RESEARCH ARTICLE

Multisensory simultaneity recalibration: storage of the aftereffect in the absence of counterevidence

Tonja-Katrin Machulla · Massimiliano Di Luca · Eva Froehlich · Marc O. Ernst

Received: 26 July 2011 / Accepted: 30 November 2011 / Published online: 30 December 2011 © Springer-Verlag 2011

Abstract Recent studies show that repeated exposure to an asynchrony between auditory and visual stimuli shifts the point of subjective simultaneity. Usually, the measurement stimuli used to assess this aftereffect are interleaved with short re-exposures to the asynchrony. In a first experiment, we show that the aftereffect declines during measurement in spite of the use of re-exposures. In a second experiment, we investigate whether the observed decline is either due to a dissipation of the aftereffect with the passage of time, or the result of using measurement stimuli with a distribution of asynchronies different from the exposure stimulus. To this end, we introduced a delay before measuring the aftereffects and we compared the magnitude of the aftereffect with and without delay. We find that the after-

T.-K. Machulla (⊠) · M. Di Luca · E. Froehlich · M. O. Ernst Multisensory Perception and Action Group, Max Planck Institute for Biological Cybernetics, Spemannstr. 41, 72076 Tübingen, Germany e-mail: tonja.machulla@tuebingen.mpg.de

T.-K. Machulla Graduate Training Centre of Neuroscience, International Max Planck Research School, University of Tübingen, Österbergstr. 3, 72074 Tübingen, Germany

M. Di Luca University of Birmingham, Edgbaston, Birmingham B15 2TT, UK

E. Froehlich

Department of Experimental and Neurocognitive Psychology, Freie Universität Berlin, Habelschwerdter Allee 45, 14195 Berlin, Germany

M. O. Ernst

Department of Cognitive Neuroscience, Bielefeld University, Universitätsstr. 25, 33615 Bielefeld, Germany

effect does not dissipate during the delay but instead is stored until new sensory information in the form of measurement stimuli is presented as counterevidence (i.e., stimuli with an asynchrony that differs from the one used during exposure).

Keywords Temporal recalibration · Audiovisual integration · Temporal order judgment · Multisensory time perception · Subjective simultaneity

Introduction

The temporal coincidence of stimuli in different sensory modalities provides an important cue for determining which stimuli belong together and hence should be integrated into a unified percept (de Gelder and Bertelson 2003; King 2005). However, the perception of simultaneity is not as straightforward as it may seem, since stimuli that are processed by different sensory modalities differ substantially in their physical transmission and physiological transduction times. Signals that originate from the same event might therefore become perceptually available at different points in time. Usually, we are not aware of temporal inconsistencies between corresponding signals because several cognitive mechanisms work unceasingly to perceptually align inputs between the senses (King 2005; Spence and Squire 2003; Vroomen and Keetels 2010). For instance, a few minutes of exposure to a constant temporal discrepancy between two signals will subsequently cause similar discrepancies to appear less pronounced than before. Perception is altered so that the point of subjective simultaneity (PSS; i.e., the physical time difference at which the two stimuli appear to be simultaneous) shifts toward the exposure asynchrony. For instance, the reader

will probably have had the experience of watching a video clip for which the auditory and the visual streams have not been properly aligned in time. If the asynchrony is not too extreme, the initially distracting discrepancy will have quickly become less perceptually noticeable. This phenomenon has been interchangeably termed *adaptation* or *recalibration* (Di Luca et al. 2009; Fujisaki et al. 2004; Hanson et al. 2008; Harrar and Harris 2005, 2008; Heron et al. 2007, 2010; Keetels and Vroomen 2007a, b; Stetson et al. 2006; Takahashi et al. 2008; Vatakis et al. 2007, 2008; Vroomen et al. 2004). In this paper, the two terms will be used with specific meanings in the discussion.

Most experiments that investigate the effect of repeated exposure to asynchrony adopt similar paradigms: participants are exposed to temporally asynchronous stimuli and the perception of simultaneity is measured after (and in some studies before) this exposure (for a different paradigm see Miyazaki et al. 2006). During measurement, pairs of stimuli are presented for which participants perform temporal-order judgments (TOJ) or simultaneity judgments. From these responses, a PSS can be derived. The difference between two PSS measurements is taken to reflect the aftereffect of repeated exposure to the asynchrony. This could either be the difference between the PSS measured before and after exposure (e.g., Harrar and Harris 2008) or between the PSS measured after two different exposure conditions such as to auditory-leading versus visual-leading asynchrony (e.g., Keetels and Vroomen 2007a).

