EFFECTS OF SENSORY FEEDBACK ON DURATION REPRODUCTION

A Bayesian Approach to Characterize Sensorimotor Temporal Estimation

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Summary

Most studies, investigating human time perception, have demonstrated a difference between subjective and objective timing. Very common are, for example, results showing that visual intervals are judged shorter than physically equivalent auditory intervals. Recent studies have also found differences between motor and perceptual timing. Considering those perceived differences, the idea has been proposed that the brain might employ distributed (modality-specific) timing mechanisms rather than one amodal timing mechanism. Distributed timing mechanisms and therefore independent temporal estimates would be convenient in the computation for reliability-based multisensory or sensorimotor integration, as predicted by Bayesian inference. Several studies have shown that multisensory temporal estimates can be predicted by reliability-based integration models, as for example the Maximum Likelihood Estimation (MLE) model. Reliability-based integration studies in time research are still fairly rare and discussed controversially, and especially studies investigating sensorimotor integration are mostly missing. The aim of this cumulative thesis was to investigate sensorimotor temporal reproduction with a focus on the influence of sensory (mainly auditory) feedback on motor timing. Here fore, in all studies a sensorimotor temporal reproduction paradigm was employed, and sensory and motor estimates were treated as different/independent estimates. First, we investigated the effect of onset and offset delayed sensory feedback on temporal reproduction (Chapter 2.1). Second, perceptual and motor timing were compared explicitly and then a reliability-based model was used to predict the observed sensorimotor reproduction times (Chapter 2.2). In a third study, we manipulated the prior representation of the standard duration, using different adaptation conditions (Chapter 2.3). The findings showed that if the onset of a feedback stimulus was delayed in relation to an action (in contrast to when the feedback signal was started before the action), reproduced durations increased immediately, as soon as a delay is introduced. Offset-delayed sensory feedback, on the other hand, only induced a minor decrease in reproduction times and this effect could only be observed with auditory feedback. In comparison to auditory comparison estimates, which were shown to be fairly precise, pure motor reproduction as well as auditory reproduction was found to be consistently overestimated. The observed overestimation bias in auditory reproduction was reduced, compared to pure motor reproduction. This pattern of result could be shown for various standard durations and different signal-to-noise ratios (SNR) in the compared/reproduced tones. Further, a reliability-based model

predicted observed auditory reproduction biases successfully. In the third study, we could show that shifting the temporal range of accuracy feedback, manipulating the SNR of the reproduced tone, as well as introducing a manipulation of the reproduced tone onset, led to significant changes in the prior representation of the standard duration. Only manipulating the reproduced tone onset during the adaptation phase induced a reduction of auditory weights, which could be observed during the test phase. Additional trial-wise analysis confirmed that the adapted prior representation is shifted back to normal dynamically over time, once no accuracy feedback is provided anymore. The differences between observed sensory and motor estimates of time are discussed. We concluded that the finding that onset and offset delay influenced reproduction performance differentially implies that participants rather rely on the sensory feedback as a start-timing signal (at least if a causal relationship between action and sensory feedback can be established), while the motor stop is used as primary stop-timing signal. Observed sensorimotor reproduction biases and variability could be described as the weighted integration of the auditory estimate and the motor estimate. The integration reflects the brain combines multiple timing signals to improve overall performance. The prior knowledge of the standard duration in the reference memory is updated dynamically in that current sensorimotor estimates are constantly integrated with the history of duration estimates. In the end, overall implications of all the results for time perception, as well as sensory integration research are discussed. In summary, this thesis helps to improve our knowledge about sensorimotor temporal integration in a sensorimotor reproduction task on the basis of behavioral findings as well as probabilistic modeling.

CONTENTS

Chapter 1: General Introduction

1.1 Time perception

The perception of time is an interesting phenomenon. We consciously perceive the passage of time and use temporal information for everyday activities, like talking, walking and playing music or sports (Buhusi & Meck, 2005). Interval timing in the subsecond to minute range has been proven to be important for motor control (Buhusi & Meck, 2005). But even though we process time and use the temporal information constantly, time perception has so far not been investigated as thoroughly as spatial perception, and there are still a lot of open questions, about how humans perceive time. Interestingly, for example, no particular sense organ for physical time has been found, and also unlike specialized brain areas as for example the auditory cortex for the initial decoding of tones, there is no evidence for one specialized brain area primarily dedicated for time perception (Wittmann, 2009). Temporal information can be inferred from inputs of all the sensory organs, and many cognitive processes, like attention, memory and decision processes, have been shown to contribute to the perception of time (Church, 1984; Gibbon, Church, & Meck, 1984; Zakay & Block, 1996). Up to date, the question about how the brain processes time is still far from being answered completely (Wittmann, 2013).

1.1.1 Models of time perception

A classic and well known model of time perception is the pacemaker-accumulator model (Church, 1984). This model consists of several parts: a pacemaker, a switch, an accumulator, a working memory store, a reference memory store and a decision process/comparator (see Figure 1). During a to-be-timed interval the accumulator collects pulses that are generated by the pacemaker (Church, 1984). The switch is necessary to gate the pulses; the switch closes, when we start timing and when it opens again the accumulation stops, as no pulses can any longer be transferred from pacemaker to accumulator. The collected pulses are then transferred to the working memory for time (Church, 1984). Temporal information represented in the working memory is compared to reference memories (where previous temporal information is stored, for example a representation of a standard duration that was learned before). The actual comparison process depends on the task and a behavioral response can only happen after a decision, based on the comparison, has been made (Wearden, 2004). The model is easy to understand and intuitive, and – most importantly – can account for large behavioral data as well as for physiological data, at least qualitatively (Buhusi & Meck, 2005a; Simen, Balci, de Souza, Cohen, & Holmes, 2011). Individual parts of the model can be validated by independently manipulation in experiments. Meck (1983, 1996), for example, has shown that different drugs interfere with temporal processing at different levels: Methamphetamines, a psychostimulant acting on dopaminergic neurons, increases clock speed. On the other hand, vasopressin or oxytocin, neuropeptides thought to be involved in learning and memory processes (Walter, Hoffman, Church, Flexner, & Flexner, 1982), affects the transformation of temporal information into the working memory (Meck, 1983). Also other studies could successfully demonstrate changes in pacemaker speed (Burle & Bonnet, 1999; Droit-Volet & Wearden, 2002; Penton-Voak, Edwards, Percival, & Wearden, 1996) or altered switch processes in humans (Droit-Volet, 2003; Wearden, Edwards, Fakhri, & Percival, 1998) affect subjective time. An important feature of the pacemaker-accumulator model is the scalar property of the temporal information. Typically, temporal estimation has been shown to resemble Weber's law[1] in that the estimation error and variability is proportional to the physical duration of the to-be-estimated interval (Gibbon et al., 1984). This means that after normalization of the estimates of different standard durations, the same form of distribution of relative time and constant timing sensitivity can be found. Some researchers have even argued that this scalar property does not only apply to behavioral estimates, but also to the neural activation in the brain (Buhusi & Meck, 2005; Hinton & Meck, 2004; Meck & Malapani, 2004).

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[1] Weber's law, as formulated by Ernst Weber, 1831, highlights the relationship between the physical intensity of a stimulus and the sensory experience that the stimulus causes. An increase in stimulus intensity that is needed to produce a just-noticeable difference is constant.

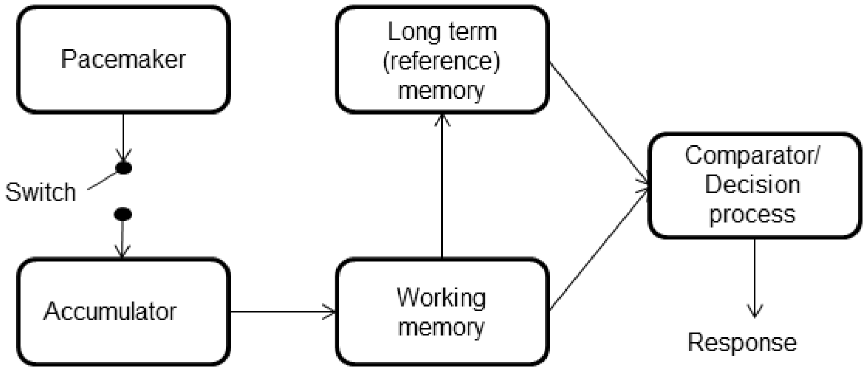

Figure 1. Outline of the pacemaker-accumulator model. The left side shows the clock, the middle panel the memory stores, and the right side the decision level (adapted from Wearden, 2004).

