

# **Absence of direction-specific cross-modal visual-auditory adaptation in motion-onset ERPs**

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## **Abstract**

Adaptation to visual or auditory motion affects within-modality motion processing as reflected by visual or auditory free-field motion-onset evoked potentials (VEPs, AEPs). Here, a visual-auditory motion adaptation paradigm was used to investigate the effect of visual motion adaptation on VEPs and AEPs to leftward motion-onset test stimuli. Effects of visual adaptation to (i) scattered light flashes, motion in the (ii) same or in the (iii) opposite direction of the test stimulus were compared. For the motion-onset VEPs, i.e. the intra-modal adaptation conditions, direction-specific adaptation was observed: The change-N2 (cN2) and change-P2 (cP2) amplitudes were significantly smaller after motion adaptation in the same than in the opposite direction. For the motion-onset AEPs, i.e. the cross-modal adaptation condition, there was an effect of motion history only in the change-P1 (cP1), and this effect was not direction-specific: cP1 was smaller after scatter than after motion adaptation to either direction. No effects were found for later components of motion-onset AEPs. While the VEP results provided clear evidence for the existence of a direction-specific effect of motion adaptation within the visual modality, the AEP findings suggested merely a motion-related, but not a direction-specific effect. In conclusion, the adaptation of veridical auditory motion detectors by visual motion is not reflected by the AEPs of the present study.

## Introduction

The perception of moving auditory or visual objects is of fundamental importance for our interaction with the environment. Previous studies on the neural mechanisms of motion analysis indicated the existence of highly specific, direction-selective processing in the visual (Tootell *et al.*, 1996; Heeger *et al.*, 1999; Huk *et al.*, 2001; Lortelje *et al.*, 2007) as well as in the auditory domain (e.g. Griffiths *et al.*, 1998; Baumgart *et al.*, 1999; Warren *et al.*, 2002). In recent years, multisensory mechanisms of motion perception have received increasing attention by human brain imaging (Lewis & Van Essen, 2000; Bremmer *et al.*, 2001; Baumann & Greenlee, 2007; Alink *et al.*, 2008; Soto-Faraco & Völjamäe, 2012), electrophysiological (Stekelenburg & Vroomen, 2009; Getzmann & Lewald, 2014), and behavioural studies (Kitagawa & Ichihara, 2002; Alais & Burr, 2004; Meyer *et al.*, 2005; Jain *et al.*, 2008). To focus on temporal features of the underlying neural processes in the auditory modality, auditory evoked potentials (AEPs) to the onset of motion of an initially stationary sound source were used (Ducommun *et al.*, 2002; Getzmann & Lewald, 2010a; b; Grzeschik *et al.*, 2010, 2013). These studies demonstrated a fronto-central motion-onset response complex, comprising a negative component (change-Negativity, cN1) at around 140 ms and a positive component (change-Positivity, cP2) at around 230 ms. Sometimes, an early fronto-central positivity (cP1) was also observed (Krumbholz *et al.*, 2007; Getzmann, 2009; Getzmann & Lewald, 2012). Visual motion onset evoked responses at occipital/occipito-temporal recording sites that are dominated by a P1 around 100-130 ms and a N2 around 150-200 ms (Clarke, 1972; 1973; Kubová *et al.*, 1990; Bach & Ullrich, 1994; Snowden *et al.*, 1995; Heinrich 2007).

Investigating motion processing requires the identification of veridical motion detectors. These can be recognized on the basis of the direction specificity of their responses (Borst & Egelhaaf, 1989; Wagner *et al.*, 1997), i.e., a veridical motion detector will show a stronger response to a stimulus moving in its preferred direction than in the opposite direction (DeYoe & Van Essen, 1988). In mass responses, such as evoked potentials, paradigms assessing direction-specific motion adaptation enable the investigation of the contribution of such motion detectors (Mather *et al.*, 1998). Here, the response of veridical motion detectors should be more reduced after adaptation to their preferred, than non-preferred, motion direction.