Stimuli used to assess the PSS after exposure are usually interleaved with short periods of re-exposure to the asynchrony (e.g., Fujisaki et al. 2004; Takahashi et al. 2008; Vroomen et al. 2004). Ideally, the quantity, duration, and frequency of these re-exposure stimuli should be chosen such as to prevent changes in the magnitude of the aftereffect. However, it is not clear whether in practice this is the case as none of the available studies report how re-exposure stimuli have been selected and how effective they are. It is therefore possible that in some studies, the measured aftereffect was polluted by changes that took place during measurement. Such failure to stabilize the aftereffect might in fact explain inconsistent results present in the literature. For instance, while the aftereffect of repeated exposure to asynchrony has by now been reported for all bimodal combinations of the visual, auditory, and tactile senses (e.g., Hanson et al. 2008; Keetels and Vroomen 2007b; Stetson et al. 2006), some studies failed to find shifts in PSS for certain combinations of modalities (Harrar and Harris 2008; Navarra et al. 2005, 2007) or even found an effect opposite to the predicted minimization of asynchrony (Harrar and Harris 2005). Another example of such inconsistency of results is found in studies investigating whether the aftereffect is confined to one modality combination (e.g., audiovisual) or whether it transfers to other bimodal combinations (e.g.,

audiotactile or visuotactile). While some find such a transfer (Di Luca et al. 2009), others do not (Harrar and Harris 2005, 2008). All of these studies differ to some degree in the details of their experimental designs and in the type of stimuli they used. It is possible that an aftereffect is present only for some combinations of these conditions, which would explain why some studies failed to find an aftereffect. Another possibility, however, is that an aftereffect was initially present in all of the previous studies, but in some of them, the re-exposure stimuli failed to prevent changes in the magnitude of the aftereffect, and thus, artifactual null results were created.

In a first experiment, we investigate the stability of the aftereffect over the course of measurement. We chose an experimental design and procedure very similar to the one used in the study by Vroomen et al. (2004). This study uses a high ratio of re-exposure to measurement stimuli, as well as long exposure and short measurement periods (all of these are likely to influence the measured aftereffect magnitude). This design, therefore, seemed to be most effective in stabilizing the aftereffect. We find that the aftereffect dissipates throughout measurement in spite of the re-exposure stimuli. In a second experiment, we investigate the cause underlying the observed dissipation.

Experiment 1

Methods

Participants

Two of the authors (M.D.L., E.F.) and 14 students of the Eberhard Karls University Tuebingen participated in the experiment, all of whom gave their informed consent prior to their inclusion in the experiment. The participants (10 females and 7 males; aged 22–34 with a mean age of 26) were recruited via the Max Planck Institute subject database. The data of one participant were not included in the analysis because of the participant's inability to perform the experimental task (temporal order judgments). The students were naïve to the purpose of the experiment and received a compensation of 8 Euros per hour of participation. All participants reported normal or corrected-to-normal vision and good hearing. The study was approved by the local Ethics committee of the Tuebingen University.

Apparatus and stimuli

Stimuli were generated using Matlab (Mathworks) and a custom-made apparatus capable of producing co-located sound and light with high temporal accuracy (0.1 ms). Observers sat at arm-length from the device. Auditory

stimuli were presented via two vertically mounted speakers, set 7.5 cm apart. Halfway between these speakers a 7×5 array of red LEDs (1.6 cm \times 1.3 cm) presented the visual stimuli. A multi-channel sound card (M-audio 1010LT) was used together with identical power amplifiers to drive both LEDs and speakers and insure sub-millisecond precision and accuracy. The audio card produced 20-ms sinusoids with frequencies of 2,000 Hz and 150 Hz, respectively, for the audio and visual stimuli, with 5 ms linearly ramped onset and offset. Stimulus intensities were 76 dB SPL and 41 cd/m², respectively. In order to ensure that subjects paid attention throughout the presentation of the stimuli, 1–9 oddball stimuli with a deviating sound frequency (1,000 Hz) or light intensity (76.5 cd/m²) were presented among the standard stimuli during the exposure phase.

Design

The experiment was run in 3 sessions on consecutive days. Each session consisted of 4 experimental blocks, each of which in turn consisted of an exposure phase and a measurement phase. We manipulated two within-subject factors: firstly, during the exposure phase, either an auditory stimulus preceded a visual stimulus by 150 ms (condition auditory-leading) or vice versa (condition visual-leading). Each of these two conditions was presented 6 times throughout the experiment in a randomized order. Secondly, in the measurement phase, the stimulus onset asynchrony (SOA) between the visual and auditory stimuli was varied (-240, -120, -90, -60, -30, 0, 30, 60, 90, 120, and 240 ms, where negative values indicate light first and positive values auditory first). In each experimental block, all 11 SOAs were presented 7 times in randomized order.

