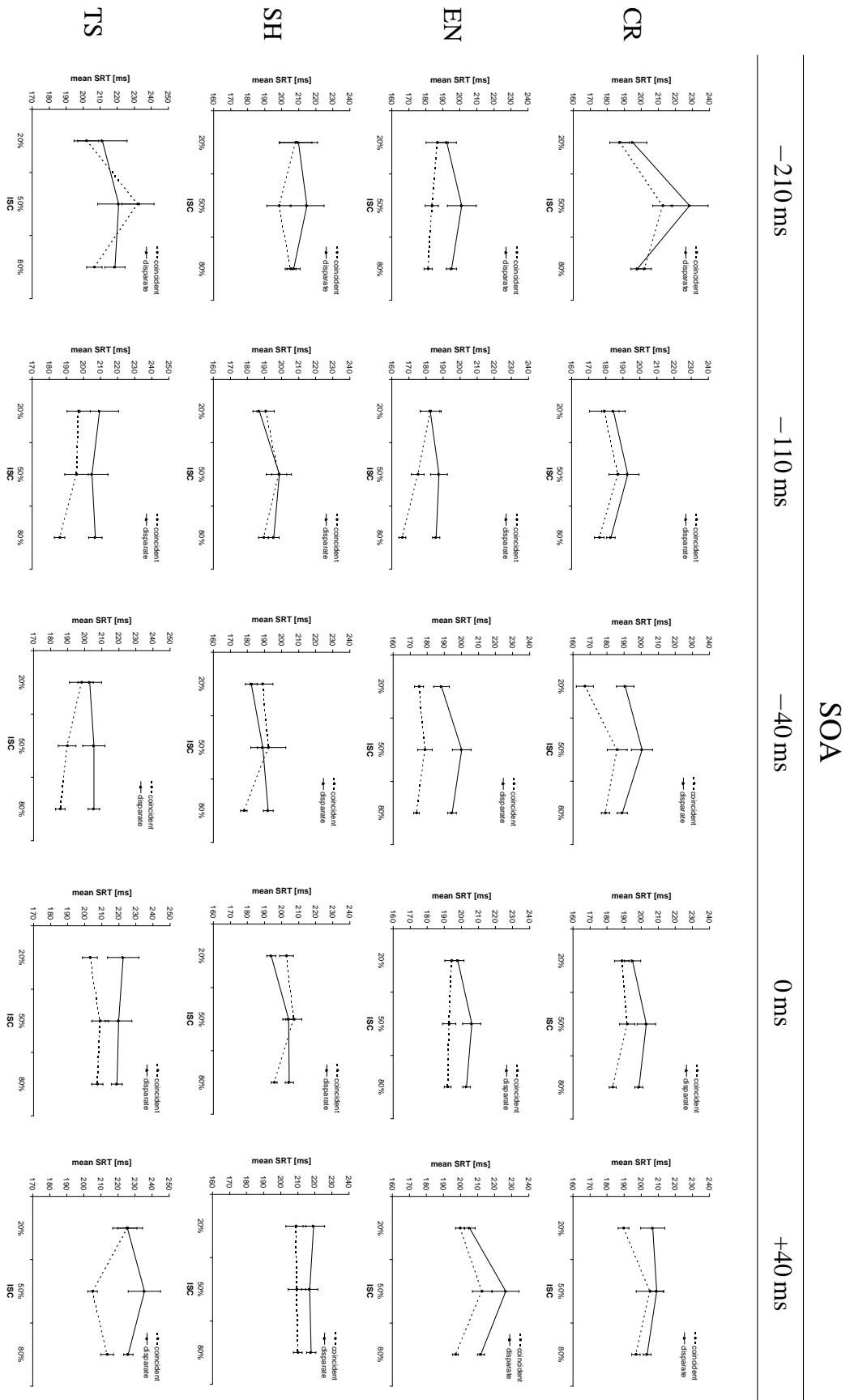


Figure 3.2: Interstimulus contingency (ISC) effects separated by stimulus onset asynchrony (SOA) and spatial congruence (coincident vs. disparate). The effects are significant in SOA = -210 ms and -40 ms for subject CR, and in SOA = +40 ms for subject EN.

Table 3.1: *Relative frequency of catch responses for each subject according to effective contingency validity.*

| Subject | Contingency validity | | | TOTAL |
|---------|----------------------|---------------|---------------|---------------|
| | 20% | 50% | 80% | |
| CR | 32/130 = 0.25 | 8/106 = 0.08 | 27/116 = 0.23 | 67/352 = 0.19 |
| EN | 30/158 = 0.19 | 16/151 = 0.11 | 35/148 = 0.24 | 81/457 = 0.18 |
| SH | 10/116 = 0.09 | 9/115 = 0.08 | 3/118 = 0.03 | 22/349 = 0.06 |
| TS | 11/110 = 0.10 | 5/102 = 0.05 | 13/98 = 0.13 | 29/310 = 0.09 |

3.2.2.2 Saccade amplitudes

First, differences in the three ISC validities were investigated and, second, these differences were compared to those obtained in catch response trials. Separate ANOVAs were conducted for each subject and rightward *vs.* leftward saccades with ISC validity and spatial congruence (coincident *vs.* disparate) as unreplicated factor. Subject CR showed a significant contingency effect in leftward saccades ($F_{2,324} = 10.81, p < 0.001$, amplitudes in 20% and 80% ISC being 1.5° and 1.2° longer on average than in 50% ISC), and a marginally significant effect in rightward saccades ($F_{2,313} = 11.67, p < 0.059$, amplitudes in 80% ISC being 0.6° longer on average than in 50% ISC). Subjects EN and SH only showed a significant ISC effect in one direction of gaze: (EN: $F_{2,465} = 7.21, p < 0.016$, leftward amplitudes in 80% ISC being 0.4° shorter on average than in 50% ISC; SH: $F_{2,343} = 7.32, p < 0.098$, rightward amplitudes in 20% ISC being 0.5° longer on average than in 50% ISC). Subject TS did not show any contingency effects in saccade amplitudes. The remaining three subjects exhibited a significant interaction effect of contingency and spatial congruence.

In a second analysis, for each subject the catch response amplitudes were submitted to separate t-tests, comparing the responses in the different ISC conditions. This analysis reached significance in subject EN in rightward saccades only ($t_{1,18} = 2.33, p < 0.031, 4.7^\circ$), indicating longer amplitudes to catch trials interspersed in 80% than in 20% ISC blocks.

3.2.2.3 Visual-auditory facilitation in saccadic reaction times

A one-way ANOVA compared the saccadic reaction times across all ISC conditions with the reaction times obtained in the control trials in which the subjects either responded to the visual or auditory stimulus presented alone. This analysis was highly significant ($F_{2,6806} = 562.3, p < 0.001$) indicating shorter saccadic reaction times to unimodal auditory and bimodal stimulation (200 ms and 207 ms) than to the unimodal visual stimulus (236 ms).

3.2.2.4 Catch responses

Table 3.1 shows that the relative frequency of catch responses varied considerably between subjects. Chi-square tests were carried out comparing the relative frequency of catch responses in the different ISC conditions between trials in which the subjects correctly withheld the response with those in which the subjects falsely responded to a catch trial. These Chi-square tests were significant only for subject CR. Inspection of Table 3.1 revealed that she less often falsely responded to the catch trials interspersed in the 50% ISC than to the catch trials interspersed in the 20% and 80% ISC. In a second analysis, the catch response SRTs of each subject were submitted to separate ANOVAs with ISC validity as unrepeated factor, but none of these ANOVAs reached significance.

3.2.2.5 Recency effects

In a final analysis, we examined catch trial recency effects which have been observed in previous studies (*e.g.*, Jüttner & Wolf, 1992). The SRTs of each subject were separated into those trials following a bimodal trial, and the trials following a catch trial. The SRTs were then submitted to separate ANOVAs for each subject with catch recency (bimodal *vs.* catch), SOA, and ISC (20%, 50% or 80%) as unrepeated factors. All of the subjects showed a significant catch recency effect with latencies in trials presented after a bimodal trial being 15 ms faster on average than latencies in trials presented after a catch trial. No interaction effect of catch recency * ISC validity was found. Catch recency did interact with SOA in all but one subject (CR). For subjects SH and TS a significant three-fold interaction of catch recency * SOA * ISC was found. Separate ANOVAs for each SOA revealed that it was only the SOA = -210 ms that contained the significant interaction effect of catch recency and ISC (SH: $F_{2,266} = 5.1, p < 0.007$; TS: $F_{2,223} = 2.9, p < 0.057$). Graphical inspection suggested that these interaction effects consisted in significant ISC effects in trials following a catch trial, but no ISC effects in trials following a bimodal trial.

3.2.2.6 Summary

Experiment 2 revealed significant main effects of SOA, spatial congruence and ISC validity on saccadic reaction times (SRT). The lack of interactions showed that the effects of SOA and spatial congruence (coincident *vs.* disparate) were largely independent. Also, the effects of spatial congruence were largely independent of interstimulus contingency effects. However, the contingency effects did interact with SOA, indicating that contingency effects occurred when the auditory stimulus was presented either 210 ms before or 40 ms after the visual target.

The main effect of ISC validity indicated shorter reaction times in 20% and 80% ISC than in 50% ISC. This effect reached significance only in two subjects when the data were analysed separately for each subject. The analyses of catch recency and saccade amplitudes further showed that in 20% and 80% ISC one subject was less prone to committing catch trial responses, and the two subjects either showed shorter or longer saccade amplitudes than in 50% ISC. Another two subjects did not show any contingency effects in reaction times or amplitudes, but they did show a significant interaction effect of ISC and

catch recency in $SOA = -210$ ms, indicating significant ISC effects on saccadic latencies in trials following a catch trial, but no ISC effects in trials following a bimodal trial. All subjects showed significant effects of catch recency, with latencies in trials presented after a bimodal trial being 15 ms faster on average than latencies in trials presented after a catch trial. None of the subjects showed more than 0.1% express saccades.

3.2.3 Discussion

The systematic variation of interstimulus contingencies revealed shorter saccadic reaction times to positively and negatively correlated bimodal stimuli in comparison to no correlation. This finding is consistent with the results of Schwarz (1996) who reported shorter manual reaction times in negatively correlated letters. However, the results are in clear contrast to the findings in spatial cueing experiments in which longer saccadic reaction times are typically reported in invalid trials. Whether our results were due to the specific task requirements of interstimulus contingencies or to the inclusion of catch trials will be investigated in the next experiment and in Experiment 5.

Note that the effects of spatial congruence (coincident *vs.* disparate) and interstimulus contingency (20%, 50%, and 80%) were largely independent. This result indicated that the learning about contingencies did not interfere with spatial contiguity or bimodal interaction effects (see Sections 1.5). On the other hand, the contingency effects did interact with SOA in two subjects. They were most prominent for long mean latencies, *i.e.*, for $SOA = -210$ ms and $SOA = 40$ ms. This finding implied that the processing of interstimulus contingencies needs some minimum time before they can be used for optimal performance.

Two subjects did not show any contingency effects in reaction times and/or amplitudes, but they did show a significant interaction effect of ISC and catch recency in $SOA = -210$ ms. SRTs in this SOA condition were generally almost as long as when the auditory stimulus was presented simultaneously or after the visual target. We therefore conclude that the longer SRTs in $SOA = -210$ ms represent a specific effect of the auditory catch trials as subjects had to wait for the occurrence of the visual target to decide whether they actually were allowed to respond in that trial. According to their informal self-report given at the end of the sessions, these two subjects tried to ignore as much as possible the auditory stimulus in order to render the task easier. This strategy might explain why they did not show any contingency effects except for trials with $SOA = -210$ ms following a catch trial. Only in a situation in which they had just been reminded to take notice of the auditory stimulus in order to correctly withhold the response in a catch trial, and in which they had to wait for the visual stimulus to be presented, these subjects actually made use of the contingency information contained in the auditory stimulus. In other words, it seems that our task left a certain margin for the subjects in considering the auditory stimulus. Only when they almost had no choice but to act on it did they use the contingency information the auditory stimulus contained.

The fact that none of the subjects showed a significant amount of express saccades might be explained by the specific task constraint of auditory catch trials. In order to decide whether they were actually asked to respond, the subjects had to wait for the presence of the visual target. This uncertainty on whether and when to respond may have increased

the threshold to reach a decision for saccade execution (see Cavegn & d'Ydewalle, 1996, for further discussion of this issue).

The observation that two subjects exhibited contingency effects in the saccade latencies and amplitudes confirmed our conclusion in Experiment 1 (see Chapter 2) that the processing of interstimulus contingencies affects motor processing. Whether these contingency effects on saccade amplitudes are similar to those on the saccade latencies will be discussed in more detail in the Experiments 4 and 5.

Finally, the catch recency effects are consistent with the general finding that subjects react faster in trials following a target trial than in trials following a catch trial. The analysis further revealed that the subjects, having tried to ignore the auditory stimulus, showed an interaction effect of catch recency with contingency. On the other hand, those subjects who paid attention to the contingency information contained in the auditory stimulus did not show an interaction of catch recency with contingency. This pattern of results suggested that the interstimulus contingencies only affected saccadic reaction times and amplitudes if the subjects paid attention to the auditory stimulus and, thus, seemed to be more or less insensitive to the catch trials. 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 in which visual catch trials were employed.

3.3 Experiment 3: Visual catch trials

In Experiment 3 we replaced the unimodal auditory trials by unimodal visual trials. The subjects were instructed to make an eye movement to the visual target only if the auditory stimulus was present. Otherwise, subjects were asked to continue looking in the middle (catch trial). With these visual catch trials, subjects had to wait for the auditory stimulus in order to make a saccade. We thus wanted to incite subjects to pay attention to the auditory stimulus in each trial. The hypothesis was that the subjects should show stronger contingency effects than in Experiment 2, because they should pay even more attention to the auditory stimulus and, thereby, to the contingency information it contained.

Furthermore, the variation in the modality of the catch stimulus would allow to confirm the finding in Experiment 2 that no contingency effects occurred, if the subjects showed an interaction effect of catch recency and contingency. We hypothesised that no interaction effect of catch recency with contingency should occur, because the stimulus modality containing the contingency information did not constitute the catch stimulus.

As one subject in Experiment 2 showed an effect of contingency even when the auditory stimulus was presented closely after the visual target, the range of SOAs was enlarged and the auditory stimulus presented even later after the visual target. One group of subjects was presented with the same SOAs as in Experiment 2, the other group was presented with a new range of SOAs (also see Experiment 1).

3.3.1 Method

3.3.1.1 Participants

Seven students (mean age 23 ± 4 years) of the University of Oldenburg took part in the experiment. Subjects EN, SH, and TS already participated in Experiment 2. The remaining four subjects had not participated in psychophysical experiments before. All but one subject (TS) had right eye dominance. All subjects had normal hearing and normal or corrected-to-normal vision. They were either paid or received partial course credit for participation. All subjects gave their informed consent prior to their inclusion in the study. They were not informed about the specific hypotheses under study.

3.3.1.2 Task and procedure

Experiment 3 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, but to withhold a response if only the visual target was present (catch trials). Second, the 20% and 80% ISC blocks contained 50 bimodal and 20 catch trials, and the 50% ISC blocks contained equal numbers of bimodal and catch trials. Finally, saccades to unimodal visual or auditory stimuli were measured in separate blocks at the end of the sessions.

3.3.2 Results

If not mentioned otherwise, trials in the 20% and 80% ISC blocks were recoded according to their effective validity (see right panel of Figure 2.1).

3.3.2.1 Saccadic reaction times

Express saccades Graphical inspection of SRTs revealed that the four subjects having performed under the negative SOAs showed a large number of anticipatory and express saccades. For subjects MA and MW, these saccades formed separate populations in their saccade latency distributions. Also, both types of saccades were characterised by a large scatter in saccade amplitudes. An analysis of the relative frequencies of gaze direction showed that all four subjects gazed more often in the direction of the stimuli presented coincidentally than in direction of the auditory stimulus when presented disparate to the visual target. However, sometimes the subjects even gazed opposite to both stimuli.

To examine the effect of contingencies on express saccade behaviour, the correct express saccades were sorted by effective ISC validity. By effective ISC validity we mean that those trials, in which the visual and auditory stimuli were presented in 80% of the bimodal trials at the same or opposite location, were defined as 80% valid, whereas the remaining 20% of the bimodal trials were defined as 20% valid (see right panel of Figure 2.1). The number of express saccades in each ISC condition was then divided by the total number of bimodal trials measured in the respective ISC condition in order to account for the different numbers of trials obtained especially in 20% and 80% ISC. The relative frequency of express gaze is summarised in Table 3.2 separately for each subject.

Table 3.2: *Relative frequency of correct express saccades sorted by effective contingency validity for each subject.*

| Subject | Contingency validity | | |
|---------|----------------------|---------------|----------------|
| | 20% | 50% | 80% |
| MA | 13/273 = 0.05 | 22/270 = 0.08 | 66/1085 = 0.06 |
| MW | 9/238 = 0.04 | 3/226 = 0.01 | 38/969 = 0.04 |
| SH | 4/219 = 0.02 | 4/223 = 0.02 | 14/911 = 0.02 |
| TS | — | 3/149 = 0.02 | 18/636 = 0.03 |

Chi-square tests on the relative frequencies shown in Table 3.2 did not reach significance in any subject. Finally, the saccade amplitudes of the correct express saccades were submitted to separate t-tests for each subject, direction of gaze (rightward or leftward), and for each comparison of ISC validity. None of these t-test reached significance.

As the subjects performed under different combinations of SOAs, the remaining regular SRTs were analysed separately for each SOA.

SOA = -210 ms The SRTs were analysed separately for each subject, because subjects MA and MW produced saccades mainly before the presentation of the visual target or with latencies less than 80 ms. These anticipations (Kalesnykas & Hallett, 1987) were sorted by gaze direction (coincident, visual disparate, auditory disparate, and opposite to coincident). The anticipations were also separated for ISC validity, but this time ISC validity was defined in terms of the trials as they were presented together in one experimental block of ISC (see left panel of Figure 2.1). Thus, in the top panels of Figure 3.3 each main column of ISC contains all anticipatory saccades measured under that type of ISC. Note however that the relative trial frequency in each ISC condition should not be directly compared with the relative frequency subjects gazed at those stimuli, because the columns of Figure 3.3 only contain anticipatory saccades. Regular saccades, express saccades, blinks, or other errors were not included in this analysis.

Separate chi-square tests were conducted on the relative frequencies as illustrated in the top panels of Figure 3.3. For each subject, these tests compared the effects of ISC validity on each direction of gaze: Both subjects gazed more often to the coincident stimuli in 80% ISC than in 20% and 50% ISC, and they also gazed more often to the auditory disparate stimulus in 20% ISC than in 50% and 80% ISC. Even more interesting, the subjects gazed more often in the direction of the to-be-presented disparate visual target in 20% ISC (in 80% of the trials stimuli were presented disparately) than in 80% ISC (only in 20% of the trials stimuli were presented disparately). These results showed clearly that the subjects anticipated the respective relative frequency of stimulus events in the different ISC conditions.

The bottom panels of Figure 3.3 show the SRTs of subjects SH and TS. Separate ANOVAs with spatial congruence (coincident vs. disparate) and ISC validity as unreplicated factors revealed a significant ISC effect for subject TS ($F_{2,157} = 4.35$, $p < 0.014$):

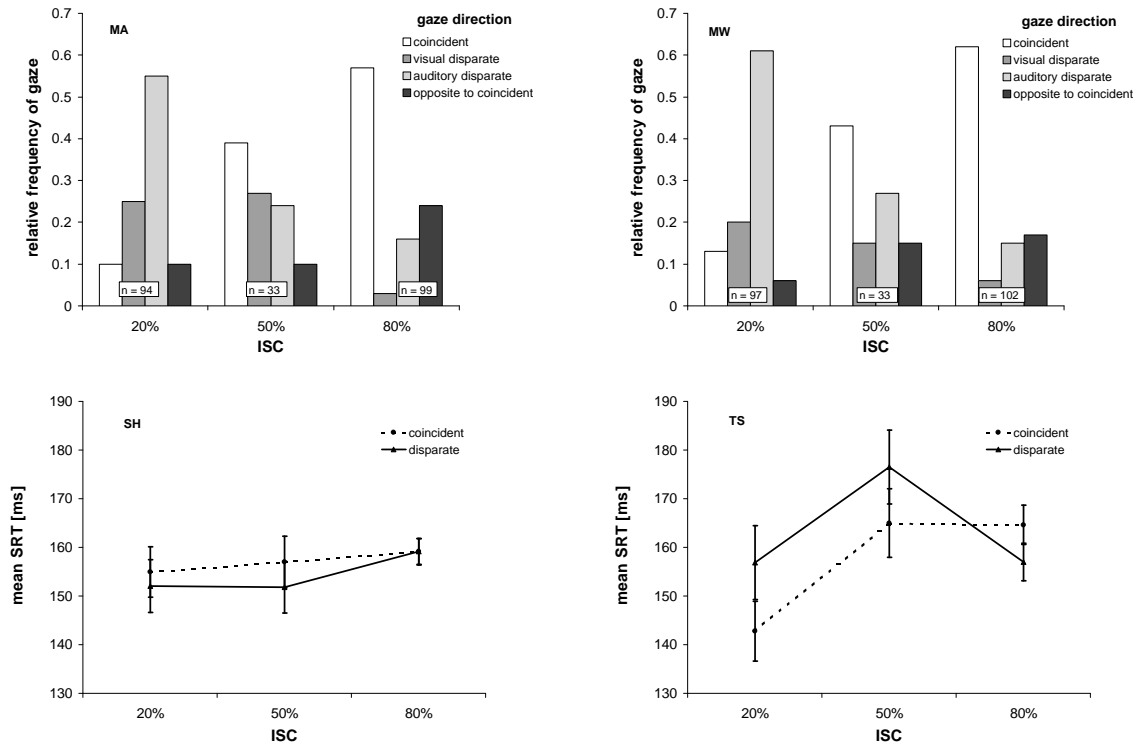


Figure 3.3: Anticipatory or regular saccades in $SOA = -210$ ms. The upper panels illustrate the relative frequency of anticipatory saccades separated by gaze direction and interstimulus contingency (ISC) for two subjects (MA and MW). ISC validity is defined in terms of the trials as they were presented during the experiment. Note that the relative trial frequency in each ISC condition should not be directly compared with the relative frequency subjects gazed at these stimuli, because the graph does not include express or regular saccades obtained in the same conditions. The lower panels illustrate the mean latencies of regular saccades (SRT) of two subjects (SH and TS) according to recoded ISC validity. coincident:= stimuli presented at the same location; disparate:= stimuli presented at opposite locations.

She responded 21 ms faster on average in the 20% ISC than in the 50% ISC. No other factors or interaction terms reached significance.

SOA = -110 ms The regular saccades in SOA = -110 ms were submitted to a two-way ANOVA with spatial congruence (coincident *vs.* disparate) and ISC (20%, 50% or 80%) as repeated factors. The analysis revealed a marginal effect of ISC ($F_{2,3} = 3.52, p < 0.09$), no other effects reached significance. When the SRTs were analysed separately for each subject, three of the four subjects (MA, MW, and TS) showed a significant effect of ISC with responses in 20% ISC being 27 ms faster on average than responses in 50% ISC. Subject TS showed a significant interaction effect of spatial congruence and ISC ($F_{2,201} = 4.16, p < 0.017$): The ISC effect only was significant in the coincident trials.

SOA = -40, 0, and +40 ms The SRTs of all seven subjects were submitted to separate two-way ANOVAs for each SOA with spatial congruence (coincident *vs.* disparate) and ISC (20%, 50% or 80%) as repeated factors. In all SOAs the main effect of ISC was significant (SOA = -40 ms: $F_{1,6} = 5.39, p < 0.054$; SOA = 0 ms: $F_{1,6} = 5.89, p < 0.045$; SOA = +40 ms: $F_{2,6} = 9.18, p < 0.005$). In SOA = -40 and 0 also the main effect of spatial congruence was significant (SOA = -40 ms: $F_{1,6} = 6.28, p < 0.046$; SOA = 0 ms: $F_{1,6} = 6.45, p < 0.044$). No such effect was found in SOA = +40 ms, nor were the interaction effects significant. In a second step, the SRTs were analysed separately for each subject and SOA. In these analyses only three of the seven subjects showed a significant ISC effect (see Figure 3.4). Subject MW showed significant ISC effects in all three SOAs and a significant interaction effect of spatial congruence and ISC in SOA = -40 ms; subject SH showed a marginal ISC main and interaction effect of spatial congruence * ISC in SOA = -40 ms, and a significant ISC effect in SOA = +40 ms; subject TS showed a significant ISC effect in SOA = -40 ms.

SOA = +80 and +120 ms Separate two-way ANOVAs for each SOA were conducted with spatial congruence (coincident *vs.* disparate) and ISC validity (20%, 50% or 80%) as repeated factors. None of these factors reached significance. However, in separate ANOVAs for each subject and SOA, subject AN showed a marginal ($F_{2,239} = 2.9, p < 0.057$), and subject EN a significant main effect of ISC validity ($F_{2,263} = 6.39, p < 0.002$) in SOA = +80 ms. As can be seen in Figure 3.5, on average both subjects reacted about 33 ms faster in 20% ISC and 25 ms faster in 80% ISC than in 50% ISC. For SOA = +120 ms only subject EN showed a significant ISC effect ($F_{2,263} = 5.71, p < 0.004$): SRTs were 46 ms faster on average in 80% ISC than in 50% ISC. None of the interaction effects reached significance.

3.3.2.2 Saccade amplitudes

Saccade amplitudes of all regular saccades were submitted to separate ANOVAs for each subject and rightward *vs.* leftward saccades with ISC validity and spatial congruence (coincident *vs.* disparate) as unrepeated factors. Five of the seven subjects showed a significant effect of ISC validity in at least one direction of gaze. Three of them exhibited shorter amplitudes in 50% ISC than in 20% and 80% ISC in rightward saccades (mean

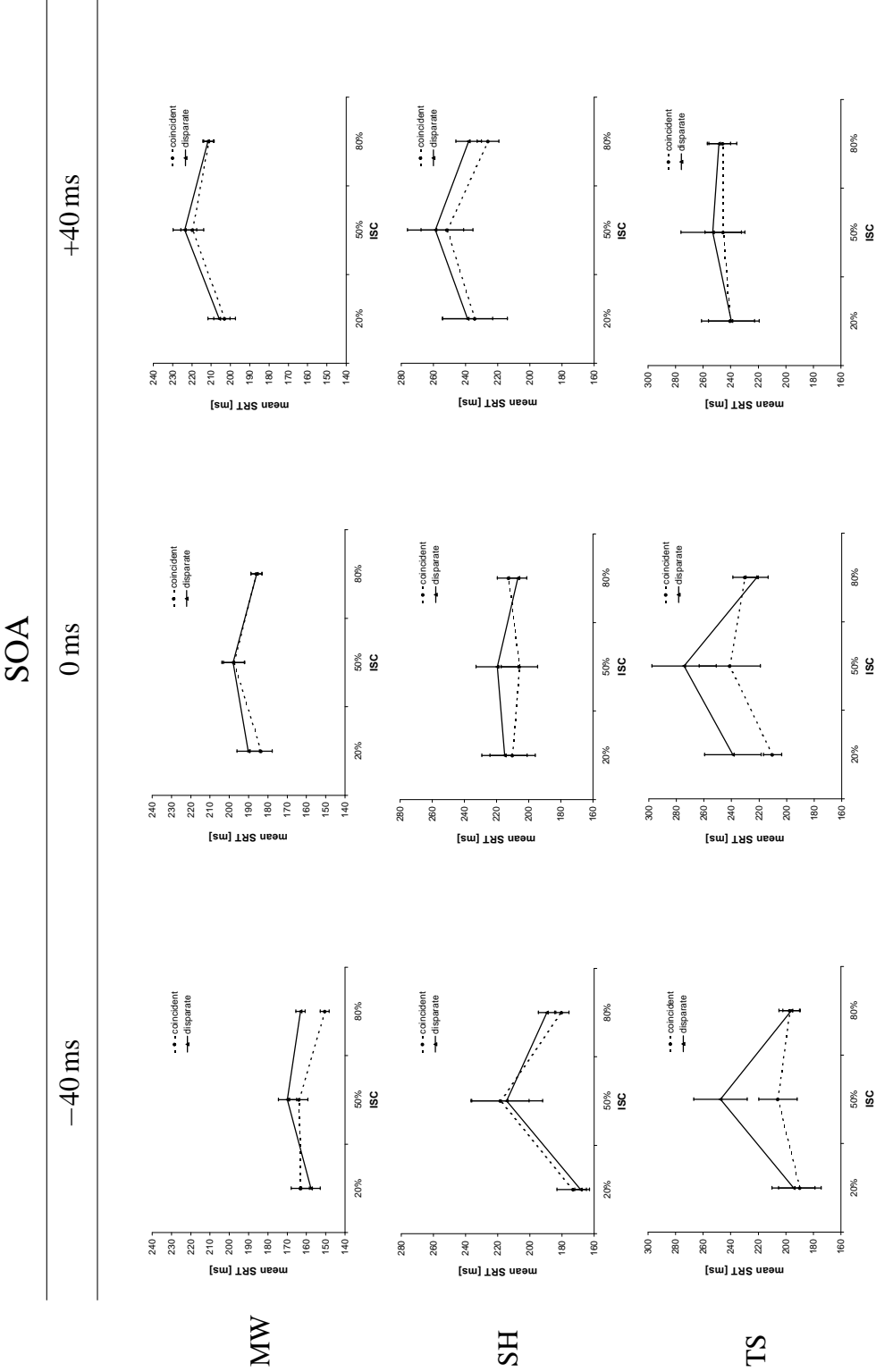


Figure 3.4: Interstimulus contingency (ISC) effects separated by stimulus onset asynchrony (SOA) and spatial congruence (coincident vs. disparate). Subject MW exhibited significant ISC effects in all SOAs, subject SH in SOA = + 40 ms, and subject TS in SOA = -40 ms.

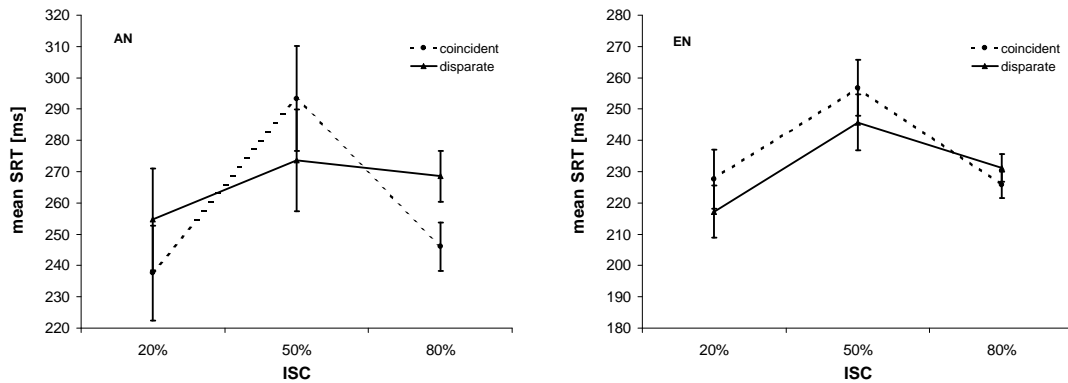


Figure 3.5: *Interstimulus contingency (ISC) effects in SOA = +80 ms for the two subjects either exhibiting marginally (AN) or significantly (EN) shorter mean saccadic reaction times (SRT) in 20% and 80% ISC than in 50% ISC. coincident:= stimuli presented at the same location; disparate:= stimuli presented at opposite locations.*

difference = 0.8° , $SD = 0.09^\circ$). However, the remaining two subjects, and one subject of the former group (SH), exhibited longer amplitudes in 50% ISC than in 20% and 80% ISC in leftward saccades (mean difference = 0.8° , $SD = 0.21^\circ$). Five subjects showed a significant interaction effect of ISC validity * spatial congruence.