In the present study, a well-established approach to assess the direction selectivity of motion-onset visual evoked potentials (VEPs; Bach & Ullrich, 1994; Hoffmann *et al.*, 1999,

2001; Bach & Hoffmann, 2000; Hoffmann & Bach, 2002; Maurer & Bach, 2003; Heinrich *et al.*, 2004; Lorteije *et al.*, 2008) and AEPs (Grzeschik *et al.*, 2013) was adapted to study the influence of visual motion adaptation on auditory motion processing. Applying free-field auditory and visual motion, the impact of visual motion history on motion-onset VEPs and motion-onset AEPs was assessed.

## **Methods**

### *Subjects*

The subjects took part in the study after passing a pure-tone audiometric hearing screening (Oscilla USB100, Inmedico, Lystrup, Denmark) with a hearing loss less than 20 dB at all audiometric frequencies. All subjects reported normal or corrected to normal vision. They were unaware of the scientific background of the study. The subjects gave their written informed consent to participate in the study and were paid for their participation. The procedures followed the tenets of the Declaration of Helsinki (World Medical Association, 2000), and the protocol was approved by the Ethical Committee of the Medical Faculty of the Ruhr University Bochum, Germany. A total of 22 healthy subjects took part in the experiment and data of 21 (median age 25 years, range 19–47 years, 10 female, all right-handed) entered the analysis (one was excluded due to a defective EEG data set).

### *Apparatus, stimuli, and procedure*

The subject sat on a vertically adjustable chair in an unlit, soundproof and anechoic room (Guski, 1990; Getzmann *et al.*, 2004). The position of the subject's head was held constant by a chin rest. Auditory stimuli were presented by an array of 91 broad-band loudspeakers (SC 5.9, Visaton, Haan, Germany) that were mounted in front of the subject with a distance of 1.5 m from the centre of the head (for details, see Lewald *et al.*, 2004). The loudspeakers were arranged at ear level in the horizontal plane ranging from  $-90^\circ$  (left) to  $90^\circ$  (right) in steps of  $2^\circ$ , with the central loudspeaker at  $0^\circ$ . All loudspeakers were selected on the basis of similar efficacy and frequency response curves. The loudspeakers were controlled by custom-made amplifiers and software. For the visual stimuli, white light-emitting diodes (LEDs; diameter 10 mm, luminance 0.05 mcd) were mounted directly below each of the loudspeakers. An additional red LED located below the central loudspeaker served as fixation target. To improve the impression of a smoothly moving visual target (see below), subjects wore

spectacles with blurred glasses during the experiment. Both visual and auditory motion was presented at a velocity of  $180^\circ/\text{s}$  for motion-adaptation and motion-test stimuli.

Auditory stimuli were generated digitally using CoolEdit 2000 (Syntrillium Software Co., Phoenix, AZ, USA) and consisted of a continuous, band-pass-filtered (lower and upper cut-off frequencies 250 Hz and 20 kHz, respectively), 100-Hz sine-wave amplitude modulated white noise (modulation depth 12%; starting phase  $0^\circ$ ) with rise/decay times of 15 ms and 66 dB(A) sound level. Visual stimuli consisted of 50-ms light flashes emitted by the LEDs. The generation of virtual visual/auditory motion followed a previously applied procedure (Getzmann & Lewald, 2011; 2012). Visual/auditory motion was generated by successively activating one loudspeaker/white LED after the other along the horizontal loudspeaker/LED arrangement. The signals were shaped by envelopes (rise/decay times 3 ms) and switched between LEDs and loudspeakers. The distance between adjacent loudspeakers ( $2^\circ$ ) was substantially below the minimum audible movement angle (Chandler & Grantham, 1992) for the velocity used here, resulting in the percept of a smoothly moving auditory object. In the visual domain, such a successive activation of LEDs is known to produce a percept of apparent motion (Kolers, 1972).