Procedure

Observers were seated in a dark, sound-attenuated room. They were instructed to maintain fixation on the LED throughout the entire experiment. To acquaint observers with the TOJ task and the order of the answer keys, 20 training trials were administered in the beginning of each session. In each of these trials, an audiovisual stimulus pair was presented with a large random SOA (100–500 ms). Participants judged which of the two stimuli had been presented first (temporal order judgment—TOJ) and entered their response over a regular keyboard using the right hand. The left arrow and the down arrow keys served as answer keys; the assignment of key and answer was randomly chosen for each participant. During these training trials, auditory feedback was given after each response indicating which answer key had been pressed (however, not whether the response had been correct).

Experimental blocks consisted of an initial exposure phase lasting 3 min, followed by a post-exposure measurement phase (see Fig. 1). During the exposure phase, a series of audiovisual stimulus pairs with random ISI (range: 250– 400 ms) was presented. For the first minute of the exposure phase, the lag between the auditory and the visual stimulus of the pair continuously increased from 0 to 150 ms. In order to ensure that observers attended to both the auditory and the visual stimuli, they were asked to count the number of oddball stimuli (one to nine brighter lights or lower pitch tones). Observers reported this number at the end of the experimental block.

The exposure phase was followed by a measurement phase consisting of 77 test trials. On each test trial, an audiovisual stimulus pair was presented and participants were required to perform a TOJ. Each test trial was preceded by a short re-exposure (eight stimulus pairs with the same asynchrony as used in the exposure phase). The interval between participants' TOJ and the beginning of the next short re-exposure was approximately 1 s. After each experimental block, participants took a 5-min break outside the experimental room performing normal actions without any particular task in order to decrease fatigue.

Results and discussion

Participants performed well on the oddball task during the exposure phase (98% mean correct responses), thus





Fig. 1 Depiction of stimulus presentation in one experimental block. Each participant performed 12 such blocks, 6 in the auditory-leading condition (shown), and 6 in the visual-leading condition



Fig. 2 Change in aftereffect magnitude (in ms and in % of the exposure SOA) over the course of the experiment. The aftereffect magnitude (Δ PSS, i.e., the difference of PSS between the two experimental conditions auditory-leading or visual-leading asynchrony) is repeatedly computed using a running window (the *shaded rectangle*): for the first iteration of the window, Δ PSS is obtained from the first 30 consecutive trials of each experimental block and plotted as a function of the

demonstrating that their attention had been directed to the exposure stimuli. For each participant, TOJ data were analyzed separately for the two conditions (auditory-leading and visual-leading) using a running window. For the first iteration of the window, the data of the first 30 test trials of each experimental block (totaling 180 trials for each condition) were extracted, and the percentage of "auditory first" responses was computed as a function of SOA. These data were fitted with a cumulative Gaussian function using the psignifit toolbox (Wichmann and Hill 2001). From this fit, the point of subjective simultaneity (PSS) was obtained, which refers to the SOA at which the auditory and the visual stimuli are equally likely perceived to be first. The magnitude of the aftereffect was captured by ΔPSS , which was computed as the difference between the PSS in the auditory-leading and the visual-leading condition. This value is represented in Fig. 2 as the first point of the graph. The procedure was repeated 48 times, each time on 30 consecutive trials extracted from the next iteration of the moving window (i.e., the first analysis was performed on trials 1-30 of all experimental blocks, the next on trials 2-31, and so forth, until the last analysis, which included trials 48-77).

Inspection of the results of this analysis (Fig. 2) suggests that the aftereffect magnitude varies during measurement with an overall tendency to decline: the first value of ΔPSS is 17 ± 6 ms (SEM), which corresponds to 6% of the exposure asynchrony and the last value of ΔPSS is 4 ± 6 ms (SEM), which corresponds to 1%. In order to quantify this trend, a line of the form y = m * x + b was fitted on the data of each participant, such that y corresponds to ΔPSS at each iteration of the moving window and x is the corresponding iteration number. Average value of b obtained across participants is 26 ± 7 ms (SEM), which significantly differs from 0 (t(14) = 3.1, P = 0.008). This confirms the presence

trial at the center of the window. The 30-trial window is then shifted to include trials 2–31 for the next iteration, and so on. The *dotted line* depicts the best-fitting regression line (for illustrative purpose only). The *dark shaded area* represents the standard error of the mean across participants. The *upper-right inlay* shows participants' PSS for the two experimental conditions (exposure to auditory-leading or visual-leading asynchrony)

of an aftereffect immediately after the end of the exposure phase. The aftereffect declines over the course of measurement as the average slope $m = -0.32 \pm 0.14$ ms/iteration is significantly different from 0 (t(14) = 2.4, P = 0.03). In other words, on each following trial, the aftereffect declines by approximately one-third of a millisecond.