Depending on the total number of trials (see Table 3.3), the catch response amplitudes were analysed with separate ANOVAs or t-tests for each subject with ISC validity as unrepeated factor. None of these analyses reached significance.

3.3.2.3 Visual-auditory facilitation in saccadic reaction times

A one-way ANOVA compared the saccadic reaction times across all ISC conditions in the SOAs = -40 ms, 0 ms, and $+40$ ms with the reaction times obtained in the control trials in which the subjects either responded to the visual or auditory stimulus presented alone. This analysis was highly significant ($F_{2,9380} = 273.8, p < 0.001$). Student-Newman-Keuls post-hoc tests indicated that the SRTs to unimodal auditory stimuli were significantly shorter than SRTs to bimodal stimulation (186 ms and 217 ms) which in turn were shorter than SRTs to unimodal visual targets (227 ms).

3.3.2.4 Catch responses

As can be seen in Table 3.3, the relative frequency of catch responses varied strongly across subjects. The relative frequency of catch responses in the different ISC conditions between trials in which the subjects correctly withheld response were compared with those in which they falsely responded to a catch trial. Chi-square tests reached significance only for the subjects AN and EN. The catch trials interspersed in the 50% ISC blocks were less often falsely responded to than catch trials interspersed in the 20% and 80% ISC blocks (*cf.* Table 3.3). In a second analysis, the catch response SRTs were submitted to separate ANOVAs for each subject with ISC validity as unrepeated factor. For two subjects (EN and TS) this analysis reached significance (EN: $F_{2,130} = 3.9, p < 0.023$;

Table 3.3: *Relative frequency of catch responses for each subject according to effective contingency validity.*

| Subject | Contingency validity | | | TOTAL |
|---------|----------------------|----------------|----------------|----------------|
| | 20% | 50% | 80% | |
| AN | 156/242 = 0.65 | 119/250 = 0.48 | 161/238 = 0.68 | 463/730 = 0.63 |
| DS | 121/235 = 0.51 | 90/235 = 0.38 | 112/232 = 0.48 | 323/702 = 0.46 |
| EN | 58/256 = 0.23 | 21/255 = 0.08 | 52/258 = 0.20 | 131/769 = 0.17 |
| MA | 11/275 = 0.04 | 5/274 = 0.02 | 13/269 = 0.05 | 29/818 = 0.04 |
| MW | 17/305 = 0.06 | 7/270 = 0.03 | 13/292 = 0.04 | 37/867 = 0.04 |
| SH | 63/229 = 0.28 | 47/226 = 0.21 | 70/231 = 0.30 | 180/686 = 0.26 |
| TS | 23/109 = 0.21 | 13/115 = 0.11 | 23/116 = 0.20 | 59/340 = 0.17 |

TS: $F_{2,57} = 2.97, p < 0.06$), but their pattern of SRTs was adverse: Subject EN responded to catch trials in 20% ISC blocks 12 ms faster on average than in 50% ISC blocks, but subject TS responded to catch trials in 20% ISC blocks 38 ms longer on average than in 50% ISC blocks.

3.3.2.5 Recency effects

In order to examine catch trial recency effects, the data were separated into those trials following a bimodal trial, and the trials following a catch trial. The regular SRTs were then submitted to separate ANOVAs for each subject with catch recency (bimodal vs. catch), SOA, and ISC validity as unreplicated factors. Except for subject TS, all subjects showed a significant main effect of catch recency with latencies in trials presented after a bimodal trial being 20 ms (SD = 11 ms) faster on average than latencies in trials presented after a catch trial. The main effect of ISC validity was significant in all but subjects MA and SH. Only in subject AN a significant interaction effect of catch recency * ISC validity occurred ($F_{2,1033} = 2.98, p < 0.05$). This subject and subject SH also showed a significant three-fold interaction effect of catch recency * ISC validity * SOA. Separate ANOVAs for each SOA revealed that subject AN showed a significant interaction of catch recency * ISC validity only in SOAs = +40 ms and +80 ms, and subject SH showed this effect in SOA = -40 ms. Graphical inspection indicated that these interaction effects consisted in significant ISC effects in trials following a catch trial, but no ISC effects occurred in trials following a bimodal trial. Four subjects showed a significant interaction effect of catch recency * SOA.

3.3.2.6 Summary

We found significant interstimulus contingency effects in all but one subject. The SOA range in which contingency effects occurred reached from -210 ms to +80 ms. Saccade amplitude effects were significant in the bimodal trials: Amplitudes in 50% ISC were either shorter or longer than in 20% and 80% ISC, depending on the subject and direction

of gaze. The relative frequency of catch responses varied considerably among subjects. Two of the three subjects who performed under the positive SOAs exhibited significantly less catch responses in the 50% ISC blocks than in the remaining contingency conditions. All but one subject showed significant effects of catch recency, with latencies in trials presented after a bimodal trial being 20 ms faster on average than latencies in trials presented after a catch trial. Two subjects showed significant interaction effects of catch recency and ISC validity: They only showed contingency effects in trials following a catch trial.

Two of the subjects who performed under the negative SOAs exhibited a large number of anticipatory and express saccades. The interstimulus contingencies did not affect the relative frequency of express saccades. However, they did affect the relative frequency of gaze direction in anticipatory saccades: The subjects anticipated the respective relative frequency of stimulus events in the different ISC conditions.

3.3.3 Discussion

The variation of stimulus onset asynchronies showed that interstimulus contingency effects can occur over a large time window. Meredith, Nemitz, & Stein (1987) recorded visual-auditory neurons in the cat's superior colliculus (SC) and found optimal response enhancement when a visual and an auditory stimulus were presented in a time window of 100 ms, while the neuron still exhibited significant activity when the stimuli were presented 200 ms apart. This wide temporal window seems especially adapted if one considers the different travelling times of the respective sensory energies and thus the different times these inputs reach the SC (Stein & Meredith, 1993).

Note that the subjects in the present study not only did exhibit shorter SRTs with bimodal stimulation than with either unimodal stimulus, but somehow used the contingency information in the auditory stimulus for even shorter responding. This is not to say that interstimulus contingencies are processed in the SC, such a conclusion lies beyond the purpose of this study, but it seems however possible that the processing of contingencies in a selective attention task with simple visual and auditory stimuli already takes place in early visual areas in extrastriate cortex (Handy, Hopfinger & Mangun, 2001; Martinez, DiRusso, Anllo-Vento *et al.*, 2001)

The four subjects who performed under the negative SOAs showed a considerable number of express saccades when the auditory stimulus was presented before the visual target. However, none of the subjects showed any contingency effects on express saccade behaviour, neither in terms of the percentage of occurrence nor in the saccade amplitudes. This result confirmed our observation in Experiment 1 (see Chapter 2) that the occurrence of express saccades was related to a general facilitation effect.

However, the analysis of anticipatory saccades in $SOA = -210$ ms indicated that the two subjects having exhibited the most express saccades showed a tendency to anticipate the respective frequencies of stimulus events in the different contingency conditions. Furthermore, the very same subjects also exhibited contingency effects in the regular saccades. These results hint at a trade-off between saccade programming and contingency processing: In anticipatory saccades subjects tried to anticipate the location of the visual target on the basis of the location of the auditory stimulus: They released the saccades too early, sometimes even before the presentation of the visual target. However, they showed

contingency effects in the relative frequencies of gaze directions. In the express saccades, on the other hand, subjects did not show any effects of interstimulus contingency. In fact, they might sometimes have released the saccade too early in an effort to use the contingency information on the basis of the location of the auditory stimulus, so that in the end they made about as many errors as in the anticipatory saccades. Only if the subjects waited long enough to correctly localise and identify both stimuli, they made no errors and exhibited contingency effects in the mean latencies of the regular saccades.

Contrary to our hypothesis, two subjects exhibited significant interaction effects of catch recency and contingency even with visual catch trials. This result, in combination with the findings in Experiment 2, showed that the interaction effects of catch recency and contingency do not depend on catch modality but, rather, on the specific processing of the catch trials per se. Note that the two subjects exhibiting interaction effects in the present experiments also showed significant contingency effects in the mean regular saccades. Thus, there may not exist a direct relation between the occurrence of contingency effects and interaction effects of catch recency and contingency, as hypothesised in the introduction to this experiment. For the moment, we conclude that some subjects are specifically sensitive to catch trial effects in contingencies.

3.4 Experiment 4: Contingency pre-information

The purpose of Experiment 4 was to further investigate our consistent finding that subjects responded faster in 20% and 80% ISC than in 50% ISC. Why did subjects react faster even in the rare cases of 20% ISC? Subjects had always been informed about the contingency condition that was going to be investigated in the next block of trials. On the basis of this information, it is possible that they held the hypothesis that the 20% and 80% ISC conditions were somehow more important than the 50% ISC condition, and that therefore, they were more motivated to exhibit their very best performance in the correlated contingency conditions. In order to control for this possible response strategy, we decided to falsely inform subjects about the contingencies. When presenting 20% ISC they were told that it was 50% ISC, and vice versa. The 80% ISC was excluded as it is too easily identified (Kareev, 1995).

The rationale was that subjects should show shorter saccadic reaction times in the true 50% ISC than in the true 20% ISC, if they were more motivated to respond faster in the alleged correlated condition (true 50% ISC). If, however, subjects showed the same pattern of reaction times as before, we would conclude that they were insensitive to the pre-information they were given, and that their former performance did not depend on motivation but on the processing of the respective contingency conditions.

In order to directly compare results, we asked subjects MW, SH, and TS to take part in the experiment. Each subject was presented with the one SOA in which she had shown the strongest contingency effect in Experiment 3.

3.4.1 Method

3.4.1.1 Participants

Three students (mean age 22) of the University of Oldenburg took part in the experiment. They also had participated in Experiment 2 and/or 3. All but one subject (TS) had right eye dominance. They had normal hearing and normal or corrected-to-normal vision. They were paid for participation. All subjects gave their informed consent prior to their inclusion in the study. They were not informed about the specific hypothesis under study. After data collection, we apologised to the subjects and explained the purpose of the deception.

3.4.1.2 Task and procedure

Experiment 4 was in all aspects identical to Experiment 3, except for the following: Subjects MW and TS were only presented with the SOA = -40 ms (the auditory stimulus being presented before the visual target), and subject SH was only presented with the SOA = $+40$ ms (the auditory stimulus being presented after the visual target). Second, all subjects were only presented with 20% and 50% ISC blocks. They were falsely informed about which contingency condition was going to be investigated in the next block of trials.

3.4.2 Results

Trials in the true 20% ISC condition were recoded according to their effective validity. That is, those bimodal trials in which the stimuli were presented in 80% of the trials at the opposite location were defined as 80% valid, and the remaining 20% of the trials were defined as 20% valid (see right panel of Figure 2.1).

3.4.2.1 Saccadic reaction times

As the subjects were submitted to different SOAs, saccadic latencies were analysed separately for each subject. ANOVAs with ISC validity (20%, 50%, and 80%) and spatial congruence (coincident *vs.* disparate) as unreplicated factors revealed significant main effects of ISC validity in each subject. The main effect of spatial congruence reached significance in subject MW with SRTs to coincident trials being 22 ms shorter on average than SRTs to disparate trials. Figure 3.6 illustrates the contingency effects for all subjects: Latencies in 50% ISC were longer than in 20% ISC or in 80% ISC.

A comparison of Figures 3.6 and 3.4 illustrated that subjects SH and MW showed very similar results whether they were correctly or falsely informed about the contingencies. Subject TS showed a slightly different pattern of saccade latencies: While in Experiment 3 she showed a contingency effect in the coincident trials, in the present experiment she showed a similar effect only in the disparate trials.

3.4.2.2 Saccade amplitudes

Only saccade amplitudes of the bimodal trials were analysed, as subjects exhibited less than 10 catch responses in the three test blocks measured. Separate t-tests for each subject,

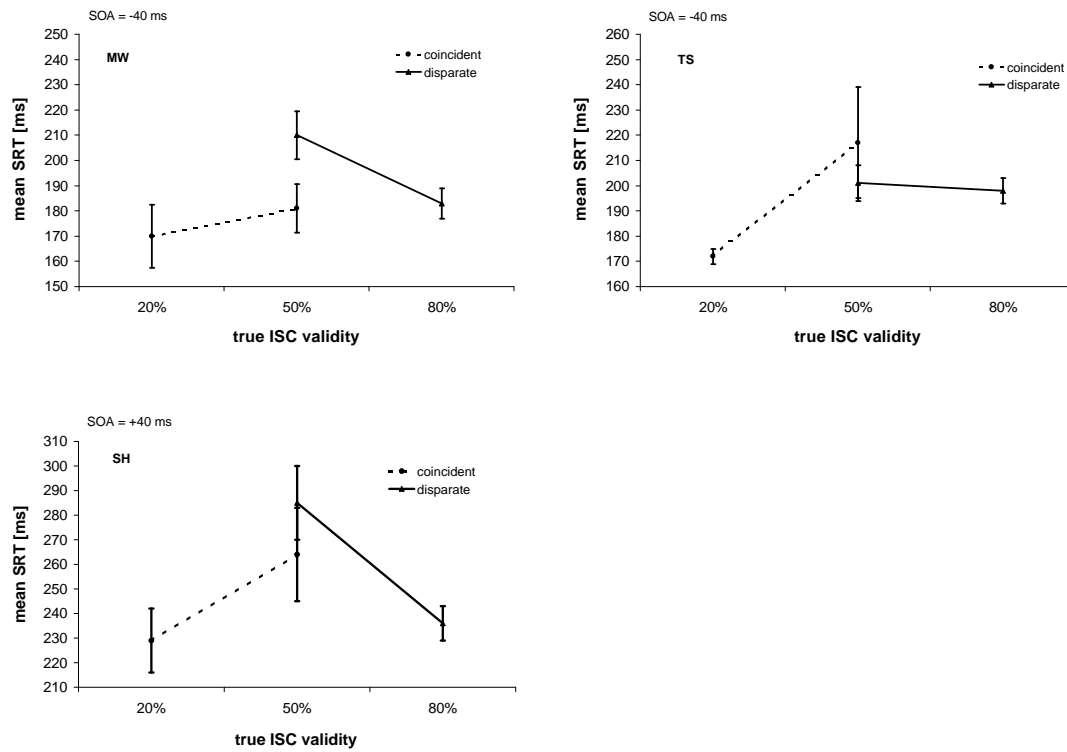


Figure 3.6: Saccadic reaction times (SRT) according to true validity of interstimulus contingency (ISC) separated by spatial congruence (coincident vs. disparate). Subject SH was presented with the stimulus onset asynchrony (SOA) = +40 ms (the auditory stimulus being presented after the visual target). Subjects MW and TS were presented with SOA = -40 ms (the auditory stimulus being presented before the visual target). Only 20% and 50% ISC were investigated.

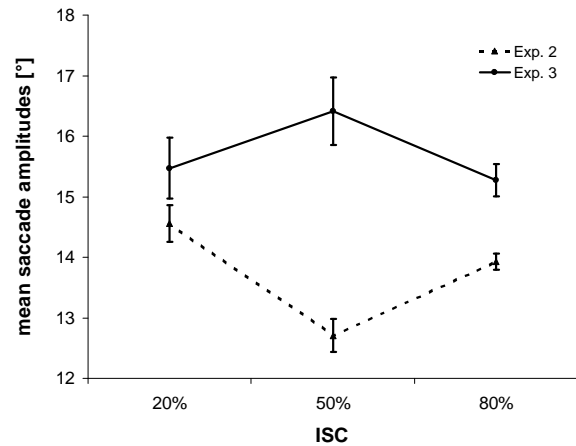


Figure 3.7: *Mean saccade amplitudes to the right according to interstimulus contingency (ISC) in Experiments 3 and 4 for subject SH. Only data in SOA = +40 ms is compared. Both experiments contained visual catch trials. In Experiment 3 the subject was correctly informed about ISC, whereas in Experiment 4 she was told 20% ISC when actually 50% ISC was presented, and vice versa. The data in 20% ISC only contain coincident trials, and the data in 80% ISC only contain disparate trials. The data in 50% ISC represent the mean of the coincident and disparate trials.*

direction of gaze (rightward vs. leftward), and comparison of ISC validities only reached significance in subject SH in the rightward saccades¹: She exhibited significantly shorter amplitudes in 20% and 80% ISC than in 50% ISC (mean difference 0.9° and 1.1°, see Figure 3.7).

In a second step, the saccade amplitudes obtained in the Experiments 3 and 4 in the same subject were compared. t-tests on the overall amplitudes in the two experiments, separated by gaze direction (rightward vs. leftward), revealed that all subjects exhibited shorter mean amplitudes in Experiment 3 than in Experiment 4. For subject SH a two-way ANOVA with experiment and ISC validity as unreplicated factors was conducted, indicating a significant interaction effect of experiment and ISC validity in the rightward saccades. As Figure 3.7 shows, amplitudes in Experiment 3 in 20% and 80% ISC were longer than in 50% ISC, while in the present experiment they were shorter.

3.4.2.3 Recency effects

Catch trial recency effects were analysed separately for each subject with catch recency (bimodal vs. catch) and ISC validity as unreplicated factors. Only subject SH showed a significant main effect of catch recency indicating longer SRTs in trials following a catch trial than in trials following a bimodal trial (mean difference 47 ms). The main effect of ISC validity was significant in subjects SH and TS. The interaction effect of catch recency * ISC validity did not reach significance in either subject.

¹Note that subject MW did not show any contingency effects on saccade amplitudes in Experiment 3 either.

3.4.2.4 Summary

All three subjects showed the same pattern of reaction times in the different contingency conditions as in Experiment 3: SRTs in 20% or 80% ISC were shorter than in 50% ISC. A comparison of saccade amplitudes in Experiments 3 and 4 revealed that all subjects exhibited shorter overall amplitudes in Experiment 4. One subject showed a significant interaction effect of experiment and ISC validity: She exhibited shorter amplitudes in 20% and 80% ISC than in 50% ISC in the present experiment, while in Experiment 3 she showed the opposite pattern of ISC validities on saccade amplitudes. The same subject also showed a significant effect of catch recency indicating shorter reaction times in trials following a bimodal trial than in trials following a catch trial.

3.4.3 Discussion

The results of Experiment 4 replicated our general finding that subjects responded faster in 20% and 80% ISC than in 50% ISC. This is the more interesting as here subjects were misled about the correct contingency conditions employed. When we apologised to the subjects at the end of the session, it became clear that they had not been aware of the contingency mix-up. We concluded that the reduction of reaction times to positively or negatively correlated contingencies did neither result from the subjects' motivation nor conscious strategy of using this kind of task information. The subjects must have implicitly learned the contingency relation between the auditory and the visual stimulus.

Note that this conclusion is in good accord with Carlson and Flowers (1996), Flowers and Smith (1998), Lambert, Naikar, McLachlan, & Aitken (1999), and Lambert *et al.* (2000) who, in different tasks, revealed the implicit nature of learning about interstimulus contingencies. However, in our task the subjects were explicitly (falsely) informed about the contingency condition to be investigated in the next block of trials. Our finding of similar contingency effects on saccade latencies as in Experiment 3 thus strengthened the conclusion that the processing of interstimulus contingencies implies implicit learning.

The analysis of saccade amplitudes shed some additional light on whether subjects processed the contingencies the same way as when informed correctly. In particular, the comparison of amplitude effects in Experiments 3 and 4 showed a specific pattern of contingency effects in subject SH in the rightward saccades: When correctly informed, she exhibited longer saccade amplitudes in the correlated contingencies than in the uncorrelated condition, but, when falsely informed, this pattern of contingency effects was reversed. It is possible that SH showed longer amplitudes in 50% ISC in Experiment 4, because she believed that it was 20% ISC. This would mean that the subject had built specific kinematic response patterns for each contingency condition. Also, the assumption would predict that the subject would show shorter amplitudes in 20% and 80% ISC in Experiment 4, because she believed that she responded to 50% ISC. As the results have shown, this was actually the case. We thus concluded that our contingency mix-up had a specific effect on the subject's kinematic response behaviour. However, we still believe that the subjects were not aware of our exchange of contingency conditions. Note that the above assumption does not explain how exactly the subjects built the kinematic response

behaviour in each contingency condition. Further research will be necessary to elucidate this point.

In summary, all subjects showed the same pattern of response times whether correctly or falsely informed about the contingencies. Therefore, we concluded that the subjects had implicitly learned to use the correlational patterns involved. However, one subject showed a change in saccade amplitudes between experiments indicating a specific reaction to our misleading information on the contingency conditions.

3.5 Experiment 5: Catch trial frequency

Experiment 5 investigated another concern about the experimental set-up. It is possible that the contingency effects depend on the total number of catch trials included in each block of trials. So far, all the 50% ISC blocks contained more catch trials than the 20% and 80% ISC blocks. As mentioned above, reaction times are the longer the more catch trials are being used (Alegria, 1978; Jüttner & Wolf, 1992). Thus, one might argue that the longer reaction times found in 50% ISC did not constitute a specific contingency effect but were simply due to more catch trials presented in these blocks of trials. Therefore, in the final experiment the total number of catch trials was held constant across contingency conditions.

3.5.1 Method

3.5.1.1 Participants

Three students (mean age 22) of the University of Oldenburg took part in the experiment. They also had participated in Experiments 3 and 4. All but one subject (TS) had right eye dominance. All subjects had normal hearing and normal or corrected-to-normal vision. They were paid for participation. All subjects gave their informed consent prior to their inclusion in the study. They were not informed about the specific hypothesis under study.

3.5.1.2 Task and procedure

Experiment 5 was identical to Experiment 3 in all aspects, except for the following: First, all blocks of trials either contained 29% or 50% catch trials. The order of the catch trial conditions was varied among subjects: Subjects SH and TS were first presented with 29% catch trials, and subject MW started with 50% catch trials. Second, in the 29% catch trial condition all subjects were presented with SOAs = -40 ms, 0 ms, and $+40$ ms. For reasons of economy, in the 50% catch trial condition subjects were only presented with two SOAs: Subjects MW and TS were presented with SOAs = -40 ms and 0 ms (the auditory stimulus being presented before or simultaneously with the visual target), and subject SH was presented with SOAs = 0 ms and $+40$ ms (the auditory stimulus being presented simultaneously or after the visual target). Third, all subjects were only presented with 50% and 80% ISC blocks.

Table 3.4: *Relative frequency of catch responses for each subject according to effective contingency validity.*

| Subject | Contingency validity | | |
|---------|----------------------|--------------|--------------|
| | 50% | 80% | TOTAL |
| MW | 7/23 = 0.31 | 10/47 = 0.21 | 17/70 = 0.24 |
| SH | 3/23 = 0.13 | 8/47 = 0.17 | 11/70 = 0.16 |
| TS | — | 2/34 = 0.06 | 2/48 = 0.04 |

3.5.2 Results

Trials in 80% ISC were recoded according to their effective validity. That is, those bimodal trials, in which the stimuli were presented in 80% of the trials at the same location were defined as 80% valid, and the remaining 20% of the trials were defined as 20% valid (see right panel of Figure 2.1). In the following, only those trials in which the saccade amplitudes started at less than 1° off the fixation point were considered for the analysis of saccade latencies and amplitudes. In a first step, data in the 29% and 50% catch frequency conditions were analysed separately in order to evaluate the contingency effects within each catch trial condition.

3.5.2.1 29% catch trials

The SRTs of all subjects were submitted to a three-way ANOVA with SOA, spatial congruence (coincident *vs.* disparate), and contingency validity (20%, 50%, and 80%) as unreplicated factors. One main effect, but no significant interaction effects emerged. The main effect of SOA ($F_{2,238} = 16.47, p < 0.001$) indicated longer latencies the later the auditory stimulus was presented.

Catch responses As Table 3.4 shows the relative frequency of catch responses varied considerably among subjects. Chi-square tests comparing the relative frequency of catch responses in the two ISC conditions between trials, in which the subjects correctly withheld response with those in which they falsely responded to a catch trial, did not reach significance in any subject.

Saccade amplitudes For each subject the saccade amplitudes in the bimodal trials were analysed with separate t-tests for each saccade direction and all combinations of ISC validity. Subjects MW and TS showed longer saccade amplitudes in 80% ISC than in 50% ISC in the leftward saccades. The same effect was obtained for subject SH in the rightward saccades, while she showed shorter amplitudes in 20% and 80% ISC than in 50% ISC in the leftward saccades. For subject SH this pattern of contingency effects on saccade amplitudes corresponded to the effects observed in Experiment 3. Subject MW did not show any amplitude effects in Experiment 3, and subject TS exhibited similar effects as found in the present experiment, but only in the rightward saccades.

Table 3.5: *Relative frequency of catch responses for each subject according to effective contingency validity.*

| Subject | Contingency validity | | |
|---------|----------------------|---------------|---------------|
| | 50% | 80% | TOTAL |
| MW | 16/113 = 0.14 | 23/149 = 0.15 | 39/262 = 0.15 |
| SH | 17/120 = 0.14 | 21/116 = 0.18 | 38/236 = 0.16 |
| TS | 5/67 = 0.07 | 21/177 = 0.12 | 26/244 = 0.11 |

Recency effects The SRTs of each subject were separated into those trials following a bimodal trial, and the trials following a catch trial. A two-way ANOVA with catch recency (bimodal *vs.* catch), and ISC validity as unrepated factors revealed one significant main effect. No interaction effect reached significance. The main effect of catch recency indicated that subjects responded 14 ms faster on average in trials following a bimodal trial than in trials following a catch trial.

3.5.2.2 50% catch trials

The SRTs of all subjects were analysed separately for each SOA with three-way ANOVAs including catch recency (bimodal *vs.* catch) and ISC validity (20%, 50%, and 80%) as un-repeated factors. Note that the analysis of SRTs in each SOA included different numbers of subjects (SOA = -40 ms: two subjects; SOA = 0 ms: three subjects; SOA = +40 ms: one subject). The main effect of catch recency was significant in SOAs = -40 ms and 0 ms indicating shorter SRTs in trials following a bimodal trial than in trials following a catch trial (SOA = -40 ms: 22 ms; SOA = 0 ms: 29 ms). The main effect of ISC validity did not reach significance in either SOA, nor did the interaction effect of catch recency * ISC validity.

Catch responses As can be seen in Table 3.5, all subjects showed about the same total number of catch responses. Separate chi-square tests for each subject, comparing the relative frequency of catch responses in the two ISC conditions between trials in which the subjects correctly withheld response with those in which they falsely responded to a catch trial, did not reach significance in any subject.

Saccade amplitudes For each subject saccade amplitudes in the bimodal trials were analysed with separate t-tests for each direction of gaze and all combinations of ISC validity. None of these tests reached significance.

3.5.2.3 Comparison of 29% and 50% catch frequency conditions

The latencies were analysed separately for each subject. Only responses to identical SOAs in both catch trial conditions were considered. The raw SRTs of each subject were submitted to three-way ANOVAs, with number of catch trials (29% *vs.* 50%), SOA, and ISC validity (50% *vs.* 80%) as unrepated factors. In all subjects only the main effect of

Table 3.6: Comparison of reaction time differences between 50% ISC in 50% catch trials and 80% ISC in 29% catch trials in Experiment 3 and 5.

| Subject | 50% ISC _{50%catch} – 80% ISC _{29%catch} | |
|---------|---|--------------|
| | Experiment 3 | Experiment 5 |
| MW | 11 ms | 5 ms |
| SH | 25 ms | 9 ms |
| TS | 30 ms | 3 ms |

SOA reached significance, indicating longer latencies the later the auditory stimulus was presented.

One-way ANOVAs conducted on the saccade amplitudes with frequency of catch trials (29% vs. 50%) as unreplicated factor revealed significant differences for all subjects: Subjects MW and SH exhibited significantly shorter saccade amplitudes with 50% catch trials than with 29% catch trials in the rightward saccades (mean difference = 0.8°). In the leftward saccades subjects MW and TS also exhibited significantly shorter saccade amplitudes with 50% catch trials than with 29% catch trials (mean difference = 0.9°), while subject SH showed the opposite pattern (50% catch > 29% catch, 0.4°).

Finally, we calculated the differences of mean SRTs between 50% ISC in 50% catch trials and 80% ISC in 29% catch trials (see Table 3.6), because these combinations of ISC validity and catch frequency condition had actually been used in Experiment 3. If the calculated differences were smaller than those in Experiment 3, the contingency effects of Experiment 3 could not be explained solely on the basis of different frequencies of catch trials occurring in the correlated and uncorrelated contingency blocks. If, on the other hand, the calculated differences were at least as large as in Experiment 3, the contingency effects observed in Experiment 3 may in fact constitute an effect of the different frequencies of catch trials rather than a specific effect of contingency processing.

Table 3.6 compares the SRT differences predicted on the basis of the present experiment with those observed with identical SOAs and with the very same subjects in Experiment 3. This comparison clearly showed that the SRT differences observed in Experiment 3 were much larger than those in the present data. Separate ANOVAs for each subject with ISC validity (50% vs. 80%) as unreplicated factor confirmed that the latency differences between 80% ISC in 29% catch trials and the 50% ISC in 50% catch trials in the present study did not reach significance in any subject.