The time courses of the different stimulus types are schematically shown in Fig. 1. They comprised three consecutive phases that were presented in a cyclic design: (a) a visual '*adaptation phase*' (duration 1342 ms); (b) a '*stationary phase*' (duration 1000 ms); (c) a '*test phase*' (duration 330 ms) in which the motion-onset event-related potentials (ERPs) were measured; and (d) an interstimulus interval (duration 828 ms). In phases (b) and (c), either visual or auditory stimuli were presented. ERPs to the onset of leftward motion were measured for the following three conditions that differed in their history, i.e., the type of preceding adaptation (a). The adaptation phase comprised one out of three different types of visual stimulation: (1) '*Scatter*': adaptation to a randomized sequence of light flashes that were homogeneously distributed across LED locations, thus minimizing the impression of consistent motion; (2) '*Adaptation Same*': adaptation to visual motion in the same direction as the test stimulus (i.e., leftward); and (3) '*Adaptation Opposite*': adaptation to visual motion in the direction opposite to the test stimulus (i.e., rightward). The Scatter condition (1) was employed to determine motion onset potentials with poor motion history (duty cycle of motion 9%) in a previous approach (Getzmann, 2009). Here, in the adaptation phase, a flickering image generated by successively activated LEDs within the spatial range from  $-60^\circ$  to  $60^\circ$  was presented, following a pseudorandom scheme for the spatio-temporal distribution of locations (local stimulus duration 11 ms; rate of location change  $90/\text{s}$ ). The adaptation

conditions (2) and (3) were used to determine motion onset potentials with rich motion history (duty cycle of motion 48%). For the Adaptation-Same condition, a 671-ms stimulus moving from  $60^\circ$  to  $-60^\circ$  (i.e., leftward) was presented twice in the adaptation phase. For the Adaptation-Opposite condition, the 671-ms stimulus moved from  $-60^\circ$  to  $60^\circ$  (i.e., rightward). For all conditions, a static stimulus was presented at  $0^\circ$  in the stationary phase (b) that was followed by a motion onset stimulus moving from  $0^\circ$  to  $-60^\circ$  in the test phase (c).

To maintain a constant level of vigilance during the experimental session, and to test whether motion detection was modulated by adaptation, subjects had to perform a simple detection task. In six of 115 presented trials, the test stimulus moved from the centre ( $0^\circ$ ) to the right ( $60^\circ$ ), i.e., in the direction opposite to adaptation. The subject had to respond to those deviant motion via button press with the index finger of the dominant hand. The ERPs to these catch trials were discarded from analysis. Altogether, 109 trials were obtained per condition for each participant.

The time courses of the different blocks are schematically shown in Fig. 2. Each block was preceded by a 2-min motion adaptation phase. Here, 105 repetitions of the motion adaptation stimulus that was also used for top-up adaptation during the adaptation phase of the recordings (visual leftward or rightward motion or scatter, depending on conditions) were presented, with 500-ms silence between each of the adaptation stimuli. The blocks were followed by a 10-min recovery break during which the subjects were allowed to look around freely.

Each session began with a practice block (about 20 trials) to familiarize the subjects with the stimuli and the task. The motion-onset ERPs were recorded in six separate blocks. Each of the six blocks comprised one specific visual adaptation condition (*Scatter*, *Adaptation Same*, *Adaptation Opposite*) and either a visual or auditory test stimulus. The block-sequence was counter-balanced across subjects.

### *Electrophysiological recordings*

Multi-channel-recordings consisting of 57 EEG channels referenced to FCz and 2 pairs of electrooculography (EOG) channels (one bitemporal horizontal EOG and one vertical EOG of the left eye) were performed using an EEG cap (Head Cap, GVB Gelimed, Bad Segeberg, Germany) with equidistantly arranged Ag-/AgCl-sintered ring electrodes based on the international 10–10 system (American Encephalographic Society, 2006), amplified with two cascaded physiological amplifiers (NuAmps amplifier, NeuroScan Labs, Sterling, VA, USA), and digitised at 500 Hz. A ground electrode was centred on the forehead, just above the

nasion. Two additional electrodes were placed on the left and right mastoids. Impedances were kept below 5 k $\Omega$ .