However, as most classic time research was based on animal research, researchers did not account for modality differences in timing, but rather implicitly assumed that only one dedicated (amodal) mechanism is responsible for measuring temporal intervals. Only more recent studies, employing brain imaging techniques, found diverse activations in the brain, which rather speak for modality specific timing mechanisms employed by humans during a timing task (Bueti, Bahrami, & Walsh, 2008; Ghose & Maunsell, 2002; Lewis & Miall, 2003). Therefore, researchers have started to argue for distributed, modality specific timing mechanisms in the brain (for a review see, Bueti, 2011). These so called intrinsic models (for reviews on dedicated vs. intrinsic models see Ivry & Schlerf, 2008; Wittmann, 2013), in contrast to the dedicated amodal models (like the classic pacemaker-accumulator account), propose the idea that sensory and cognitive processes can make inferences about temporal information in addition to their main sensory processing function (Buhusi & Meck, 2005; van Wassenhove, 2009). Based on findings from electrophysiological recordings in animals (Lebedev, O'Doherty, & Nicolelis, 2008; Leon & Shadlen, 2003), a fairly promising recent, neurologically plausible, model assumes that temporal estimation is achieved by 'climbing' neural activation (Simen et al., 2011; Wittmann, 2013). In these studies it has been observed that neural activity increases and peaks at the end of a to-be-estimated duration. This idea would be in agreement with the idea that one area in the brain works as a central clock (one central, amodal memory store) and reads out neural signals from other brain regions (modality specific pacemakers and accumulators). On the other hand, it is also reasonable to assume that different neural networks are activated, dependent on the task characteristics that represent temporal information in addition to their other functions (Wittmann, 2013). Up until now, however, evidence for the climbing activity model is hardly found in human research (for an exemption, see Wittmann, Simmons, Aron, & Paulus, 2010) and is therefore still under discussion (Kononowicz & van Rijn, 2011; Wittmann, 2013).

1.1.2 Physical time versus subjective time

Many studies have demonstrated that subjective time is not equal to physical time, but can actually vary quite dramatically. Already over a century ago, Albert Einstein described the phenomenon that time perception often depends on the context: "When a man sits with a pretty girl for an hour, it seems like a minute. But let him sit on a hot stove for a minute – and it's longer than any hour" (as cited in Mirsky, 2002, p.102). In agreement with Einstein's metaphor, several studies have demonstrated that the emotional state of an observer influences the perceived time (Angrilli, Cherubini, Pavese, & Mantredini, 1997; Shi, Jia, & Müller, 2012). Also stimulus properties like intensity, motion (speed) or flicker could be shown to have an effect on time estimations (Eagleman, 2008; Johnston, Arnold, & Nishida, 2006; Kaneko & Murakami, 2009; van Wassenhove, Buonomano, Shimojo, & Shams, 2008). Further, as mentioned earlier various pharmacological agents, like cocaine, methamphetamine, or vasopressin have been shown to affect the perceived duration of a temporal interval (Buhusi & Meck, 2005; Meck, 1983, 1996). When a voluntary action or a saccade starts a to-be-timed interval, this interval is usually overestimated, compared to the interval started automatically (Park, Schlag-Rey, & Schlag, 2003; Yarrow, Haggard, Heal, Brown, & Rothwell, 2001). This overestimation effect is known as the "chronostasis effect", describing the phenomenon of the impression that the second hand of a clock seems to stop when you turn to look at the clock. However, the opposite effect (underestimation after voluntary action or saccade) has been shown as well (Haggard, Clark, & Kalogeras, 2002; Morrone, Ross, & Burr, 2005). This opposite illusion, in which participants perceive an interval between a voluntary action and a sensory stimulus as shorter than its actual physical duration, has been termed "intentional binding", demonstrating that a voluntary action is attracted towards its sensory effect to keep a causal relationship between the action and the effect consistent (Engbert, Wohlschläger, & Haggard, 2008; Engbert, Wohlschläger, Thomas, & Haggard, 2007; Haggard et al., 2002).

As mentioned before, researchers have argued for distributed, modality-specific timing mechanisms in the brain as subjective time has been found to depend on the sensory modality a temporal duration is presented in. In general, a temporal interval is perceived longer if the duration is conveyed by auditory signals than visual signals, even though physically it has the same duration (Walker & Scott, 1981; Wearden et al., 1998). There is also similar evidence that physically same length durations are judged longer if they are presented as auditory tones than as tactile durations (Jones, Poliakoff, & Wells, 2009). The subjective bias (i.e. the estimated difference from the actual physical duration) as well as the variability of a temporal estimate, therefore, can vary quite dramatically dependent on the modality. Further, multiple durations can be easily kept in the memory, if the durations are presented in different modalities (Gamache & Grondin, 2010). It seems reasonable to assume that this improvement in memory is caused by the fact that the temporal intervals are stored as different memory representations dependent on the modality they are presented in (Bueti, 2011). In the brain, modality-specific temporal processing has also been demonstrated in several imaging studies (for a review see, Bueti, 2011). One study, for example, using transcranial magnetic stimulation could show that the disruption of the visual area V5/MT+ affects the estimation of visual durations, but not of auditory intervals (Bueti, Bahrami, & Walsh, 2008). All these findings rather speak for modality-specific temporal encoding, than for an amodal internal clock, and highlight the perceptual differences and variability of subjective time perception.

1.1.3 Motor timing

Time perception in the millisecond to one second range is important especially for action (Buhusi & Meck, 2005). Timing in this range is thought to rather depend on cerebellar representation in contrast to timing in the range of seconds, where activation of the cerebellum is hardly ever found (Buhusi & Meck, 2005; Ivry & Spencer, 2004; Koekkoek et al., 2003). Most studies investigating motor/action timing have either used sensorimotor synchronization or reproduction methods paradigms. In sensorimotor synchronization participants are generally asked to tap a finger (or a foot) along with an auditory, visual or sometimes even tactile rhythm. Especially of interest is here, how movement is synchronized with an external event and the associated error correction mechanisms (for a review see, Repp, 2005). Note however, that in sensorimotor synchronization sensory stimuli appear at a regular beat and participants have to tap along with this beat. Therefore, the task has a rhythmic element and it has been suggested that rhythmic movements might be different from non-rhythmic movement, usually applied in temporal reproduction tasks (Davis, 1962; Treisman, 1963). Non-rhythmic temporal reproduction research on the other hand is quite diverse. An important problem here is that different paradigms are summarized under the term reproduction. For most studies employing a temporal reproduction method, participants are asked, after the presentation of a standard duration, to stop a second temporal interval at the point in time when they think that this second interval has been presented for the same duration as the standard interval (Wearden, 2003). This method has also been termed “reproduction by waiting” and is the most frequently reported method used in temporal reproduction research (Wearden, 2003). In some other studies temporal reproduction was achieved by pressing a button once to start a reproduction of a reference interval and then press a button again, when participants think that the duration is equal to the reference duration (see for example, Meegan, Aslin, & Jacobs, 2000). Importantly, in both reproduction methods described the actual reproduced duration is unfilled or rather filled with perceptual information (like a tone or a visual stimulus). Only few studies have used ‘filled’ reproduction method - pressing a button for a certain duration to produce the reference interval (i.e. filled duration reproduction) (Bueti, Walsh, Frith, & Rees, 2008; Bueti & Walsh, 2010; Walker & Scott, 1981). Analogue to differences found for empty and filled auditory and visual duration discrimination (Grondin, 1993; Rammsayer & Lima, 1991), one could assume that there might also be a estimation difference for filled and unfilled temporal reproduction.

Because of the diversity of methods used in order to investigate motor timing, common models for motor timing are rare. An exemption, are models on sensorimotor synchronization (Vorberg & Wing, 1996; Wing, 1977). It has been proposed that temporal reproduction might consist of two consecutive processes: initiating a response when the to-be-timed duration is similar to a given standard duration, and executing of a motor response (i.e. pressing a button) (Wearden, 2003). The initiation and execution of the response also takes time and generally leads to an over-reproduction of standard intervals (idea adapted for interval timing from Wing and Kristofferson’s model for repetitive tapping, Wing & Kristofferson, 1973). However this can only be true for the reproduction of unfilled intervals, as in the production of a filled duration delays due to initiation and termination of a response may cancel each other out.

Most studies focused on common mechanism of motoric and perceptual timing, trying to support the idea of a single “clock” – being responsible for all time perception - in our brain. In a study by Keele and colleagues, a correlation between the acuity of perceptual judgments and the regularity of motor production was reported (Keele, Pokorny, Corcos, & Ivry, 1985). In one task participants had to produce regular intervals by tapping either their finger or foot and in the other task they compared durations of time intervals between clicks. Motor accuracy correlated with an amount of 0.6 with accuracy of perceptually based time judgments. The results were replicated, confirming with a method of slope analyses that time-dependent variability is equal for perceptual and motor timing (Ivry & Hazeltine, 1995). Arguments for common motoric and perceptual timing mechanisms are also in line with cerebellar patient studies, which showed performance impairments for both – perceptual and motor - tasks (Ivry & Keele, 1989). Further evidence for common timing mechanisms comes from an fMRI study which showed that the neural network supporting time perception involves the same brain areas that are responsible for temporal planning and coordination of movements (Schubotz, Friederici, & von Cramon, 2000). It has also been demonstrated that training on a perceptual timing task showed a significant transfer to a motor timing task (Meegan et al., 2000), further strengthening the argument for common timing mechanisms for motoric and perceptual timing.