Similar ANOVAs, conducted on the saccade amplitudes for each subject separately, revealed significant effects of ISC validity in all subjects. In leftward saccades subjects MW and TS exhibited longer saccade amplitudes to 80% ISC in 29% catch trials than to 50% ISC in 50% catch trials, while subject SH showed the opposite pattern. The latter subject also showed a significant effect in the rightward saccades indicating longer saccade amplitudes to 80% ISC in 29% catch trials than to 50% ISC in 50% catch trials. Figure 3.8 illustrates the contingency effects in saccade amplitudes in Experiment 3 and 5 (29% catch trials), including the comparison of 80% ISC in 29% catch trials and 50% ISC in 50% catch trials obtained in Experiment 5 (comparison). The effects of the number of catch trials on saccade amplitudes differed among subjects: While the comparison

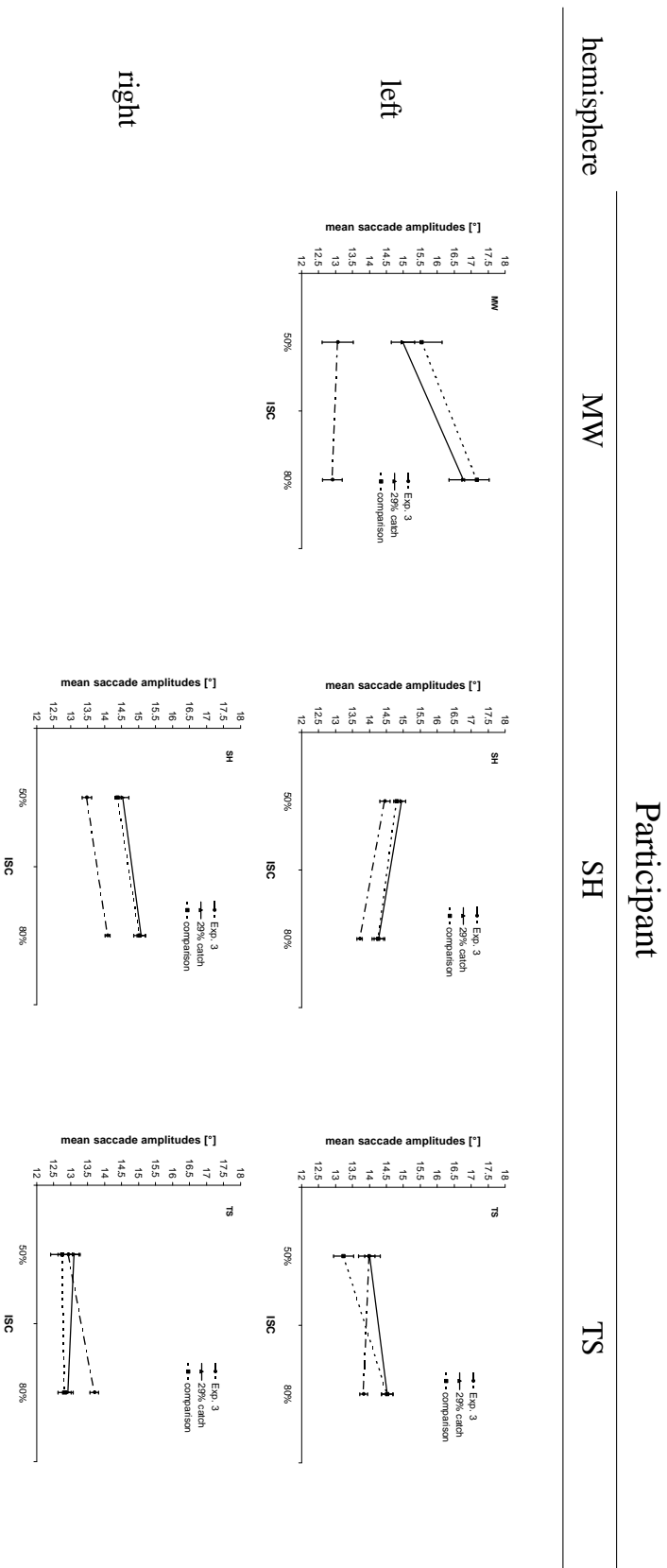


Figure 3.8: Mean saccade amplitudes to the left and/or right for three subjects having participated in Experiments 3 and 5. Each panel contains the amplitudes obtained in Experiment 3 with 50% ISC in 50% visual catch trials and 80% ISC in 29% visual catch trials (Exp. 3), the amplitudes obtained in the identical contingency and catch trial conditions in two separate parts of Experiment 5 (comparison), and the amplitudes obtained in the first part of Experiment 5 with 29% visual catch trials (29% catch).

of contingency conditions and frequency of catch trials in Experiment 5 (see comparison and Exp. 3) predicted rather well the pattern of saccade amplitudes obtained in Experiment 3 in both directions of gaze in subject SH, the same comparison did not hold for subject MW, as she did not exhibit any amplitude effects in Experiment 3. The pattern of amplitude effects appeared even more complicated in subject TS in that the comparison of contingency conditions and frequency of catch trials in Experiment 5 (see comparison and Exp. 3) would predict a significant contingency effect on saccade amplitudes in the leftward saccades of Experiment 3. Actually, it was obtained only in the rightward saccades.

3.5.2.4 Summary

Separate analyses of contingency effects on saccadic reaction times either with 29% catch trials or with 50% catch trials did not reach significance. However, the analysis of saccade amplitudes revealed significant contingency effects in 29% catch trials in all subjects. These contingency effects were comparable to those obtained in Experiment 3 for two subjects. The analysis of catch recency effects reached significance either with 29% catch trials or with 50% catch trials, indicating overall shorter reaction times in trials following a bimodal trial than in trials following a catch trial. While with 29% catch trials the number of catch responses varied considerably among subjects, the subjects exhibited about the same number of catch responses with 50% catch trials.

The comparison of catch frequency conditions revealed significant differences in saccade amplitudes, but not in saccadic reaction times. All subjects exhibited shorter overall amplitudes with 50% catch trials than with 29% catch trials in at least one direction of gaze.

Finally, mean SRTs and amplitudes in 50% ISC and 50% catch trials were compared to those obtained in 80% ISC and 29% catch trials. The difference in saccadic reaction times did not reach significance and was much smaller than the effects obtained in Experiment 3. The comparison of saccade amplitudes did reach significance in all subjects, but for two subjects these differences did not correspond to the effects obtained in Experiment 3.

3.5.3 Discussion

Experiment 5 investigated the influence of two different frequencies of catch trials (29% or 50%) on contingency effects. Catch trial frequency had no significant effect on saccadic reaction time nor on the size of the contingency effects. This finding clearly suggested that the frequency of catch trials used in the present study did not affect the processing of interstimulus contingencies on the level of saccadic latencies.

However, saccade amplitudes were different for the two catch frequency conditions. When the frequency of catch trials was low (29%), each subject showed a specific pattern of saccade amplitudes between the correlated and uncorrelated contingency conditions. Moreover, the relative frequencies of catch responses varied considerably among subjects. On the other hand, when the percentage of catch trials was high (50%), no specific contingency effects on saccade amplitudes were found, nor did the relative frequency of catch responses vary among subjects. This indicated that subjects actually exhibited con-

tingency effects in the low catch trial condition, but these effects did not show up in the reaction times. The finding that all three subjects exhibited contingency effects on saccade amplitudes with 29% catch trials is even more interesting considering the fact that one of the subjects had not shown any such effect in Experiment 3.

The observation that the analysis of saccadic reaction times and amplitudes did not reach significance in the 50% catch trial condition shed some further light on the conditions under which contingency effects may be observed. In fact, it is possible that the number of catch trials interspersed in a block of trials played a crucial role in the processing of contingencies. If the non-target stimulus was sufficiently correlated with the occurrence of the target (29% catch trials) contingency effects occurred. However, if the probability for a go response was at chance, no contingency effects were observed. That is, contingency effects may only occur if subjects are biased to respond in most trials of a test block. This would also imply that the processing of interstimulus contingencies is crucially related to response preparation. Future research will show whether this hypothesis holds up over different experimental paradigms.

The comparison of the differences in reaction times between those combinations of catch trial percentage and contingency validity which had also been used in Experiment 3 confirmed that the differences in reaction times in Experiment 3 were much larger than those determined in the last experiment. Thus, it is safe to conclude that the differences observed in the present study reflect a specific consequence of the processing of interstimulus contingencies.

One might argue that subjects showed larger reaction time differences in Experiment 3, because they were presented with different frequencies of catch trials within each session. This change in catch trial frequency between test blocks might have accentuated the effects of catch trial processing. However, note that the subjects at no time realised that the frequency of catch trials changed between blocks, nor did they show any visible learning effects within each catch frequency condition in Experiments 3 and 5.

The number of catch trials had a significant influence on the programming of saccade amplitudes. With one exception, the overall mean amplitudes in 50% catch trials were significantly shorter than in 29% catch trials. It may be that subjects were less ready to respond with 50% catch trials, as in each trial there was an equal chance to be asked to respond or to withhold the saccade. The latter assumption presumes that the degree of response preparation determines the extent to which the saccade amplitude will be correct. More research is necessary to investigate this issue.

Finally, the comparison of saccade amplitudes revealed large interindividual differences. While for one subject the contingency effects on saccade amplitudes observed in Experiment 3 could be predicted rather well by differences in the frequency of catch trials, this did not hold for the other two subjects. It is also possible that the latter two subjects changed their general response strategy between experiments, since they were carried out 6 months apart. This would explain why in one subject the comparison of amplitudes in Experiment 5 predicted a significant contingency effect in the leftward saccades, while she exhibited a similar effect only in the rightward saccades.

3.6 Discussion

The results of the bimodal go/no-go experiments provided evidence for the existence of interstimulus contingency effects in saccadic reaction times and amplitudes with simple visual and auditory stimuli. In a focused attention task, subjects made faster saccades when the visual target was either positively or negatively correlated with the location of the auditory accompanying stimulus than without correlation. This is the first demonstration that interstimulus contingencies in spatial locations, rather than in the mere presence or absence of the stimuli, led to facilitation of saccadic responses. The result supported findings by Schwarz (1996) who obtained faster manual reaction times to negatively correlated target and non-target letters in a divided attention go/no-go task.

The analysis of saccadic reaction times further showed that the effects of interstimulus contingency are largely independent of spatial congruence. However, there was an interaction effect of contingency with SOA. Contingency effects mainly occurred for long mean latencies, *i.e.*, at large negative or small positive SOAs. This finding implied that the processing of interstimulus contingencies needed some minimum time before they could be used for improving performance.

On the other hand, the analyses of anticipatory and express saccades in Experiment 3 showed that the processing of interstimulus contingencies interacted with saccade latency. In fact, the comparison of contingency effects in the different types of saccades revealed a trade-off in latencies and direction errors. If subjects responded too fast and exhibited anticipatory saccades, contingency effects occurred in the relative frequencies of gaze direction. In the intermediate condition, when the subjects exhibited express saccades, no contingency effects emerged. However, subjects made many more errors than is generally reported in experiments on express saccades (*e.g.* Cavegn, 1996). However, if the subjects waited long enough to correctly localise the visual target, they made almost no errors and showed contingency effects in the mean latencies of regular saccades. In sum, the results indicated a general effect of interstimulus contingencies on saccade programming which became evident either in the number of direction errors in anticipatory saccades, or in the latency differences in the respective contingency conditions with slow-regular saccades.

A second interesting finding of the present study was the observation that the processing of interstimulus contingencies not only affected response times but also saccade amplitudes. In the correlated contingency condition, subjects either exhibited shorter or longer amplitudes than without correlation. The results in Experiment 5 further indicated that contingency effects in saccade amplitudes only occur if subjects are biased to prepare a response, that is, in those conditions in which only a few catch trials were presented. Furthermore, one subject in Experiment 4 exhibited different amplitude effects when falsely informed about the contingency to be investigated in the next block of trials than when correctly informed. The same subject displayed similar contingency effects in reaction times under both conditions. Thus, the pre-information about contingencies had differential effects on reaction times and amplitudes. The hypothesis of a separate timing of a saccade and calculation of its amplitude is in good accord with models for the oculomotor system (see Findlay & Walker, 1999, for a review).

Finally, the analysis of catch recency effects confirmed the result by Jüttner and Wolf (1992) that subjects exhibit shorter saccadic reaction times in trials following a target trial

than in trials following a catch trial. This was true whether the catch stimulus was auditory or visual, and the result was independent of the frequency of catch trials. However, the results of Experiment 5 were in contrast to Jüttner and Wolf (1992) in that the overall saccadic reaction times did not depend on the frequency of catch trials interspersed in each block of trials. It is possible that the overall saccadic reaction times in the 25% and 50% catch frequency conditions of Jüttner and Wolf (1992) did not differ either. Unfortunately, they did not report any descriptive statistics on this issue.

4

Visual antisaccades

The results in the bimodal go/no-go task confirmed that the processing of interstimulus contingencies needed some minimum time before they could be used for improving performance. However, we still wondered why the subjects would exhibit shorter saccade latencies both in the positively correlated contingency and in the negatively correlated contingency.

In view of our second main finding in the bimodal go/no-go task that the saccade latencies and amplitudes were differentially affected by the interstimulus contingencies, we asked three new subjects to make a saccade in the direction opposite to the visual target. This so-called antisaccade task seemed especially well-suited to further investigate the processing of interstimulus contingencies, because it generally induces longer saccade latencies than the prosaccade task, and the subjects have to pay special attention to the calculation of the saccade amplitude and direction in order to fulfil the task demands.

In this chapter we will first describe some behavioural characteristics and neurobiological processing accounts of visual antisaccades which will be relevant for the present purposes before we will then introduce the logic of Experiment 6.

4.1 Behavioural characteristics of visual antisaccades

The antisaccade task requires a subject to generate a saccade of equal eccentricity and opposite direction to a peripheral visual stimulus. In his very first study, Hallett (1978) reported that human subjects were able to successfully look to the side opposite to the visual stimulus. However, they made quite a number of errors in the direction of the visual stimulus (prosaccade errors) before they corrected themselves by looking in the opposite direction. The mean saccade latencies of the antisaccades were longer as compared to prosaccades, their amplitudes were quite variable both between subjects and within subjects, and the peak velocities were lower than in prosaccades. Later studies confirmed the

above findings even in an animal model of antisaccade performance (Amador, Schlag-Rey & Schlag, 1998; Everling, Dorris & Munoz, 1998).

4.1.1 Visual procues

Fischer & Weber (1996) were concerned about the shortest possible latencies in an antisaccade task. When they introduced a visual cue which indicated with certainty the direction of the antisaccade (procue), the number of prosaccade errors increased, but, surprisingly, the antisaccade latencies also increased considerably. However, in a later study, Weber, Dürre & Fischer (1998) showed that the antisaccade latencies were increased only if the visual cue was presented in a gap task (the fixation point being extinguished prior to target presentation) with a cue lead time of 100 ms. If the procue was presented with larger cue lead times, the antisaccade latencies were shorter than in a control condition in which no visual cue was presented.

If the visual procue was presented always at the same side of the display and the target occurred in 50% of the trials at that location, the number of prosaccade errors was still increased, but the latencies of the antisaccades varied. Compared to a control condition in which no visual procue was presented, the antisaccade latencies were decreased if the procue and target were presented at the same location (spatial contiguity), but the latencies were about equal to the control condition if the procue and target were presented at opposite locations (Fischer & Weber, 1996; Weber *et al.*, 1998). It might thus be concluded that the principle of contiguity (Hume, 1739) also holds for the antisaccade task (see Section 1.1).

4.1.2 Prosaccade errors

When the prosaccade errors in the antisaccade task with a visual procue were analysed, it occurred that the number of errors varied considerably between subjects. Almost all of them were corrected, *i.e.* they were followed by a second saccade toward the required location (Weber *et al.*, 1998; Mokler & Fischer, 1999). An analysis of the saccade amplitudes showed that on average the second saccade corrected the error of the first saccade irrespective of the amplitude of the prosaccade error (Mokler & Fischer, 1999).

The time between the end of the first saccade and the beginning of the second saccade, the so-called correction time, could be very short with values between zero and 70 ms both in the gap and overlap tasks (Weber *et al.*, 1998).

Finally, Mokler and Fischer (1999) and Mokler, Deubel and Fischer (2000) showed that in about 60% of the prosaccade errors subjects were not aware of committing these errors. Furthermore, when the subjects were asked to discriminate a target letter in a dual-task antisaccade paradigm, discrimination performance for correct antisaccades was high at the saccade goal (opposite to the visual stimulus), but low at the opposite side (stimulus position). However, for unperceived prosaccade errors, discrimination performance was by far better at the intended saccade goal than at the actual stimulus position. Mokler *et al.* (2000) thus concluded that the unperceived prosaccade errors were not preceded by a shift of visual attention which generally leads to enhanced discrimination performance. Rather, visual attention was allocated to the planning of the voluntary movement opposite

to the visual target. The latter conclusion is in striking opposition to the general view that a saccade is always preceded by a shift of visual attention to the saccade goal (Rizzolatti, Riggio & Sheliga, 1994; Deubel & Schneider, 1996). The observations by Mokler and Fischer (2000) might indicate that at least the unperceived prosaccade errors are under strong transient, pre-attentional, automatic, and involuntary bottom-up control.

4.2 Neurobiological processing accounts of visual antisaccades

It is generally agreed that the programming of an antisaccade requires at least two intact processes: (1) the ability to suppress a reflexive saccade toward the visual stimulus, and (2) the ability to generate a voluntary saccade in the opposite direction, *i.e.* to a location void of any stimulus (Everling & Fischer, 1998). Amador *et al.* (1998) refined the former statement in suggesting that the successful performance of an antisaccade depends on the conjunction of several abilities: (1) conceptual, understanding the antisaccade instruction, (2) inhibitory, repressing reflexive orienting, (3) computational, calculating an inverted retinal error vector, (4) motor, self-initiating a saccade to an unmarked location.

Guitton, Buchtel & Douglas (1985) have shown that the frontal cortex imposes a high level control on reflexive saccades. Patients with unilateral lesions in the frontal lobes could rarely inhibit a reflexive saccade toward the visual target and rarely corrected their prosaccade errors by a second saccade. Guitton *et al.* thus suggested that the frontal eye fields (FEFs) and/or the supplementary eye fields (SEFs) were the critical structures for correct performance in the antisaccade task.

Note, however, that the findings by Guitton *et al.* (1985) were not confirmed by later lesion studies which pointed to the dorsolateral prefrontal cortex and anterior cingulate cortex as critical structures for the inhibition of reflexive saccades (Pierrot-Deseilligny, Rivaud, Gaymard & Agid, 1991; Gaymard, Rivaud, Cassarini, *et al.*, 1998; Gaymard, Ploner, Rivaud-Péchaux *et al.*, 1999, but see also Walker, Husain, Hodgson, & Kennard, 1998). Lesions in the parietal and temporal lobe have been reported not to affect the performance in the antisaccade task. However, positron emission tomographic studies and single-cell recordings indicated that the FEFs, SEFs, posterior parietal cortex, and temporal cortex alter their activity during the performance of an antisaccade task compared with a prosaccade task (see Everling & Fischer, 1998, for a review, but see also Paus, 1996). This discrepancy on the locus of inhibitory control still remains an unresolved issue.

Evdokimidis, Constantinidis, Liakopoulos & Papageorgiou (1996), in an admittedly oversimplified attempt, tried to differentiate the contributions of frontal and parietal cortex in the control of antisaccade latencies. They showed that antisaccade latencies are prolonged in comparison to prosaccade latencies only if the target location of the antisaccade is unpredictable. Evdokimidis *et al.* (1996) thus pointed to the importance of parietal cortex, and more specifically to the lateral intraparietal area (LIP), in coding the target location and converting this signal into a motor plan (Anderson & Gnadt, 1988). The latter processing account was supported by electrophysiological recordings (EEG) on human subjects investigating an antisaccade task with visual cue (see Section 4.1.1). Everling, Spantekow, Krappmann & Flohr (1998) showed that the execution of a correct

antisaccade was preceded by a shift of a negative potential from the parietal hemisphere contralateral to the visual stimulus toward the parietal hemisphere ipsilateral to the stimulus. These results support the hypothesis that the parietal cortex participates in coding the target location opposite to the visual stimulus before generating a motor signal for the performance of an antisaccade.

4.2.1 Prosaccade errors

Everling, Dorris & Munoz (1998) examined the role of prestimulus build-up neural activity in the SC for the generation of a prosaccade error. They showed that the activity of build-up neurons before the arrival of the visual signal in the SC was higher in prosaccade errors than in correct antisaccades if the visual stimulus was presented into the response field of the neuron. Furthermore, this prestimulus build-up activity predicted well the number of prosaccade errors and correct antisaccades committed by the monkeys. These findings support the hypothesis that a high level of prestimulus build-up activity in the SC at the location of the visual target predicts the generation of prosaccade errors in the antisaccade task (Everling *et al.*, 1998).

4.3 Experiment 6: Visual antisaccades

The experimental procedure of Experiment 6 was identical to Experiment 1, only the subjects were asked to make an antisaccade to the visual stimulus instead of a prosaccade. Contingency information was provided in the location of the auditory accompanying stimulus. As the antisaccade task leads to longer saccade latencies than the prosaccade task (see Section 4.1), we hypothesised that the subjects should exhibit even larger interstimulus contingency effects in their antisaccade latencies than in the former experiments, because they should have more time to use the contingency information provided in the auditory accompanying stimulus.

We further were interested in determining whether we would replicate the observation by Fischer & Weber (1996, see Section 4.1.1) of longer antisaccade latencies with a 100% valid visual precue than in the control condition without precue. In analogy to the intersensory facilitation effect (see Section 1.5) we hypothesised that in our experiment antisaccade latencies should be faster with a 100% valid auditory precue than in the control condition with unimodal visual stimulation. According to our findings in the former experiments we further hypothesised that the antisaccade latencies with a 100% valid precue should be faster than with 80% contingency validity.

In accord to Fischer & Weber (1996) our third hypothesis was that antisaccade latencies should show spatial contiguity effects. Finally, in correspondence to Weber *et al.* (1998) and Mokler and Fischer (1999), we decided to analyse the prosaccade errors with respect to their latency, amplitude, number of corrections, correction times, and amplitudes of corrective saccades. In analogy to Everling *et al.* (1998) we hypothesised that the subjects should commit more errors with shorter latencies in 80% ISC than in 50% ISC, because the prestimulus build-up activity in the SC should be higher with correlated contingencies than without correlation (Dorris & Munoz, 1998).

4.3.1 Method

4.3.1.1 Participants

Four students (age 21-26 years) of the University of Oldenburg took part in the experiment. Subject MW already participated in Experiments 1 to 5. All subjects had right eye dominance. They had normal hearing and normal or corrected-to-normal vision. They were either paid or received partial course credit for participation. All subjects gave their informed consent prior to their inclusion in the study. They were not informed about the specific hypotheses under study.

4.3.1.2 Task and procedure

Experiment 6 was identical to Experiment 1, except for the following: The task was to make an eye movement as quickly and as accurately as possible opposite to the visual target and to use the accompanying auditory stimulus as a possible, but unreliable, cue for the location of the visual target. Feedback was given if the saccades fell in the direction of the visual target (prosaccade error). For experimental parsimony the SOA was varied only on three levels with equal probability: The auditory stimulus appeared either 40 ms before (–), simultaneously, or 40 ms after (+) the visual target. The different ISC conditions were measured in separate sessions in order to allow subjects to (implicitly) learn about the contingencies. All ISC blocks contained 60 bimodal and no unimodal trials. Saccades directed opposite to unimodal visual or auditory stimuli were measured in separate block at the end of the sessions. For investigating the visual procue effect in Fischer & Weber's study (1996), in the last training session before the main experiment the auditory accompanying stimulus was presented with 100% ISC validity either coincident or disparate to the visual target in separate blocks of trials.

4.3.2 Results

Trials in the 20% and 80% ISC blocks were recoded according to their effective validity (see right panel of Figure 2.1). In the following, only those trials in which the saccade amplitudes started at less than 1° off the fixation point were considered for the analysis of the saccade latencies and amplitudes.

4.3.2.1 Saccadic reaction times

The data of subject MW will be considered separately, because she only had time to participate in SOA = 0 ms. All subjects showed less than 0.1% express saccades. The regular SRTs were submitted to a three-way ANOVA with SOA, spatial congruence (coincident vs. disparate), and ISC validity (20%, 50%, or 80%) as repeated factors. Two main effects and one interaction effect emerged. The main effect of SOA ($F_{2,2} = 105.6, p < 0.001$) indicated shorter latencies the earlier the auditory accompanying stimulus was presented before the visual target. The second main effect of spatial congruence ($F_{1,2} = 28.9, p < 0.033$) was due to 16 ms shorter latencies on average to coincident than to disparate stim-

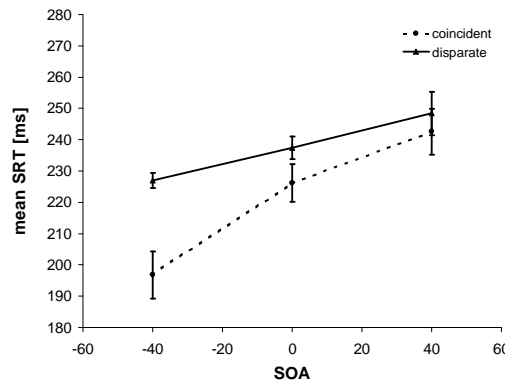


Figure 4.1: *Effects of stimulus onset asynchrony (SOA) and spatial congruence (coincident vs. disparate) on the mean saccadic reaction times (SRT) of the correct antisaccades. The auditory accompanying stimulus was presented 40 ms before (–), simultaneously, or 40 ms after (+) the visual target.*

uli. The interaction effect of SOA * spatial congruence indicated 30 ms shorter SRTs on average in coincident than in disparate trials in SOA = –40 ms (see Figure 4.1).

When the SRTs were analysed with separate ANOVAs for each subject, three main effects and two interaction effects emerged. All subjects showed main effects of SOA¹, spatial congruence, and ISC validity, and an interaction effect of SOA¹ * spatial congruence as it is described above. However, Newman-Keuls post-hoc tests revealed that the main effect of ISC validity differed between subjects (see Figure 4.2): Subject MK exhibited longer SRTs in 20% ISC than in 50% and 80% ISC; subject RS showed shorter SRTs in 80% ISC than in 50% and 20% ISC; in subject TL the post-hoc tests did not reach significance; subject MW exhibited shorter SRTs in 20% and 80% ISC than in 50% ISC. Finally, subjects RS and MW showed an interaction effect of spatial congruence * ISC validity indicating shorter SRTs in 20% ISC than in 50% ISC in the coincident trials, and shorter SRTs in 80% ISC than in 50% and 20% ISC in the disparate trials (see Figure 4.2).

4.3.2.2 Saccade amplitudes

Separate ANOVAs were conducted for each subject and rightward vs. leftward saccades with ISC validity and spatial congruence (coincident vs. disparate) as unrepeated factors. Only those effects are reported which were accompanied by equivalent effects in the peak velocities. All but subject MW showed a significant main effect of ISC validity in at least one direction of gaze. They showed longer saccade amplitudes in 20% and 80% ISC than in 50% ISC in the rightward saccades (mean = 2.6°, SD = 1.05°), and shorter saccade amplitudes in 80% ISC (and 20% ISC, two subjects) than in 50% ISC in the leftward saccades (mean = 2.3°, SD = 1.34°). All subjects showed a significant interaction effect of spatial congruence * ISC validity in at least one direction of gaze.

¹Subject MW only participated in SOA = 0 ms and therefore did not show any effect of SOA.

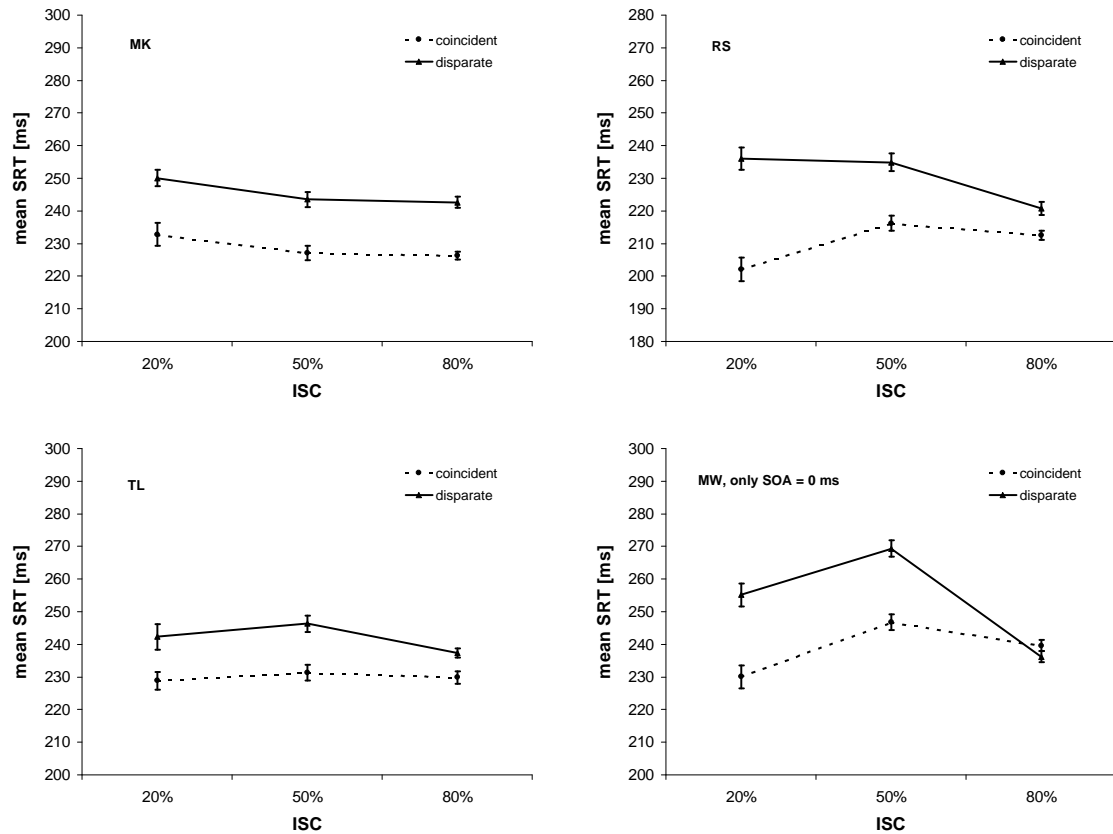


Figure 4.2: *Interstimulus contingency (ISC) effects on the mean antisaccades latencies (SRT). Subject MK exhibited longer SRTs in 20% ISC than in 50% and 80% ISC, subject RS showed shorter SRTs in 80% ISC than in 50% and 20% ISC and subject MW exhibited shorter SRTs in 20% and 80% ISC than in 50% ISC. The interaction effect of ISC validity with spatial congruence reached significance in the subjects RS and MW indicating shorter SRTs in 20% ISC than in 50% ISC in the coincident trials, and shorter SRTs in 80% ISC than in 50% and 20% ISC in the disparate trials.*

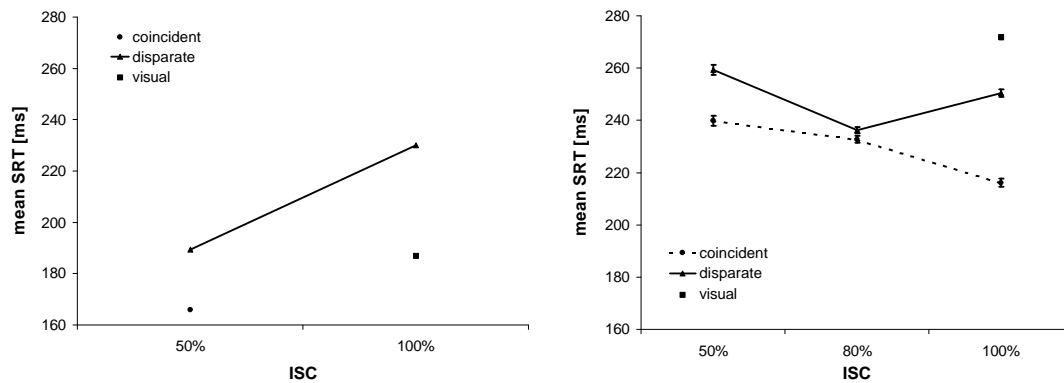


Figure 4.3: *Procue effects on the saccadic reaction times (SRT) of correct antisaccades. The left panel reprints the mean SRTs in the unimodal visual and bimodal trials (coincident vs. disparate) of Fischer and Weber (1996). The right panel illustrates the same types of trials in the present experiment. While in Fischer and Weber (1996) the latencies in the disparate trials were about as long or significantly longer than in the unimodal visual trials, in the present experiment they were shorter. However, in both studies, the latencies in the disparate trials of 100% ISC were longer than in 50% ISC. Fischer and Weber (1996) used a visual procue, whereas in the present experiment it was auditory.*

4.3.2.3 Visual-auditory facilitation in saccadic reaction times

A one-way ANOVA compared the SRTs across all ISC conditions with the latencies obtained in the control trials where the subjects either made saccades opposite to the visual or auditory stimulus presented alone. This analysis was highly significant ($F_{2,2126} = 293.9, p < 0.001$) indicating shorter SRTs of saccades in direction opposite to the unimodal auditory stimulus than to bimodal stimulation which in turn was shorter than saccades directed opposite to the unimodal visual stimulus (272 ms, visual, 236 ms, auditory, and 240 ms, bimodal). In separate ANOVAs for each subject, two subjects showed a slightly different result in that they exhibited shorter SRTs in the bimodal trials than in the unimodal auditory trials (227 ms, bimodal, and 244 ms, auditory) which in turn were shorter than in the unimodal visual trials (272 ms).