### *Data analysis*

Trials were analyzed offline with BrainVision Analyzer 2.0 (Brain Products, Gilching, Germany) and Igor Pro V6.1 (WaveMetrics Inc., Lake Oswego, OR, USA) for an interval from -2342 to 1058 ms relative to motion onset. This interval was chosen to cover nearly the entire trial duration (2342 ms adaptation and stationary phases, 330 ms test phase, and 728 ms pause) and thus to gain an overview of the quality of the ERPs. The data were digitally band-pass filtered (cut-off frequencies 0.5 and 25 Hz; slope 48 dB/octave) and re-referenced to the average of the 58 EEG-channels (56 EEG and 2 mastoid electrodes). The raw data were inspected manually to avoid obvious artifacts. Thereafter, the EEG channels were corrected for ocular artifacts using the Gratton, Coles, and Donchin procedure (Gratton *et al.*, 1983). This method allows keeping segments with eye blinks. Remaining individual epochs that exceeded a maximum-minimum difference of 200  $\mu$ V (maximal allowed voltage step / sampling point: 50.00  $\mu$ V; minimal/maximal allowed amplitude:  $\pm$ 100.00  $\mu$ V; lowest allowed activity [max - min]: 0.50  $\mu$ V) were excluded from further analysis (automatic artifact rejection as implemented in the BrainVision Analyzer software). The traces were baseline corrected to the 100 ms interval preceding motion onset and averaged separately for each subject and condition. Peaks were defined as maximal negativity and positivity, respectively, and detected automatically within a time window of 100 ms width, covering the cluster range resulting from the statistical analysis.

### *Statistical analysis*

For group-level statistical analysis of the ERP and to assess the spatial distribution of the electric responses at the scalp, i.e., to recognize sites with potential significant effects, a cluster randomization analysis (Maris & Oostenveld, 2007) was used. Further, this method addresses the problem of multiple comparisons due to the analysis of the entire waveforms. Here, the sum of  $t$ -values across a cluster was compared to the distribution of maximum cluster sums of  $t$ -values derived from a randomization procedure (1000 randomizations). Statistically significant differences between conditions were reported when the  $p$ -value of the cluster was below the critical  $\alpha$ -level (0.05) after correction for multiple comparisons, i.e., a Bonferroni correction was conducted with  $\alpha$  set to 0.025 divided by the number of significant clusters (for details see Sambrook & Goslin, 2014). According to previous studies (Altmann *et al.*, 2012), the different conditions were compared using a two-tailed Student's  $t$ -test in the

time window of 50-350ms after motion onset. This time window was chosen in order to cover potential effects on both early and late event-related responses. Clusters with at least four neighbouring electrodes showing significant differences between conditions entered a further analysis, which was conducted for validation of the cluster analysis. In these analyses, the traces of the electrode cluster were averaged and the peak amplitudes were determined for each individual. Subsequently, the conditions that were identified to be different in the preceding cluster analysis were tested for significance using post-hoc Student's *t*-tests.

## Results

### *Behavioural performance*

The analysis of the catch trial data revealed a comparatively high hit rate (mean 87.2%, SEM 4.3%) for the detection of test stimuli moving in the direction opposite to adaptation. Two-way ANOVAs failed to indicate any significant effects of the type of adaptation (Scatter, Adaptation Opposite, Adaptation Same) on the hit rate, neither for the auditory test stimuli ( $F_{2,40} = 0.52$ ,  $P > 0.05$ ; partial  $\eta^2 < 0.03$ ), nor for the visual test stimuli ( $F_{2,40} = 0.18$ ,  $P > 0.05$ ; partial  $\eta^2 < 0.01$ ). The false alarm rate (i.e., a response to test stimuli moving in the direction of adaptation) was extremely small (mean 0.12%, SEM 0.03%), and was not further analyzed. In sum, vigilance of the subjects did not depend on adaptation condition, neither in the intra-modal visual condition, nor in the cross-modal visual-auditory condition.