Figure 2 (inset) also shows the change in PSS separately for the auditory-leading and visual-leading conditions. Relatively speaking, it would appear that the visual-leading condition contributes more to the trend we have observed, i.e., it has the steeper slope. There are various possible explanations for this. For instance, the aftereffect of exposure to asynchrony could be different in the two exposure conditions. For audiovisual pairs, the pre-exposure PSS usually differs from 0 (for a review, see van Eijk et al. 2008). If the perceived magnitude of the exposure asynchrony is determined with respect to the PSS and if the aftereffect magnitude is a certain percentage of that perceived magnitude, it follows that the aftereffect will be larger in one condition than in the other. Also, the measured change in the PSS over the course of the experiment would be larger in the condition that led to a larger initial aftereffect. Alternatively, the difference in the amount of dissipation in the insert of Fig. 2 could be due to the different effectiveness of exposure stimuli in stabilizing the PSS in the two conditions.

This result illustrates that the magnitude of the aftereffect is not constant while it is being measured. In fact, it gradually declines during the measurement phase to a point where it is no longer apparent. There are two explanations for this change; they are not mutually exclusive.

First, the aftereffect could be the result of a progressive desensitization at the neuronal level, resulting from the unusually intense stimulation during the exposure phase. This has sometimes been referred to as neuronal "fatigue" Fig. 3 Distributions of measurement and re-exposure stimuli within one experimental block (here for the auditoryleading condition of Experiment 1)



(Kohler and Wallach 1944). Recent studies have produced behavioral results that are in accordance with the interpretation that repeated stimulation causes a decreased response of stimulus-specific neurons in a neural population that codes temporal properties of stimuli (Heron et al. 2011; Roach et al. 2010). Recovery of neuronal responsiveness, whenever it is due to fatigue, should spontaneously occur once the exposure ceases. The observed decline in the measured aftereffect would therefore reflect such a natural recovery of normal functioning over time.

The second possible explanation is that the brain strives to maintain a well-calibrated state across sensory modalities, and every piece of sensory evidence is used to adjust this state (Wozny and Shams 2011). In this view, the measured aftereffect is the result of a recalibration of the perceived relative timing of auditory and visual events, which was initiated by the unbalanced distribution of sensory evidence that was presented during exposure. If this is the case, the new calibration state (i.e., the aftereffect) is not expected to change with the passage of time, but only with the presentation of new sensory evidence. The measurement stimuli in the current experiment could constitute such new sensory information, since they differ considerably from the exposure stimuli. While the SOAs of the exposure stimuli originated from a single-valued distribution at 150 ms (i.e., a distribution of SOAs conforming to a delta function), the SOAs of the measurement stimuli were chosen from a discrete uniform distribution with a mean asynchrony of 0 and a range spanning 480 ms (from -240to 240 ms). Figure 3 illustrates these distributions. Thus, while the exposure stimuli caused a recalibration of the PSS in the direction of their distribution's mean (SOA of 150 ms), the measurement stimuli may have caused a shift of the PSS toward the mean of their respective distribution (SOA of 0 ms). If this is so, the introduction of the measurement stimuli should progressively cancel out the aftereffect induced by the exposure phase.

In a second experiment, we investigated which of these two mechanisms—neuronal fatigue or recalibration underlies the decline of the aftereffect found in Experiment 1. To this end, we assessed the change in perceived simultaneity in two conditions. One condition resembled Experiment 1 in that the measurement of the aftereffect started immediately after the exposure phase. In the other condition, measurement was delayed for a few minutes. No stimuli were presented during this interval. If the change observed in Experiment 1 reflected a change over time, the magnitude of the aftereffect should be reduced after this delay interval. However, if the change was induced by the measurement procedure itself, the passage of time should have no effect on the magnitude of the aftereffect. The new perceptual state should be stable as long as no new information is presented (i.e., stimuli that are different from the exposure asynchrony).