Test of the visual procue effect in Fischer and Weber (1996) An ANOVA on the antisaccade latencies of all subjects with stimulus modality (unimodal vs. bimodal) as unrepeated factor revealed significantly shorter latencies in all bimodal trials than in the unimodal visual trials (see the right panel of Figure 4.3).

A second ANOVA with spatial congruence (coincident vs. disparate) and ISC validity (50%, 80%, and 100%) as unrepeated factors revealed two significant main effects and a significant interaction effect of spatial congruence * ISC validity. As can be seen in the right panel of Figure 4.3, the latencies in the coincident trials were faster than in the disparate trials, and they were faster in 80% ISC and 100% ISC than in 50% ISC. However, the interaction effect of spatial congruence * ISC validity indicated shorter

Table 4.1: *Relative frequency of prosaccade errors for each subject. The second column indicates the relative frequency with which these errors were corrected by a second saccade crossing the midline of presentation in the direction opposite to the visual target.*

| Subject | Type of trial | |
|---------|---------------|--------------|
| | Error | Corrected |
| MK | 18/792 = 0.02 | 12/18 = 0.67 |
| RS | 82/859 = 0.09 | 82/82 = 1.00 |
| TL | 70/888 = 0.08 | 70/70 = 1.00 |
| MW | 31/579 = 0.05 | 28/31 = 0.90 |

latencies in 100% ISC than in 80% ISC in the coincident trials, but the reverse was true in the disparate trials.

4.3.2.4 Prosaccade errors

In this subsection we will first describe some general descriptive statistics on the relative frequency, latencies, and saccade amplitudes of the prosaccade errors. In a second step, we will analyse whether the prosaccade errors were affected by interstimulus contingency effects. By prosaccade errors we mean those trials where the subjects gazed at the visual target. Corrected errors are defined as those trials where the subjects first gazed at the visual target and then, after a certain time interval, made a second, corrective saccade which crossed the midline of presentation (meridian) in direction opposite to the visual target (antisaccade).

Descriptive statistics Table 4.1 shows that the subjects committing the most errors corrected them all, whereas subject MK committed less errors and corrected them less often. Separate Chi-square tests for each subject further showed that all but subject MW exhibited significantly more prosaccade errors in the disparate trials than in the coincident trials.

Separate ANOVAs for each subject comparing the SRTs of correct and erroneous saccades reached significance in all subjects indicating 53 ms shorter latencies on average in the erroneous prosaccades than in the antisaccades (see Table 4.2).

The saccade amplitudes were submitted to separate t-tests for each subject and direction of gaze comparing correct antisaccades with corrected errors. These t-tests reached significance in all subjects indicating overall shorter amplitudes in the first, erroneous saccade of corrected errors than in the correct antisaccades (mean difference = 5.3° , $SD = 1.12^\circ$, leftward; mean difference = 6.6° , $SD = 2.07^\circ$, rightward). t-tests comparing the landing positions of the second, corrective saccade of corrected errors with the amplitudes of correct antisaccades were significant in subjects RS and MW indicating landing positions of the second, corrective saccades of corrected errors to be further away from

Table 4.2: Means and standard deviations of the latencies of correct antisaccades and prosaccade errors.

| Subject | Correct antisaccades | Prosaccade errors |
|---------|----------------------|-------------------|
| MK | 232 ± 29 | 205 ± 54 |
| RS | 219 ± 30 | 160 ± 22 |
| TL | 237 ± 30 | 165 ± 22 |
| MW | 244 ± 24 | 190 ± 28 |

fixation than the landing positions of correct antisaccades (mean difference = 2.2°, SD = 0.52°, leftward; mean difference = 4.9°, rightward).

Interstimulus contingency effects Table 4.3 for each subject the relative frequency of prosaccade errors separated by effective ISC validity. The number of prosaccade errors in each contingency condition was divided by the total number of bimodal trials in that condition in order to account for the different numbers of trials obtained especially in 20% and 80% ISC.

Separate Chi-square tests were conducted for each subject comparing the number of prosaccade errors in the different contingency conditions with the number of correct trials in the same conditions. Only in subject RS the Chi-square test reached significance. As can be deduced from Table 4.3, she exhibited more errors in 20% ISC and less errors in 80% ISC than would be expected.

The saccade latencies of all prosaccade errors in the different ISC conditions were compared for each subject with separate t-tests. Only subject TL showed marginally shorter SRTs in 80% ISC than in 50% ISC (163 ms vs. 174 ms). When the latencies of the second, corrective saccade of corrected errors were analysed, subject MK exhibited marginally shorter latencies in 80% ISC than in 20% ISC (229 ms vs. 267 ms), and subject TL exhibited significantly shorter latencies in 80% ISC than in 50% ISC (262 ms vs. 292 ms). We calculated the time interval between the end of the first and the start of the second, corrective saccade in corrected errors for those trials where the corrective saccades crossed the meridian in direction opposite to the visual target (antisaccade task). This so-called correction time was affected by interstimulus contingencies in subject TL. She exhibited shorter correction times in 80% ISC than in 20% and 50% ISC (42 ms vs. 65 ms). Also, subjects MK and TL showed significant contingency effects on the time interval between the start of the first, erroneous saccade and the start of the second, corrective saccade of corrected errors in those trials where the corrective saccades crossed the meridian in direction opposite to the visual target. For subject MK this correction interval was significantly shorter in 80% ISC than in 20% ISC (45 ms vs. 78 ms), and it was shorter in 80% ISC than in 50% ISC for subject TL (100 ms vs. 118 ms).

As the number of prosaccade errors in subjects MK and MW was too small to be separated by direction of gaze and ISC validity, only the prosaccade errors of subjects RS and TL were submitted to an analysis of saccade amplitudes. Separate t-tests for each

Table 4.3: *Relative frequency of prosaccade errors for each subject according to effective contingency validity.*

| Subject | Contingency validity | | |
|---------|----------------------|---------------|---------------|
| | 20% | 50% | 80% |
| MK | 6/121 = 0.05 | 5/187 = 0.03 | 7/484 = 0.01 |
| RS | 20/129 = 0.16 | 28/226 = 0.12 | 34/504 = 0.07 |
| TL | 8/131 = 0.06 | 15/213 = 0.07 | 47/544 = 0.09 |
| MW | 8/88 = 0.09 | 6/148 = 0.04 | 17/343 = 0.05 |

subject and direction of gaze compared the different contingency conditions². Only those effects are reported which were accompanied by equivalent effects in the peak velocities. Only subject RS showed 2.5° longer amplitudes on average in 80% ISC than in 50% ISC in the rightward saccades. She also exhibited 5.4° longer amplitudes on average in 20% ISC than in 50% ISC in the rightward direction of the second, corrective saccade of corrected errors. Finally, an analysis of the endpoints of the corrective saccades reached significance in subjects RS and TL. They showed endpoints further away from fixation in 20% ISC or 80% ISC than in 50% ISC in the rightward saccades (mean difference = 3.7°, SD = 0.04°) while subject TL also showed endpoints 2.1° nearer to fixation in 80% ISC than in 50% ISC in the leftward saccades.

4.3.2.5 Summary

The saccadic reaction times showed main effects of SOA and spatial congruence. Latencies were shorter the earlier the auditory accompanying stimulus was presented before the visual target, and when the stimuli were presented coincidentally. When the latencies were analysed separately for each subject, the main effect of ISC validity was evident in all subjects. However, they showed large interindividual differences in that one subjects showed shorter SRTs in 80% ISC than in 50% ISC, one showed longer SRTs in 20% ISC than in 50% and 80% ISC, and two subjects exhibited an interaction effect of spatial congruence and ISC validity. All but one subject exhibited longer saccade amplitudes in 20% and 80% ISC than in 50% ISC in the rightward saccades, and shorter saccade amplitudes in 80% ISC (and 20% ISC, two subjects) than in 50% ISC in the leftward saccades. All subjects showed a significant interaction effect of spatial congruence and ISC validity in at least one direction of gaze.

The analysis of contingency effects on prosaccade errors revealed interindividual differences in response strategy. Subject RS exhibited more errors in 20% ISC and less errors in 80% ISC than would be expected. Subject TL showed shorter SRTs in 80% ISC than in 50% ISC in all prosaccade errors, in the second, corrective saccade of corrected errors, and in the correction times. Subjects TL and MK showed shorter correction intervals in

²In this analysis also the saccades starting $\pm 1^\circ$ off fixation were included because of lack of trials.

80% ISC than in 50% or 20% ISC. Finally, subject RS showed longer amplitudes in 80% ISC than in 50% ISC in the rightward saccades of all prosaccade errors, and longer amplitudes in 20% ISC than in 50% ISC in the rightward direction of the second, corrective saccade of corrected errors. Subjects RS and TL exhibited endpoints further away from fixation in 20% ISC or 80% ISC than in 50% ISC in the rightward saccades while subject TL also showed endpoints 2.1° nearer to fixation in 80% ISC than in 50% ISC in the leftward saccades.

In general, saccade latencies were shorter in saccades directed opposite to unimodal auditory and bimodal stimulation than to the unimodal visual stimulus. If the auditory accompanying stimulus was presented with 100% validity either coincident or disparate to the visual target, the antisaccade latencies were shorter in 80% ISC than in 100% ISC in the coincident trials, but the reverse was true in the disparate trials.

The latencies of the prosaccades errors were about 53 ms shorter than the latencies of correct antisaccades. All but one subject committed more errors in the disparate trials than in the coincident trials. The saccade amplitudes in the first, erroneous saccade of corrected errors were smaller than in the correct antisaccades. In two subjects the landing position of the second, corrective saccade of corrected errors was further away from fixation than the landing position of correct antisaccades.

4.4 Discussion

When performing visual antisaccades, all subjects exhibited significant interstimulus contingency effects at least in the antisaccade latencies. We replicated the general observation that antisaccade latencies are significantly longer compared to prosaccade latencies. This additional processing time in the generation of antisaccades may have contributed to the interstimulus contingency effects.

Note, however, that the size of the contingency effects was comparable to those obtained in the former experiments. This finding rather points to similar processing in all experiments. However, in the antisaccade task subjects exhibited large interindividual differences in the contingency effects. The latter result is in clear opposition to the contingency effects obtained in the bimodal go/no-go task (see Chapter 3) in which all subjects exhibited shorter latencies both with positively and negatively correlated contingencies. It might thus be concluded that the contingency effects found in the bimodal go/no-go task were specific to the experimental procedure as the subjects in the antisaccade task were more candid in adapting different response strategies.

Interestingly, however, all but one subject showed very similar interstimulus contingency effects in the antisaccade amplitudes. This was all the more remarkable as the amplitudes in the antisaccade task are known to vary considerably both within and between subjects (see Section 4.1). The large variability in antisaccade amplitudes, however, did not prevent interstimulus contingency effects to occur. On the other hand, the variability in the antisaccade amplitudes might explain the size of the contingency effects which was larger than in the former experiments.

Note that the difference in interindividual variability between the antisaccade latencies and amplitudes supports our conclusion of Experiment 5 (see Section 3.5) which pointed

to different interstimulus contingency effects on saccade latencies and amplitudes. For a discussion of this issue see the General Discussion in Chapter 6.

The antisaccade latencies were the shorter the earlier the auditory accompanying stimulus was presented before the visual target, and if the stimuli were presented at the same location. These results thus confirmed our second hypothesis which held that antisaccade latencies show spatial and temporal contiguity effects. The significant interaction effect of SOA and spatial congruence further indicated that the two items of the principle of contiguity (see Section 1.1), spatial and temporal proximity, in combination lead to the shortest antisaccade latencies if the auditory stimulus is presented 40 ms before the visual target at the same location.

The lack of significant interaction effects of either SOA or spatial congruence and contingency further showed that the contingency information was processed independently of the contiguity effects. Note, however, that the analysis of the training session with 100% ISC revealed a significant interaction effect of spatial congruence and contingency. This interaction effect was due to shorter antisaccade latencies in 100% ISC than in 80% ISC in the coincident trials, while the reverse was true for the disparate trials.

At first view, this result seems to indicate that the contingency information was not processed independently of spatial congruence. On the other hand, it should be noted that in the training session the subjects only were presented with 50% ISC and 100% ISC. Therefore, it might be hypothesised that the significant interaction effect rather was due to a reference frame effect of the subjects. The latter assumption was supported by the main effect of contingency indicating overall shorter antisaccade latencies in 100% ISC than in 50% ISC. If it is further acknowledged that the learning of contingencies is more difficult in the disparate than in the coincident trials, the reference frame account supports our conclusion of independent processing of interstimulus contingencies. If this was true, the size of the latency difference between 80% ISC and 100% ISC in the disparate trials would be indicative of a lower bound of learning from the first to the last session in 80% ISC. Further research will be necessary to systematically investigate this point.

Fischer & Weber (1996) observed longer antisaccade latencies compared to a control condition if a visual procue was always presented opposite to the visual target (see Section 4.1.1). However, the reverse was true in the present experiment (see Figure 4.3). The subjects always responded faster in the bimodal trials than in the unimodal visual trials. This result confirmed that antisaccade latencies show an intersensory facilitation effect.

In the light of this IFE, the longer antisaccade latencies with a visual procue in Fischer & Weber's study need further explanation. In fact, Ross & Ross (1981), and later Walker, Kentridge & Findlay (1995) showed that the presentation of a visual stimulus (cue) opposite to the visual target leads to shorter prosaccade latencies than without cue. It was concluded that the cue serves as a warning signal and elicits the programming of a saccade to the location of the warning event. On the basis of these conclusions, it might thus be assumed that the warning effect of the visual procue in Fischer & Weber's study entailed an automatic (covert) shift of attention and the pre-programming of a saccade in the direction of the cue. However, as the subjects were instructed to make an antisaccade to the visual target (in the direction of the cue), the inhibition of the initial saccade program in direction of the cue (warning effect) and the inhibition of the saccade program in direction of the visual stimulus may have interfered with the antisaccade program in

the same direction as the cue leading to the prolonged latencies compared to the warning effect (see Dorris, Taylor, Klein & Munoz, 1999, and Rizzolatti, Riggio & Sheliga, 1994, for details).

If the latter hypothesis was true, we need to explain why in the present study no such interference effect occurred due to the auditory accompanying stimulus. One main difference between experiments was that Fischer & Weber (1996) employed a gap task in which the fixation point was extinguished 200 ms prior to target presentation, while in the present study the fixation point was extinguished at the same time as the target was presented. The gap task is generally known to facilitate saccadic response times (see Everling *et al.*, 1998). However, Reuter-Lorenz, Oonk, Barnes & Hughes (1995) and Forbes & Klein (1996) showed that this reduction in saccade latencies is significantly reduced in the antisaccade task. Therefore, we may conclude that the different timing in fixation off-set may not have caused the difference in interference between our experiment and Fischer and Weber's study (1996).

A second difference between experiments obviously lied in the modality of the procue. While the assumption of a smaller warning effect of the auditory accompanying stimulus than the visual procue would contradict common understanding (i.e., Ross & Ross, 1981), it might be hypothesised that the auditory accompanying stimulus was less effective in eliciting a saccade pre-program than the visual procue. This hypothesis was supported by Sheliga, Riggio & Rizzolatti (1994) who were interested in the saccade trajectories in a spatial cueing paradigm (see Section 1.4.2). They found that the trajectory of vertical saccades deviated in the direction opposite to a visual or auditory target (right or left of fixation) if the target was presented in the hemisphere in which it was expected. Note however, that this deviation in saccade trajectory was much smaller with auditory targets than with visual targets. This observation thus might indicate that an auditory stimulus is less effective in eliciting a saccade pre-program leading to saccade deviation or antisaccade latency interference (Fischer & Weber, 1996).

Finally, the analysis of prosaccade errors revealed that two subjects exhibited shorter latencies in 80% ISC than in 50% ISC in all prosaccade errors, in the second, corrective saccade of corrected errors, and in the correction times and intervals. These results thus supported our hypothesis of higher prestimulus build-up activity and thus shorter latencies of the prosaccade errors in 80% ISC than in 20% ISC (Dorris & Munoz, 1998; Dorris, *et al.*, 1997; Everling *et al.*, 1998).

Note, however, that all but one subject committed more errors in the disparate trials than in the coincident trials. Furthermore, one subjects committed more errors in 20% ISC and less errors in 80% ISC than would be expected. In analogy to the former discussion on the smaller interference effect in antisaccade latencies with an auditory procue than with a visual procue, it might be hypothesised that the auditory stimulus in the disparate trials automatically activated a pre-program for a saccade in the direction of the stimulated field (Rizzolatti *et al.*, 1994). However, as the subjects were instructed to make an antisaccade, a central program may have counteracted this pre-program causing a bias in the opposite direction (Tassinari, Biscaldi, Marzi & Berlucchi (1989). If, then, the visual target was presented at the opposite side of the auditory stimulus, the higher prestimulus build-up activity due to the central bias may have triggered the prosaccade errors. This mechanism thus would explain the higher frequency of prosaccade errors in the disparate trials than

in the coincident trials. However, more research will be necessary to investigate the exact mechanisms underlying the shorter latencies in the prosaccade errors of 80% ISC than in 20% ISC on the one hand, and the higher frequency of errors in 20% ISC than in 80% ISC on the other hand.

The analysis of prosaccade amplitudes showed that the primary, erroneous saccades were significantly shorter than the amplitudes of correct antisaccades. This result and the observation of very short correction times confirmed Mokler and Fischer's conclusion (1999) that reflexive errors and voluntary antisaccades may be prepared in parallel. During the preparation of the antisaccade, a prosaccade bottom-up command may have reached the superior colliculus (SC). This command may have been processed automatically leading to a saccade before the command for the voluntary antisaccade reached the SC (Mokler & Fischer, 1999). However, the command of the antisaccade may have interrupted the prosaccade in mid-flight which would explain the shorter amplitudes of the prosaccade errors (Weber *et al.*, 1998).

Note, that the subjects exhibited landing positions of the second, corrective saccades of corrected errors that overshoot the landing positions of the correct antisaccades. This result contradicted Mokler and Fischer (1999) who reported that the amplitudes of the second saccades corrected the amplitudes of the first, erroneous saccades. Our finding indicated that voluntary antisaccades are planned in orbitocentric co-ordinates, *i.e.* with respect to the outer space of the observer, rather than just by inverting the direction vector of the prosaccade (error), because there would be no reason to overshoot the landing positions of correct antisaccades by inverting the direction, but retaining the amplitude of the prosaccade (error) which, as Kowler (1990) indicated, may be stored in working memory.

In summary, all subjects exhibited coherent contingency effects in the antisaccade amplitudes. However, they showed large interindividual differences in the contingency effects on the antisaccade latencies. Therefore, we concluded that the shorter latencies both in the positively and negatively correlated contingencies in the former experiments were due to the bimodal go/no-go task. The discussion of the warning effect of either an auditory or visual procue indicated that the auditory accompanying stimulus was less effective in eliciting a collicular pre-program thus leading to less antisaccade latency interference than a visual procue (Fischer & Weber, 1996). On the other hand, this auditory pre-program may have caused a central bias in the opposite direction leading to more frequent prosaccade errors in the disparate trials than in the coincident trials. Note, however, that the latter mechanism alone could not explain why some subjects showed shorter prosaccade latencies in 80% ISC than in 20% ISC, while another subject exhibited more errors in 20% ISC than in 80% ISC. Finally, the analysis of prosaccade errors indicated that antisaccades are programmed in orbitocentric co-ordinates, because the landing positions of the second, corrective saccade of corrected errors overshoot the landing positions of the correct antisaccades.

5

Auditory prosaccades

To date only a few researchers have attempted to determine the behavioural characteristics and neurobiological basis of saccades in the direction of an auditory target. In fact, the orienting in the direction of a sound source is not as tightly coupled to a saccadic eye movement as the orienting to a light. The location of a sound source is primarily represented in craniotopic co-ordinates, *i.e.* with respect to the head. These co-ordinates have to be transformed into oculocentric co-ordinates in order to calculate the position of the sound source with respect to the eyes before a saccade can be made.

A recent study by Groh, Trause, Underhill, Clark & Inati (2001) indicates that already in the primate inferior colliculus (ICC), a structure in the brainstem which converges the information of binaural cues, the representation of sound location is intermediate between craniotopic and oculocentric co-ordinates. This code appeared sufficient for later neural stages, as *e.g.* the superior colliculus (SC), to calculate the position of sounds with respect to the eyes (Groh *et al.*, 2001). In contrast to the auditory pathway, however, the visual information reaching the retina is transduced without any co-ordinate transformation onto the retinotopically organised SC, a midbrain structure, which converges this information to the brainstem premotor circuitry to trigger an eye movement toward the source of stimulation (see Schall, 1991, for a review). While the auditory information has to be recoded before a saccadic eye movement can be made, the visual information can be used directly to trigger the movement. In this sense, saccadic eye movements to auditory targets cannot be directly compared to visually guided saccades.

In this chapter we will first briefly describe some behavioural characteristics and the neurobiological processing accounts of auditory prosaccades before we will then introduce the logic of Experiment 7.

5.1 Behavioural characteristics of auditory prosaccades

In an auditory prosaccade task subjects are asked to make a saccade in the direction of an auditory target. Zahn, Abel, & Dell'Osso (1978) reported that human subjects were able to successfully perform this task requirement, but the latencies of auditory prosaccades were longer than in visual prosaccades. While later studies confirmed the latter observation (Zahn, Abel, Dell'Osso & Daroff, 1979; Zambarbieri *et al.*, 1982), they also showed that the latencies of auditory prosaccades critically depend on the eccentricity of the auditory target. Saccadic latencies increased with eccentricity for visual targets, but they decreased with eccentricity for auditory targets (Yao & Peck, 1997; Zambarbieri *et al.*, 1995). Jay & Sparks (1990) systematically compared the auditory prosaccade latencies in humans and macaque monkeys. They found that humans showed overall shorter latencies to auditory targets than to visual targets, but the reverse was true for the monkeys (also see Whittington, Hepp-Reymond & Flood, 1981).

5.1.1 Visual distractor task

Lueck, Crawford, Savage & Kennard (1990) investigated the effects of auditory-visual interaction on the amplitudes of auditory prosaccades. In a focussed-attention task, subjects were presented with an auditory target at 15° right or left of fixation, while a visual distractor could occur at any of twelve positions, with equal probability. If the stimuli were presented in the same hemifield, the saccade latencies and amplitudes to the auditory target were shorter than if the stimuli were presented in opposite hemifields. It can thus be concluded that auditory prosaccades follow the principle of spatial contiguity (see Section 1.1).

Lueck *et al.* (1990) further determined that unimodal auditory prosaccades show a larger scatter in saccade amplitudes and lower peak velocities than unimodal visual prosaccades (also see Jay & Sparks, 1990).

5.1.2 Express saccades

Shafiq, Stuart, Sandbach, Maruff & Currie (1998) examined the contributions of attention and oculomotor fixation on the occurrence of express saccades in the auditory prosaccade task. In a gap task, subjects exhibited a few express saccades which did not form a separate mode in the saccade-latency distribution. In a control condition with visual prosaccades, however, the same seven subjects did not show any express saccades either. On the basis of this result, it is difficult to decide whether the lack of express saccades in the auditory prosaccade task was inherent in the programming of auditory prosaccades or whether it occurred due to the subject sample or experimental procedure, because the subjects did not show any express saccades in the visual prosaccades either. Note that Shafiq *et al.* (1998) presented their subjects with an auditory 'fixation' stimulus. When the subjects were presented with a visual fixation point and auditory targets, Fendrich, Hughes & Reuter-Lorenz (1991) obtained a similar gap effect as with visual prosaccades.

This observation was later confirmed by Taylor, Klein & Munoz (1999) who found a gap effect to auditory targets only if either a visual or auditory fixation point was extinguished 200 ms prior to target presentation. Unfortunately, neither of the latter authors analysed their data with respect to the occurrence of express saccades. However, the finding of a smaller gap effect with auditory targets and/or auditory fixation (33 ms and 46 ms) than with visual targets and/or visual fixation (69 ms and 55 ms) might indicate that the auditory prosaccade task is less apt in eliciting express saccades than the visual prosaccade task.

5.2 Neurobiological processing accounts of auditory prosaccades

There are several neural sites which show movement-related auditory responses. Wallace, Wilkinson & Stein (1996) showed that the deep layers of the monkey's SC contain auditory-responsive unimodal and multimodal neurons. These neurons responded best to broad-band noise bursts and were excited by stimuli presented at the contralateral side. Each multisensory neuron has multiple receptive fields, one for each modality to which it responds. These receptive fields are in spatial register to one another so that a sensory cue, regardless of modality, activates neurons in the same SC location - the location that corresponds to the position of the stimulus with respect to the observer (Stein, 1998; King, Schnupp & Thompson, 1998). Furthermore, these sensory maps are also in register with the premotor maps in the SC so that they can direct the eyes, ears and head to the source of stimulation (Stein & Meredith, 1993).

The SC neurons receive sensory input from a large number of subcortical and cortical sources (see Schall, 1991, for a review). One direct cortical input comes from the frontal eye fields (FEFs) which have been shown to play a role in visually and aurally guided eye movements (Russo & Bruce, 1994). All FEF neurons with movement-related activity preceding visual targets also were active in precedence of saccades to auditory targets, while the activity in conjunction with aurally guided saccades was somewhat weaker. Meredith (1999) further showed that the saccade-related neurons in the FEF preferentially target the multisensory neurons in the deep layers of the SC thereby controlling unimodal and multimodal processing in the SC.

A second cortical structure with direct connections into the FEF and the SC is the lateral intraparietal area (LIP) of the posterior parietal cortex. Linden, Grunewald & Anderson (1999) compared the activity of neurons in area LIP of two macaque monkeys in a visually guided and aurally guided memory-saccade task. They found that the auditory-responsive neurons were more activated in the memory-saccade task than during fixation, while the visual-responsive neurons did not show such a change in response behaviour. As Linden *et al.* found a link between auditory activity and oculomotor behaviour in area LIP they suggested that the behavioural modulation of responses to an auditory stimulus reflects the significance of that stimulus as a potential target for an eye movement.

Finally, the basal ganglia is a key structure in controlling the cortical input by the FEFs and LIP into the SC. Contrary to the cortical areas, the basal ganglia do not provide a drive, but select one that is appropriate (see Hikosaka, Takikawa & Kawagoe, 2000, for

a review). The neurons of the substantia nigra pars reticulata (SNr), which is one of the output structures of the basal ganglia, exert tonic inhibition on presaccadic neurons in the SC, but remove the inhibition occasionally to allow a saccade to the contralateral side. Hikosaka & Wurtz (1983) showed that the SNr of macaque monkeys contained a small portion of auditory-responsive neurons. The response of these neurons was enhanced when the monkey used the stimulus as a target for saccadic eye movements. In sum, the functional role of SNr may consist in the suppression of inappropriate movements and forthcoming movements which are ready to go, but must be kept from being triggered (Hikosaka *et al.*, 2000).

5.2.1 Express saccades

Shafiq *et al.* (1998) argued that they obtained only a few express saccades in the auditory prosaccade task, because the task was novel and therefore, the disinhibition of neurons in the SC by the FEFs may have been more difficult to achieve. In fact, they propose that the occurrence of express saccades in visual prosaccades is related to the FEFs exhibiting inhibitory control via the SNr over the SC neurons to prevent fast-latency movements (Dias & Bruce, 1994). However, with training, the FEFs may habituate to the point where the saccades are controlled (only) by subcortical mechanisms producing express saccades. If, however, the task is novel and thus the FEFs do not habituate as in the visual prosaccade task, the inhibitory control of the SNr on the SC may thus preclude express saccades to occur (see also Reuter-Lorenz, Hughes & Fendrich, 1991, Section 4.4).

The former hypothesis relies on the assumption that the fixation cells in the rostral pole of the SC are less prone to be modulated by an auditory fixation stimulus than by a visual fixation stimulus. However, the psychophysical data illustrated in Section 5.1.2 and single cell recordings in the cat's SC showed that auditory stimuli are as effective as visual stimuli in modulating the discharge rate of the fixation cells of the SC (Peck & Baro, 1997). In accord with Taylor *et al.* (1999) we thus conclude that the gap effect (and possibly also the occurrence of express saccades) may be related to intracollicular (des)inhibition (Munoz & Istvan, 1998) of saccade-related neurons in the intermediate layers by the fixation cells in the rostral pole of the SC (Dorris & Munoz, 1995). Furthermore, the smaller gap effect with auditory targets than with visual targets may be explained by the reduced saccade-related activity of burst neurons in the SC (van Opstal & Frens, 1996). To the extent that the disappearance of the fixation stimulus releases inhibition on the movement-related cells, the less active saccade-related burst neurons with auditory targets may thus lead to a smaller gap effect or may need more time to exert their effects (Taylor *et al.*, 1999).

5.3 Experiment 7: Auditory prosaccades

Experiment 6 with visual antisaccades showed that the subjects exhibited large interindividual differences in the saccade latencies, but similar interstimulus contingency effects in the saccade amplitudes. Note that the programming of an antisaccade requires the ability to suppress a reflexive saccade toward the visual stimulus, and to generate a voluntary

saccade in the opposite direction (see Section 4.1). The analysis of amplitudes of correct antisaccades and landing positions of corrected prosaccade errors further indicated that the generation of a voluntary saccade might entail the coding of the target location in orbitocentric co-ordinates. It might thus be hypothesised that the (re-)coding of target co-ordinates was the constituent part in the processing of interstimulus contingencies which led to the reliable contingency effects on antisaccade amplitudes, whereas the subjects in the former visual prosaccade tasks without (re-)coding of the target location exhibited less coherent contingency effects in the prosaccade amplitudes.

To test this hypothesis, the subjects in Experiment 7 were asked to make a saccade in the direction of the auditory target (auditory prosaccade). Contingency information was provided in the location of the accompanying visual stimulus. Note that the location of a sound source in the auditory pathway is primarily represented in craniotopic co-ordinates. These co-ordinates have to be transformed into oculocentric co-ordinates in order to calculate the position of the sound source with respect to the eyes before a saccade can be made (see introduction to this chapter). It thus appears that auditory prosaccades are especially adapted in testing our hypothesis that the re-coding of target co-ordinates leads to interstimulus contingency effects at least in the saccade amplitudes.