Only in recent research, differences between motoric and sensory timing have been investigated more critically. In agreement with the argument for distributed, intrinsic timing mechanisms in the brain, differences between perceptual timing and motor timing have been proposed, as well (Bueti & Walsh, 2010). Only several studies have explicitly compared action/motor and perceptual/sensory timing. Ivry, for example, postulated the idea that there could be processed in different units that are specific to a task, like specific timing mechanisms for each limb and for each input modality (Ivry, 1996). This idea was based on findings that if participants were asked to tap with two hands to a rhythm, within-hand temporal variability is reduced when the movements of one hand is accompanied by the in-phase movements of the other hand (Franz, Ivry, & Helmuth, 1996; Helmuth & Ivry, 1996). Here, the authors argue that the two timing signals for each hand (or other limbs) become averaged and therefore tapping is less variable with two limbs compared to tapping with one limb. However, differences between sensory and motor timing are not addressed specifically. Two other, fairly recent, studies (Bueti, Walsh, Frith, & Rees, 2008; Bueti & Walsh, 2010) have directly addressed the question about differences between action and sensory timing. It could be shown that in comparison to a perceptual task, where temporal estimations were not affected, performance in the action timing task (where participants had to press and hold down a button to reproduce an auditory or a visual duration) dropped if a delay between the end of the standard and begin of the reproduction was introduced (Bueti & Walsh, 2010). Additionally, in the action timing task, several areas in the brain were more activated than compared to the perceptual task (Bueti, Walsh, Frith, & Rees, 2008). A different and wider cortical network, including the cerebellar vermis, prefrontal and parietal cortex, was activated during the action condition compared with the more "simple" perceptual time estimation condition.

Assuming that the brain employs independent mechanisms for motor timing compared to perceptual timing, different temporal variances and biases should arise, dependent on the task.

1.2 Sensory cue integration

In everyday life we are confronted with multiple sensory information and our actions are accompanied by sensory feedback. For example, we can see and hear a car passing by on the street and we can see and feel our hand grasping a pen. However, combining those sensory inputs that derived from the same event and separating those inputs that come from differential events is a challenging task for the brain. Usually, in our environment there is not only one event we are confronted with at the same time, but multiple. The assignment of whether sensory inputs derive from the same event is further complicated, by the fact that sensory input is not always accurately encoded, but is rather noisy. An example for inaccurate sensory integration is that people often perceive two flashes, when a single flash is accompanied with two auditory beeps (Shams, Kamitani, & Shimojo, 2000). It is thought that the most important factors of how the brain groups sensory inputs are spatial proximity and temporal coincidence (Alais, Newell, & Mamassian, 2010). Sensory inputs are likely to be integrated when the signals originate from proximal locations and reach the brain at about the same time.

1.2.1 Models of sensory cue integration

Early multisensory research has argued for a 'modality appropriateness hypothesis' (Welch & Warren, 1980). The idea here is that the input from the most accurate sensory modality dominates in multisensory perception. Due to its higher spatial resolution vision often dominates over audition in spatial tasks, while in temporal tasks audition dominates over vision. The crossmodal interactions are often described as visual or auditory capture effects, resulting in a neglect of the other (additionally presented) modality. It has been argued that the modality appropriateness hypothesis might be a too simplistic explanation of multisensory integration, as it has been shown that if in a spatial localization tasks visual signals are degraded, the typically found visual dominance in the task can be reversed, so that participants rather trust an auditory signal over a degraded visual signal (Alais & Burr, 2004). Also, it was shown that an auditory click was perceived as earlier in time when it was preceded by a visual flash and as later when it was followed by a flash, similar (but smaller in amount) to capture effects shown for visual stimuli by auditory events (Fendrich & Corballis, 2001). Moreover, it has been demonstrated that the brain might combine information from different senses in a probabilistic way, rather than simply choosing information from only one sensory input and neglecting the other. One well known model is the Maximum Likelihood Estimation (MLE) model (Alais & Burr, 2004; Ernst & Banks, 2002; Ernst & Bülthoff, 2004) which uses Bayesian statistics to quantitatively account for multisensory integration. The MLE model suggests that an ideal observer will combined two independent, sensory signals in a linear-weighted fashion, such that the combined estimate has highest reliability (Ernst & Banks, 2002). The optimal weights used for the multimodal integration are proportional to the reliability (i.e., the inverse of its variance) of each estimate. Therefore, the modality that provides less variable information in a given situation will have a higher weight and a greater influence on the final percept. With an ideal observer, the MLE estimate is the best estimate among any linear-weighted combination, because it is least variable and maximally reliable. The winner-take-all estimate suggested by the modality appropriateness hypothesis (Welch & Warren, 1980) would be less optimal since it only takes information from one modality while neglecting others (Alais et al., 2010; Ernst & Bülthoff, 2004; Ernst & Di Luca, 2011; Vilares & Kording, 2011). This increased reliability in cue integration, enhances object discrimination and identification, and facilitates a reaction to the external world (Vroomen & Keetels, 2010).

The principles of MLE can be illustrated, if one considers an audiovisual signal, providing two sources of information about an event (e.g. during an audiovisual localization task), estimated by the auditory and visual system (auditory localization estimate $\hat{S}_a$, visual localization estimate $\hat{S}_v$). The bimodal estimate of the audiovisual location $\hat{S}_{av}$ results from the integration of the two sensory cues and is a weighted linear combination:

$$\hat{S}_{av} = w_a \hat{S}_a + w_v \hat{S}_v \qquad (1)$$

where $w_a = 1/\sigma_a^2 / \left(1/\sigma_a^2 + 1/\sigma_v^2\right)$, $w_v = 1 - w_a$, and σ_a^2, σ_v^2 are variances of the auditory and visual localization estimates (see Figure 2). Importantly, the MLE model predicts both the mean bimodal estimate and its variance.

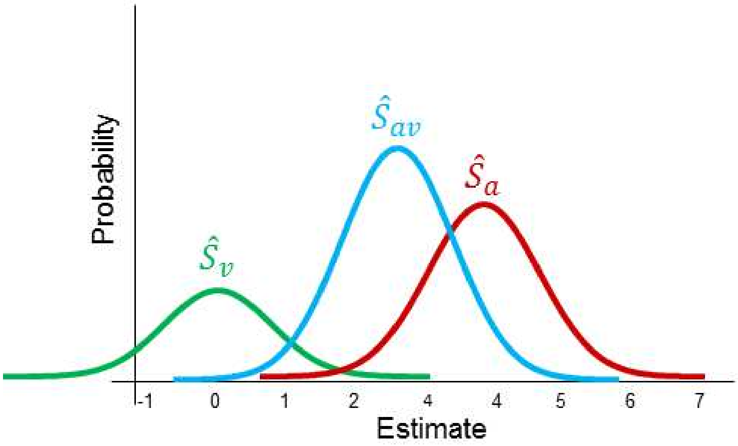

Figure 2. Audiovisual integration according to the MLE model. The audiovisual estimate $\hat{S}_{av}$ results from a linear combination of the unimodal estimates $\hat{S}_a$ and $\hat{S}_v$, with each weight set in proportion to its reliability.

Many studies have tested and verified the predictions of the reliability-based integration models in spatial perception (for a review, see Alais et al., 2010). Ernst and Bank could show that visual and haptic information about size is integrated as predicted by the MLE model (Ernst & Banks, 2002). Also integration of audio-visual localization cues (Alais & Burr, 2004; Battaglia, Jacobs, & Aslin, 2003) and even the integration of independent cues within a single modality, as for example the integration of texture and motion or texture and binocular disparity has been demonstrated (Hillis, Ernst, Banks, & Landy, 2002; Jacobs, 1999; Knill & Saunders, 2003). Even though, reliably-based models often assume that the two sensory signals have a single cause and are unbiased, accurate estimates, a recent study demonstrated that even biased estimates of stereo vision and motion cues are integrated in accordance with the reliability-based model and that this integrated estimate of biased stimuli is still more beneficial than non-integrated/unimodal estimation (Scarfe & Hibbard, 2011).

Optimal integration has been proven to play a role in minimizing uncertainty also in sensorimotor control. Studies could show that additional sensory feedback will be optimally integrated in order to perform more accurately on sensorimotor tasks (Bays & Wolpert, 2007; Izawa & Shadmehr, 2008; Körding & Wolpert, 2004; Shadmehr, Smith, & Krakauer, 2010; van Beers, Sittig, & Van der Gon, 1999). For example van Beers and colleagues asked their participants to align their left hand with either a visual target or a proprioceptive target (their unseen right hand) (van Beers, Sittig, & Van der Gon, 1996). Results showed that the variability in the estimates obtained when subjects combined proprioceptive and visual information was smaller than the variability obtained when participants could use one of the senses. In a further study, it could be shown that participants tend to rely on the most accurate cue: proprioceptive information was rather used for depth estimation, as proprioception gives more reliable information about depth, while for azimuth participants rather rely on visual information (which has been shown to be the more reliable source of information) (van Beers, Sittig, & Van der Gon, 1998).