### *Auditory motion-onset after adaptation to visual motion*

In Fig. 4, the response topography of the auditory test stimuli is shown for the three types of adaptation: Scatter, Adaptation Opposite, and Adaptation Same. In accordance with previous studies, the topographies were dominated by a fronto-central response. At cluster levels, significant differences were observed for the fronto-central positivity for two clusters that were significant at the 0.00227 threshold set by Bonferroni correction (= 0.025 divided by 11 found clusters): (i) Scatter vs. Adaptation Opposite (cluster  $\Phi$  between 88 and 126 ms;  $P = 0.0006$ ) and (ii) Scatter vs. Adaptation Same (cluster  $\Sigma$  between 96 and 136 ms;  $P = 0.0006$ ). The grand mean traces for the responding group sites are shown in Fig. 5A, C. The main effect of motion history was an increase of cP1, as these deflections reached significance only for the conditions Adaptation Opposite and Adaptation Same (obtained by running *t*-test; not shown). This positivation of the motion-onset AEP (cP1) upon adaptation was assessed quantitatively with a single-peak analysis of the amplitude (Fig. 5B, D). Paired *t*-tests demonstrated that the cP1-amplitudes for Adaptation Opposite and Adaptation Same were larger than for Scatter ( $t_{20} = 3.51$ ,  $P = 0.002$  and  $t_{20} = 2.73$ ,  $P = 0.013$ , respectively),



indicating a motion-related effect. In contrast, although showing a similar trend, this effect did not reach significance for the cP2 amplitude (Fig. 5C;  $t_{20} = -0.982$ ,  $P = 0.338$ ). Furthermore, there was no direction-specific effect, i.e., no significant difference between Adaptation Opposite and Adaptation Same.

#### *Visual motion-onset after adaptation to visual motion*

In analogy to the motion-AEP literature (Krumbholz *et al.*, 2007; Getzmann, 2009; Getzmann & Lewald, 2010a; b; Grzeschik *et al.*, 2010; Grzeschik *et al.*, 2013), the motion-VEP components P1 (around 100-130 ms), N2 (around 150-200 ms) and P2 (around 230 ms) will be referred to cP1, cN2, and cP2. Figure 6 shows the response topographies for the visual test stimuli in the three adaptation conditions (Scatter, Adaptation Opposite, Adaptation Same). Due to the average-reference they are dominated by a strong positive fronto-central response and a negative occipital response. At cluster level, significant differences were observed for Adaptation Opposite vs. Adaptation Same in three clusters that were significant at the 0.00057 threshold set by Bonferroni correction (= 0.025 divided by 44 found clusters): (i) fronto-parietal (Fig. 7A; cP1 cluster  $\Psi$  between 132 and 178 ms;  $P = 0.0003$ ), (ii) fronto-central (Fig. 7C; cP2 cluster  $\Omega$  between 224 and 352 ms;  $P = 0.0004$ , and (iii) occipital (Fig. 7E; cN2 cluster  $\Pi$  between 164 and 270 ms;  $P = 0.0002$ ). This reduction of the motion-onset VEP upon adaptation was assessed quantitatively with a single-peak analysis of the amplitudes cP1, cP2, and cN2 (Figs. 7B, D, F). Paired  $t$ -tests demonstrated that the amplitudes for Adaptation Same were significantly smaller than for Adaptation Opposite (cP1:  $t_{20} = 3.346$ ,  $P = 0.003$ ; cP2:  $t_{20} = -2.812$ ,  $P = 0.011$ ; cN2:  $t_{20} = -3.393$ ,  $P = 0.003$ ), indicating a direction-specific effect of adaptation. There was no significant difference of Adaptation Opposite vs. Scatter and Adaptation Same vs. Scatter.