We further hypothesised that the subjects should show overall shorter saccade latencies than in the antisaccade task, and possibly shorter overall latencies than in the visual prosaccade task. In analogy to Lueck *et al.* (1990), the third hypothesis was that the subjects should exhibit spatial contiguity effects at least in the saccade amplitudes. In accord with Taylor *et al.* (1999) we further hypothesised that the auditory prosaccade task is less effective in eliciting express saccades than the visual prosaccade task. Finally, in order to compare the results as closely as possible with the data of Experiment 6, we decided to analyse the direction errors with respect to their latency, amplitude, number of corrections, correction times, and amplitudes of corrective saccades (see Section 4.3.2.4).

5.3.1 Method

5.3.1.1 Participants

Five students (age 21-26 years) of the University of Oldenburg took part in the experiment. Subjects SN and ST already participated in Experiment 1, and subjects MK and RS already participated in Experiment 6. The fifth subject had never participated in any psychophysical experiment before. All subjects had right eye dominance. They had normal hearing and normal or corrected-to-normal vision. They were either paid or received partial course credit for participation. All subjects gave their informed consent prior to their inclusion in the study. They were not informed about the specific hypotheses under study.

5.3.1.2 Task and procedure

Experiment 7 was identical to Experiment 6 (anti), except for the following: First, the task was to make an eye movement as quickly and as accurately as possible to the auditory target and to use the accompanying visual stimulus as a possible, but unreliable, cue for the location of the auditory target. Second, feedback was given if the saccades fell in

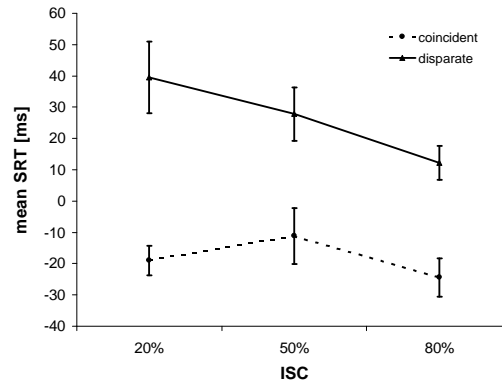


Figure 5.1: *Effects of interstimulus contingency (ISC) on the mean saccadic reaction times (SRT). Prior to this analysis, the SRTs of each subject were normalised by subtracting their overall mean SRT. The contingency effects only reached significance in the disparate trials: Latencies in 80% ISC were shorter than in 50% ISC which in turn were shorter than in 20% ISC.*

the direction of the visual accompanying stimulus when it was presented opposite to the auditory target. Finally, in order to facilitate the comparison of results with those of Experiment 1, subject SN was presented with 12 additional (16.7%) unimodal auditory trials interspersed into the bimodal trials, while for subject ST the order of ISC blocks was counterbalanced within each session.

Note that the definition of SOAs was identical to the former experiments: In $SOA = -40$ ms the auditory target was presented before the visual accompanying stimulus, whereas in $SOA = +40$ ms, the target was presented after the accompanying stimulus.

5.3.2 Results

Trials in the 20% and 80% ISC blocks were recoded according to their effective validity (see right panel of Figure 2.1). In the following, only those trials in which the saccade amplitudes started at less than 1° off the fixation point were considered for the analysis of saccade latencies and amplitudes.

5.3.2.1 Saccadic reaction times

All but subject SN (2.9%) exhibited less than 0.5% express saccades. For better comparability, the regular SRTs of each subject were normalised by subtracting their overall mean SRT. These normalised SRTs were submitted to a three-way ANOVA with SOA, spatial congruence (coincident vs. disparate), and ISC validity (20%, 50%, or 80%) as repeated factors. Two main effects and one significant interaction effect emerged. The main effect of SOA ($F_{2,4} = 14.67, p < 0.002$) indicated that the SRTs were the shorter the later the auditory target was presented after the visual accompanying stimulus. The second main effect of spatial congruence ($F_{1,4} = 14.02, p < 0.02$) indicated 45 ms shorter SRTs on average to coincident than to disparate stimuli. The interaction effect of spatial congruence

* ISC validity ($F_{1,2} = 5.9, p < 0.027$) was due to a significant effect of ISC validity only in the disparate trials: SRTs in 80% ISC were 17 ms shorter on average than in 50% ISC which in turn were 12 ms shorter than in 20% ISC (see Figure 5.1).

When the SRTs were analysed with separate ANOVAs for each subject, three significant main effects and three interaction effects emerged. All subjects exhibited main effects of spatial congruence and ISC validity. Newman-Keuls post-hoc tests indicated overall shorter SRTs in 80% ISC than in 50% ISC in four subjects, and longer SRTs in 20% ISC than in 50% ISC in two subjects (see Figure 5.2). The main effect of SOA reached significance in all but one subject. Respectively, two subjects showed significant interaction effects of SOA * spatial congruence, SOA * ISC validity, and spatial congruence * ISC validity. The interaction effect of SOA * spatial congruence indicated shorter latencies in the SOA = +40 ms when the stimuli were presented coincidently. The interaction effect of SOA * ISC validity in subject SN was due to significant contingency effects only in the SOA = -40 ms and +40 ms while in subject MK it indicated in shorter latencies in 20% and 80% ISC than in 50% ISC in all but SOA = +40 ms in which she exhibited similar mean latencies in 50% and 20% ISC but shorter latencies in 80% ISC. Finally, the interaction effect of spatial congruence * ISC validity was due to significant contingency effects only in the disparate trials.

Express saccades The express saccades of subject SN were separated by effective ISC validity (see Experiment 1) and then divided by the number of bimodal trials in the respective ISC condition in order to account for the different numbers of trials obtained especially in 20% and 80% ISC. A Chi-square test comparing the number of errors and bimodal trials in the respective contingency conditions did reach significance. This subjects exhibited significantly more express saccades in 80% ISC than would be expected. Only one of twenty-four express saccades was an error being directed to the visual accompanying stimulus.

5.3.2.2 Saccade amplitudes

Separate ANOVAs were conducted for each subject and rightward vs. leftward saccades with ISC validity and spatial congruence (coincident vs. disparate) as unreplicated factors. Only those effects are reported which were accompanied by equivalent effects in the peak velocities. Four of the five subjects showed a significant main effect of ISC validity in at least on direction of gaze. In all these cases saccade amplitudes in 20% ISC and/or 80% ISC were shorter than in 50% ISC (mean difference = 1.7° , SD = 0.62°). The same four subjects also showed a significant interaction effect of ISC validity * spatial congruence. All but one subject exhibited a main effect of spatial congruence in one direction of gaze indicating overall shorter saccade amplitudes to coincident than to disparate stimuli (mean difference = 2.95° , SD = 1.84°).

5.3.2.3 Visual-auditory facilitation in saccadic reaction times

A one-way ANOVA compared the SRTs across all ISC conditions with the reaction times obtained in the control trials where the subjects either responded to the visual or auditory

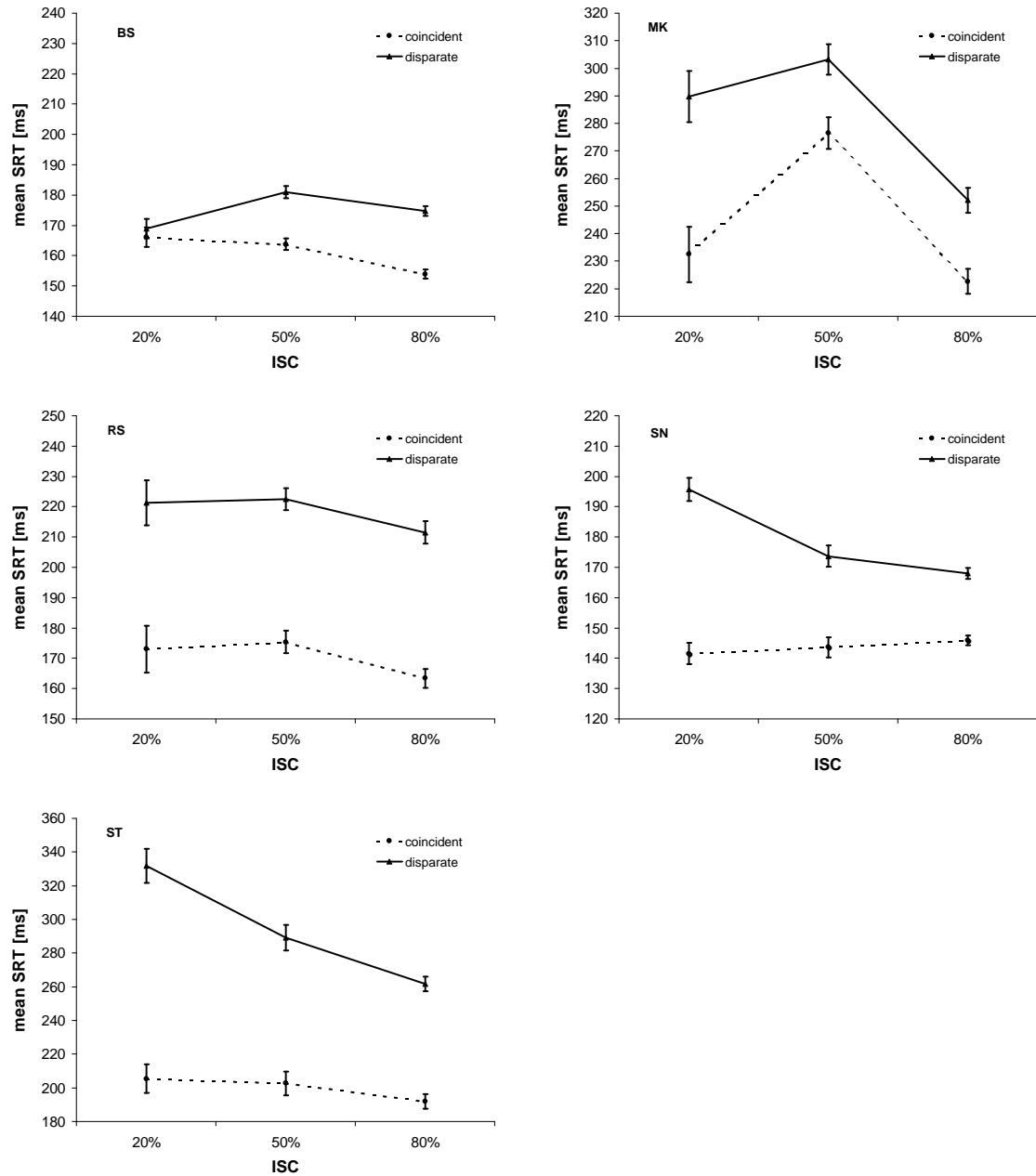


Figure 5.2: *Interstimulus contingency (ISC) effects on saccadic reaction times (SRT) for each subject separately. Subjects BS, MK, RS and ST showed shorter SRTs in 80% ISC than in 50% ISC, while subjects SN and ST exhibited longer SRTs in 20% ISC than in 50% ISC and significant interaction effects of contingency validity with spatial congruence.*

Table 5.1: *Relative frequency of direction errors for each subject. The second column indicates the relative frequency with which these errors were corrected by a second saccade crossing the midline of presentation in the direction of the auditory target.*

| Subject | Type of trial | |
|---------|---------------|--------------|
| | Error | Corrected |
| BS | 11/698 = 0.02 | 11/11 = 1.00 |
| MK | 42/660 = 0.06 | 15/42 = 0.36 |
| SN | 40/803 = 0.05 | 31/40 = 0.77 |
| ST | 56/877 = 0.06 | 33/56 = 0.59 |
| RS | 12/517 = 0.02 | 12/12 = 1.00 |

stimulus presented alone. This analysis was highly significant ($F_{2,3244} = 47.2, p < 0.001$) indicating shorter saccadic reaction times to unimodal auditory and unimodal visual stimuli (177 ms and 182 ms) than to bimodal stimulation (199 ms).

In a second step, we separated the bimodal trials by spatial congruence (coincident vs. disparate) and conducted separate ANOVAs for each with stimulus modality as un-repeated factor. The analysis of the coincident trials revealed shorter latencies in unimodal auditory and bimodal stimulation than to the unimodal visual stimulus ($F_{2,2221} = 4.84, p < 0.008$; 176 ms and 177 ms versus 182 ms), while the analysis of the disparate trials showed shorter latencies in the unimodal visual and auditory trials than in the bimodal trials ($F_{2,2094} = 220.1, p < 0.001$; 177 ms and 182 ms versus 224 ms).

5.3.2.4 Direction errors

In this subsection we will first describe some general descriptive statistics on the relative frequency, latencies, and saccade amplitudes of the direction errors. In a second step, we will analyse whether the direction errors were affected by interstimulus contingency effects. By direction errors we mean those trials where the subjects gazed at the visual accompanying stimulus when it was presented opposite to the auditory target. Corrected errors are defined as those trials where the subjects first gazed at the visual accompanying stimulus and then, after a certain time interval, made a second, corrective saccade which crossed the midline of presentation (meridian) in direction of the auditory target.

Descriptive statistics As can be seen in Table 5.1, the subjects exhibiting the less errors (BS and RS) corrected them all, while the subjects with more errors (MK and ST) corrected them less often. Separate Chi-square tests for each subject revealed a significant effect for subject SN. She more often corrected her errors by crossing the meridian in direction of the auditory target than holding her gaze at the wrong direction, that is, on the visual accompanying stimulus (see Table 5.1).

Table 5.2: Means and standard deviations of the latencies of correct auditory prosaccades and direction errors.

| Subject | Auditory prosaccades | Direction errors |
|---------|----------------------|------------------|
| BS | 167 ± 27 | 166 ± 37 |
| MK | 255 ± 54 | 259 ± 54 |
| SN | 158 ± 29 | 172 ± 30 |
| ST | 237 ± 69 | 211 ± 71 |
| RS | 193 ± 39 | 199 ± 39 |

Separate ANOVAs for each subject comparing the SRTs of correct and erroneous saccades reached significance in subjects SN and ST. This analysis indicated shorter latencies in the correct than erroneous saccades for subject SN, while the reverse was indicated for subject ST (see Table 5.2).

All subjects exhibited significant differences in the saccade amplitudes of correct saccades and corrected errors¹ (mean difference = 4.3°, SD = 1.21°, leftward; mean difference = 4.9°, SD = 0.66°, rightward) indicating overall shorter saccade amplitudes in the first, erroneous saccade of corrected errors. t-tests comparing the landing positions of the corrective saccades with the amplitudes of correct saccades were significant in subjects MK, SN, and ST indicating landing positions of the second, corrective saccades of corrected errors to be nearer to fixation than the landing positions of correct saccades (mean difference = 2.4°, SD = 0.7°, leftward; mean difference = 3.4°, SD = 0.19°, rightward).

Interstimulus contingency effects For each subject the relative frequency of direction errors separated by effective ISC validity is shown in Table 5.3. The number of direction errors in each contingency condition was divided by the total number of bimodal trials in that condition in order to account for the different numbers of trials obtained especially in 20% and 80% ISC.

Separate Chi-square tests were conducted for each subject comparing the number of direction errors in the different contingency conditions with the number of correct trials in the same conditions. In all but subject RS these tests were significant. As can be deduced from Table 5.3, the subjects exhibited more errors in 20% ISC and less errors in 80% ISC than would be expected.

Finally, for each subject the saccade latencies of all direction errors in the different ISC conditions were compared with separate t-tests. Subjects MK and SN showed significantly shorter SRTs in 80% ISC than in 50% and/or 20% ISC. When the latencies of the second, corrective saccade of corrected errors were analysed, subjects BS and SN exhibited significantly shorter latencies in 80% ISC than in 20% ISC (subject BS: 280 ms vs 452 ms; subject SN: 259 ms vs. 302 ms). We calculated the time interval between the end of the first and the start of the second, corrective saccade in corrected errors for those tri-

¹In this analysis also the saccades starting ± 1° off fixation were included because of lack of trials.

Table 5.3: *Relative frequency of direction errors for each subject according to effective contingency validity.*

| Subject | Contingency validity | | |
|---------|----------------------|---------------|---------------|
| | 20% | 50% | 80% |
| BS | 5/91 = 0.05 | 1/231 = 0.01* | 5/376 = 0.01* |
| MK | 25/89 = 0.28 | 11/208 = 0.05 | 6/363 = 0.02 |
| SN | 14/120 = 0.12 | 14/204 = 0.07 | 12/479 = 0.03 |
| ST | 25/141 = 0.18 | 10/178 = 0.06 | 21/558 = 0.04 |
| RS | 3/66 = 0.05 | 7/172 = 0.04 | 2/279 = 0.01* |

** If the relative frequency was too small, a procedure for the correction of ties was applied.*

als where the corrective saccades crossed the meridian in direction of the auditory target. This so-called correction time was affected by interstimulus contingencies in subjects BS and MK. They exhibited shorter correction times in 80% ISC than in 20% ISC (subject BS: 76 ms vs. 217 ms; subject MK: 101 ms vs. 252 ms). An analysis of the correction intervals (see Section 4.3.2.4) did not reach significance. The number of direction errors was too small to be separated by direction of gaze and ISC validity in order to be submitted to an analysis of saccade amplitudes.

5.3.2.5 Summary

The saccadic reaction times showed main effects of SOA and spatial congruence, and an interaction effect of spatial congruence and ISC validity. Latencies were the shorter the later the auditory target was presented after the visual accompanying stimulus, and if the stimuli were presented coincidently. The interaction effect was due to shorter latencies in the disparate trials of 80% ISC than in 50% ISC which in turn were shorter than in 20% ISC, but no contingency effects in the coincident trials. When the latencies were analysed separately for each subject, four subjects showed shorter latencies in 80% ISC than in 50% ISC, and two subjects showed longer latencies in 20% ISC than in 50% ISC. One subject exhibited a significant number of express saccades. She exhibited significantly more express saccades in 80% ISC than would be expected. All but one subject exhibited main effects of spatial congruence and ISC validity and an interaction effect of spatial congruence and ISC validity in the saccade amplitudes. The main effects consisted in shorter saccade amplitudes in coincident than in disparate trials, and shorter amplitudes in 20% ISC and/or 80% ISC than in 50% ISC.

The analysis of direction errors indicated that all but one subject exhibited more errors in 20% ISC and less errors in 80% ISC than would be expected. Three of the five subjects showed contingency effects on the saccade latencies and amplitudes of the direction errors. Two subjects respectively exhibited shorter latencies in 80% ISC than in 50% and/or

20% ISC in the latencies of all errors, in the latencies of the second, corrective saccade of corrected errors, and in the correction times.

In general, the saccade latencies were shorter to unimodal auditory and unimodal visual stimuli than to bimodal stimulation. A second analysis, however, showed that this was true only for the disparate trials of bimodal stimulation. In the coincident trials, the latencies to unimodal auditory and bimodal stimulation were shorter than to the unimodal visual stimulus. All subjects exhibited shorter saccade amplitudes in the first, erroneous saccade of corrected errors than in correct saccades. In three subjects the landing position of the second, corrective saccades of corrected errors was nearer to fixation than the landing position of correct saccades.

5.4 Discussion

In the auditory prosaccades task, four of the five subjects exhibited shorter saccade amplitudes both in the positively and/or negatively correlated contingency than in the control condition. This reliable contingency effect on saccade amplitudes and the higher variability of the amplitudes compared to visual prosaccades might thus confirm our hypothesis that the re-coding of target co-ordinates was the constituent part in the processing of interstimulus contingencies which also might have led to the contingency effects in the antisaccade amplitudes in Experiment 6.

Note, however, that the pattern of contingency effects was different in the amplitudes of auditory prosaccades than in the amplitudes of the antisaccades. While the subjects exhibited similar effects in both directions of gaze in the auditory prosaccades, the contingency effects differed between gaze directions in the antisaccade task (see Section 4.3.2.2). This result is difficult to reconcile with the hypothesis that the contingency effects in both experiments were due to the re-coding of target co-ordinates.

A second main finding of the auditory prosaccade task was that in the disparate trials the subjects exhibited shorter saccade latencies in the positively correlated contingency, but longer latencies in the negatively correlated contingency than in the control condition. This result confirms the finding of spatial cueing tasks which generally show shorter reaction times in the valid trials than in the invalid trials (see Section 1.4.1). However, the result contrast with our findings in the prosaccade tasks (see Chapters 2 and 3) in which the subjects exhibited shorter latencies both in the positively and negatively correlated contingencies. We thus conclude that the learning about contingencies requires different processes in visual prosaccades than in auditory prosaccades (see General Discussion for details).

The analysis of visual-auditory interaction effects revealed shorter latencies to the unimodal visual and auditory stimulus than to bimodal stimulation. At first view, this result seems in clear opposition to the intersensory facilitation effect (see Section 1.5) which predicts shorter latencies in bimodal trials than in unimodal trials. In fact, the comparison of the latencies to unimodal and bimodal stimulation indicated that the visual accompanying stimulus inhibited the processing of the auditory target in the bimodal trials. However, the second analysis showed that this was true only for those bimodal trials in which the auditory target was presented opposite to the visual accompanying

stimulus. The latencies in the coincident bimodal trials were as short as the latencies to the unimodal auditory stimulus which in turn were shorter than the latencies to the unimodal visual stimulus. It might thus be concluded that auditory prosaccades show an intersensory facilitation effect if the stimuli are presented at the same location, but intersensory inhibition if the stimuli are presented in opposite locations.

The intersensory inhibition effect might be explained by the auditory spatial code which has to be recoded from craniotopic to oculocentric co-ordinates before a saccade can be made. When the visual stimulus was presented opposite to the auditory target, this recoding procedure may have taken some time so that the pre-program of the auditory stimulus was less effective in eliciting the saccade-related burst neurons in the SC than the pre-program of the visual stimulus. Consequently, the pre-program of the visual stimulus first was to be inhibited before a saccade to the auditory target could be made. Note that this explanation would support our conclusion in Section 4.4 that the auditory 'precue' was less effective in eliciting a saccade pre-program than the visual precue in Fischer & Weber's study (1996) leading to less interference in the antisaccade latencies than the visual precue.

Furthermore, the intersensory inhibition effect with disparate stimulation might not be explained by auditory-responsive multimodal neurons in the deep layers of the superior colliculus. In single-cell recordings of macaque monkeys, Wallace, Wilkinson & Stein (1996) showed that auditory-responsive neurons in the SC respond best if the auditory stimulus is presented in the contralateral hemisphere. The recordings further indicated that auditory-responsive multimodal neurons exhibit cross-modal depression if one of the stimuli falls within the inhibitory portion of the response field of that neuron. In the case of our disparate stimulation, it might thus be hypothesised that the best response to the auditory target was found in the auditory-responsive neurons of the contralateral SC. If it is further acknowledged that the multimodal neurons in the same hemisphere provided an inhibitory signal that degraded the excitatory input of the visual accompanying stimulus, it is predicted that the latencies to the auditory target should be as fast as latencies to unimodal auditory targets. However, our data revealed much longer latencies with disparate bimodal stimulation. On the basis of this result, we thus conclude that the longer latencies in the disparate bimodal trials than in the unimodal trials may have been related to the recoding of auditory co-ordinates rather than multimodal inhibitory mechanisms within the deep layer of the SC.

The analysis of saccadic reaction times revealed that auditory prosaccades show spatial and temporal contiguity effects. This result thus confirmed the findings of Lueck *et al.* (1990) of shorter latencies to coincident than to disparate stimuli. The interaction effect of SOA and spatial congruence further indicated that the latencies were the shortest in the coincident trials when the visual accompanying stimulus was presented 40 ms after the auditory target. This result may indicate that the visual stimulus was more significant in guiding the saccadic eye movement in the coincident trials than the auditory target. The latter hypothesis was supported by our observation in the visual prosaccade task in which the subjects were the fastest the earlier the auditory accompanying stimulus was presented before the visual target (see Figures 2.3 and 3.1). When the auditory stimulus in the auditory prosaccade task was presented 40 ms before the visual accompanying stimulus, it may thus have elicited a similar intersensory facilitation effect as in the visual

prosaccade task. Note that the hypothesis of visual dominance in response preparation further supports our conclusion that the longer latencies in the disparate bimodal trials were related to the recoding of auditory co-ordinates and, correspondingly, the inhibition of visual discharge in the SC.

The interaction effects of spatial congruence and SOA with contingency further demonstrated that the processing of interstimulus contingency was interdependent with contiguity. Contingency effects only occurred in the disparate trials, and for two subjects the contingency effects were the largest when the visual accompanying stimulus was presented 40 ms before the auditory target. We already pointed to the significance of spatial disparity when discussing the possible mechanisms underlying the longer latencies in the bimodal trials than in the unimodal trials. It remains an interesting issue to determine whether the processing of contingency in the auditory prosaccade task was related to spatial disparity or, in more general terms, to the choice of direction.

In accord to Shafiq *et al.* (1999), only one of our subjects showed a small amount of express saccades. It might thus be concluded that the auditory prosaccade task is less effective in eliciting express saccades than the visual prosaccade task. Note, however, that the occurrence of express saccades in the auditory task may depend on the dominant modality of each subject (Giard & Peronnet, 1999). This hypothesis was supported by informal reports at the end of the experiment in which the subject exhibiting some express saccades was the only one of five subjects for whom it appeared easy to localise the auditory target even at the start of the training sessions. On the other hand, it should be noted that the subjects in the auditory task were only presented with small SOAs which in the visual tasks led to only quite a few express saccades either. More experiments will be necessary to determine the conditions responsible for the occurrence of express saccades in the auditory prosaccade task.

Finally, the subjects exhibited 2% to 6% of errors in the direction of the visual accompanying stimulus. As the subjects showed less than 0.5% of errors in the visual prosaccade tasks, this result supports our hypothesis of visual dominance in response preparation in the auditory prosaccade task. Furthermore, four of the five subjects exhibited more errors in 20% ISC and less errors in 80% ISC than would be expected. This result might further support our hypothesis of visual dominance in response preparation. In the 80% ISC blocks, the subjects were prepared to respond to 80% coincident trials. Therefore, in the 20% disparate trials the subjects were less prepared to inhibit the visual stimulus opposite to the auditory target, thus leading to more errors. However, in the 20% ISC blocks, the subjects were prepared to inhibit the visual accompanying stimulus which occurred opposite to the auditory target in 80% of the trials. This preparation thus may have precluded the occurrence of errors. The hypothesis of stronger response preparation in 80% ISC than in 20% ISC was further supported by the two subjects, respectively, who showed shorter latencies in the first and/or second saccade of the direction errors and shorter correction times in 80% ISC than in 20% ISC.

In summary, the auditory prosaccade task revealed coherent contingency effects in all subjects both in the saccade latencies and amplitudes. The subjects exhibited shorter saccade latencies in the positively correlated contingency, and longer latencies in the negatively correlated contingency than in the control condition, but only in the disparate trials. We discussed the need to recode the auditory co-ordinates and to inhibit the vi-

sual accompanying stimulus as a possible mechanism to account for these effects. Our hypothesis of visual dominance was supported by the observations (1) that the latencies were the shortest when the auditory target was presented 40 ms before the visual stimulus, (2) the subjects exhibited a considerable number of direction errors while they exhibited almost no errors in the visual prosaccade tasks, and (3) the direction errors in 80% ISC were more frequent, and had shorter latencies and correction times than in 20% ISC.

6

Visual prosaccades with outline boxes

In the last experiment, we addressed the question why the subjects in Experiment 7 exhibited contingency effects only in those trials in which the auditory target was presented opposite to the visual accompanying stimulus. In these disparate trials, did the subjects had to inhibit an automatic saccadic orienting response to the sudden onset of the accompanying visual stimulus (intersensory inhibition), or did they deliberately choose the proper direction of the saccade target (see Chapter 5)? We introduced two outline boxes right and left of fixation which indicated the possible locations for the visual target. The outline boxes were presented throughout the duration of each trial. Subjects thus realised at the beginning of each trial that they had to choose between the two possible locations for the visual target.

Note that the presentation of two outline boxes bears a resemblance to experiments on the effects of a visual distractor on visually guided responses. Therefore, in this chapter we will first briefly describe some behavioural characteristics and neurobiological processing accounts of visual prosaccades in a visual distractor paradigm before we will then introduce the logic of Experiment 8.

6.1 Behavioural characteristics of visual prosaccades in a visual distractor task

Presenting a visual cue, a distractor, simultaneously with a visual target affects either the timing (increased reaction times) or the metrics ('averaged saccades') of visual prosaccades, depending on the position of the distractor relative to the target (Walker, Deubel, Schneider & Findlay, 1997). When these authors presented their subjects with either a target in one hemisphere (unilateral) or the same target, but accompanied by a distractor at the opposite location (bilateral, remote distractor), the subjects exhibited about 30 ms longer saccadic reaction times in the distractor condition.

Similar results were obtained in several electrophysiological studies investigating the evoked brain potentials (ERPs) related to covert visual spatial attention (see Mangun & Hillyard, 1995; Hillyard, Vogel & Luck, 1998, for reviews). For example, Mangun and Hillyard (1991) compared a simple manual response to a single vertical grating with a choice response to one of two gratings presented in opposite hemispheres. In the latter bilateral condition, the target was defined by the height of the grating. The subjects exhibited much longer manual reaction times in the bilateral choice reaction than in the unilateral, simple response. When Lange, Wijers, Mulder & Mulder (1999) compared similar unilateral and bilateral gratings, but in both conditions the subjects were instructed to release a single button at target presentation, they found about 16 ms longer manual reaction times in the bilateral than in the unilateral condition.

Finally, Walker, Kentridge & Findlay (1995) asked subjects to saccade to either one of two identical bilateral targets. In the first experiment, the subjects exhibited about 20 ms longer overall saccadic reaction times than in the control condition with the unilateral target. In the third experiment, the subjects knew in advance when and where the target was going to be presented. The distracting stimulus appeared at different time intervals before, simultaneously, or after the target. In this case, the saccadic reaction times were the longest when the distracting stimulus was presented simultaneously with the target and decreased rather quickly to 80 ms that the distracting stimulus was presented before or after the target. Therefore, Walker *et al.* (1995) concluded that the inhibitory effect of a second, bilateral visual stimulus on visual prosaccade latencies is short-lasting.

6.1.1 Express saccades

Weber and Fischer (1994) investigated the effects of a visual distractor presented opposite to the saccade target on visual prosaccade latencies. When the distractor had the same form and size as the target and the subjects knew in advance in which hemisphere the target was going to be presented, the number of express saccades was significantly reduced compared to a control condition without distractor. However, in their fifth experiment Weber and Fischer (1994) presented the distractor permanently throughout the duration of each trial. In this case the onset of the target (change of orientation) was a sudden change in the periphery leading to automatic, covert orienting of attention to the location of the target. The same subjects as in the former experiment exhibited slightly increased overall mean latencies, but about the same number of express saccades as in the control condition. This result thus indicated that a continuously presented distractor has only a weak effect on visual prosaccade latencies (Weber & Fischer, 1994).

6.2 Neurobiological processing account of visual prosaccades in a visual distractor task

There are several neural sites which show differential effects on the presentation of either single or bilateral visual stimulation. Olivier, Dorris and Munoz (1999) recorded the neural activity in the intermediate layers of the Superior Colliculus (SC) of a macaque monkey. In a gap task (300 ms gap), a visual target was presented on the neuron's response

field, while a distractor was presented in the opposite location. Olivier *et al.* (1999) found a transient inhibitory pause in the discharge of these saccade-related neurons compared to a control condition without distractor. They argued that this inhibition occurred simultaneously to the target activating saccade-related neurons in the remote SC. Due to the lateral inhibitory interconnection of the intermediate layers of the two SCs (Munoz & Istvan, 1998), the inhibition of the distractor delayed the saccade-related activity in the remote SC from reaching the level of discharge required to initiate a saccade and therefore delayed its initiation. In sum, Olivier *et al.* (1999) explained the longer saccadic reaction times in a remote distractor task by lateral inhibitory interconnections of the two SCs of a macaque monkey.