1.2.2 Temporal integration

Multisensory events that coincide in time have been shown be integrated to a coherent temporal percept, similar to multisensory spatial integration. Analogous to the spatial ventriloquist effect, several studies have reported a temporal ventriloquist effect, demonstrating that visual temporal order judgments are enhanced by the presentation of two auditory stimuli, one presented slightly prior to the first visual flash and the second shortly after the second flash (Morein-Zamir, Soto-Faraco, & Kingstone, 2003; Shimojo et al., 2001). Studies in time have long favored the modality appropriateness hypothesis (Welch & Warren, 1980) in temporal integration, as most studies only demonstrate auditory influence on visual temporal judgments (Bertelson & Aschersleben, 1998; Morein-Zamir et al., 2003). For example, Klink and colleagues argued that while irrelevant auditory intervals are automatically used when the brain estimates visual durations, irrelevant visual durations have no effect on the estimation of auditory durations (Klink, Montijn, & van Wezel, 2011). Only over the last decade, researchers have started to use Bayesian inference to model multisensory integration in the temporal domain. However, the results are still diverse. Employing an audio-tactile temporal-order judgments (TOJ) task, Ley et al. showed that the bimodal temporal estimates were optimal as predicted by the MLE model (Ley, Haggard, & Yarrow, 2009). However, Burr and colleagues only found a rough fit of the MLE model for their audio-visual temporal-bisection data (Burr, Banks, & Morrone, 2009). The only "somewhat" consistent pattern found in studies investigating temporal multisensory integration is that of well predicted temporal estimates, but no maximal reduction of the variability. This pattern has been confirmed in an apparent motion study, implicitly measuring perceived durations (Shi, Chen, & Müller, 2010), in a recent audio-visual temporal bisection task (Hartcher-O'Brien & Alais, 2011), as well as in a visual-tactile reproduction task (Tomassini, Gori, Burr, Sandini, & Morrone, 2011). More strikingly, sensorimotor temporal integration has been neglected, so far.

The reasons for the missing reduction in the observed variability reported in temporal integration studies are not clear yet. It seems possible that the neuronal processes for temporal estimates from different sensory modalities might not be completely distributed and statistically independent, as indicated by the amodal time theories (Church, 1984; Coull, Vidal, Nazarian, & Macar, 2004; Gibbon, Malapani, Dale, & Gallistel, 1997; Ivry & Hazeltine, 1995; Keele et al., 1985; Treisman, 1963). Also the assumption of Gaussian noise might not be appropriate for temporal estimations (Burr et al., 2009). There could also be accuracy limits in some sensory systems so that variability could not be further reduced. The time perception research community is only starting to understand multisensory temporal integration and to investigate differences in comparison to spatial multisensory integration.

1.2.3 Remapping and delay perception

As mentioned before temporal coincidence is an important factor for perceiving a common source and integrating two signals. In order to detect temporal coincidence, however, the brain needs to calibrate for physical temporal discrepancies induced by physical transmit speed (as sound and light travels at different speeds), as well as for different neural processing time for the different sensory modalities (King & Palmer, 1985; Stone et al., 2001). For example, neural transmission times for auditory information are much shorter, than for visual input (Levitin, MacLean, Mathews, & Chu, 2000). For touch, the origin of the stimulation has to be considered, because the transmission time is shorter from the face to the brain than from the toes (Vroomen & Keetels, 2010). Therefore, it has been proposed that the temporal integration window has to be relatively wide, in order to allow for more multisensory integration. In speech perception, for example the auditory signal can be delayed by as much as 250 ms before the de-synchronization with the visual input becomes apparent (Dixon & Spitz, 1980). Additionally, the brain should be able to recalibrate and adapt to temporal asynchronies in order to deal with continuous changes in the body (e.g. limbs growth or the increase in head size) and the environment. Indeed, several studies have shown that the brain can adapt to small temporal asynchronies between multisensory or sensorimotor events (Fujisaki, Shimojo, Kashino, & Nishida, 2004; Harrar & Harris, 2008; Keetels & Vroomen, 2008; Stetson, Montague, & Eagleman, 2006). One psychophysical study examined the repeated exposure to an introduced audio-visual asynchrony and demonstrated that after adaptation judgments of subjective simultaneity were shifted towards the adapted asynchrony (Fujisaki et al., 2004). Also for other modalities a comparable shift in perceived simultaneity has been demonstrated (Di Luca, Machulla, & Ernst, 2009; Hanson, Heron, & Whitaker, 2008; Harrar & Harris, 2008; Takahashi, Saiki, & Watanabe, 2008).

Adaptation to even larger asynchronies and larger effects than those reported for adaptation to sensory-sensory asynchrony have been found in sensorimotor temporal asynchrony recalibration studies (Kennedy, Buehner, & Rushton, 2009; Stetson et al., 2006; Sugano, Keetels, & Vroomen, 2010). For example, it has been shown that after exposure to a delayed visual feedback of a button press action, flashes that were triggered by the button press without delay were perceived as having occurred before the button press (Stetson et al., 2006). The authors have argued that in order to maintain the expected causality between button press and visual feedback, the visual event was shifted dynamically towards the onset of the action. This idea goes along with other research arguing that a delayed sensory effect is perceived as having appeared slightly earlier in time if it follows a voluntary action (Eagleman & Holcombe, 2002; Haggard, Clark, & Kalogeras, 2002) – a phenomenon referred to as "intentional binding". On speaks of intentional binding if a voluntary action is attracted towards its sensory consequence, so that the action is perceived as having occurred slightly later in time and the perceived feedback delay is shorter than the actual delay (Engbert, Wohlschläger, & Haggard, 2008; Engbert, Wohlschläger, Thomas, & Haggard, 2007; Haggard et al., 2002). It is assumed that everyday experience leads the brain to calibrate sensorimotor synchrony between the start of a motor action and its sensory effect (Heron, Hanson, & Whitaker, 2009). It has also been argue that due to increased mapping uncertainty for sensorimotor signals compared to for example the mapping of texture and disparity estimates, adaptation is faster for sensorimotor than for multisensory or within-modality asynchronies (Ernst & Di Luca, 2011). Further, Wenke and Haggard have argued for a transient slow-down of an internal clock after a voluntary action (Wenke & Haggard, 2009). However, whether sensorimotor temporal recalibration is due to timing changes in the motor system or in the perceptual system is still discussed controversial (Kennedy et al., 2009; Sugano et al., 2010).

1.2.4 Effects of priors on multisensory/sensorimotor estimation

The Bayesian framework does not only describe the integration of two sensory or of a sensor and a motor estimates, but also prior knowledge can be integrated in order to achieve a more reliable estimate. Prior knowledge is understood as general knowledge about the world (as for example the assumption that light comes from above – Dror, Willsky, & Adelson, 2004) or task specific knowledge that has been achieved through experience with a certain task (Berniker, Voss, & Kording, 2010). For example, if we watch TV, even though the sound actually comes from a different location than the visual image (speakers on the side), our beliefs (= prior knowledge) combines sound and visual input to a coherent perception of a common origin of the visual and auditory stream. Several studies have demonstrated that humans combine sensory information with previously acquired knowledge (prior), relying more on the prior when sensory information is relatively unreliable and vice versa (Brouwer & Knill, 2009; Gerardin, Kourtzi, & Mamassian, 2010; Körding & Wolpert, 2004; Tassinari, Hudson, & Landy, 2006). In general, in studies using the MLE model to describe a multisensory reliability-based integration process it is assumed that the prior knowledge is flat and stable over time and therefore, plays no role in the integration process (Alais & Burr, 2004; Ernst & Banks, 2002). This assumption is not only often implicated because of computational convenience, but also because studies have shown that prior knowledge can stay fairly stable across time (Beierholm, Quartz, & Shams, 2009). However, several recent studies have pointed out that prior knowledge is dynamically updated and can be implicitly modulated by short-term experience on a trial-by-trial basis (Acerbi, Wolpert, & Vijayakumar, 2012; Jazayeri & Shadlen, 2010; Petzschner & Glasauer, 2011).

As mentioned before, in time perception, it has often been found that the temporal context, the modality of a to-be-timed stimulus, as well as the order of the presentation has an influence on discrimination and estimation performance (Dyjas, Bausenhart, & Ulrich, 2012; Grondin, 2010; Gu & Meck, 2011; Jazayeri & Shadlen, 2010; Lejeune & Wearden, 2009; Penney, Gibbon, & Meck, 2000; Wearden, Edwards, Fakhri, & Percival, 1998). Recently, researchers have used the Bayesian framework and explicitly the dynamical update of prior knowledge to account for these temporal illusions (for a review see Shi, Gibbon, & Meck, in press). Taking the internal clock model into account, the process of the memory stage, where the current estimate is transferred to the reference memory, can be easily be described in the Bayesian framework, as the integration of the sensory likelihood with the prior knowledge in the memory. One would therefore predict that every time a to-be-timed interval is presented, the current estimate is integrated with the history of previous estimations and therefore affects the prior representation of the standard duration in the memory. The idea is in line with a recent model, which considers the buildup of the reference memory of a standard duration not to be based on a single memory trace, but rather as a dynamic process that changes temporal estimations over trials based on experiences (Taatgen & van Rijn, 2011). Also the central-tendency effect, observed when long and short standard durations are intermixed, where participants tend to perceive short durations longer and long durations shorter (Gu & Meck, 2011) could be explained by the effect of prior knowledge that has so far been implicitly assumed to be learned by participants over time (Acerbi et al., 2012; Jazayeri & Shadlen, 2010). Jazayeri and Shadlen, for example, could show that participants reproduce the same duration differently depending on the mean distribution of the presented durations (Jazayeri & Shadlen, 2010). This sort of integration behavior helps participants to decrease the observed variability in their duration estimates. Note however, that the authors implicitly assume that participants can learn and use statistical properties of stimulus distributions. In agreement with spatial integration studies, it has further been demonstrated that if participants are less variable in their temporal perception, as expert drummers are for example, the influence of the prior knowledge (i.e. central tendency effect) is less strong (Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012); however, if participants are more variable in their temporal perception, as for example Parkinson's disease (PD) patients, tested off their dopaminergic medication, they rely stronger on the prior memory representation than the actual presented interval (Malapani et al., 1998). All of these described studies highlight the importance of acknowledging the dynamic influence of prior knowledge in multisensory or sensorimotor time perception.