Experiment 2

Methods

Participants

Seventeen new participants were recruited from the MPI subject database, two of whom had to be excluded from the analysis due to the failure to finish all experimental sessions or the inability to perform TOJs. The remaining participants, 10 of whom were females, were between the ages of 20 and 33 years (average age 25 years).

Apparatus, stimuli, design, and procedure

The apparatus was identical to that reported for Experiment 1; design, procedure, and stimuli were adjusted as illustrated in the following. We included a further within-subject factor into the design. As before, we varied leading stimulus type during the exposure phase (auditory or visual) and the SOA (-240, -120, -90, -60, -30, 0, 30, 60, 90, 120, and 240 ms) in the measurement phase. Additionally, the measurement phase started either immediately after the exposure phase (henceforth, immediate condition) or after a delay (henceforth, delayed condition, see Fig. 4). The experiment was run on 3 consecutive days, with a total of 8 experimental blocks per day. All four combinations of leading stimulus type with the immediate/delayed measurement were presented six times throughout the experiment. The 11 SOAs were randomized and presented two times in



Fig. 4 Experimental design of Experiment 2

the experimental blocks of the delayed condition (totaling 22 trials) and 4 times in the blocks of the immediate condition (totaling 44 trials). In the immediate condition, the test trials were administered as soon as the exposure phase had ended. In the delayed condition, observers sat quietly in the dark for an additional couple of minutes before testing began. The duration of this delay was determined before each experimental block of the delayed condition by calculating the average time required to finish the first half (22) trials) of all experimental blocks of the immediate condition so far administered. This way, measurement in the delayed condition started at approximately the same time as the second half of the immediate condition. In an effort to reduce the overall length of the experiment, the SOA of the exposure stimuli was changed to 100 ms and the number of re-exposure stimuli presented before each measurement stimulus was decreased to 4.

Results and discussion

Participant performed the oddball task during the exposure phase accurately (98% mean correct responses). For each participant, the percentage of "auditory first" responses was calculated as a function of SOA, separately for all combinations of the visual-first and the auditory-first conditions with the immediate and the delayed conditions. In the immediate condition, this analysis was applied separately to the first and the second half of the trials (henceforth referred to as first and second measurement of the immediate condition). A cumulative Gaussian function was fitted to the data as described in Experiment 1. Again, the ΔPSS was computed as the difference between the PSS in the auditory-first condition and visual-first condition, yielding our measure of the magnitude of the aftereffect.

The magnitude of the aftereffect computed from the TOJ responses is shown in Fig. 5. We find a significant aftereffect in both the delayed condition (Δ PSS of 12 ± 5 ms (SEM) corresponding to 6% of the exposure asynchrony) and the first measurement of the immediate condition (Δ PSS of 17 ± 6 ms (SEM) corresponding to 8.5% of the exposure asynchrony), but not in the second measurement



Fig. 5 Δ PSS obtained for the immediate and the delayed condition in Experiment 2. The *large gray cross* indicates that in the delayed condition, no measurements were taken during the time interval following the exposure phase

of the immediate condition (ΔPSS of -3 ± 6 ms (SEM) corresponding to 1.5% of the exposure asynchrony; onetailed t tests of ΔPSS against zero with Bonferroni correction for the overall number of t tests performed on each data set: t(14) = 2.8, P = 0.007; t(14) = 2.5, P = 0.014; t(14) = 0.48, P = 0.68). The latter result replicates the finding of Experiment 1, indicating a decline of the aftereffect size as the measurement progresses. Further, we compared the aftereffect magnitude in the second measurement of the immediate condition with the aftereffect magnitude in the delayed condition. Even though a comparable amount of time had passed between the end of the exposure phase and the beginning of measurement in each of these two cases $(167 \pm 3 \text{ s vs. } 183 \pm 4 \text{ s})$, the aftereffect was significantly larger in the delayed condition (paired-sample t test: t(14) = 2.9, P = 0.006). On the other hand, the magnitudes of the aftereffect in the first measurement of the immediate condition and the delayed condition do not differ (pairedsample t test t(14) = 0.67, P = 0.74). These findings demonstrate that the recalibration state is stored after the exposure phase, i.e., the mere passage of time leaves the aftereffect unaffected. We conclude that the change in the measured magnitude of the aftereffect we observed in Experiment 1 is caused by the information presented during the measurement phase.