Braun, Weber, Mergner and Schulte-Mönting (1992) compared the saccadic reaction times between unilateral and bilateral stimulation in patients with focal frontal or parietal lesions. In the bilateral task, the patients with parietal lesions exhibited more direction errors and a higher variability in saccadic reaction times than patients with frontal lesion or control subjects. This result thus indicated that the parietal cortex may be involved in early steps of saccade preparation such as the encoding of the direction of intended saccades (Gnadt & Anderson, 1988).

Platt and Glimcher (1997) refined this observation by single-cell recordings in the lateral intraparietal area (LIP) of macaque monkeys. They showed that the LIP neurons responded more strongly in association with the saccade target than in association with the same visual stimulus when it was the remote distractor. Platt and Glimcher (1997) thus suggested that the bilateral stimulation activated two populations of LIP neurons, each associated with one of the two visual stimuli, or with one of the two simultaneously planned movements. After one of the stimuli had been identified as the saccade target, the associated population of LIP neurons responded more strongly than the population associated with the distractor.

Schall and his group (Schall & Hanes, 1998; Bichot & Schall, 1999) investigated the neural correlates of saccade target selection in a visual search task. They recorded the activity of neurons in the frontal eye fields (FEFs) of macaque monkeys trained to shift gaze to a unique stimulus among similar distractors. The initial visual response of most visually responsive neurons in the FEF did not discriminate whether the target or one of the distractors appeared in their receptive field. However, before saccades initiation, the activity of most visually responsive cells in the FEF evolved to signal the location of the target through attenuation of the activity associated with the distractors. This attenuation of distractor activity was most significant when the distractor was presented opposite to the target (Bichot & Schall, 1999).

Hasegawa, Matsumoto and Mikami (2000) recorded the neural activity in the dorso-lateral prefrontal cortex (DLPFC) of macaque monkeys. In a delayed visual search task, an array of six small circular gratings was presented at symmetric locations. After the gratings disappeared, the monkeys had to hold fixation for a variable delay period, before they then were to make a saccade to the former target location which was defined by a different spatial frequency than the distractors. The neural activity at the time of stimulus presentation was determined by the identity of the stimulus as the target. If the same stimulus was a distractor, the discharge of the DLPFC neurons was comparable to the control condition without distractors. As the population activity in the control condition

was significantly lower than in the search condition, Hasegawa *et al.* (2000) concluded that neurons in the monkey dorsolateral prefrontal cortex respond to a stimulus in a complex array only if the stimulus dictates a behavioural choice as in the search task (also see Rowe, Toni, Josephs *et al.*, 2000).

Finally, the investigation of event-related potentials associated with covert spatial attention (see above) revealed differential effects of unilateral versus bilateral visual stimulation in the occipito-temporal areas of human subjects (Hillyard, Vogel & Luck, 1998). The presentation of bilateral targets resulted in two separate components: A positive wave (P1) about 80–130 ms poststimulus, and a negative wave (N1) occurring 140–200 ms after stimulus presentation. However, when the subjects were presented with a single, unilateral visual stimulus, only the positive P1-component was observed. Therefore, it was concluded that the increment in the P1-amplitude reflects facilitation of early visual processing. The N1 component, on the other hand, was associated with the application of a discrimination process to the attended location (Vogel & Luck, 1999). As in the unilateral, simple response condition subjects had no need to discriminate the features of the stimulus to perform the task, this would explain why only the initial pathway bias reflected in the P1 enhancement was evident in this condition (Mangun & Hillyard, 1991).

6.3 Experiment 8: Visual prosaccades with outline boxes

The subjects in Experiment 7 exhibited significant interstimulus contingency effects only in those trials in which the auditory target was presented opposite to the visual accompanying stimulus. We discussed two possible explanations for this result (see Chapter 5). First, the processing of contingency effects might have been related to the discrimination of stimulus modality. As the subjects were asked to make a saccade to the auditory target, in the disparate trials they first had to identify the modality of both stimuli before initiating the saccadic response in the direction of the auditory target. Second, as the contingency effects only occurred in the disparate trials, their processing might have been related to the choice of direction for the saccadic eye movement.

In order to test between these possibilities, we introduced two outline boxes right and left of fixation which indicated the possible locations for the visual target. If the processing of interstimulus contingencies was related to stimulus modality, subjects should show a similar null result as in Experiment 1 on visual prosaccades without outline boxes (see Chapter 2). However, if the contingency effects occurred due to the choice of target direction, the subjects should exhibit similar or even larger contingency effects than in Experiment 7.

The summary of the literature on visual prosaccades in a visual distractor task (see above) indicated that the presentation of two visual stimuli with equal amplitude, but in opposing hemispheres, has a significant effect on visual prosaccade latencies. However, as the experiments by Walker *et al.* (1995) and Weber and Fischer (1994) showed, this effect was less evident when the visual distractor was presented simultaneously with the target and permanently throughout the duration of each trial. Accordingly, we expected our outline boxes to show only a minor effect on the prosaccade latencies.

Also, we hypothesised that the subjects should exhibit about as much express saccades as in Experiment 1 (Weber & Fischer, 1994). The third hypothesis was that the subjects should show similar effects of intersensory facilitation and temporal as well as spatial contiguity as in Experiment 1 (see Chapter 2). As the saccade amplitudes were pre-determined by the outline boxes, we did not expect them to be affected by interstimulus contingencies. Finally, in order to compare the results as closely as possible with the data of Experiment 7, we decided to analyse the direction errors with respect to their latency, amplitude, number of corrections, correction times, and amplitudes of corrective saccades (see Section 5.3.2.4).

6.3.1 Method

6.3.1.1 Participants

Three students (age 19-24 years) of the University of Oldenburg took part in the experiment. They had not participated in any psychophysical experiment before. All subjects had right eye dominance. They had normal hearing and normal or corrected-to-normal vision. They received partial course credit for participation. All subjects gave their informed consent prior to their inclusion in the study. They were not informed about the specific hypotheses under study.

6.3.1.2 Task and procedure

Experiment 8 was identical to Experiment 7 (see Chapter 5), except for the following: First, two outline boxes ($1^\circ \times 1^\circ$, approximately 11 cd/m^2) defined the target locations. The boxes were horizontally aligned. They were visible throughout the duration of each trial. The visual target was presented in the middle of either one of the boxes at 15° right or left of a central fixation point. Second, the task was to make an eye movement as quickly and as accurately as possible to the visual target and to use the accompanying auditory stimulus as a possible, but unreliable, cue for the location of the visual target. Third, no feedback was given. Finally, saccades directed to the unimodal visual or auditory stimulus, either presented alone or in one of the outline boxes, were measured in separate blocks at the end of the sessions.

6.3.2 Results

Trials in the 20% and 80% ISC blocks were recoded according to their effective validity (see right panel of Figure 2.1). In the following, only those trials in which the saccade amplitudes started at less than 1° off the fixation point were considered for the analysis of saccade latencies and amplitudes.

6.3.2.1 Saccadic reaction times

The regular SRTs were submitted to a three-way ANOVA with SOA, spatial congruence (coincident vs. disparate), and ISC validity (20%, 50%, or 80%) as repeated factors. Three main effects and a marginally significant interaction effect of SOA * ISC validity

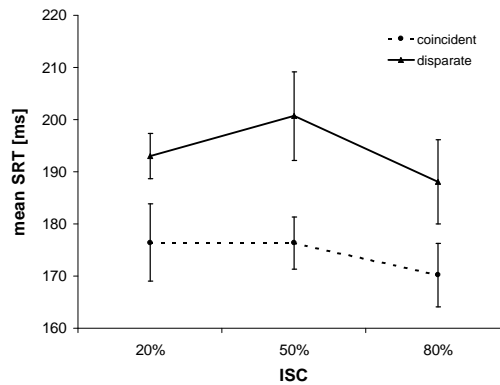


Figure 6.1: *Interstimulus contingency (ISC) effects on the saccadic reaction times (SRT). Latencies were significantly shorter in 80% ISC than in 50% and 20% ISC.*

emerged. The main effect of SOA ($F_{2,2} = 49.3, p < 0.002$) indicated that the latencies were the longer the later the visual target was presented after the auditory accompanying stimulus. The second main effect of spatial congruence ($F_{1,2} = 286.7, p < 0.003$) indicated 20 ms shorter latencies on average to coincident than to disparate stimuli. The third main effect, the effect of ISC validity ($F_{2,2} = 8.2, p < 0.038$), was due to shorter latencies in 80% ISC than in 50% ISC and 20% ISC (see Figure 6.1). The marginally significant interaction effect of SOA * ISC validity was due to shorter latencies in 80% ISC than in 50% and 20% ISC in the SOA = -40 ms.

When the SRTs were analysed with separate ANOVAs for each subject, the main effects of SOA, spatial congruence, and ISC validity were significant in all subjects. Newman-Keuls post-hoc tests indicated that the main effect of ISC validity consisted in overall shorter SRTs in 80% ISC than in 20% ISC and 50% ISC in all subjects (see Figure 6.2). Subject MF showed significant interaction effects of SOA * ISC validity, SOA * spatial congruence, and spatial congruence * ISC validity. The interaction effect of SOA * spatial congruence, which also was marginally significant in subject RN, was due to shorter latencies in the coincident trials of SOA = -40 ms. The interaction effects of SOA * ISC validity indicated significant contingency effects only in SOA = +40 ms. Finally, the interaction effect of spatial congruence * ISC validity was due to significant contingency effects only in the disparate trials.

Express saccades Subjects MF and NS exhibited a significant number of express saccades. An analysis of the relative frequencies of gaze direction showed that they gazed more often in the direction of the stimuli presented coincidently and to the auditory stimulus when presented disparate to the visual target than to the visual target when presented disparate to the auditory stimulus. Sometimes they even gazed opposite to both stimuli.

To examine the effect of contingencies on express saccade behaviour, the correct express saccades were sorted by effective ISC validity (see right panel of Figure 2.1). The number of express saccades in each ISC condition was then divided by the total number of bimodal trials measured in the respective ISC condition in order to account for the dif-

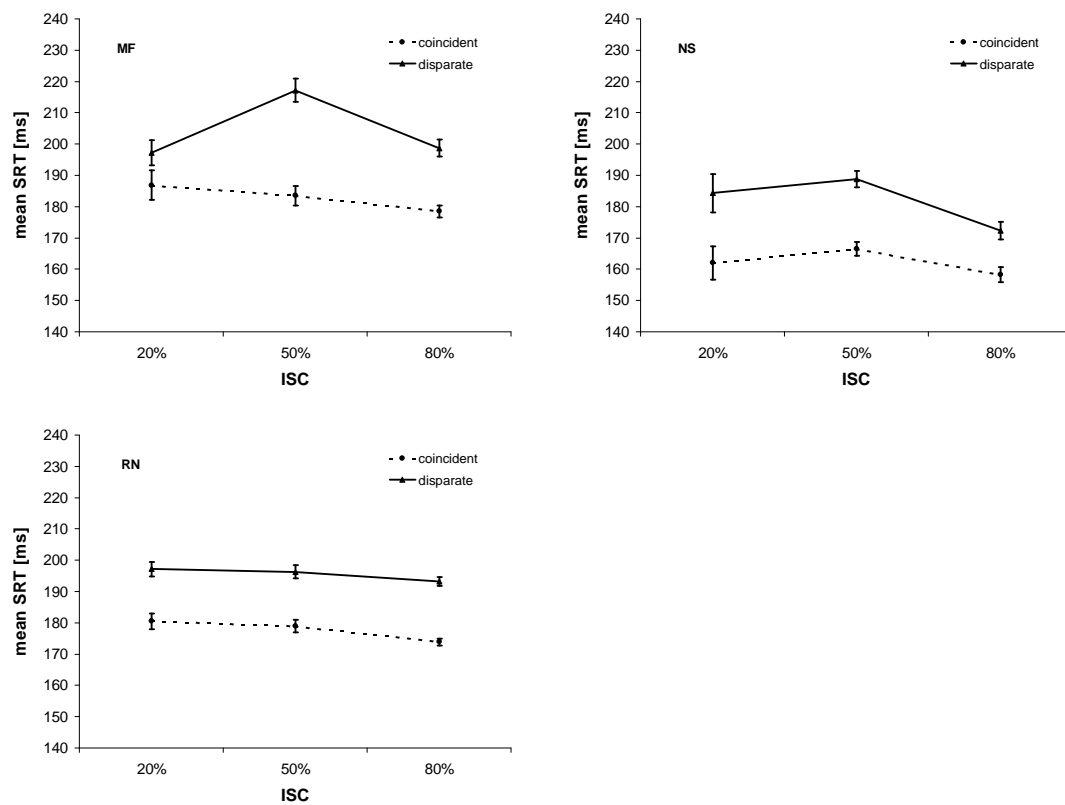


Figure 6.2: *Effects of interstimulus contingency (ISC) on the saccadic reaction times (SRT) for each subject separately. They all exhibited shorter latencies in 80% ISC than in 50% and 20% ISC. Subject MF showed a significant interaction effect of ISC validity with spatial congruence (coincident vs. disparate).*

Table 6.1: *Relative frequency of correct express saccades sorted by effective contingency validity for each subject.*

| Subject | Contingency validity | | |
|---------|----------------------|--------------|---------------|
| | 20% | 50% | 80% |
| MF | 1/103 = 0.01 | 3/177 = 0.02 | 14/418 = 0.03 |
| NS | 3/57 = 0.05 | 4/287 = 0.01 | 40/291 = 0.14 |
| RN | 1/150 = 0.01 | 2/203 = 0.01 | 3/610 = 0.01 |

ferent numbers of trials obtained especially in 20% and 80% ISC. The relative frequency of express gaze is summarised in Table 6.1 separately for each subject.

A Chi-square test on the relative frequencies of subject NS did reach significance. She exhibited more express saccades in 80% ISC and less express saccades in 50% ISC than would be expected (see Table 6.1).

6.3.2.2 Saccade amplitudes

Separate ANOVAs were conducted for each subject and rightward *vs.* leftward saccades with ISC validity and spatial congruence (coincident *vs.* disparate) as unrepeatd factors. Only those effects are reported which were accompanied by equivalent effects in the peak velocities. Only subject NS showed a significant main effect of ISC validity in the leftward saccades and significant interaction effects of spatial congruence * ISC validity in both directions of gaze. The main effect of ISC validity consisted in shorter saccade amplitudes in 20% and 80% ISC than in 50% ISC (mean difference = 1.1°, SD = 0.27°). Subject MF showed a main effect of spatial congruence in the rightward saccades indicating shorter saccade amplitudes to coincident than to disparate stimuli (mean difference = 0.6°).

6.3.2.3 Visual-auditory facilitation in saccadic reaction times

First, we analysed the results of the control trials in which the subjects either made saccades to the visual or auditory stimulus presented alone or in one of the outline boxes. Separate ANOVAs were conducted for each stimulus modality (visual or auditory) with type of presentation (with or without outline boxes) as unrepeatd factor. Saccade latencies to the unimodal visual stimulus were significantly shorter when it was presented alone than when it was presented in one of the outline boxes (211 ms, alone, 226 ms, with boxes). The reverse was true for saccades to the unimodal auditory stimulus: Latencies were significantly longer when the auditory stimulus was presented alone than when it was presented in one of the outline boxes (187 ms, alone, 203 ms, with boxes).

As in the bimodal trials of the main experiment the visual target was presented in one of the outline boxes it was compared to those control trials in which the unimodal visual and auditory stimulus were presented in the same conditions. A one-way ANOVA

Table 6.2: *Relative frequency of direction errors for each subject. The second column indicates the relative frequency with which these errors were corrected by a second saccade crossing the midline of presentation in the direction of the visual target.*

| Subject | Type of trial | |
|---------|----------------|---------------|
| | Error | Corrected |
| MF | 119/799 = 0.15 | 27/119 = 0.23 |
| NS | 159/747 = 0.21 | 9/159 = 0.06 |
| RN | 33/990 = 0.03 | 27/33 = 0.82 |

with stimulus modality (visual, auditory, or bimodal) as unrepeatd factor was highly significant ($F_{2,2504} = 120.1, p < 0.001$) indicating shorter saccadic reaction times to unimodal auditory and bimodal stimulation (187 ms and 182 ms) than to the unimodal visual stimulus (226 ms).

6.3.2.4 Direction errors

In this subsection we will first describe some general descriptive statistics on the relative frequency, latencies, and saccade amplitudes of the direction errors. In a second step, we will analyse whether the direction errors were affected by interstimulus contingency effects. By direction errors we mean those trials where the subjects gazed at the auditory accompanying stimulus when it was presented opposite to the visual target. Corrected errors are defined as those trials where the subjects first gazed at the auditory accompanying stimulus and then, after a certain time interval, made a second, corrective saccade which crossed the midline of presentation (meridian) in direction of the visual target.

Descriptive statistics Table 6.2 shows that the subject committing the less errors corrected them frequently, whereas the subjects committing much more errors corrected them less often. This observation was confirmed by separate Chi-square tests for each subject.

Separate ANOVAs for each subject comparing the SRTs of correct and erroneous saccades reached significance in all subjects indicated shorter latencies in the erroneous than in the correct saccades (see Table 6.3). About 90% of the direction errors occurred in the disparate trials. In subject NS these errors had significantly shorter latencies than the direction errors in the coincident trials ($t_{1,157} = 1.98, p < 0.05$).

All subjects exhibited significant differences in the saccade amplitudes of correct saccades and corrected errors¹ (mean difference = 3.7° , $SD = 2.17^\circ$, leftward; mean difference = 3.5° , $SD = 0.63^\circ$, rightward) indicating overall shorter saccade amplitudes in the first saccade of corrected errors. t-tests comparing the landing positions of the corrective saccades of corrected errors with the amplitudes of correct saccades reached significance

¹In this analysis also the saccades starting $\pm 1^\circ$ off fixation were included because of lack of trials.

Table 6.3: Means and standard deviations of the latencies of correct visual prosaccades and direction errors.

| Subject | Correct antisaccades | Prosaccade errors |
|---------|----------------------|-------------------|
| MF | 189 \pm 35 | 180 \pm 42 |
| NS | 172 \pm 32 | 148 \pm 42 |
| RN | 184 \pm 26 | 162 \pm 40 |

only in subject RN in the leftward saccades. She exhibited landing positions of the second, corrective saccades of corrected errors further from fixation than the landing positions of the correct saccades (mean difference = 2.9°).

Interstimulus contingency effects For each subject the relative frequency of direction errors separated by effective ISC validity is shown in Table 6.4. The number of direction errors in each contingency condition was divided by the total number of bimodal trials in that condition in order to account for the different numbers of trials obtained especially in 20% and 80% ISC.

Separate Chi-square tests were conducted for each subject comparing the number of direction errors in the different contingency conditions with the number of correct trials in the same conditions. In the subjects MF and RN these tests were significant. As can be deduced from Table 6.4, they exhibited more errors in 20% ISC and less errors in 80% ISC than would be expected.

The comparison of saccade latencies and amplitudes of the direction errors in the different contingency conditions revealed large interindividual differences. Subject NS showed shorter latencies in 20% and 80% ISC than in 50% ISC (143 ms, 139 ms, and 161 ms) in the first saccade of all errors. We calculated the time interval between the start of the first and the start of the second, corrective saccade in corrected errors for those trials where the corrective saccades crossed the meridian in direction of the visual target. This correction interval was marginally shorter in 20% ISC than in 50% ISC for subject RN (83 ms vs. 114 ms). Finally, subject MF exhibited endpoints nearer to fixation in 80% ISC than in 50% ISC in the right direction of the second, corrective saccade of corrected errors (mean difference = 2.4°). No other effects reached significance.

6.3.2.5 Summary

The saccadic reaction times showed main effects of SOA, spatial congruence, and ISC validity. Latencies were the longer the later the visual target was presented after the auditory accompanying stimulus, and if the stimuli were presented disparately. The main effect of ISC validity indicated shorter latencies in 80% ISC than in 50% ISC and 20% ISC. The same was true when the latencies were analysed separately for each subject. Two of the subjects exhibited a significant number of express saccades. One of these subjects exhibited more express saccades in 80% ISC and less express saccades in 50% ISC than

Table 6.4: *Relative frequency of direction errors for each subject according to effective contingency validity.*

| Subject | Contingency validity | | |
|---------|----------------------|---------------|---------------|
| | 20% | 50% | 80% |
| MF | 33/135 = 0.24 | 40/214 = 0.19 | 46/450 = 0.10 |
| NS | 28/82 = 0.34 | 61/344 = 0.18 | 70/321 = 0.22 |
| RN | 13/162 = 0.08 | 8/209 = 0.04 | 12/619 = 0.02 |

would be expected. The same subject showed a significant main effect of ISC validity in the amplitudes of the regular saccades to the left and significant interaction effects of spatial congruence * ISC validity in both directions of gaze. The main effect of ISC validity consisted in shorter saccade amplitudes in 20% and 80% ISC than in 50% ISC. A second subject showed a main effect of spatial congruence in the rightward saccades indicating shorter saccade amplitudes to coincident than to disparate stimuli.

The analysis of direction errors revealed that two subjects exhibited more errors in 20% ISC and less errors in 80% ISC than would be expected. The comparison of saccade latencies and amplitudes of the direction errors in the different contingency conditions further revealed interindividual differences in response strategy. Subject NS showed shorter latencies in 20% and 80% ISC than in 50% ISC in the first saccade of the direction errors. The time interval between the start of the first and the second saccade of corrected errors was marginally shorter in 20% ISC than in 50% ISC for subject RN. Finally, subject MF exhibited endpoints nearer to fixation in 80% ISC than in 50% ISC in the right direction of the second, corrective saccade of corrected errors.

In general, the saccadic reaction times to unimodal auditory and bimodal stimulation were shorter than to the unimodal visual stimulus. All subjects showed shorter latencies in the direction errors than in the correct saccades. About 90% of the direction errors occurred in the disparate trials. In one subject these errors had significantly shorter latencies than the direction errors in the coincident trials. All subjects exhibited shorter saccade amplitudes in the first saccade of corrected errors than in the correct saccades. One subject exhibited landing positions of the second, corrective saccades of corrected errors further from fixation than the landing positions of the correct saccades.

6.4 Discussion

Experiment 8 investigated visual-auditory interstimulus contingency effects in visual pro-saccades with visual outline boxes. All three subjects exhibited significantly shorter saccade latencies in the positively correlated contingency than in the control condition. We thus concluded that the processing of interstimulus contingencies was related to the choice of saccade direction.

Note that the auditory prosaccades in the disparate trials of Experiment 7 and the visual antisaccades in Experiment 6 also implied a choice in saccade direction (see Chapters 5 and 4.1). Correspondingly, the contingency effects observed in all three experiments may be explained by the same processing account (see General Discussion for details).

However, the overall saccade latencies in the present study were about as short or even shorter than the auditory prosaccades and the visual antisaccades. In this sense, the present experiment is the first to provide evidence that interstimulus contingencies can affect the preparation of very short saccade latencies.

Contrary to our hypothesis, one of the subjects exhibited a main effect of contingencies on the saccade amplitudes. Also, two subjects showed shorter saccade amplitudes in the coincident than in the disparate trials. As the subjects also exhibited shorter saccadic reaction times in the latter conditions, the amplitude effects might hint to a speed-accuracy trade-off in the processing of interstimulus contingencies and spatial contiguity. Note that this result further supports our conclusion that the present study establishes a lower bound for the speed and accuracy in the processing of interstimulus contingencies.

The analysis of the control trials showed that the outline boxes had differential effects on the saccade latencies of unimodal visual and auditory stimuli. With visual stimulation the latencies were shorter when the target was presented without outline boxes, but the reverse was true for the auditory stimuli. In the visual domain, this result confirmed the general observation in a visual distractor task that reaction times are longer with bilateral stimulation. Note, however, that this effect was much smaller than in the study by Walker *et al.* (1997). The difference in the remote distractor effect may be explained by the form of the visual stimuli. While in the visual distractor task the subjects generally are presented with two different visual forms which have to be discriminated in order to identify the target, in the present study only one target was presented in one of the outline boxes and the subjects only had to choose the saccade direction. Therefore, the difference in saccade latencies between the two visual control conditions may estimate the minimum time it takes to choose the saccade direction.

The difference in saccade latencies in the auditory control trials, on the other hand, may have been related to an intersensory facilitation effect (see Section 1.5). In fact, the auditory latencies with outline boxes were about as fast as the bimodal latencies in the main experiment. In the auditory domain, the visual outline boxes thus did not interfere with but facilitated the preparation of auditory prosaccades.

Note that the overall IFE effect as well as the temporal and spatial contiguity effects were comparable to Experiment 1 on visual prosaccades without outline boxes. Furthermore, for two of the three subjects the contingency effects occurred independently of contiguity. Note that a similar result was obtained in Experiment 6 on visual antisaccades. Therefore, we might conclude that interstimulus contingencies generally are processed independently of contiguity effects.

The analysis of express saccades confirmed the results by Weber and Fischer (1994) that continuously presented distractors or outline boxes only have a small effect on their occurrence. In fact, the subjects exhibited about as much express saccades as in Experiment 1 without outline boxes (see Chapter 2), but the range of SOAs in the present study was much smaller. This result might indicate that the presentation of the outline boxes facilitated the occurrence of express saccades, possibly due to the IFE effect in the

processing of the unimodal auditory stimulus presented in one of the outline boxes (see above). Further research is necessary to investigate this question.

Finally, the analysis of direction errors showed that about 90% of these errors occurred in the disparate trials, and two of the three subjects exhibited more errors in 20% ISC and less errors in 80% ISC than would be expected. These results further support our conclusion that the processing of contingencies is related to the choice of saccade direction. In the 80% ISC blocks, the subjects were prepared to respond to 80% coincident trials. Therefore, in the 20% disparate trials the subjects were less prepared to inhibit the auditory stimulus opposite to the visual target, thus leading to more errors. However, in the 20% ISC blocks, the subjects were prepared to inhibit the auditory accompanying stimulus which occurred opposite to the visual target in 80% of the trials. This preparation thus may have precluded the occurrence of errors. The hypothesis of stronger response preparation in 80% ISC or 20% ISC than in 50% ISC was further supported by the two subjects who showed shorter latencies in the first saccade of the direction errors and shorter correction times in the correlated contingencies than in the control condition.

In summary, all subjects exhibited shorter saccade latencies in the positively correlated contingency than in the control condition. This result confirmed our hypothesis that the processing of interstimulus contingencies was related to the choice of saccade direction which was operationalised in the presentation of two outline boxes. Our hypothesis was further supported by the observations (1) that most of the direction errors occurred in the disparate trials and (2) two of the three subjects exhibited more errors with shorter latencies or correction times in 20% ISC than in 80% ISC.

Furthermore, because of the short overall saccade latencies, the present study provides evidence that interstimulus contingencies can affect early stages of saccade preparation. However, these contingency effects on saccade latencies might occur at expense of accuracy as was indicated by the less accurate saccade amplitudes of two subjects. Finally, the present data and the results of Experiment 6 on visual antisaccades indicated that interstimulus contingencies are processed independently of temporal and spatial contiguity.

7

The ILAT model

In the literature on oculomotor control, mainly two classes of models can be distinguished. Neural field models (Kopocz, 1995; Grossberg, Roberts, Aguilar & Bullock, 1997) demonstrated that saccadic reaction times can be accounted for by the dynamic coordination of artificial neurons which closely reflect the activity patterns of real neurons, *e.g.* in the superior colliculus of primates (Trappenberg *et al.*, 2001). The second class of models can be characterised as sequential sampling or accumulator models such as diffusion and Linear Approach to Threshold with Ergodic Rate (LATER) models. These models suppose that in response to a stimulus, a signal in the brain grows until it reaches a threshold, thereby triggering a motor response to the stimulus.

In this chapter, we will first describe the LATER model by Carpenter (1981) before we will then explain in detail the modifications which have been introduced in this thesis in order to account for visual-auditory interstimulus contingency effects in auditory prosaccades (see Chapter 5). In the last sections, we will estimate the parameters of the new model by Monte Carlo simulations, and the results of the simulations will be discussed with respect to the data obtained in Experiment 7.

7.1 The LATER model by Carpenter (1981)

Carpenter (1981), and later Carpenter and Williams (1995), were concerned about the variability which is characteristic of saccadic reaction times (SRTs). Carpenter (1981) argued that the steady increase in presaccadic activity of visuomotor neurons in the brainstem and several cortical areas as *e.g.* the frontal eye fields (FEFs) of macaque monkeys may constitute a possible physiological counterpart of the variability in SRTs. As the responses of visuomotor neurons have been shown to be more closely related to the subsequent saccade than to the processing of the stimulus (see Schall, 1991, for a review), Carpenter (1981) and Carpenter & Williams (1995) proposed that the variation of saccade latencies may be due to the stochastic nature of decision processes rather than due to the noise in the target detection times (also see Carpenter & Reddi, 2001).

Their assumption was confirmed in several single-cell recordings investigating the countermanding task. In some infrequent trials, subjects were presented with an imperative stop-signal. They were asked to withhold the impending movement if the stop-signal occurred (stop trials) or to make a saccade to the visual target if no stop-signal was present (control trials). Hanes and Schall (1996) showed that the latency-distributions generated by a monkey in the control trials could be predicted by a simulation of the LATER model using parameters derived directly from measures of the activity of individual neurons in the monkey's frontal eye fields. Also, the maximum level of activity that was measured in successfully inhibited stop trials was shown to be significantly less likely to reach the trigger threshold than in trials when the monkey executed the movement. These results thus confirmed that the variability in the timing of saccadic eye movements is a consequence of a particular form of stochastic variability in neural circuits carrying the decision signal to initiate a voluntary movement (also see Hanes, Patterson & Schall, 1998; Schall, Hanes & Taylor, 2000).

7.1.1 Description of the LATER model

The LATER model assumes that a decision signal S starts to rise at s_0 in response to the target at a constant rate r until, at a time t , it crosses a fixed threshold level θ at which point a response is initiated (see Figure 7.1). The rate r is assumed to vary randomly from trial to trial, with a Gaussian distribution of mean μ and variance σ^2 . On any one trial, the (saccade) latency t thus can be described as $(\theta - s_0)/r$. However, because the rate r varies from trial to trial, so does the latency t , resulting in a skewed latency distribution as is commonly observed for (saccadic) reaction times.

In the terminology of the model, the decision signal S reflects a measure of the accumulated information that a particular response to a possible stimulus is required. The threshold θ corresponds to the confidence level required before commitment to a particular course of action (Reddi & Carpenter, 2000). The mean rate of rise μ is related to the attentional or motivational significance of the stimulus evoking it (Carpenter, 1981).

Carpenter & Williams (1995) further predicted that the initial activity level s_0 depends on the prior probability of the target being present, and when reduced causes an increase in saccade latency (see Figure 7.1). They tested this prediction by systematically varying the probability that a visual target was presented either to the left or right of fixation. In an overlap task, human subjects were asked to make a saccade to the peripheral target. After some practice, subjects' latencies gradually changed to reflect these prior probabilities, *i.e.* latencies to expected targets became shorter, whereas latencies to unexpected targets became longer. When the latency-distributions in each probability condition were plotted cumulatively with a reciprocal time axis and probit ordinate, all distributions fell on straight lines as was predicted by the model (see Carpenter, 1981, for details).