1.3 Aim of this thesis

In everyday life our actions are generally accompanied by sensory feedback. We are so used to causally related action feedback that we do not even perceive small temporal delays between an action and the sensory feedback (Engbert et al., 2008, 2007; Haggard et al., 2002), which in principal would be in the range of being detectable for us. In the spatial domain, researchers have long investigated the question how sensorimotor information is integrated, how sensory feedback enables monitoring actions and how sensory feedback is used to learn new movements (Bays & Wolpert, 2007; Körding & Wolpert, 2004; Shadmehr et al., 2010; van Beers et al., 1996). However, in time research the effect of sensory information on action timing has only sparsely been investigated and is missing completely in terms of duration perception – in comparison to point-in-time perception. The purpose of the three studies presented in this thesis was to get a better understanding of action timing and the effect of sensory feedback on it. So far sensorimotor timing, i.e. filled-duration sensorimotor timing has only been sparsely investigated. As mentioned before, only in the last decade researchers have started to accept distributed timing mechanisms in the brain (for a review see Bueti, 2011). Especially action-perception differences in time estimation have only been proposed recently. Interestingly, striking differences between action and perception time have been reported. For example, Walker and Scott, as mentioned earlier, once found that motor reproduction, relying only on kinesthetic information (i.e. action timing), was overestimated by about 12 perception for an auditory standard duration (Walker & Scott, 1981). Investigating modality differences and particularly action-perception differences in time estimation is important to help getting a clearer picture on the time processing mechanisms of the brain that are not well understood yet. In this thesis sensorimotor timing is investigated closely, using three different approaches to get a better understanding of action and perception time estimations and their interactions. First, the effects of a delay manipulation are explored. So far the effects of delay between an action and a sensory stimulus have only been investigated for point-in-time estimations (e.g. Stetson et al., 2006). Different delay manipulations might highlight differences between action and perception timing. Further, it should shed some light on what information (i.e. action or perception information) is used by participants in order to reproduce a given standard duration as accurately as possible. Also intentional binding effects, so far only observed for sensorimotor point-in-time estimations (Engbert et al., 2008, 2007), might also be present during filled-duration sensorimotor time reproduction and might lead to further insights on the underlying processes of intentional binding. Second, action and perception timing were compared directly to observe differences in temporal bias and variability. Applying a reliability-based model allowed us to look at the benefits of integrating biased temporal estimates. Using different temporal biases rather than different physical durations might open new opportunities for looking at reliability-based temporal integration. Third, we compared different adaptation procedures to dynamically affect the prior representation of the standard duration. Prior knowledge as an additional source of information during sensorimotor timing will always affect reproduction performance. Previous studies have assumed that additional knowledge, for example about the statistical distribution of the presented stimuli, will affect time reproduction (Acerbi et al., 2012; Jazayeri & Shadlen, 2010), however, nobody has explicitly attempted to modulate prior knowledge and investigate trial-wise effects. Overall, this thesis attempts to give readers a better understanding of action and perception timing and about the integration and interaction of the two time information sources.

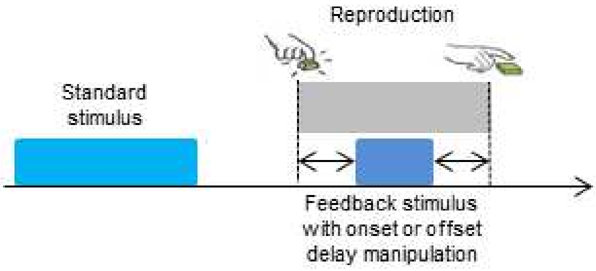

Figure 3. Illustration of the temporal reproduction task with sensory feedback used in all three studies of the thesis. A standard duration is presented first. Participants are asked to reproduce the standard by pressing a button. Another stimulus is fed back to participants based on the action. The onset or the offset of the feedback stimulus could be delayed (onset and offset were never delayed at the same time).

In order to explicitly investigate action and perception time, we adopted and modified a temporal reproduction task with feedback (see Figure 3), as introduced by Bueti and Walsh (2010). Here, participants had to reproduce a standard duration, by pressing and holding down a button. In the sensorimotor condition a feedback signal was presented while participants were holding down the button. The term feedback signal refers to the stimulus presented during the reproduction to highlight the causal relationship between action and sensory stimulus. Participants were always instructed to focus on reproducing the standard duration and not pay attention to the feedback. With the exemption of the third study, no accuracy feedback (too long, too short) was provided to the participants. This is important as we are interested in pure temporal estimates that we assume to be biased and the biases are thought to be dependent on the modality (action vs. perception timing). The same task was used in all three studies included in this thesis. It enabled us to compare filled-interval action timing with filled-interval perception timing. Using only filled durations was considered as being important, as we assume that temporal estimation might be most different/independent for these kind of durations, compared to unfilled durations which might employ more similar mechanisms in the brain as the information presented in unfilled intervals (i.e. nothing) is more comparable for action and perception time here. In the action timing task kinesthetic and tactile (touch sense) feedback due to the button press is considered as one, unitary motor component. That this might be an oversimplification of processes underlying motor reproduction is highlighted by the results of a previous sensorimotor tapping study, where it could be shown that blocking peripheral feedback leads to an increase in the variability in synchronizing the pacing signal with the tap (Aschersleben, Gehrke, & Prinz, 2001). Further, in the second and third study presented, we completely focused on auditory timing. Auditory timing is generally found to be more accurate and automatic than visual or tactile time perception (Jones et al., 2009; Klink et al., 2011; Repp, 2005; Walker & Scott, 1981; Wearden et al., 1998). Also several researchers have argued for a privileged link between the auditory and the motor system for timing, leading to a more direct access of auditory information in the motor system (Jäncke, Loose, Lutz, Specht, & Shah, 2000; Jantzen, Steinberg, & Kelso, 2005; Zatorre, Chen, & Penhune, 2007). For these reasons, the testing of temporal integration mechanisms was considered to be easier and less variable for auditory timing only.

In a first study (Chapter 2.1), the effect of sensory feedback on action timing was investigated, by means of investigating how action timing is affected by asynchronous-feedback signals. Feedback onset, as well as feedback offset was manipulated. Feedback (visual or auditory), presented while participants were pressing a button, was either synchronized with the button press or either the onset or the offset could be delayed in relation to button press onset or offset. Further, the feedback could either be presented in the same or in a different modality than the standard stimulus. The main question was whether participants would rely either on action/motor timing or on the perceptual timing, even though perception timing would be considered as more unreliable as it was delayed during some trials. In the case that participants completely rely on their action/motor timing (as actually instructed), no (or only small) effects of feedback delay were expected. However, if perceptual timing is considered by participants during the task as well, reproduction errors should differ for conditions in which the feedback was synchronized with the button press, compared to conditions in which the feedback was delayed. In four, out of five experiments, the feedback delay was systematically arranged and always the same (200 ms). In the fifth experiment, the feedback delay varied randomly near the onset or offset of the button press. In this study, visual, auditory and also crossmodal audio-visual timing (visual standard and auditory feedback vs. auditory standard and visual feedback) was investigated.

The second study (Chapter 2.2) focused on the question whether the integration of a feedback signal during a temporal reproduction task could be modeled using a reliability-based approach. We compared estimation and variability for three different tasks: auditory duration comparison, motor reproduction (without feedback signal) and auditory reproduction (with synchronous feedback signal). Estimates and variability of the auditory comparison and the motor reproduction task measured perceptual and action/motor time processing and were considered as being independent. Further, the unimodal biases and variability were used to predict estimation biases and variability in the auditory reproduction task. We explicitly introduced temporal biases (which are usually disregarded in Bayesian integration models) in the quantitative model. It was expected that in the sensorimotor task (auditory reproduction) temporal bias is reduced, as auditory and motor biases are combined in a linear weighted fashion. Further, we expected sensorimotor variability to be decreased compared to the two unimodal tasks, as predicted by reliability-based models. Dynamic weight adjustment (as predicted by the classical MLE) was investigated by introducing two different signal-to-noise ratios (SNR) for the comparison/reproduced tone and two different standard durations. Importantly, only auditory stimuli were used in this study.