General discussion

Repeated exposure to a constant asynchrony causes a change in perceived simultaneity. In order to quantify this change, the magnitude of the aftereffect induced by the exposure needs to be measured. This measurement, however, cannot be performed instantaneously. Instead, it requires the successive presentation of a number of stimuli to be judged by the participant. In the present paper, we investigated (1) how stable the aftereffect is over the course of its measurement, and (2) which mechanism-recalibration or neuronal fatigue-underlies the aftereffect. Our results can be summarized as follows. In Experiment 1, we obtained an aftereffect that decayed almost completely within the measurement period in spite of the interleaved presentation of re-exposure stimuli. In Experiment 2, we measured either immediately after the exposure phase, or we measured after a delay lasting a few minutes during which no stimuli were presented. In the delayed measurement condition, we found no signs of dissipation of the aftereffect whereas in the immediate measurement condition, the aftereffect decayed completely within a time span comparable to the delay. We interpret these findings to show that the effect of repeated exposure to asynchronous stimuli is stored during the interval until measurement and does not decay with the mere passage of time, at least not within the time span used in the present study (about 3 min). Instead, the aftereffect is affected by the measurement stimuli that are used to assess its magnitude. This does not support the view that the aftereffect is due to desensitization at the neuronal level. If the decay in the immediate measurement condition reflected a recovery from a previous loss in sensitivity, the aftereffect in the delayed condition should decay with a similar time course (i.e., during the delay). We conclude that the aftereffect resulting from repeated exposure to an asynchrony is the result of a durable adjustment of the calibration between the involved sensory modalities.

To date, the aftereffect of exposure to asynchrony has interchangeably been named *adaptation aftereffect* (Stetson et al. 2006;) or *recalibration aftereffect* (e.g., Hanson et al. 2008; Vroomen et al. 2004), often even within the same publication (e.g., Di Luca et al. 2009; Fujisaki et al. 2004; Harrar and Harris 2005; Heron et al. 2010). While a recalibration mechanism clearly serves an adaptive purpose, the converse is not necessarily true (i.e., adaptation does not always result from a recalibration process). An adaptive change could also result from alternative mechanisms such as a loss of responsiveness after excessive exposure to the same type of stimulus. We explicitly distinguish this sensitivity loss from recalibration. The former should be temporary, while we consider the latter to reflect a durable adjustment of the mapping between two sensory dimensions (or between a sensory and a physical dimension). To the best of our knowledge, the present research is the first to provide conclusive evidence that adaptation to a temporal discrepancy is indeed the result of a recalibration process.

It is useful to examine our results within the framework of Helson's (1947, 1964) adaptation level theory, which provides a simple model of sensory recalibration processes. Many phenomenological dimensions are bipolar with a null point, which Helson called adaptation level (AL). The presentation of a physical stimulus that corresponds to this phenomenological null point will elicit a "neutral" perception. In our case, on the dimension of the perceived order of two sensory events, the AL is the point at which both events are perceived as simultaneous (measured by the PSS). According to Helson, the value of the null point is not hard-wired but it rather is a function of all present and past stimuli, weighted according to various factors (e.g., recency or frequency of occurrence). Each individual stimulus biases the AL by pulling it toward its own value-a notion that has recently also been endorsed by Wozny and Shams (2011)—and the perception elicited by each stimulus' is determined in relation to the current AL. Such a system serves reasonably well in providing a calibration between the null points of perceptual and physical dimensions when receiving a wide variety of environmental inputs. However, in situations that show strong variations in statistical regularities compared to "normal" sensory input (like a large number of presentations of the same stimulus), substantial and measurable shifts of the AL can occur within a short period of time (for simultaneity perception this has been demonstrated by Miyazaki et al. 2006). In our case, repeated exposure to an asynchrony changes the AL such that the asynchrony becomes perceptually less and less pronounced. Stimuli that originally fell onto the null point are now perceived to belong to the side of the bipolar continuum that is opposite to the side of the exposure stimulus (this has been termed negative or contrastive aftereffect, cf. Mollon 1974).

Helson's (1947, 1964) theory allows us to interpret the PSS changes resulting from temporal recalibration as a change of the null point of the phenomenological dimension with regard to its physical counterpart. We would like to make two clarifications with regard to this model. First, the phenomenological dimension need not consist of equidistant points (as the physical dimension does). Therefore, the amount that the two dimensions shift with regard to each other need not be uniform for all stimuli. Evidence for such uneven changes along the phenomenological dimension has recently been provided by Roach et al. (2010). Their results show that repeated exposure exerts the largest influence on stimulus pairs with an asynchrony similar to the exposure asynchrony. Second, it is important to note that even though the dimension of audiovisual order

perception—for which the recalibration is described here is multisensory in nature, temporal recalibration, at least in part, results from a modification of unisensory processing latencies as has been demonstrated recently (Di Luca et al. 2009; Navarra et al. 2009). A comprehensive model of adaptation to asynchrony has to take these previous findings into account.