#### *Comparison of average and linked-mastoids reference*

In accordance with the relevant literature on motion-onset AEPs (Krumbholz *et al.*, 2007; Getzmann, 2009; Getzmann & Lewald, 2010a; b; Grzeschik *et al.*, 2010; Grzeschik *et al.*, 2013), the analysis described above was conducted on data that were referenced to an average reference. This reference can be confounded depending on distribution and spatial sampling of the responses (Junghöfer *et al.*, 1999). In particular, occipito-temporal responses differed from the fronto-central responses, i.e., they were, relative to the fronto-central response complex, inverted in their polarity. For better comparability of the results of the present study with previous work (e.g., Hoffmann *et al.*, 2001; Heinrich *et al.*, 2004), we additionally analyzed the influence of the reference used in the previous motion-onset VEP studies. Thus,

an assessment of the VEPs was performed also with the VEPs referenced to linked mastoids (Fig. 8A) at the same electrodes as used in previous motion-onset VEP studies, i.e., Cz, PO7, Oz, and PO8. The average and linked-mastoids reference comprised largely similar response signatures of the grand mean traces. The responses of the motion-onset VEP upon adaptation were assessed quantitatively with a single-peak analysis of the amplitude cP2 (electrode Cz; peak time for Scatter condition 292 ms) and cN2 (electrodes PO7, Oz, PO8; peak times for Scatter condition 218, 214, and 214 ms) (Fig. 8B). One-way repeated-measures ANOVAs for the factor condition demonstrated a significant effect for cP2 amplitude at Cz ( $F_{1,20} = 7.785$ ,  $P = 0.001$ ) and for cN2 amplitude at Oz and PO8 ( $F_{1,20} = 7.52$ ,  $P = 0.002$  and  $F_{1,20} = 6.622$ ,  $P = 0.003$ , respectively), but not at PO7. Subsequent post-hoc tests (paired  $t$ -tests sequentially Bonferroni-corrected; (Holm, 1979) confirmed for Cz that cP2 amplitudes for Adaptation-Same were significantly smaller than for Scatter and Adaptation-Opposite conditions ( $t_{20} = -3.071$ , uncorrected  $P = 0.006$ , corrected  $P = 0.012$  and  $t_{20} = -3.24$ , uncorrected  $P = 0.004$ , corrected  $P = 0.012$ , respectively). In contrast, for the occipital electrodes, cN2 amplitudes for Adaptation-Same and Scatter conditions were significantly smaller than for Adaptation-Opposite (Oz:  $t_{20} = 4.003$ , uncorrected  $P = 0.0007$ , corrected  $P = 0.0021$  and  $t_{20} = -2.919$ , uncorrected  $P = 0.008$ , corrected  $P = 0.016$ , respectively; PO8:  $t_{20} = 3.453$ , uncorrected  $P = 0.003$ , corrected  $P = 0.009$  and  $t_{20} = 2.806$ , uncorrected  $P = 0.011$ , corrected  $P = 0.022$ ).

## Discussion

This study revealed a direction-specific intra-modal effect of visual motion adaptation on motion-onset VEPs, indicated by a reduction of cN2 and cP2 amplitudes for the Adaptation-Same condition with reference to the Adaptation-Opposite condition. However, the cross-modal visual-auditory effect (i.e., the effect of visual motion adaptation on motion-onset AEPs) was not specific for direction. The cP1 was more positive for both conditions, i.e. Adaptation-Opposite and Adaptation-Same, than for the Scatter condition. Consequently, there was an influence of visual motion adaptation on auditory motion processing that did, in contrast to motion-onset VEPs, not appear to be specific for the motion direction of the adapting stimulus.

### *Motion-related effect of visual motion history on auditory cP1*

In line with previous studies, the onset of auditory motion elicited an AEP with a fronto-central cP1, cN1, and cP2 complex (e.g., Krumbholz *et al.*, 2007; Getzmann, 2009; Getzmann & Lewald, 2012). A modulation of the motion-onset AEPs by visual motion adaptation was located mainly at fronto-central electrodes. Specifically, the cP1 amplitudes (in the range of

80-140 ms after motion onset) were more enhanced for Adaptation Same and Adaptation Opposite than for Scatter. Such a modulation was not found at later points in time or at electrodes covering other brain areas. The effect was more prominent at electrodes on the left hemisphere for the Adaptation-Opposite condition, i.e., at the hemisphere contralateral to the rightward moving adaptor. In contrast, the effect was more spread over electrodes on both hemispheres for the Adaptation-Same condition, i.e., with the leftward moving adaptor.