In the third study (Chapter 2.3), we addressed the question whether the buildup of the prior representation of the standard duration can be explicitly manipulated by adaptation. Comparable to the previous studies, participants had to do a sensorimotor temporal reproduction task. During an adaptation phase participants received a feedback (i.e. accuracy feedback) about their performance accuracy. Here, we manipulated once the accuracy feedback range, the signal-to-noise ratio (SNR) of the reproduced tone and in the last experiment the reproduced tone onset. During an immediately following test phase no accuracy feedback was provided, but we introduced an onset-delay, which allowed us, again using a Bayesian framework, to infer the weights of auditory estimations from the slope when the reproduced duration is regressed against delay time. Shifting the accuracy range of the feedback was expected to shift the whole prior representation in the direction of the shift. Since we adapted participants to an accuracy range that was 100 ms short of the true accuracy range, lower reproduction durations for the shifted compared to the baseline feedback condition were hypothesized. A manipulation of the SNR of the reproduced auditory tone was also thought to affect the actual reproduction durations after adaptation, leading to shorter reproduction times after low SNR adaptation, compared to longer reproduction times after high SNR adaptation. Additionally, a change in auditory weights due to the different sound intensities was predicted (i.e. lower auditory weights after low SNR adaptation). Adaptation with a random-tone onset, compared to synchronous tone onset adaptation, was also expected to have an effect on the associated auditory weights, which should lead to a change in slope when reproduced duration is regressed against delay time. As we had so far only established that auditory reproduction can be predicted by the MLE model, again, only auditory stimuli were used in this study.

Chapter 2: Cumulative Thesis

This cumulative thesis consists of two studies that were peer-reviewed and accepted for publication in scientific journals and one unpublished manuscript. In the following, the papers are presented, each introduced by a short summary of the paper. The contribution of the author of this thesis to the respective papers/manuscript is indicated.

2.1 Duration reproduction with sensory feedback delay: differential involvement of perception and action time

2.1.1 Summary

It has been shown that delayed feedback events can be attracted by voluntary action towards the action, and that motor-sensory temporal order judgments can be reversed after sensorimotor delay adaptation. In this first study, we investigated how feedback delays can influence duration reproduction performance, as the effects of delays on duration reproduction are still unclear. A sensorimotor duration reproduction task was adapted, investigating within modality (auditory, visual) and across audiovisual modalities reproduction performance. We injected an onset- or offset delay to the sensory feedback signal generated during the reproduction. When an onset delay was introduced to the sensory feedback signal, we observed that the reproduced duration increased, independent whether standard and feedback signal was presented in the same modality (visual or auditory) or in different modalities (crossmodal condition: auditory standard and visual feedback and vice versa). The increase in reproduced duration could be observed immediately as soon as the delay was introduced. Interestingly, there was almost no effect of onset-delay, if the feedback signal was started before the action. On the other hand, when the offset of the feedback signal was delay, reproduction durations decreased. However, this effect was weaker and could only be observed when the feedback signal was a tone (rather than a visual stimulus). We therefore concluded that participants mix together the onset of the motor timing and the onset of the feedback signal when the feedback is delayed. However, participants heavily rely on the action-stop signal rather than the feedback-stop signal in their reproduction. Additionally, we found that auditory durations were overestimated compared to visual durations in crossmodal feedback conditions. This overestimation/underestimation effect was independent of the delay manipulation.

2.1.2 Author contributions

This work was carried out under the supervision of Zhuanghua Shi and Hermann J. Müller; S.G. conceived the idea and S.G and Z.S. designed the research. SG performed research. S.G. and Z.S. discussed the results and wrote the paper. H.J.M. commented on the manuscript.

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Duration reproduction with sensory feedback delay: differential involvement of perception and action time

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Previous research has shown that voluntary action can attract subsequent, delayed feedback events toward the action, and adaptation to the sensorimotor delay can even reverse motor-sensory temporal order judgments. However, whether and how sensorimotor delay affects duration reproduction is still unclear. To investigate this, we injected an onset- or offset-delay to the sensory feedback signal from a duration reproduction task. We compared duration reproductions within (visual, auditory) modality and across audiovisual modalities with feedback signal onset- and offset-delay manipulations. We found that the reproduced duration was lengthened in both visual and auditory feedback signal onset-delay conditions. The lengthening effect was evident immediately, on the first trial with the onset-delay. However, when the onset of the feedback signal was prior to the action, the lengthening effect was diminished. In contrast, a shortening effect was found with feedback signal offset-delay, though the effect was weaker and manifested only in the auditory offset-delay condition. These findings indicate that participants tend to mix the onset of action and the feedback signal more when the feedback is delayed, and they heavily rely on motor-stop signals for the duration reproduction. Furthermore, auditory duration was overestimated compared to visual duration in crossmodal feedback conditions, and the overestimation of auditory duration (or the underestimation of visual duration) was independent of the delay manipulation.

Keywords: action, audition, time perception, time reproduction, vision

INTRODUCTION

Accurate timing is essential for our everyday activities, like dancing, playing music, or catching a moving object. In order to accomplish precise timing in a complex environment, our brain has to frequently update its internal representation of multiple sensory inputs. Precisely inferring the timing and duration of events as well as correctly judging temporal order in the sub-second range can be challenging, since neural representations of time may be confounded by noise and delay perturbation in sensory pathways. For example, the neural transmission time can vary across different sensory modalities (King and Palmer, 1985; Regan, 1989), and physical transmission distances (Campbell et al., 1981; Shadmehr et al., 2010), as well as stimulus intensities (Purpura et al., 1990). Continuous changes of the body and the environment provide a further challenge for accurate action timing (Shadmehr et al., 2010). However, in daily life, accurate sensorimotor temporal coordination remains possible, indicating that our brain is able to calibrate and compensate for temporal inconsistencies among different sensory inputs as well as delays in the sensorimotor loop.

Indeed, research has demonstrated that the brain can dynamically realign the perceived timing of multisensory or sensorimotor events. For example, Fujisaki et al. (2004) have shown adaptive changes in synchrony perception between vision and audition: after exposure to a fixed audiovisual asynchrony, the point of subjective simultaneity (PSS, a measure of point in time at which observers perceive maximum simultaneity) of an audiovisual event was shifted toward the previous "lagging" modality. Other work has revealed similar temporal recalibration mechanisms across other modalities (Vroomen et al., 2004; Navarra et al., 2005; Hanson et al., 2008; Harrar and Harris, 2008; Takahashi et al., 2008; Di Luca et al., 2009). Temporal recalibration has also been found between an action and its sensory feedback. The first study that demonstrated compensation for temporal delays in the visuomotor feedback loop confronted participants with a visual-motor lag (delayed visual feedback while controlling the horizontal movement of a small airplane as it moved down the screen through an obstacle field) (Cunningham et al., 2001). Participants' performance improved after some time of practice. Interestingly, when the lag was removed after the adaptation, the adapted behavior persisted and participants, suffering from the adaptation, often made movements too early, leading to more crashes. In another study, Stetson et al. (2006) demonstrated that following brief exposure to delayed visual feedback of a voluntary action the subjective temporal order of a motor-sensory event might even be reversed when the delay was removed. This effect was attributed to dynamical shifts of the appearance of the visual stimulus with respect to the perceived timing of the key press, in order to maintain appropriate causality perception. This proposal goes along with earlier findings that a delayed sensory effect is perceived as having appeared slightly earlier in time if it follows a voluntary action (Eagleman and Holcombe, 2002; Haggard et al., 2002)—a phenomenon referred to as "intentional binding." Studies have also demonstrated that intentional binding attracts a voluntary action toward its sensory effect, so that the action is perceived as having occurred slightly later in time and the interval between the action and its sensory feedback as shorter than the actual interval (Haggard et al., 2002; Engbert et al., 2007, 2008). Wearden et al. (2009) proposed that the shortening effect is driven by a transient slowdown of an internal clock after a voluntary action, and this shortening effect might be reinforced by everyday experience which leads us to assume sensorimotor synchrony between the start of a motor action and its sensory consequence (Heron et al., 2009). However, whether sensorimotor temporal calibration is due to timing changes in the motor system or in the perceptual system is still under debate. Some researchers have suggested that sensorimotor temporal calibration is induced mainly by a temporal shift in the motor system (Sugano et al., 2010), whereas others have attributed sensorimotor temporal calibration to pure perceptual learning (Kennedy et al., 2009).

Alternatively, sensorimotor temporal (re-)calibration has been taken to only reflect modification of predictive feed-forward actions, reducing the errors between the internal prediction and the external feedback (Miall and Jackson, 2006; Shadmehr et al., 2010). Such error correction mechanisms have been used for explaining sensorimotor synchronization, as for instance in the frequently used paradigm of finger tapping to an external pacing source (metronome). When the changes of the pacing source are detectable and regular, participants are able to reduce their sensorimotor asynchronies by predicting upcoming changes. When temporal changes are unpredictable, the time to the next motor response is automatically adjusted in proportion to the asynchrony in the previous sensorimotor event (Repp, 2005).

However, it is important to note that most of the aforementioned studies focused on sensorimotor calibration of a point in time. By contrast, the effects of delayed feedback on the voluntary duration reproduction are as yet little understood. Unlike a point in time, subjective duration can be distorted in many ways, such as by a saccadic eye movement shortly before or after the to-be-estimated event (Morrone et al., 2005), a voluntary action immediately prior to the critical event (Park et al., 2003), the emotional state of the observer (Angrilli et al., 1997; Shi et al., 2012), stimulus properties (such as intensity) (Eagleman, 2008), or pharmacological agents (such as cocaine or methamphetamine) (Meck, 1996) (see review Buhusi and Meck, 2005). Perceived durations in different modalities can also differ. For example, sounds are often perceived as longer than light flashes of the same physical duration (Walker and Scott, 1981; Wearden et al., 1998). Furthermore, there is evidence that the auditory system dominates the visual system, causing the durations of visual stimuli, presented simultaneously with an auditory stimuli, to be perceived as longer than they physically are (Walker and Scott, 1981; van Wassenhove et al., 2008; Burr et al., 2009; Chen and Yeh, 2009; Shi et al., 2010a; Klink et al., 2011). In addition, not only the use of different signal modalities during a timing task, but also the encoding of multiple signal durations, can lead to distortions in temporal memory—an effect recently termed as "memory-mixing" (Gu and Meck, 2011). Such high variability in subjective timing is quite surprising considering how important accurate timing is for our actions.