In Experiment 1, we showed that the PSS changes while it is being measured, despite a number of re-exposure stimuli, which were interleaved to maintain the aftereffect constant. This change might be interpreted as a decay of an aftereffect over time. However, Helson's account predicts that the null point should not simply change with the passage of time but rather be stored until new sensory information requires further adjustments of the AL. In accordance with this prediction, we showed in Experiment 2 that the PSS is stored in the absence of sensory stimulation and only changes once the measurement phase has begun. As mentioned earlier, the distribution of measurement stimuli differs substantially from the stimuli presented during the exposure phase (Fig. 3). We believe that the stimuli in the two phases induce shifts of the AL in opposing directions, which cancel each other out. Theoretically, observers' AL before the experiment is based on naturally occurring stimuli, whose distribution is more similar to the measurement stimuli than to the exposure stimuli (for an overview, see van Eijk et al. 2008). Hence, while the tendency of the AL to shift toward the mean of the measurement stimuli might appear like dissipation toward some "default" level, it, in fact, reflects a recalibration process.

At this point, it is interesting to note that each measurement trial consisted of either eight or four re-exposure stimuli (Experiment 1 and Experiment 2, respectively) and only 1 measurement stimulus (see Fig. 3). In spite of this imbalance in sensory evidence in favor of the re-exposure stimuli, measurement stimuli exerted a larger influence on the magnitude of the AL. The reason for this is still unclear. Possibly, measurement stimuli receive a higher weighting in the computation of the AL because observers are required to make active decisions concerning the temporal order of the auditory and visual events and act upon these decisions. Re-exposure stimuli, on the other hand, require no decisions and therefore might be perceived in a passive and less attentive way. This interpretation is supported by Heron et al. (2010) study. They found that explicitly instructing participants to pay attention to the asynchrony presented during the exposure phase increases the magnitude of the aftereffect. Indeed, subsequent questioning of our participants revealed that most observers were not aware that the stimulus pairs presented during exposure and re-exposure were asynchronous. This indicates a lack of attention toward temporal properties of the repeated stimuli, as a discrepancy of 150 ms is certainly noticeable for pairs of simple stimuli presented in isolation.

Lastly, it is also of interest that the aftereffect in our study disappeared quite rapidly during testing in spite of interleaved re-exposures. We do not believe that this fast decay might be a peculiarity of the stimuli or the exposure and measurement procedures we used, since we made an effort to choose a conservative set of parameters in designing this study. We used a large number of stimuli in the exposure phase, as well as a high ratio of re-exposure stimuli to measurement stimuli. The magnitude of our initial aftereffect was in both experiments around 6-8% of the exposure asynchrony, a value that is within the range of previous findings (e.g., 6.7% average shift reported in Vroomen et al. 2004). Our data therefore indicate that measurement of the aftereffect should not be extended over too many measurement trials per block. In fact, our results might explain why some studies were not able to show a recalibration of the PSS in some of their conditions (Harrar and Harris 2005, 2008; Navarra et al. 2005, 2007) while others did (Di Luca et al. 2009; Hanson et al. 2008). For instance, Harrar and Harris (2005, 2008) report that they measured the temporal recalibration aftereffect with 210 consecutive measurement trials after each exposure phase (for comparison, the aftereffect in our experiments had completely disappeared within 44-77 trials). They also used an especially low ratio of re-exposure stimuli to measurement stimuli, probably in order to reduce the overall duration of the experiment. In cases like these, the analysis of the results over trials (with a method similar to that used in Experiment 1) might provide insights to whether an initially present aftereffect might have been canceled out during measurement.

Acknowledgments T.-K.M. and M.D.L. contributed equally to this work. This work was supported by Deutsche Forschungsgesellschaft (Sonderforschungsbereich 550-A11), EU Grants "Immer-Sence" (IST-2006-027141), and "THE" (IST-2009-248587) and the Max Planck Society.

Conflict of interest The authors declare that they have no conflict of interest.