A modulation of the early cP1 of the motion-onset AEP is unexpected and it should be noted that the functional relevance of the P1 in the auditory modality is yet not well understood. It is believed that the auditory P1 mainly reflects basic sensory functions of sound detection that largely depend on features of the sound stimuli (Grunwald *et al.*, 2003). However, from the visual domain, there is also evidence that the positivity around 100 ms, also termed P1, is a correlate of early sensory selection (Heinze *et al.*, 1990). Specifically, within the sensory “gain control” model of Hillyard *et al.* (1998), the P1 is assumed to be an early ERP index of attentional control that interacts with bottom-up sensory processing. The suppression of the cP1 observed after Scatter adaptation could therefore reflect a reduction in motion sensitivity: While the visual adaptors in the Adaptation-Same and Adaptation-Opposite conditions were both perceived as continuous sideward motion, the Scatter adaptor rather triggered the perception of a discontinuous, unsystematical position change.

Apart from being correlate of early sensory selection, the visual P1 (or P100) component is also attributed to a spatial-attention effect, i.e., directing attention to the location of a stimulus enhances the P1 amplitude (Posner & Dehaene, 1994; Hillyard & Anllo-Vento, 1998; Luck *et al.*, 2000). Furthermore, Luck *et al.* (1994) pointed out that the P1 reflects changes in sensory-level processing (e.g., brightness and spatial frequency) and “costs” of attention, i.e., a suppression of P1 if the target is outside the attended area. Posner & Dehaene (1994) reported in their visual-search experiment an enhanced P1 if cue and following stimulus were the same. If the stimulus was miscued, the P1 was suppressed. Assuming similar mechanisms in the auditory modality, the results of these studies suggest that the enhancement of the cP1 in the Adaptor-Same and Adaptor-Opposite conditions relative to Scatter, as was found here, could be due to a kind of stimulus recognition on a basic level (“basis dimension effect”). The two moving adaptation stimuli were substantially easier to perceive as a coherently moving object than the adaptation stimulus presented in the Scatter condition. Therefore, stimuli in the Adaptor-Same and Adaptor-Opposite conditions may have attracted more attention while crossing the fixation LED than the Scatter stimulus that was randomly distributed across space. Following the rationale of Posner & Dehaene (1994), the

cP1 was enhanced, when the test stimulus (which was always moving from the front position to the left) was preceded by a moving adaptor stimulus, regardless of the direction of motion, i.e., “cue” and stimulus were the same. Following the Scatter adaptation, the test stimulus was “miscued” and therefore led to a suppression of cP1. In any case, the present results would indicate a motion-related, rather than direction-specific, cross-modal visual-auditory adaptation mechanism. Since little is known about this early component of the auditory motion-onset potential, further research is required to shed light into this issue.

#### *No visual-auditory interaction at cN1 or cP2*

Only few ERP studies on visual-auditory interaction with real motion have investigated the influence of visual motion on auditory motion processing, while the vast majority of studies have dealt with the reverse issue, that is, the influence of auditory motion on visual motion processing. In this study, visual-auditory interaction was present at early processing levels (cP1), but not at later components, such as cN1 or cP2. The absence of a significant cross-modal effect at those components might be due to differences in spatial and temporal processing, with spatial information being rather processed by the visual system, and temporal information by the auditory system (Sanders & Astheimer, 2008). However, Getzmann & Lewald (2014) described for simultaneous visual and auditory stimulation an influence of visual motion on the auditory component around 170 ms, revealed by topographical analyses, whereas the analysis of the cN1 amplitude at Cz failed to indicate any significant effects of cross-modal interactions. Further, they observed an absence of a cross-modal effect at a later component cP2 which was reasoned by the parallel recording of behavioural and ERP data, leading to an overlap of motor responses and motion-onset AEPs. In the present study overt responses were only required in the few catch trials and auditory and visual stimulation was not simultaneous but separated in time. Thus, an overlap of responses cannot be attributed to the absence of a significant effect at cP2 reported here. Alternatively, the lack of cross-modal effects at late components might have had methodological reasons. For example, it could be that the motion adaptation induced by the adaptor stimuli was not strong enough to influence the response to auditory motion onset. However, the result that adaptation strongly affected the VEP responses under intra-modal conditions argue against this possibility. Alternatively, one might argue that the lack of cross-modal effects could be due to the fact that the subjects could not see (or did not attend to) the adaptation stimuli. However, the analysis of the catch trials revealed a hit rate of nearly 90%, indicating that the subjects were well able to detect the direction of motion and thus perceived the moving stimuli.