The purpose of the present study was to investigate how asynchronous-feedback signals would influence motor timing. We adopted an action-based duration reproduction paradigm combined with feedback onset- and, respectively, offset-delay manipulations. That is, participants had to reproduce auditory or visual durations and received (auditory or visual) feedback signals[1]. The feedback could either be synchronized or delayed with participants' button presses (onsets or offsets), and could be delivered in the same or different modality. We specifically asked participants to focus on the reproduction of the standard duration and not pay attention to the feedback. There are two sources of temporal information available for duration reproduction: motor timing (i.e., the duration of the button press) and the feedback timing. If participants only rely on the motor timing for their ongoing reproduction, reproduction errors would be expected to be the same or similar across all trials, no matter whether the feedback is synchronous or delayed. If participants get influenced by the feedback signal during their reproduction, despite the instruction, different reproduction errors for synchronized versus delayed feedback would be predicted. Furthermore, we examined influences of action-effect causal relationship on the duration reproduction, by presenting the feedback signal randomly near the onset or offset of participants' action.

GENERAL METHODS

SUBJECTS

Sixty nine naive volunteers (53 females, mean age 27.6) participated in each experiment for payment (Experiments 1–4: 14 participants, Experiment 5: 13 participants). All participants had normal or corrected-to-normal vision; none of them reported any history of somatosensory disorders. They gave written informed consent before the experiments.

STIMULI AND APPARATUS

All experiments were conducted in a dimly lit cabin (0.21 cd/m^2). Auditory tones (400 Hz and 600 Hz, 64 dB) and LED lights (84 cd/m^2 blue and 67 cd/m^2 red) were presented as stimuli. Stimulus presentation and data acquisition were controlled by a National Instrument PXI system, ensuring highly accurate timing (<1 ms). The experimental programs were developed using MatLab and the Psychophysics Toolbox (Brainard, 1997). The auditory stimuli were delivered to participants via headphones (Pro-luxe XL-300); the LED stimuli (two LEDs, blue and red)

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[1] In this study we refer to the second stimulus—that is presented during the reproduction—as a "feedback signal" to highlight the causal relationship between the action and sensory effect. The terms "feedback signal" and "feedback" are used interchangeably in the text.

were positioned 2 cm apart horizontally. The response button was placed on the table in-between the participant and the LEDs. Reproduction times were measured using the response button, which participants pressed with their right-hand index finger.

PROCEDURE

We adopted and modified an action-based duration reproduction task with feedback, as introduced by Bueti and Walsh (2010). Each trial started with a standard duration, either 800 or 1200 ms in length, in the form of an auditory tone (Experiments 1 and 4) or an LED light (Experiments 2 and 3). Following the presentation of the standard duration, participants were asked to reproduce the duration as accurately as possible by button press, with reproduction duration demarcated by the onset and offset of the press action. Pressing the button also induced a feedback signal (a tone in Experiments 1 and 3, an LED light in Experiments 2 and 4) whose onset or offset could deviate from the onset or offset of the button press (see **Figure 1** and next paragraph). Subjects were told that feedback signal could be either dependent or independent of their button press. They were specifically instructed to reproduce the standard duration as accurately as possible by pressing down the button, regardless of the feedback signals (see the detail instruction in the "Appendix"). To distinguish and counter-balance the standard and feedback stimuli, half of the participants received high tones (or red lights) as standard stimuli and low tones (or blue lights) as the ± feedback stimuli, and vice versa for the other half.

For the first four experiments, there were three different temporal manipulations of feedback signals: synchronous-feedback, onset-delay feedback, and offset-delay feedback. In the synchronous-feedback condition, the onset and offset of the feedback occurred synchronously with the onset of the button press and the release of the button. In the onset-delay condition, the onset of the feedback signal was delayed by 200 ms following the onset of the button press, while feedback offset occurred synchronously with the release of the button. In the offset-delay condition, the feedback signal started synchronously with the button press, but the feedback offset occurred only 200 ms after the release of the button. These three conditions were varied block-wise, with 10 trials per block. Both the onset- and offset-delay blocks were preceded and followed by a synchronous-feedback block. The order of the onset- and offset-delay blocks was randomized.

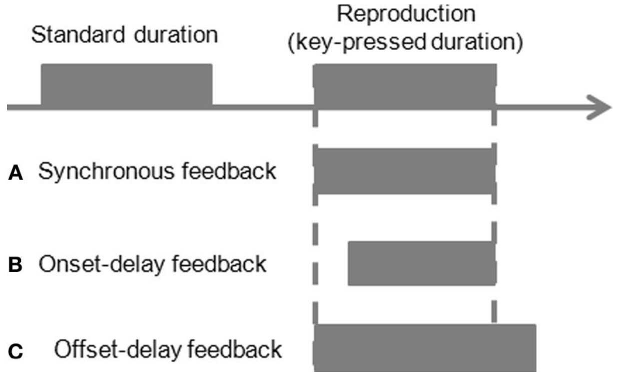

FIGURE 1 | Schematic illustration of the experimental design. A standard duration reproduction paradigm with manipulation of feedback delays during reproduction. An auditory or visual stimulus is presented first as a standard duration. Participants reproduce the standard by pressing a button. Another auditory or visual stimulus is fed back to participants based on the action. The feedback signal could be synchronous to the key press (**A** synchronous-feedback condition), or be delayed 200 ms at the onset of the feedback but simultaneously stops at button release (**B** onset-delay feedback condition), or starts synchronously with the button press but stops 200 ms after the button release (**C** offset-delay feedback condition).

In Experiment five, we used the same block-design as in previous experiments, but randomized the onset and offset of the feedback signal relative to the button press. To do this, for each synchronous-feedback block we measured the mean reproduction durations for 800 and 1200 ms, and the mean response onset asynchrony. During the onset-manipulation blocks, the feedback signal started independently of the button press, with random jittering ±200, ±100, or 0 ms around the mean response onset asynchrony measured in the preceding synchronous block. The feedback signal stopped when the button was released. During the offset-manipulation blocks, the feedback signal started synchronously with the button press, but stopped automatically with a duration randomly jittering ±200, ±100, or 0 ms around the mean reproduction duration (either 800 or 1200 ms corresponding to the duration in the current trial) measured in the preceding synchronous block. The random jittering was used in order to ensure that participants would not be able to predict the onset or offset of the manipulated feedback signal, thus we could obtain about half of all trials with feedback prior to participants' actions. We further increased the number of the trials to 20 for the onset- and offset-manipulation blocks to ensure enough trials with the feedback before participants' action. The task instruction was kept the same as during the previous four experiments.

Note that the standard and feedback stimuli were kept within the same modality in Experiments 1, 2, and 5, but presented in separate modalities in Experiments 3 and 4 (see **Table 1**).

In the first four experiments, there were 10 repetitions for the onset- and offset-delay blocks and 20 repetitions for the synchronous-feedback signal blocks. Participants took a short break after every eight blocks. In Experiment 5, there were eight repetitions for the onset- and offset-manipulation blocks (each consisting of 20 trials) and 16 repetitions for the synchronous-feedback signal blocks (each consisting of 10 trials). Here, participants took a short break after four blocks

Table 1 | Modalities of the standard and feedback stimuli.

Experiment	Standard	Feedback
1	Auditory	Auditory
2	Visual	Visual
3	Visual	Auditory
4	Auditory	Visual
5	Auditory	Auditory

(= 60 trials). In addition, there were two practice blocks with the synchronous-feedback signal condition run prior to the formal experiment.

DATA ANALYSIS

Mean measures and standard deviations of time reproduction have been shown to vary linearly with standard durations, so that after normalization the same form of distribution of relative time and constant timing sensitivity can be found (Gibbon et al., 1984). In line with this, reproduction errors (i.e., the difference between the reproduced duration and the standard duration) in the present study exhibited differences between the two standard durations (800 and 1200 ms), that is, the amount of over-/underestimation (in ms) is proportional to the respective standard duration. To take this into account, we calculated reproduction errors and then normalized them by the corresponding physical duration. Normalized reproduction errors of zero indicate perfect reproduction, positive values an overestimation, and negative values an underestimation of the standard duration. In order to examine dynamic influences of the onset- and offset-delay manipulation, we selected four trials from the synchronous block prior to and the synchronous block after the delay manipulation. The first four trials served as baseline and the last four trials for analyzing after-effects of the delay manipulation. Henceforth, we refer to the former four synchronous-feedback trials as baseline phase, the latter four synchronous-feedback trials as post phase, and the 10 trials from the (intervening) delay block as delay phase. We omitted the middle two trials in the synchronous-feedback block to separate the post and baseline phases. Repeated-measures analyses of variance (ANOVAs) of the normalized reproduction errors in the three different phases (baseline phase, delay phase, and post phase) were run separately for the onset- and offset-delay conditions. Bonferroni-corrected *t*-tests for multiple comparisons were carried out for a-posteriori comparisons to assess differences in reproduction errors.