Furthermore, as prior probability increased, the cumulative distributions became shallower and converged onto a constant infinite-time intercept of the ordinate. These observations clearly indicated that the reduction in latency with increasing prior probability was due to the shorter distance between the fixed threshold θ and the initial activity level s_0 rather than due to a change in the mean rate μ (of the decision signal S) which would have displaced the curves parallel to one another (Carpenter & Williams, 1995).

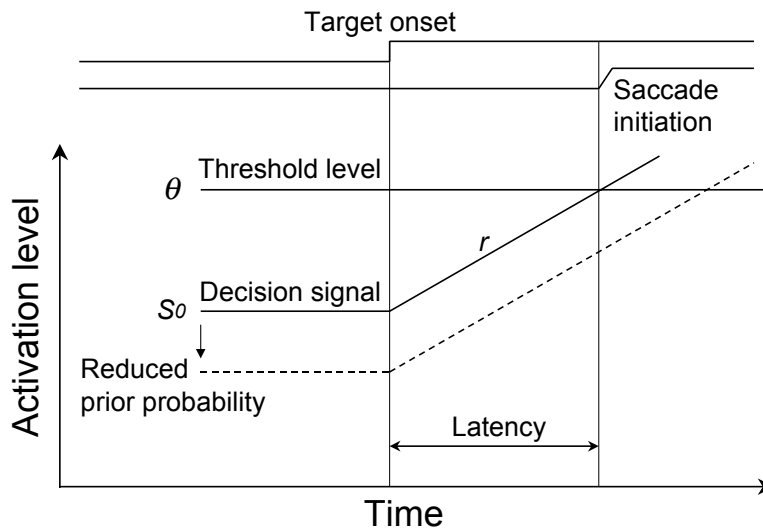


Figure 7.1: *The LATER model for initiating saccades. A decision signal S , initially s_0 , starts to rise in response to a target at a constant rate r until it crosses a fixed threshold level θ at which time a saccade is initiated. The initial activity level s_0 depends on the prior probability of the target being present [at a certain location], and when reduced causes an increase in latency. Reprinted from Carpenter and Williams (1995).*

7.1.2 Comparison of LATER to diffusion models

There may be three major differences between LATER and diffusion models. First, the rate of rise, which in LATER varies from trial to trial, varies also during a trial in diffusion models (Ratcliff, 1978; 1988). Diffusion models assume that the drift (equivalent to rate of rise) is accumulated continuously over time instead of in discrete steps as in LATER. The slope of the mean drift is often directly related to stimulus characteristics as *e.g.* stimulus intensity (Diederich, 1995). It was argued that a high intensity stimulus provides more information than a weak intensity stimulus and thus should have a larger drift rate. A process with a larger drift rate should reach the decision boundary sooner which means that the response times should be shorter. With alike assumptions, diffusion models thus can directly account for different stimulus characteristics of the target, while LATER models suppose a more simple, linear process to account for later stages of processing, such as the decision to initiate a movement.

The second difference between LATER and diffusion models lies in the definition of response time. In LATER, response time is defined as the time when the decision signal crosses the response threshold, whereas in diffusion models a constant time of encoding and response execution is added to the time of reaching the boundary. Conceptually speaking, diffusion models thus place all variability in the early stage of sensory processing.

Finally, the number of boundaries (equivalent to thresholds) to be reached by the drift define the third difference between LATER and diffusion models. While LATER as-

sumes one single threshold, diffusion models postulate two boundaries, *e.g.* one for each response in a two-choice decision task (Ratcliff, van Zandt & McKoon, 1999). Erroneous responses are explained by the variability of the drift which, during anyone trial, may drive the accumulation process to the wrong boundary and thus may initiate the wrong response.

Note that diffusion models directly relate the occurrence of errors to the noise in the accumulation process carrying sensory information. However, as Ratcliff (2001) argued, LATER has no such explicit mechanism to account for errors. On the other hand, LATER can explain the occurrence of errors if two independent processes are assumed to race against each other (Carpenter & Reddi, 2001). In the countermanding task (see Section 7.1), if the go-process reaches the threshold before the stop-process, a response is initiated. Simulations of this LATER race model correctly predicted the probability of successful saccade inhibition and also the latency-distributions of erroneous responses in stop trials (Hanes & Carpenter, 1999; Colonius, Özyurt & Arndt, 2001). In sum, both kinds of models can account for errors. Diffusion models relate them to the noise in a single sensory signal moving to one out of two boundaries, while LATER models relate errors to at least two independent decision signals racing to a single response threshold.

7.2 The ILAT model for visual-auditory contingency effects in auditory prosaccades

In order to explain the interstimulus contingency effects observed in Experiment 7, we decided to adopt the logic of LATER, because this model emphasises the decision stage which was supposed to be the most relevant part in the processing of interstimulus contingencies (see Section 6.4).

7.2.1 Description of ILAT

The LATER model by Carpenter (1981) was changed in several significant ways. First, we assumed two separate decision signals for the visual and auditory stimulus respectively (S_A and S_V). Their respective rate of rise will be called r_A and r_V . In Experiment 7, the visual accompanying stimulus was presented 40 ms before (–), simultaneously, or 40 ms after (+) the auditory target. In order to account for these stimulus onset asynchronies (SOAs) in the model we allowed S_V or S_A to start 40 ms before the respective alternative signal. For the SOAs unequal to zero we thus subdivided the time axis into two separate time intervals. This division into separate time intervals defined the name of the new model: per Interval Linear Approach to Threshold (ILAT). In the model, each time interval was defined by a separate rate of rise r which could either be unimodal or bimodal. The second rate of rise in the second time interval started at the final activation level of the first rate of rise in the first time interval (see Figure 7.2). The overall process finished when the second, bimodal rate of rise r_{AV} reached the fixed threshold¹.

¹Note that the latter restriction to finish the process only if the bimodal rate crosses the threshold is no necessary condition for the correct functioning of the model. It was introduced in a first approach in order

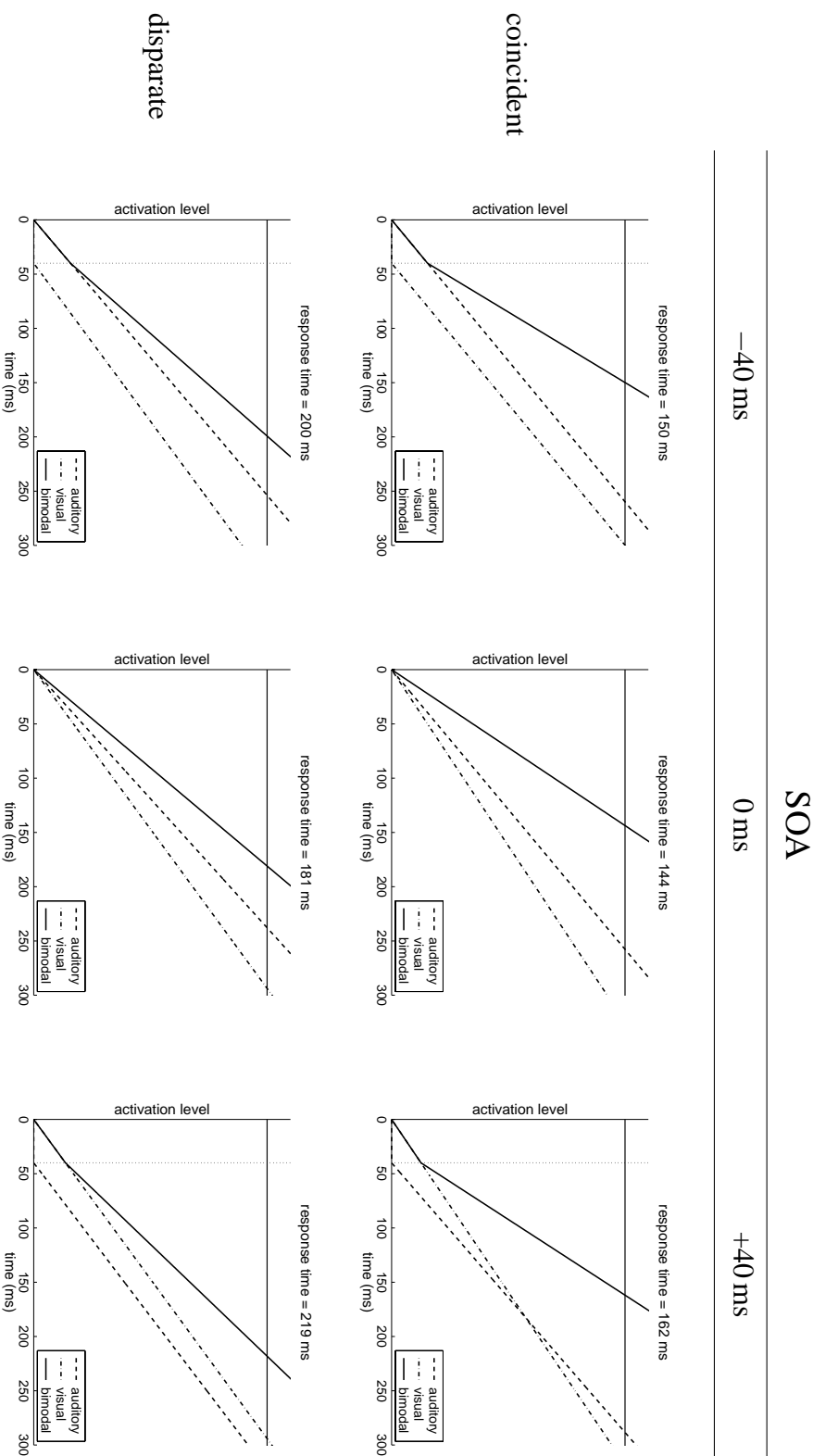


Figure 7.2: Illustration of ILAT. In hypothetical trials, the respective rates of the visual and auditory stimulus rise toward the fixed threshold (horizontal dotted line). At the time that the auditory and visual stimulus are presented in parallel, their rates form a combined rate as is defined in Expression 7.1. The first signal crossing the threshold defines the reaction time which is indicated at the top of each panel. In the stimulus onset asynchrony (SOA) = -40 ms, the bimodal rate of rise first is defined only by the auditory signal until - after 40 ms - the visual accompanying stimulus is presented (indicated by the vertical dotted line) and vice versa in the SOA = +40 ms. The first respective the second three panels illustrate the predictions in the coincident and disparate trials.

For the time interval in which the visual and auditory stimulus were presented in parallel, they were assumed to coactivate a common process which was expressed as the sum of auditory and visual rates of rise. With this assumption we accounted for intersensory integration effects (see Section 1.5). Furthermore, for the disparate trials in which the auditory target was presented opposite to the visual accompanying stimulus, the spatial parameter d was subtracted from the sum of both rates of rise. In so doing we accounted for interhemispheric inhibition.

In analogy to Carpenter and Williams (1995), the effects of interstimulus contingency were expressed as the prior probability (bias) that the locations of the visual and auditory stimulus were correlated. Carpenter and Williams showed that the prior probability of target occurrence was best reflected in the initial activity level s_0 . In a similar vein, in the present model the bias was added to the compound bimodal rate of rise r_{AV} . Expression 7.1 defines the bimodal rate of rise for the coincident and disparate trials.

$$r_{AV} = \begin{cases} r_A + r_V + \text{bias} & \text{for coincident trials} \\ r_A + r_V - d + \text{bias} & \text{for disparate trials} \end{cases} \quad (7.1)$$

Remember that the visual and auditory stimulus in the present thesis were always presented with equal probability either to the right or left of fixation. Interstimulus contingency was defined as the conditional probability that the auditory target was presented at the same or opposite location as the visual accompanying stimulus. If the subjects were to use this kind of contingency information for improving their performance, they had to wait for the visual accompanying stimulus to be presented in order to build a spatial expectancy for the future location of the auditory target. For this reason, the bias in the model was added to the bimodal rate of rise r_{AV} rather than to the initial activity level s_0 (Carpenter & Williams, 1995).

Note that the latter assumption was the most parsimonious possible, because in the $\text{SOA} = +40$ ms, the subjects actually had more time to build the spatial expectancy on the basis of the location of the visual accompanying stimulus (see right panels of Figure 7.2) than was expressed in the bias. On the other hand, in the $\text{SOA} = -40$ ms, the auditory target was presented before the visual accompanying stimulus so that the subjects had less time to use the bias, because they almost already knew where to look at the time the visual accompanying stimulus was presented.

7.2.2 Predictions of ILAT

Generally speaking, ILAT makes the same predictions as the LATER model by Carpenter (1981) plus some extensions specifically related to intersensory interaction:

1. Response times are the faster the larger the mean rate of rise μ , as $\bar{t} = (\theta - s_0)/\mu$.
2. They directly depend on the difference between the initial activation level s_0 or bias and the threshold θ (Carpenter & Williams, 1995; Reddi & Carpenter, 2000).

to account for the correct responses in Experiment 7 in which the subjects always made a saccade in the direction of the auditory target in the presence of the visual accompanying stimulus.

If the threshold is fixed and the bias is increased, response times should be faster. However, if the bias is reduced, response times should be increased relative to a control condition (bias set to zero).

3. Stimulus onset asynchronies have a significant effect on response times. If the visual and auditory stimulus are presented simultaneously, response times should be faster than if they are presented with any temporal delay (see Figure 7.2).
4. Response times directly depend on the spatial congruence of the visual and auditory stimulus. If the stimuli are presented at the same location, response times should be faster than if they are presented with spatial disparity (subtraction of the spatial parameter d).
5. The variation of bias has a stronger effect if the stimuli are presented with spatial disparity rather than at the same location due to the overall shallower slope of the decision signal with disparate stimulation (subtraction of the spatial parameter d).
6. If any of the unimodal decision signals S_A or S_V reaches the boundary before the alternative signal was presented, the response is determined by that signal.

7.3 Test of ILAT by Monte Carlo simulations

The first five² predictions of ILAT were tested on the data set of Experiment 7. In analogy to the simulations of the LATER model in the countermanding task (Hanes & Carpenter, 1999; Colonius *et al.*, 2001), we conducted Monte Carlo simulations of ILAT whereby estimating the parameters of the model by minimising the sum of squared deviations between the mean saccadic reaction times observed in Experiment 7 and the mean of the simulated response times. For the minimisation, an unconstrained non-linear optimisation algorithm was used (fminsearch implemented in Matlab Version 5.3).

7.3.1 Procedure

The saccadic reaction times of each subject were separated by experimental conditions, resulting in overall 18 conditions per subject (3 SOAs * 2 spatial congruence * 3 ISCs).

The parameters of the model were estimated separately for each subject in three steps. In the first simulation, we estimated four parameters from the mean saccadic reaction times observed in 50% ISC (3 SOAs * 2 spatial congruence). The parameters were the mean rate of rise of the auditory target μ_A , the mean rate of rise of the visual accompanying stimulus μ_V , the spatial parameter d , and the standard deviation of the Gaussian distributions σ . Note that the standard deviation was assumed to be equal across all three decision processes (visual, auditory and bimodal). In analogy to Hanes and Carpenter

²Note that the last prediction can only be tested if the overall decision process is allowed to finish if no bimodal stimulation is (yet) present (see Section 7.2.1). It will take only a few more changes in the simulation program, but some more time for the simulations before the probabilities and response times of direction errors as expressed in the sixth prediction will be tested as well.

Table 7.1: Parameter estimates of the first simulation for each subject separately.

| Subject | μ_A [Hz] | μ_V [Hz] | d [Hz] | σ [Hz] | error [ms] |
|---------|--------------|--------------|----------|---------------|------------|
| BS | 5.01 | 2.94 | 1.46 | 0.16 | 6.6 |
| MK | 2.84 | 1.25 | 0.41 | 0.20 | 17.4 |
| RS | 3.97 | 3.41 | 2.08 | 0.24 | 2.3 |
| SN | 7.53 | 1.21 | 2.67 | 0.25 | 8.7 |
| ST | 4.52 | 1.05 | 1.77 | 0.19 | 34.7 |

(1999) and Colonius *et al.* (2001), we further assumed two irreducible minimum processing times of the visual (\min_V) and auditory (\min_A) stimulus which were set to 20 ms and 60 ms respectively³.

In the second simulation, the same experimental data was used to estimate the same first three parameters, while as a result of the first simulation the standard deviation was set to 0.2. With the last two parameters we estimated the irreducible minimum processing times \min_A and \min_V . Finally, in the third simulation, we held the estimated parameters of the second simulation constant when estimating the bias parameter from the observed saccadic reaction times either in 80% ISC or 20% ISC. With this implementation of the bias parameter we assumed that the effects of interstimulus contingency were independent of SOA (see Chapter 5). As the bias parameter was added to the bimodal rate of rise r_{AV} (see Expression 7.1), it resulted in a linear shift of all six mean saccadic reaction times (3 SOAs * 2 spatial congruence) up or down the response time axis. However, due to the spatial parameter d , we nevertheless expected a larger effect of the bias parameter on the disparate than on the coincident trials (see Prediction 5).

In each simulated trial, the rate of rise values r_A and r_V were selected randomly from Gaussian distributions with parameters μ_A , μ_V , and σ . The values of the decision signals S_A and S_V started in zero. After the times of SOA and irreducible minimum had elapsed, the decision signals were incremented in 1-ms time steps by r_A and r_V respectively. In those time intervals in which S_A and S_V were presented in parallel their rates of rise were added to form one composite bimodal rate of rise r_{AV} (see Expression 7.1). The point in time at which S_{AV} reached the threshold θ (set equal to one) determined the response time for this trial. In order to account for the unequal number of trials especially in 20% and 80% ISC, we simulated exactly as many trials as were obtained in each experimental condition and subject of Experiment 7.

7.3.2 Results

The parameter values estimated during the first simulation are shown in Table 7.1.

³An auditory stimulus presented close to the ear takes approximately 13 ms to activate a superior colliculus neuron, a nearby visual stimulus requires about 65-100 ms to reach the same neuron (cf. Stein & Meredith, 1993).

As can be seen in Table 7.1, we obtained rather different parameter estimations for each subject. However, the estimates of the standard deviations were very similar across subjects. We thus decided to run a second simulation in order to investigate whether the intersubject variability was due to the irreducible minimum processing times of the auditory and visual stimulus which had been held constant at 20 ms and 60 ms respectively. In the second simulation we defined these irreducible minimum processing times as parameters and held the standard deviation constant at 0.2. The results of the second simulation are shown in Table 7.2.

Table 7.2: *Parameter estimates of the second simulation for each subject separately.*

| Subject | μ_A [Hz] | μ_V [Hz] | d [Hz] | \min_A [ms] | \min_V [ms] | error [ms] |
|---------|--------------|--------------|----------|---------------|---------------|------------|
| BS | 5.79 | 2.61 | 1.43 | 30.4 | 79.8 | 2.3 |
| MK | 3.25 | 1.11 | 0.76 | 21.5 | 55.6 | 34.3 |
| RS | 4.14 | 2.92 | 2.03 | 12.9 | 60.2 | 6.8 |
| SN | 8.42 | 0.59 | 2.50 | 29.9 | 65.7 | 7.7 |
| ST | 4.35 | 1.13 | 1.89 | 13.5 | 30.8 | 22.4 |

A comparison of Tables 7.1 and 7.2 indicated that the two simulations resulted in very similar parameter estimations for all but subject ST. For the latter subject, the first three parameters obtained similar values in both simulation, but the irreducible minima were estimated too small to be valid, physiologically speaking (cf. Stein & Meredith, 1993). At least for this subject it might be revealing in future, more extended investigations of the model to run a further simulation with the irreducible minimum processing times held constant, but estimating different standard deviations of the three Gaussian distributions for the unimodal visual, auditory, and bimodal rates of rise.

Finally, in the third simulation we used the parameter values of the first simulation and estimated the bias parameter which reflected the effects of interstimulus contingency by shifting the pattern of six mean saccadic reaction times (3 SOAs * 2 spatial congruence) up or down the response time axis. The results of this simulation are shown in Figure 7.3.

The analysis of saccadic reaction times in Experiment 7 indicated that the subjects BS, MK, RS and ST exhibited shorter latencies in 80% ISC than in 50% ISC, while the subjects SN and ST showed longer latencies in 20% ISC than in 50% ISC.

If it is further acknowledged that a larger bias leads to shorter response times (see Prediction 1), it becomes evident that at least for the subjects RS, SN and ST the former results of Experiment 7 are perfectly reflected in the bias values estimated in the third simulation (see Figure 7.3). However, for the subjects BS and MK, the bias values were estimated to be always larger than zero. This result only made sense for subject MK who exhibited shorter latencies in 80% ISC than in 20% ISC which in turn were shorter than in 50% ISC. Inspection of the latency fits by the model for the two subjects showed that especially in 20% ISC they were less convincing than for the former three subjects.

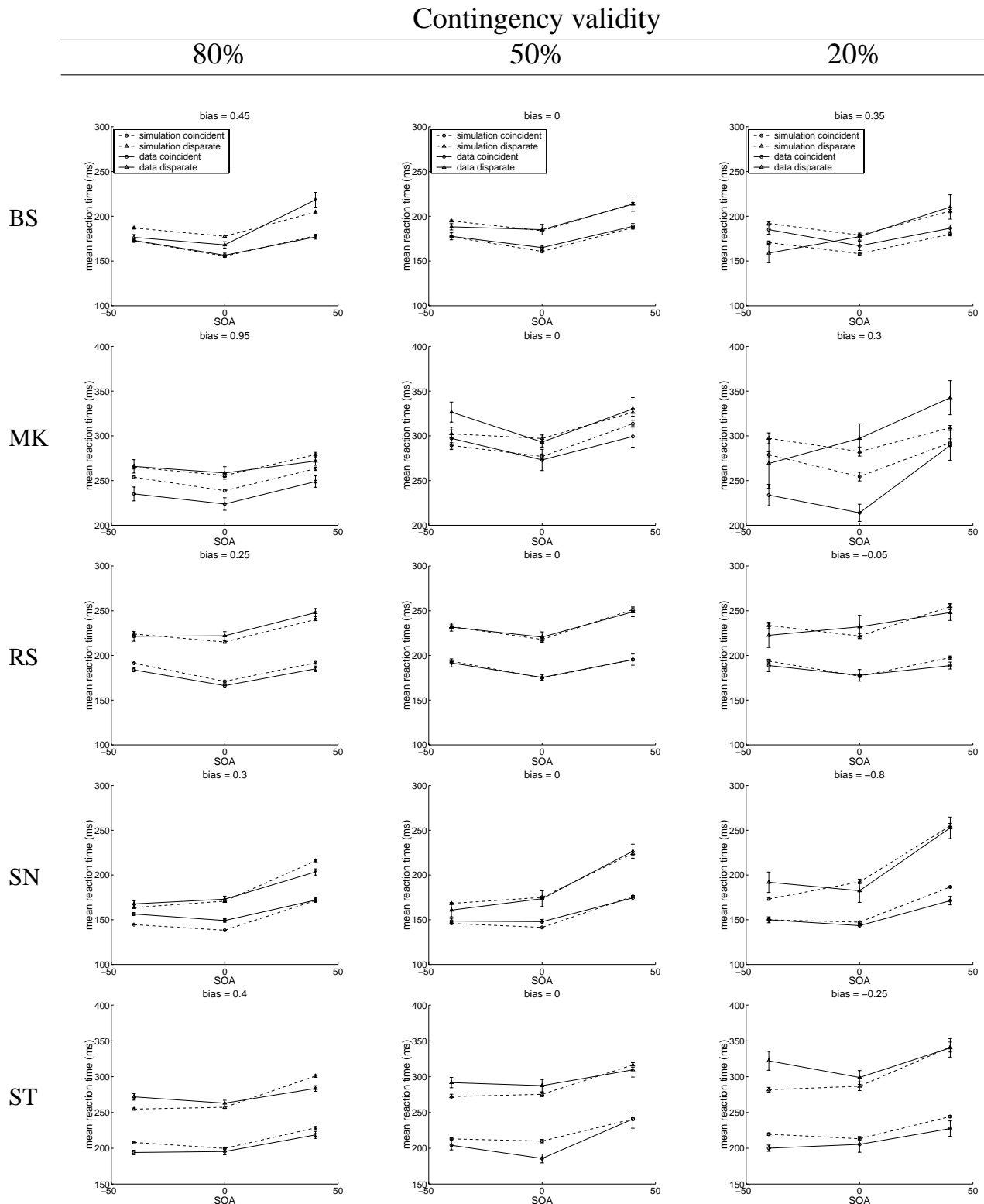


Figure 7.3: Comparison of model simulations (dotted lines) with the mean saccadic reaction times of Experiment 5 (straight lines) for each subject separately. Each panel illustrates the effects of stimulus onset asynchrony (SOA) and spatial congruence (coincident vs. disparate). The effects of interstimulus contingency (ISC) were estimated as the initial activity level (bias) resulting in a linear shift of all six mean saccadic reaction times up (+) or down (−) the response time axis. The respective bias estimates are indicated at the top of each panel.

7.4 Discussion

In this chapter, we have proposed a specific type of LATER model to account for interstimulus contingency effects in auditory prosaccades (see Chapter 5). In ILAT, two decision signals representing the visual and auditory stimulus respectively rise toward a fixed threshold. In those time intervals in which they are presented in parallel, they form a common, multimodal process which further depends on the spatial relation between the two stimuli. The response time is determined as the instance when this multimodal process reaches the response threshold. Interstimulus contingencies are expressed as a bias which linearly shifts the activation level of the multimodal decision signal toward or further away from the threshold leading to shorter or longer response times respectively.

Monte Carlo simulations of the model revealed large interindividual differences in the parameter estimates. However, this variability was independent of the common standard deviation of the three Gaussian distributions (unimodal visual, auditory and bimodal), and also occurred independently of the irreducible minimum times of the unimodal visual and auditory processes.

The estimates of the mean rates of rise of the auditory target were in the same range as corresponding estimates of the decision signals in the control trials of the countermanding task in which the subjects were asked to make a saccade to a visual target (Hanes & Carpenter, 1999; Colonius *et al.*, 2001). However, the estimates of the mean rates of rise of the visual accompanying stimulus in the present study were much smaller. These observations may confirm the assumption by Carpenter (1981) that the mean rates of rise reflect the attentional significance of the stimuli with respect to the task demands. If the visual stimulus is a target as in the control trials of the countermanding task, mean rates are high, but when the visual stimulus only has an accessory function as in the present study, mean rates are low.

Note that the mean rates of rise of the auditory target were comparable to the mean rates of visual targets in countermanding studies. This observation directly supports our interpretation in Chapter 5 that the auditory stimulus can become a target for saccadic eye movements. However, we also argued that it may be less effective in pre-programming a saccade than a visual target. It may thus be confirmed that the accumulation process in LATER models reflects the later stages of deciding to initiate a motor response to the auditory target in the presence of visual stimulation rather than earlier, sensory stages as is generally assumed in diffusion models.

In analogy to Carpenter and Williams (1995), interstimulus contingency effects were modelled as a linear shift of activation toward or away from the fixed threshold. For three subjects, this bias parameter reflected perfectly the contingency effects observed in the saccade latencies of Experiment 7. However, for further two subjects the overall fit of the model to the saccade latencies was less convincing, and the estimated biases were more difficult to interpret. This observation may indicate that the model was less powerful to the explanation of the results of these two subjects than it was for the former three subjects.

However, at this stage of evaluating ILAT it may be premature to decide whether it is actually capable of explaining the contingency effects observed in Experiment 7. A more conclusive assessment of the model could be achieved on the following lines. First, it seems desirable to run further simulations to estimate separate standard deviations for

each of the three Gaussian distributions of the visual, auditory and bimodal rates of rise, and to investigate whether the model can predict the probabilities and latencies of the direction errors (see Prediction 6). Second, it has not yet been established whether the parameter estimates are stable and whether they reflect the 'true' values of the underlying processes. For this, it seems desirable to derive the mathematical equations defining the model. These equations would allow to directly estimate the parameters rather than relying on simulations. Finally, future experiments need to investigate larger sample sizes in each experimental condition in order to fit the model to the whole empirical distributions.

8

General discussion

The principal aim of the present thesis was to determine whether human subjects exhibit interstimulus contingency effects in saccadic eye movements to simple visual and auditory stimuli. Contrary to most of the former investigations, the interstimulus contingencies were defined in the locations of a target and an accompanying stimulus rather than in the mere presence or absence of the stimuli. In all but one experiment, the subjects were asked to make a saccade in the direction of the visual (or auditory) target, and to use the auditory (or visual) accompanying stimulus as a possible, but unreliable cue, for the location of the saccade target. In the remaining antisaccade task, the subjects were asked to make a saccade opposite to the visual target. Our experimental procedure allowed to vary the respective spatial location of each stimulus separately, and to present the target with equal probability at either location thereby preventing stimulus repetition accounts.

Across all experiments, sixteen subjects exhibited interstimulus contingency effects in at least one experimental condition. This result supports the conclusion that visual-auditory interstimulus contingencies in a focussed attention task lead to facilitation of saccadic responses. The short mean latencies in the last two experiments further indicated that the learning about contingencies can be used very early in the programming of a saccadic eye movement. Lambert *et al.* (2000) investigated contingency effects in the locations of bilateral letter cues and a simple visual target. They observed about 100 ms longer mean saccadic latencies than in our last two experiments. In this sense, we established a lower bound in the time course of interstimulus contingencies. Note that this results supports the conclusion that the precise nature of the peripheral cue(s) determines the time course of interstimulus contingencies (Lambert *et al.*, 2000).

In the following, we will summarise and discuss our interstimulus contingency effects with respect to the saccadic reaction times, contiguity and intersensory facilitation effects, the occurrence of express saccades and saccade amplitudes. In the remaining sections we will outline a possible neurobiological processing account of visual-auditory interstimulus contingencies.

8.1 Saccadic reaction times

The analysis of the saccade latencies revealed reliable interstimulus contingency effects in seven of the eight experiments. They were accounted for by several different hypothesis: A minimum processing time of 200 ms, the need to recalculate the saccade amplitude, and the need to identify the target modality. The results of Experiment 8 on visual prosaccades with outline boxes indicated that the processing of interstimulus contingencies requires the choice in saccade direction. This conclusion was further supported by the observations that the subjects exhibited a considerable number of direction errors, and that these errors mainly occurred in the disparate trials and in 20% rather than in 80% ISC (see Section 6.4).

The postulate of the choice in saccade direction as a possible processing mechanism might also account for the interstimulus contingency effects in Experiment 6 on visual antisaccades. As was outlined in the introduction of Chapter 4, the programming of a visual antisaccade requires the inhibition of a reflexive prosaccade in the direction of the visual target, and the calculation of a saccade of equal eccentricity, but opposite direction to the visual target. The (cortical) structures involved in the (re-)direction of the saccadic eye movement thus may also be involved in the processing of interstimulus contingencies (see below). Note that this hypothesis cannot explain the large interindividual differences in the contingency effects of Experiment 6. As the subjects in all other experiments showed rather coherent contingency effects, the interindividual differences might constitute a specific outcome of the programming of visual antisaccades. Future research might investigate this point.