### *Direction-specific effects of motion-adaptation within the visual and auditory modalities*

While there was no direction-specific effect of adaptation across modalities, a specificity for the direction of adaptation was found within the visual and the auditory modalities. As detailed above, this is of importance as it demonstrated that the specific paradigm used here was principally able to trigger processes of adaptation. It thus may indicate that the absence of cross-modal direction-specific adaptation was not simply due to methodological issues, but rather due to the properties of the underlying neural mechanisms.

Direction-specific adaptation of VEPs to visual motion were described earlier, although for more complex motion-stimuli in a substantially lower range of velocities and for substantially smaller frame-to-frame displacement (Bach & Hoffmann, 2000; Hoffmann *et al.*, 2001; Heinrich *et al.*, 2004; Maurer *et al.*, 2004; Lorteije *et al.*, 2008). In those reports, responses after adaptation to the same direction as the test stimulus were, as in the present study, more severely reduced than after adaptation to the opposite direction. Remarkably, this effect was evident for the cN2 at occipital sites (vs. linked mastoids), but also for cP2 at Cz. This has been previously reported to be devoid of direction-specific effects of visual motion adaptation (Hoffmann *et al.*, 2001). Furthermore, in the present study, responses for the reference condition, (visual) scatter, did, apart from cP2 at Cz, not significantly exceed adaptation to the same direction and, finally, latencies of the cN2 and cP2 were comparatively high, i.e., around 220 ms and 290 ms as opposed to around 170 ms and 255 ms or less in previous studies. Taken together, this indicates that, while visual direction-specific mechanisms were isolated in the present study, they might differ from those previously described. This apparent incongruence of findings might be due to the above-mentioned differences in the stimulus features. For example, stimulus speed and displacement steps (Cavanagh & Mather, 1989) were higher and larger in the present study.

In a previously published study, direction-specific effects were described for motion-onset AEPs (Grzeschik *et al.*, 2013), using virtual moving sound sources (60°/s) generated by HRTFs (Head related transfer functions). In this auditory unimodal study, cN1 amplitudes at a fronto-central group electrode were most reduced when adaptation and test stimuli moved in the same direction, suggesting that cN1 reflects veridical auditory motion detection. Based on these results, the present study investigated a cross-modal interaction of visual and auditory motion without testing the intra-modal auditory effects. The absence of cross-modal adaptation in the present study might, apart from minor differences in methodology of the studies, reflect to some extent separate neuronal mechanisms underlying visual und auditory

motion perception. Further research is required to further disentangle the underlying mechanisms and their neural substrates.

### *Conclusions*

Motion history was shown to modulate electrophysiological correlates of subsequent motion processing for both intra-modal and cross-modal visual-auditory conditions. Direction-specific effects of motion adaptation were demonstrated only for the intra-modal, i.e., visual, condition, indicated by a decrease in motion-onset ERPs in Adaptation-Same relative to Adaptation-Opposite and Scatter conditions. A motion-related, but not direction-specific, effect was found for cross-modal (visual-auditory) conditions, suggesting that the early general feature of auditory motion processing, reflected by the cP1, might depend on visual motion history.

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### **Abbreviations**

AEP	Auditory Evoked Potential
cP1, cN1, cP2, cN2	change-P1, change-N1, change-P2, change-N2
EEG	Electroencephalography
EOG	Electrooculography
ERP	Event-related Potentials
HRTF	Head Related Transfer Function
LED	Light-emitting Diode
VEP	Visual Evoked Potential

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