References

- de Gelder B, Bertelson P (2003) Multisensory integration, perception and ecological validity. Trends Cogn Sci 7:460–467
- Di Luca M, Machulla T-K, Ernst MO (2009) Recalibration of multisensory simultaneity: cross-modal transfer coincides with a change in perceptual latency. J Vis 9:1–16
- Fujisaki W, Shimojo S, Kashino M, Nishida S (2004) Recalibration of audiovisual simultaneity. Nat Neurosci 7:773–778
- Hanson JVM, Heron J, Whitaker D (2008) Recalibration of perceived time across sensory modalities. Exp Brain Res 185:347–352
- Harrar V, Harris LR (2005) Simultaneity constancy: detecting events with touch and vision. Exp Brain Res 166:465–473

- Harrar V, Harris LR (2008) The effect of exposure to asynchronous audio, visual, and tactile stimulus combinations on the perception of simultaneity. Exp Brain Res 186:517–524
- Helson H (1947) Adaptation-level as frame of reference for prediction of psychophysical data. Am J Psychol 60:1–29
- Helson H (1964) Adaptation-level theory: an experimental and systematic approach to behavior. Harper & Row, New York
- Heron J, Whitaker D, McGraw P, Horoshenkov K (2007) Adaptation minimizes distance-related audiovisual delays. J Vis 7:1–8
- Heron J, Roach N, Whitaker D, Hanson JVM (2010) Attention regulates the plasticity of multisensory timing. Eur J Neurosci 31:1755–1762
- Heron J, Aaen-Stockdale C, Hotchkiss J, Roach NW, McGraw PV, Whitaker D (2011) Duration channels mediate human time perception. Proc R Soc B. doi:10.1098/rspb.2011.1131
- Keetels MN, Vroomen J (2007a) No effect of auditory-visual spatial disparity on temporal recalibration. Exp Brain Res 182:559–565
- Keetels MN, Vroomen J (2007b) Temporal recalibration to tactilevisual asynchronous stimuli. Neurosci Lett 430:130–134
- King AJ (2005) Multisensory integration: strategies for synchronization. Curr Biol 15:R339–R341
- Kohler W, Wallach H (1944) Figural aftereffects: an investigation of visual processes. Proc Am Philos Soc 88:269–357
- Miyazaki M, Yamamoto S, Uchida S, Kitazawa S (2006) Bayesian calibration of simultaneity in tactile temporal order judgment. Nat Neurosci 9:875–877
- Mollon J (1974) After-effects and the brain. New Scientist 61:479-481
- Navarra J, Vatakis A, Zampini M, Soto-Faraco S, Humphreys W, Spence C (2005) Exposure to asynchronous audiovisual speech extends the temporal window for audiovisual integration. Cogn Brain Res 25:499–507
- Navarra J, Soto-Faraco S, Spence C (2007) Adaptation to audiotactile asynchrony. Neurosci Lett 413:72–76

- Navarra J, Hartcher-O'Brien J, Piazza E, Spence C (2009) Adaptation to audiovisual asynchrony modulates the speeded detection of sound. Proc Natl Acad Sci USA 106:9169–9173
- Roach NW, Heron J, Whitaker D, McGraw PV (2010) Asynchrony adaptation reveals neural population code for audio-visual timing. Proc R Soc B 278:1314–1322
- Spence C, Squire S (2003) Multisensory integration: maintaining the perception of synchrony. Curr Biol 13:519–521
- Stetson C, Cui X, Montague P, Eagleman DM (2006) Motor-sensory recalibration leads to an illusory reversal of action and sensation. Neuron 51:651–659
- Takahashi K, Saiki J, Watanabe K (2008) Realignment of temporal simultaneity between vision and touch. Neurorep 19:319–322
- van Eijk RLJ, Kohlrauch A, Juola JF, van de Par S (2008) Audiovisual synchrony and temporal order judgments: effects of experimental method and stimulus type. Atten Percept Psychophys 70:955–968
- Vatakis A, Navarra J, Soto-Faraco S, Spence C (2007) Temporal recalibration during asynchronous audiovisual speech perception. Exp Brain Res 181:173–181
- Vatakis A, Navarra J, Soto-Faraco S, Spence C (2008) Audiovisual temporal adaptation of speech: temporal order versus simultaneity judgments. Exp Brain Res 185:521–529
- Vroomen J, Keetels MN (2010) Perception of intersensory synchrony: a tutorial review. Atten Percept Psychophys 72:871–884
- Vroomen J, Keetels MN, De Gelder B, Bertelson P (2004) Recalibration of temporal order perception by exposure to audio-visual asynchrony. Cogn Brain Res 22:32–35
- Wichmann FA, Hill NJ (2001) The psychometric function: I. fitting, sampling and goodness-of-fit. Perc Psychophys 63:1293–1313
- Wozny DR, Shams L (2011) Recalibration of auditory space following milliseconds of cross-modal discrepancy. J Neurosci 31:4607– 4612