An even more stringent test of our postulate that the choice in saccade direction underlies the processing of interstimulus contingencies was provided in the results of the first and seventh experiment on visual and auditory prosaccades respectively. When the subjects exhibited reflex-like prosaccades in Experiment 1 and in the coincident trials of Experiment 7, only two of the seven subjects showed contingency effects. However, when in the disparate trials of the auditory prosaccade task the subjects had to inhibit the reflex-like saccade to the visual accompanying stimulus before programming the saccade in the opposite direction (in which the auditory target was presented), all subjects showed reliable contingency effects in the saccadic reaction times. This result thus confirmed our conclusion that the processing of spatial interstimulus contingencies requires the choice in saccade direction.

Note that the contingency effects in Experiment 7 and of two subjects in Experiment 6 supported the general observation that the reaction times in the invalid trials of the spatial cueing task are longer than in the valid trials (*e.g.* Cavegn, 1996; Sheliga *et al.*, 1995). On the other hand, the results in Chapter 3 and in three subjects of the Experiments 1 and 6 contradicted this conclusion as they indicated shorter saccade latencies in the negatively correlated contingency than in the control condition. While the results of subject MW in Experiment 6 may be explained by transfer effects from the bimodal go/no-go task, the remaining contingency effects in the first experiment and in Chapter 3 cannot be related to such accounts. However, the shorter saccade latencies in the negatively correlated contingency supported Schwartz (1996) who obtained faster manual reaction times to negatively correlated target and non-target letters in a divided attention go/no-go task. It

might thus be concluded that the shorter saccade latencies in the negatively correlated contingency constitute a specific effect of the go/no-go task.

This conclusion was further supported by Lambert *et al.* (2000) who reported longer saccade latencies in the rare trials in which the target was presented opposite to the likely location (invalid trials) than in the valid trials. This result thus confirmed that the processing of spatial interstimulus contingencies with bilateral letter cues result in longer saccade latencies in the invalid trials. As Lambert *et al.* (2000) presented outline boxes right and left of fixation and the bilateral letter cues required the division of attention across the two peripheral locations, their results supported our hypothesis that the longer saccade latencies in the invalid, relatively to the valid trials are due to the choice in saccade direction.

Finally, it should be noted that all interstimulus contingency effects on the saccade latencies occurred in those (slow-regular) saccades which had mean latencies of at least 180 ms. This result thus may establish a lower limit in the time course of interstimulus contingencies.

8.2 Contiguity and intersensory facilitation effects

In all experiments, the saccadic reaction times showed effects of SOA and spatial congruence. This result confirmed the principle of contiguity and the general finding in studies on multisensory integration that the saccade latencies are shorter if a visual and auditory stimulus are presented in close spatial and temporal proximity than if the stimuli are presented alone.

Furthermore, the effects of interstimulus contingency mainly occurred independently of contiguity effects. This was especially true in two subjects of Experiment 8 on visual prosaccades with outline boxes and in Experiment 6 on visual antisaccades. On the other hand, some subjects in the bimodal go/no-go task and in the auditory prosaccade task exhibited significant interaction effects of SOA or spatial congruence with contingency. These interaction effects indicated that contingency effects mainly occur if the saccades have a minimum latency of about 200 ms and if their programming required a choice in saccade direction. It might thus be concluded that the interaction effects were more related to the specific processing requirements of interstimulus contingencies rather than demonstrating a reliable interaction effect of contiguity and contingency. In sum, if the experimental task meets the specific requirements of interstimulus contingencies, they are processed independently of temporal and spatial contiguity effects.

Finally, the comparison of unimodal and bimodal saccadic mean latencies revealed large differences between experiments. While in the visual prosaccade tasks (Experiments 1-5, and 8) and in Experiment 6 on visual antisaccades the bimodal latencies were always shorter than the unimodal visual latencies, in Experiment 7 on auditory prosaccades they were longer. However, this was only true in the disparate trials. This result indicated that the programming of a saccadic eye movement is dominated by visual stimulation (see Corneil *et al.*, 1999). This conclusion was further supported by the observation that the subjects in the disparate trials of the visual prosaccade task with outline boxes had to choose the saccade direction, but the bimodal saccade latencies showed intersensory facilitation. Therefore, the longer latencies in the disparate trials of the auditory prosac-

cade task cannot be solely explained by the choice in saccade direction, but may be related to intersensory inhibition due to the need to inhibit the reflex-like response to the visual accompanying stimulus before calculating the saccade in the direction of the auditory target.

This conclusion was tested in a post-hoc analysis comparing the latencies in the disparate bimodal trials of the visual prosaccade task with outline boxes with those in the unimodal visual trials. The comparison showed that the saccade latencies in the bimodal disparate trials were significantly shorter than in the unimodal visual trials. This result thus confirmed our conclusion that the longer saccade latencies in the disparate trials of the auditory prosaccade task were due to intersensory inhibition. Note, however, that the latter conclusion should be treated with caution as it was inferred from two experiments investigating two different subject groups. Future experiments might investigate this point more systematically.

In summary, a comparison of the contingency effects in the first and last experiment indicates that they were processed independently of intersensory facilitation effects, because the latter were comparable between experiments while only in the last experiment significant contingency effects were found. On the other hand, the discussion on the contingency effects in the disparate trials of the auditory prosaccade task suggests that they were interrelated with intersensory inhibition effects. We therefore conclude that at least with saccadic responses the processing of visual-auditory interstimulus contingencies is independent of intersensory facilitation, but only if the target is visual.

8.3 Express saccades

As outlined in the introduction, studies investigating the spatial cueing task revealed some effects specifically related to the programming of saccadic eye movements. Cavegn (1996) showed that the saccade latencies in the valid trials were of the express type whereas the responses in the invalid trials were characterised by fast-regular latencies. The analysis of express saccades in the present thesis, on the other hand, showed that the subjects in the visual prosaccade tasks (Experiments 1 and 3) exhibited about the same number of express saccades across all contingency conditions. This result led us to conclude that the occurrence of express saccades was related to a general facilitation effect (see Section 2.3).

However, note that in the auditory prosaccade task and in the visual prosaccade task with outline boxes respectively one subjects exhibited more express saccades in 80% ISC than in the remaining contingency conditions. Although these two subjects cannot be considered representative of the whole sample, the larger number of express saccades in 80% ISC supports the conclusion by Cavegn (1996) that a valid (pro-)cue leads to express saccades.

Note that Cavegn (1996) investigated a gap task in which the cue was presented and extinguished prior to target presentation, while in the present study the 'cue', that is, the auditory accompanying stimulus, was presented 40 ms before the visual target at the earliest. Therefore, the subjects had less time to use the contingency information contained in the auditory accompanying stimulus. This very fast time course in the production of ex-

press saccades further supports the general evidence that they are mediated by the superior colliculus (Fischer & Weber, 1993).

Furthermore, the larger number of express saccades in 80% ISC than in 50% ISC indicated that the two subjects had learned to use the specific contingency information contained in the auditory accompanying stimulus. In combination with the fast time course of stimulus presentation this result suggests that the learning of contingencies implied a shift in baseline neuronal activity within the SC rather than top-down influences of visual cortical areas onto the SC. The higher pretarget build-up activity in the saccade-related neurons in the intermediate layer of the SC in turn may have required less increase in discharge to surpass the burst threshold for saccade initiation therefore leading to a larger number of express saccades in 80% ISC (Dorris & Munoz, 1998; Dorris, *et al.*, 1997; Everling *et al.*, 1998).

The hypothesis of a shift in baseline activity within the SC prior to target presentation was supported by the observation that two subjects in the visual prosaccade task with visual catch trials anticipated the respective relative frequencies of stimulus events in the different contingency conditions. When the auditory accompanying stimulus was presented long before the visual target, some of these anticipatory saccades even were initiated before target presentation, but still reflected the probability of the respective stimulus events.

8.4 Saccade amplitudes

In all experiments, the interstimulus contingencies not only affected the saccadic response times but also the saccade amplitudes. The subjects either exhibited shorter or longer amplitudes in the positively and negatively correlated contingencies than in the control condition. This is the first demonstration that the processing of interstimulus contingencies affects motor control.

As outlined in the discussion of the first experiment, previous studies showed that the predictability of target location increases saccade accuracy (Coeffé & O'Regan, 1987; Bronstein & Kennard, 1987; Viviani & Swenson, 1982). Our results did not support this conclusion as the amplitudes in the correlated conditions either were shorter or longer than in the control condition. Furthermore, one subject in the last experiment on visual prosaccades with outline boxes showed shorter saccade amplitudes in the correlated contingencies than in the control condition. As the outline boxes predetermined the location of the visual target, this result supports the conclusion that the processing of spatial interstimulus contingencies did not increase the saccade accuracy. Note that this contradiction in results might be related to the difference in experimental protocol. While Coeffé and O'Regan (1987) always presented the target at the same location, in the spatial contingency task it was presented at either side of fixation with equal probability. Future experiments might probe whether this difference in target presentation can explain the difference in amplitude accuracy.

Note that the contingency effects on the saccade amplitudes were comparable across all experiments independently of the different processing demands in the respective saccade tasks. This result indicates that the contingency effects had a generalised effect

on motor control. On the other hand, one subject in Experiment 4 exhibited different amplitude effects when falsely informed about the contingency to be investigated in the next block of trials than when correctly informed. We therefore concluded that the subject had adopted a different processing mode in the correlated contingencies than in the control condition depending on the contingency pre-information (see Section 3.4). In sum, it might be concluded that spatial contingencies have a generalised effect on the saccade amplitudes, but in some subjects they might depend on the explicit contingency pre-information. Future experiments should investigate this point in more detail.

Finally, some subjects in Experiments 1 and 5 exhibited contingency effects in the saccade amplitudes, but they did not show any contingency effects in the saccade latencies. However, in very similar experimental conditions the same subjects did show contingency effects in the saccade latencies. We therefore conclude that the processing of interstimulus contingencies has differential effects on saccadic reaction times and amplitudes. This conclusion is in good accord with models for the oculomotor system which generally assume separate processes for the timing of a saccade and the calculation of its amplitude (see Becker & Jürgens, 1979).

In their comprehensive review article, Findlay and Walker (1999) described a hierarchy of processing levels through which information and command streams run in parallel in a WHERE- and a WHEN-pathway. An important aspect of the WHERE-pathway is the involvement of spatially distributed coding and the selection of the saccade target from a salience map. The exact point in time of saccade initiation is determined by the resolution of a conflict between a fixation-centre in the WHEN-pathway and a move-centre in the WHERE-pathway.

Cortical top-down influences, as *e.g.* implicit learning, are assumed to be strictly separated between the WHEN- and WHERE-pathways (Findlay & Walker, 1999). However, there is evidence that the activity in cortical centres, such as the frontal eye fields and various regions in the parietal cortex encode both the metrics and the timing of the saccade (*e.g.* Segraves, 1992). From a functional point of view, it remains to be determined how these top-down processes regulate the salience map (Taylor, 1999) and how they interact between the WHEN- and WHERE-pathways (Frens, Hooge & Goossens, 1999).

8.5 Neurobiological processing account of visual-auditory interstimulus contingencies

The most prominent neural structure to generate and guide saccadic eye movements is the superior colliculus (SC), a midbrain structure receiving converging afferents from a multitude of cortical and subcortical areas related to eye movement control (for a review, see Schall, 1991). The superior colliculus integrates information from different sensory modalities (*e.g.*, visual and auditory) and converges this information to the same brainstem premotor circuitry to trigger eye movements toward the source of stimulation (Stein & Meredith, 1993).

At rest, the SC is tonically inhibited by the substantia nigra pars reticulata (SNr) which in turn is inhibited by the caudate nucleus (Hikosaka & Wurtz, 1983a,b). Rizzolatti, Riggio & Sheliga (1994) and Sheliga, Riggio & Rizzolatti (1994; 1995a) were the first to

propose that the expectancy of a stimulus might be mediated by this tonical circuit controlling the excitability of the SC. They proposed that, 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 (Mohler & Wurtz, 1976). 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 (Rizzolatti *et al.*, 1994).

Dorris & Munoz (1998) 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 of two rhesus monkeys. In a gap task, the monkeys were presented with a visual stimulus occurring with varying probability in the response field of these neurons. Spike density functions of the same neuron superimposed for the different probability conditions showed that the build-up activity of that neuron increased with increasing probability of saccades being directed into the response field of that neuron. Moreover, this build-up activity of the neuron was negatively correlated to the saccadic reaction times indicating shorter SRTs the stronger the neuronal activity (50% vs. 100% probability). This correlation was most prominent in the epoch preceding saccade initiation (50-60 ms after target presentation). The early pre-target activity of the neurons was task-dependent, as one neuron only exhibited evident activity if the required saccade was fully predictable.

Most recently, the results by Dorris and Munoz (1998) have been implemented in a neural field model of saccade initiation in the superior colliculus (Trappenberg, Dorris, Munoz & Klein, 2001). Target probability was modelled as a weak pre-target input at the more likely target location. This pre-target input was meant to be integrated before target presentation. Simulations of the model reflected the facilitation of human saccadic reaction times with high stimulus probability especially in the gap task. Also, the simulated discharge rates of 'burst' neurons were in good accord with the results by Dorris & Munoz (1998). 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.

8.6 Survey of cortical structures mediating the choice of saccade direction

The discussion of the interstimulus contingency effects on the saccade latencies indicated that the choice of saccade direction is a constituent part in their processing. Furthermore, we outlined that this mechanism might account for all the contingency effects on the saccade latencies in the experiments six to eight, because the visual antisaccades, auditory prosaccades, and the visual prosaccades with outline boxes all required such a choice in saccade direction. This conclusion suggests that the cortical structures involved in

the programming of the former types of voluntary saccades also mediate interstimulus contingencies. We therefore decided to compare the neurobiological evidence as outlined in the introductions of the Chapters 4 to 6 in order to deduce the common cortical sites related to the choice of saccade direction.

The comparison revealed that the frontal eye fields (FEFs), the lateral intraparietal area (LIP) of the posterior parietal cortex, and in case of a visual target, the occipito-temporal cortex were involved in the programming of all three types of voluntary saccades. This result is in good accord with blood-flow neuroimaging studies which indicated 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 (*e.g.* Bushara *et al.*, 1999; Doricchi *et al.*, 1997).

The choice in saccade direction in particular might be related to the selection of the saccade target in the FEFs (Bichot & Schall, 1999) and to the coding of the target location in area LIP (Anderson & Gnadt, 1988). Note that both areas directly project onto the deep layers of the superior colliculus (SC). Furthermore, they are strongly interconnected and they both receive input from the thalamus (see Schall, 1991, for a review).

If the assumption of Rizzolatti *et al.* (1994, see above) prove correct, the FEFs and LIP might provide good candidates for the cortical motor program mediating interstimulus contingencies via the basal ganglia (SNr) onto the superior colliculus. The DLPFC might constitute a third cortical structure involved in the processing of interstimulus contingencies as this prefrontal region also has direct connections with the FEFs, area LIP, and the thalamus (see Funahashi, 2001, for a review).

More direct evidence supporting the view that interstimulus contingency effects on saccade latencies might be mediated by the FEFs, LIP and DLPFC was provided in single-cell recordings in macaque monkeys. As outlined in the introduction of Chapter 7, Hanes and Schall (1996) showed that the latency-distributions generated by a monkey in the control trials of a countermanding task could be predicted by a simulation of the LATER model (Carpenter, 1981; Carpenter & Williams, 1995) using parameters derived directly from measures of the activity of individual neurons in the monkey's frontal eye fields.

Platt and Glimcher (1999) obtained similar results in area LIP when investigating a cued visual distractor task. The monkeys were presented with two identical visual stimuli above and below the central fixation stimulus. A change in the colour of the fixation point gave the instruction to gaze to one or the other visual target. When a saccade was instructed with a probability of 0.8 the LIP neurons were more active than when the saccade was instructed with a probability of 0.2. Furthermore, this was true even before the colour of the fixation point identified the saccade target. As the probability of a response is an important variable in a decision process, Platt & Glimcher (1999) concluded that the activity of LIP neurons reflects the decision for one or the other response alternative.

Finally, Asaad, Rainer and Miller (1998) showed that DLPFC neurons reflect learning of arbitrary stimulus-response associations. First, the monkeys were presented with a picture at the central fixation stimulus. After a delay period, the monkeys had to choose the saccade direction right or left of fixation. After some practice, the monkeys learned to associate a particular, non-spatial cue with the correct saccadic response. Furthermore, the neural activity indicated the direction of the impending response progressively earlier within each successive trial. These results indicated that the monkeys had learned the

abstract rule of associating the non-spatial visual cue with a specific saccadic response (Wallis, Anderson & Miller, 2001).

In sum, there is evidence that the frontal eye fields and the lateral intraparietal area of the posterior parietal cortex not only are involved in the programming of voluntary saccades, but also mediate the decision of saccade direction. This decision process can be modelled as a rise-to-threshold mechanism as in the LATER model by Carpenter (1981; Hanes & Schall, 1996). The simulation of ILAT for interstimulus contingency effects in auditory prosaccades gave a good fit to the mean saccade latencies. Recent neurobiological evidence suggests that the bias which accounted for the different contingency conditions may be mediated by the dorsolateral prefrontal cortex.

The results of the present thesis provided evidence for a common mechanism to account for visual-auditory interstimulus contingency effects in various saccade tasks. This decision process to choose one or the other target direction was implemented as a rise-to-threshold mechanism in ILAT. The parameters and the presumptions of the model are in good accord with neurobiological evidence.

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Zusammenfassung

Die vorliegende Doktorarbeit handelt von dem Einfluß visuell-auditorischer Interstimuluskontingenzen auf die Programmierung sakkadischer Augenbewegungen. Die Versuchsteilnehmer waren aufgefordert, eine sakkadische Augenbewegung in Richtung eines visuellen (oder auditorischen) Zielreizes auszuführen. Die Wahrscheinlichkeit, daß der Zielreiz entweder links oder rechts von einem Fixationspunkt dargeboten wurde, hing von der Wahrscheinlichkeit ab, daß ein auditorischer (oder visueller) akzessorischer Reiz an demselben oder am gegenüberliegenden Ort dargeboten wurde. Im Gegensatz zu vorherigen Studien (Miller, 1987; Mordkoff & Yantis, 1991; Schwarz, 1996) war die Interstimuluskontingenz hier also nicht allein durch die Präsenz eines Ziel- oder akzessorischen Reizes, sondern durch seinen Ort definiert.

Untersuchungen von Interstimuluskontingenzen auf manuelle Reaktionszeiten in einer go/no-go Aufgabe erbrachten bisher sehr unterschiedliche Ergebnisse. Wenn das Erscheinen des Zielreizes und des akzessorischen Reizes positiv korrelierte, waren die Reaktionszeiten schneller als in der Kontrollbedingung. Wenn aber das Erscheinen des Zielreizes negativ mit dem Erscheinen des akzessorischen Reizes korreliert war, fand Mordkoff (1995) langsamere, Schwarz (1996) hingegen kürzere Reaktionszeiten als in der Kontrollbedingung. Ein erstes Ziel der vorliegenden Studie war daher, systematisch verschiedene Kontingenzvaliditäten zwischen einfachen visuellen und auditorischen Reizen zu untersuchen, um diese Unstimmigkeit in den Ergebnissen weiter zu klären.

Als Antwortmodus wurden sakkadische Augenbewegungen erhoben. In der Literatur ist das Verhalten sakkadischer Augenbewegungen auf einfache visuelle, auditorische und bimodale Reize schon recht weit erforscht (Colonius & Arndt, 2001; Corneil & Munoz, 1996; Frens, van Opstal & van der Willigen, 1995). Die Reaktionszeit visueller Prosakkaden (Sakkaden in Richtung des visuellen Zielreizes) ist kürzer, wenn gleichzeitig ein auditorischer akzessorischer Reiz dargeboten wird (bimodale Integration). Dieser Effekt ist desto größer, je zeitlich und räumlich näher die beiden Reize zueinander dargeboten werden (Stein & Meredith, 1993). Vor dem Hintergrund dieser Ergebnisse bestand ein weiteres Ziel der vorliegenden Studie darin zu bestimmen, ob die Effekte der Interstimuluskontingenz mit denen der bimodalen Integration interagieren.

In insgesamt acht Experimenten wurden jeweils unterschiedliche Typen von sakkadischen Augenbewegungen untersucht. In einem ersten Experiment mit visuellen Prosakkaden waren die Effekte der Interstimuluskontingenz auf die sakkadischen Reaktionszeiten nicht signifikant. Eine mögliche Erklärung ist, daß visuelle Prosakkaden allgemein derart automatisiert ablaufen, daß die Versuchsteilnehmer keine zusätzliche Stimulusinformation zur Antwortvorbereitung nutzen konnten (Deckeneffekt).

In den Experimenten zwei bis fünf wurden zusätzlich sogenannte catch-Reize in das Experiment eingefügt, in denen die Versuchspersonen angehalten waren, nicht auf einen 'Fang'-Stimulus zu reagieren. Diese experimentelle Variable diente also dazu, die Versuchspersonen zu motivieren, den auditorischen akzessorischen Reiz mehr zu beachten. In allen vier Experimenten mit entweder einem visuellen oder auditorischen catch-Reiz traten Kontingenzeffekte auf: Die Reaktionszeiten in den korrelierten Kontingenzzbedingungen waren schneller als in der Kontrollbedingung. Dieses Ergebnis bestätigte die Befunde von Schwarz (1995), daß negativ korrelierte Reize in einer go/no-go Aufgabe zu schnelleren Reaktionszeiten führen können als in der Kontrollbedingung. Das vierte Experiment zeigte weiterhin, daß diese Kontingenzeffekte auch dann auftreten, wenn die Versuchspersonen aufgrund der Vorinformation eine andere Kontingenzzbedingung erwarten als ihnen letztendlich präsentiert wurde. Dieses Ergebnis deutete darauf hin, daß die Kontingenzen unabhängig von der Vorinformation verarbeitet werden. Aufgrund ähnlicher Beobachtungen in der Literatur wird die Verarbeitung von Interstimulus-kontingenzen auf implizites Lernen zurückgeführt (Carlson & Flowers, 1996; Lambert, Norris, Naikar & Aitken, 2000). Eine systematische Variation der Anzahl bzw. des Prozentsatzes an catch-Durchgängen, wie sie in den vorherigen Experimenten eingestreut wurden, zeigte im fünften Experiment, daß die Kontingenzeffekte unabhängig von dieser experimentellen Variable auftreten.

Die Ergebnisse der bimodalen go/no-go Aufgabe haben gezeigt, daß sich Kontingenzeffekte auf die Reaktionszeit von sakkadischen Augenbewegungen nachweisen lassen (vgl. Lambert *et al.*, 2000). Ungeklärt blieb jedoch, ob diese Effekte auf spezifische Verarbeitungsmechanismen der catch-Reize oder der Kontingenzen zurückzuführen sind. In einem sechsten Experiment wurden die Versuchsteilnehmer daher instruiert, eine Sakkade in die entgegengesetzte Richtung zum visuellen Zielreiz auszuführen und den auditorischen Reiz als möglichen, aber nicht reliablen Hinweis für den Ort des Zielreizes zu nutzen. Diese sogenannten Antisakkaden hatten durchschnittlich 60 ms längere Reaktionszeiten als die visuellen Prosakkaden (Hallett, 1978), und alle drei Versuchspersonen zeigten Kontingenzeffekte: Entweder waren die Reaktionszeiten in der positiv korrelierten Kontingenzzbedingung kürzer als in der Kontrollbedingung oder sie waren in der negativ korrelierten Kontingenzzbedingung länger als in der Kontrollbedingung. Insgesamt zeigten diese Ergebnisse, daß die Versuchsteilnehmer auch in einer Antisakkadenaufgabe Interstimuluskontingenzen nutzen können. Wenn der Zielreiz an dem erwarteten Ort dargeboten wurde, waren die Reaktionszeiten kürzer, aber in den seltenen Fällen, in denen er am gegenüberliegenden Ort dargeboten wurde, waren die Latenzen ähnlich wie in der räumlichen cueing-Aufgabe von Posner (1980) länger. Dieses Ergebnis deutet darauf hin, daß die kürzeren Latenzen in der negativ korrelierten Kontingenzzbedingung in der bimodalen go/no-go Aufgabe auf einen spezifischen Effekt der catch-Reize zurückzuführen sind.

Als Kontrolle für die Durchgänge in Experiment 6, in denen der auditorische Reiz gegenüberliegend (disparat zum) visuellen Zielreiz dargeboten wurde, waren die Versuchsteilnehmer in Experiment 7 instruiert, eine Sakkade in Richtung des auditorischen Reizes auszuführen (auditorische Prosakkade) und den visuellen akzessorischen Reiz als Hinweis für den Ort des auditorischen Zielreizes zu benutzen. Alle fünf Versuchsteilnehmer zeigten Kontingenzeffekte auf die sakkadischen Reaktionszeiten, aber nur in den dispa-

raten Durchgängen: Die Latenzen in der positiv korrelierten Kontingenzbedingung waren kürzer als in der Kontrollbedingung, und die wiederum kürzer als in der negativ korrelierten Kontingenzbedingung. Dieses Ergebnis bestätigte die Kontingenzeffekte in der Antisakkadenaufgabe und zeigte weiter, daß die Kontingenzinformation schon sehr früh in der Programmierung einer Sakkade genutzt werden kann, denn die mittleren Latenzen der auditorischen Prosakkaden waren etwa so schnell wie die der visuellen Prosakkaden im ersten Experiment.

Auffällig war, daß die Kontingenzeffekte nur in den disparaten Durchgängen auftraten. Außerdem machten die Versuchsteilnehmer fast ausschließlich nur in diesen Durchgängen sichtlich mehr Fehler als in dem ersten Experiment mit visuellen Prosakkaden. Dieses Ergebnis deutete darauf hin, daß die Versuchsteilnehmer entweder die Modalität oder die Richtung der Stimuli diskriminieren mußten, bevor sie die entsprechende Sakkade programmieren konnten.

Um zwischen diesen Erklärungen zu unterscheiden, wurden in einem letzten Experiment zwei Umrißlinien in Form von Rechtecken links und rechts vom Fixationspunkt dargeboten. Diese beiden Rechtecke waren während der ganzen Darbietung eines Durchgangs sichtbar. Der visuelle Zielreiz wurde an der gleichen Stelle wie in den vorherigen Experimenten, aber nun in der Mitte einer der Rechtecke, dargeboten. Mit dieser experimentellen Manipulation wurden die Versuchsteilnehmer angehalten, beide Seiten des Gesichtsfeldes zu überwachen, um den Zielreiz zu detektieren und damit die Richtung der Sakkade zu entscheiden. Alle drei Versuchsteilnehmer zeigten kürzere sakkadische Reaktionszeiten in der positiv korrelierten Kontingenzbedingung als in der Kontrollbedingung. Dieses Ergebnis bestätigte die Hypothese, daß die Entscheidung der Richtung einer Sakkade bei der Verarbeitung von Interstimuluskontingenzen eine wesentliche Rolle spielt.

Da auch in der Antisakkadenaufgabe die Entscheidung der Richtung eine große Rolle spielt, lassen sich die Kontingenzeffekte in Experiment 6 ebenfalls auf diese Hypothese der Wahlreaktion als Grundlage der Verarbeitung von Interstimuluskontingenzen zurückführen. Indirekt bestätigt diese Hypothese auch unsere Schlußfolgerung in dem ersten Experiment mit visuellen Prosakkaden, daß diese zu reflexhaft durchgeführt werden als daß zusätzliche Informationen in Form von Interstimuluskontingenzen genutzt werden könnten.

In allen acht Experimenten wurden Kontiguitätseffekte nachgewiesen, d.h. die Reaktionszeiten auf zeitlich und räumlich nahe Reize waren schneller als auf disparate, zeitlich auseinanderliegende Reize. Außerdem waren die Effekte der Interstimuluskontingenz unabhängig von denen der Kontiguität, insbesondere wenn die sakkadischen Reaktionszeiten länger waren als 200 ms und die Aufgabe eine Wahlreaktion implizierte. Zusammenfassend läßt sich schließen, daß Interstimuluskontingenzen in einer Wahlreaktionszeitaufgabe zu einer Erleichterung der Sakkadenprogrammierung in positiv korrelierten Bedingungen, und zu einer Hinderung der Programmierung in negativ korrelierten Bedingungen führen, wobei diese Effekte unabhängig von (bimodalen) Kontiguitätseffekten auftreten.

Eine Wahlreaktion läßt sich sehr gut in Form eines Akkumulatormodells erklären. Bei dieser Art von Modellierung wird angenommen, daß die kortikale, sensorische Antwort auf einen Reiz solange steigt, bis sie eine konstante, kritische Grenze erreicht, die

dazu führt, daß eine motorische Antwort auf den Reiz ausgelöst wird. In der Literatur zur Sakkadenprogrammierung ist ein Sonderfall eines Akkumulatormodells bekannt, das LATER-Modell von Carpenter (1981). Hier wird angenommen, daß die Steigung der sensorischen Aktivität in jedem experimentellen Durchgang konstant ist, aber zwischen den Durchgängen variiert. In der vorliegenden Doktorarbeit wurde dieses Modell für den Fall visuell-auditorischer Stimulation erweitert, indem angenommen wurde, daß jeder der beiden Reize sensorische Aktivität hervorruft, die jeweils mit konstanter Steigung in Richtung der kritischen Grenze ansteigt. Für die Zeitintervalle, in denen die Reize gleichzeitig dargeboten wurden, wurde im Sinne der bimodalen Integration angenommen, daß die beiden Signale einen gemeinsamen Prozeß (r_{AV}) darstellen, der sich als die Summe der Aktivitäten ausdrücken läßt. Die verlangsamten Reaktionszeiten in den räumlich disparaten Durchgängen wurden durch Subtraktion eines räumlichen Parameters von diesem gemeinsamen Prozeß r_{AV} ausgedrückt. Die Effekte der Interstimuluskontingenz wurden in Anlehnung an Carpenter und Williams (1995) als Variation des Aktivitätslevels zu Beginn jedes Durchgangs erklärt. In den positiv korrelierten Durchgängen startete die Aktivität näher zur kritischen Grenze und führte aufgrund der konstanten Steigung eines Durchgangs zu kürzeren Reaktionszeiten als in den negativ korrelierten Durchgängen, die in größerer Entfernung zur konstanten, kritischen Grenze starteten.

Monte-Carlo Simulationen dieses neuen, ILAT-Modells ergaben einen guten Fit der mittleren sakkadischen Reaktionszeiten in Experiment 7 mit auditorischen Prosakkaden. Die Schätzung der Parameter ergab physiologisch sinnvolle Werte. Eine abschließender Vergleich der kortikalen Strukturen, die bei der Programmierung von Antisakkaden, auditorischen Prosakkaden und visuellen Prosakkaden in einer Wahlreaktionsaufgabe beteiligt sind, ergab, daß insbesondere die frontalen Augenfelder (FEFs) und der laterale Intraparietalkortex (LIP) bei der Programmierung von willentlichen Sakkaden und evtl. bei der Verarbeitung von Interstimuluskontingenzen beteiligt sind. Diese Hypothese läßt sich insofern bestätigen, als Hanes und Schall (1996) im FEF, und Platt und Glimcher (1999) im LIP von Affen neuronale Akkumulation wie sie im ILAT-Modell gefordert wird, nachweisen konnten.

Erklärung

Hiermit erkläre ich, dass ich die Arbeit selbständig verfasst und keine anderen als die angegebenen Hilfsmittel benutzt habe.

Oldenburg, den 28. Oktober 2001,

Lebenslauf

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