For Experiment 5, we focused on analyzing linear correlations between the onset- and offset-manipulations and normalized reproduction errors. Thus, linear regression and correlation analyses were applied. We realigned the onsets of the feedback relative to the onsets of the actual response, and compared the differential influences between the feedback before and after participants' action. For the offset-manipulation condition, we used an alternative approach: we calculated the offset jitters relative to the standard durations and analyzed the general relationship between the offset jitters and the reproduction errors. We did not align the offsets relative to the responses, since the mean feedback duration was close to the mean reproduction time, which would inevitably lead to pseudo negative correlation between the relative offset and the reproduced duration. Such correlation could not reflect the influence of the offset-manipulation. In both cases, we normalized feedback jitters with their correspondent standard durations, such that the feedback jitter has the same unit as the normalized reproduction error.

RESULTS

GENERAL REPRODUCTION RESULTS

We analyzed reproduction times for the synchronous-feedback condition for all five experiments, comparing reproduction performance after the short (800 ms) and long (1200 ms) standards. Reproduced durations in milliseconds are presented in **Figure 2**. We found a significant difference between the reproduced times of the short and long standard stimuli (all $p < 0.01$) across all five experiments, suggesting participants were actually able to perform the task.

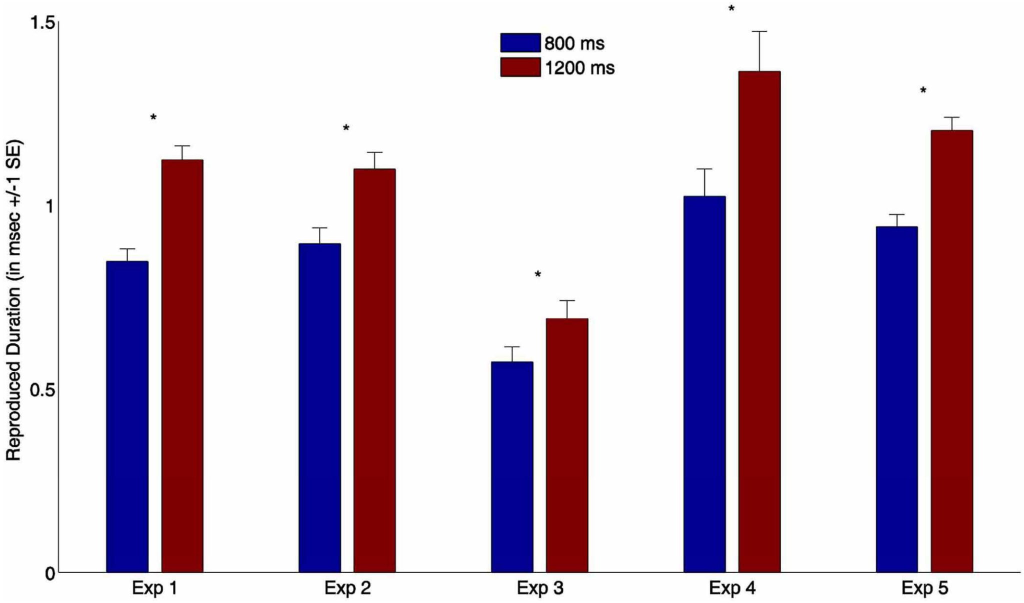

FIGURE 2 | Mean reproduction times (and associated standard errors) from all synchronous trials for all five experiments. Blue bars depict produced durations after short standard stimuli (800 ms); red bars indicate reproduction times after long standard stimuli (1200 ms) (* indicates $p < 0.01$).

EFFECTS OF UNIMODAL FEEDBACK ONSET- AND OFFSET-MANIPULATION ON THE DURATION REPRODUCTION

Normalized reproduction errors, and associated standard errors, for the first four experiments and all conditions are presented in **Table 2**. **Figure 3** shows the normalized reproduction errors for the onset- and offset-delay manipulation for the unimodal auditory and visual feedback.

In the onset-delay conditions (**Figure 3**, up-panels), normalized reproduction errors were significantly influenced by the delay manipulation, [$F_{(2,\ 26)} = 246.78$; $p < 0.01$], and [$F_{(2,\ 26)} = 43.30$, $p < 0.01$] for the auditory and visual conditions respectively. The overestimation during the onset-delay phase for both auditory and visual conditions proved to be significantly larger compared to the baseline ($p < 0.01$) and the post phase ($p < 0.01$) (**Figure 3**, low-panels). Normalized reproduction errors in the post phase (overestimation) were raised reliably relative to the baseline ($p < 0.01$) for the auditory condition, but not for the visual condition ($p = 0.16$). Interestingly, the overestimation on the onset-delay phase was 21% for the auditory and 19% for the visual, which are statistically not different from the onset-delay manipulation (all $p > 0.1$). Furthermore, the overestimation started with the first trial of the delay manipulation (condition) and stopped as soon as the delay was removed (**Figure 3**, up-panels). Paired t-tests showed no significant difference in the overestimation between the first versus the remaining trials in both delay and post phase, (all $p > 0.1$).

In contrast to the onset-delay manipulation (which made participants overestimate the standard durations), the offset-delay manipulation (**Figure 3**, mid-panels) showed different patterns for the auditory and visual conditions. In the auditory condition (**Figure 3**, middle left panel), the offset-delay led participants to significantly underestimate the standard durations during the offset-delay phase, [$F_{(2,\ 26)} = 13.73$; $p < 0.01$]. This effect derived mainly from a significantly negative increase in normalized reproduction errors during the delay phase versus the baseline ($p < 0.01$). Normalized errors were also negatively increased in the post phase compared to the baseline ($p < 0.01$). However, there was no reliable difference between the delay and post phases ($p = 0.99$). Paired t-tests showed that the underestimation started only from the second trial with delay manipulation, as there was no effect in the first trial of the delay phase (significant difference between the first and the remaining trials, [$t_{(13)} = 9.30$, $p < 0.01$]). Also, underestimation only stopped on the second trial of the post phase, with reproduction errors on the first trial still differing significantly from the errors on the other trials, [$t_{(13)} = -5.26$, $p < 0.01$]. In contrast to the auditory condition, manipulation of the visual offset-delay feedback had no significant influence on normalized reproduction, [$F_{(2,\ 26)} = 1.60$, $p = 0.22$] (baseline vs. delay: $p = 1.00$; delay vs. post phase: $p = 0.36$; baseline vs. post phase: $p = 0.45$).

EFFECTS OF CROSSMODAL FEEDBACK ONSET- AND OFFSET-MANIPULATION ON DURATION REPRODUCTION

Overall, there was strong underestimation of the visual standard with synchronous auditory feedback signal (hereafter we refer to as the visual-auditory experiment), and strong overestimation of the auditory standard with visual feedback signal (hereafter the auditory-visual experiment), all $p < 0.01$. Trial-wise normalized reproduction errors for the onset- and offset-delay manipulations are depicted in **Figure 4**.

For the onset-delay conditions (**Figure 4**, up-panels), the normalized reproduction errors were significantly modulated by onset-delays for the visual-auditory experiment, $F_{(2,\ 26)} = 185.41$, $p < 0.01$, and the auditory-visual experiment, $F_{(2,\ 26)} = 39.06$, $p < 0.01$. The underestimation (in the visual-auditory experiment, **Figure 4A**) and the overestimation (in the auditory-visual experiment, **Figure 4B**) in the onset-delay phase, were significantly different from the correspondent baseline and the post phase (all $p < 0.01$), while there were no differences between the baseline and post phase (all $p > 0.1$). Interestingly, the reproduced duration during the onset-delay phase compared to the baseline was increased 21% for the visual-auditory experiment and 16% for the auditory-visual experiment. Both are comparable to the overestimation observed in Experiment 1 and 2 (21 and 19% respectively). Further pair-wise sequential-trial analysis showed that the manipulation effect of the onset-delay in the visual-auditory experiment started on the first trial of delay manipulation ($p = 0.78$) and stopped as soon as the delay was removed ($p = 0.28$). However, in the auditory-visual experiment, participants needed one trial to adjust their behavior to the onset-delay, as evidenced by significantly different normalized reproduction errors in the first trial compared to the remaining trials of the delay phase, $t_{(13)} = -2.57$, $p < 0.05$. However, the effect ceased as soon as the delay was removed ($p = 0.59$).

For the visual-auditory experiment, a general, significant underestimation was also found in the offset-delay condition, $F_{(2,\ 26)} = 8.15$, $p < 0.01$ (**Figure 4A**, mid-panel). Relative to the baseline, the normalized reproduction error (underestimation) was negatively increased in the offset-delay phase ($p < 0.05$) and

Table 2 | Normalized reproduction errors (± standard errors) in percentage by onset- and offset-delay manipulation and different phases in Experiments 1–4.

	Onset-delay manipulation			Offset-delay manipulation		
	Baseline phase	**Delay phase**	**Post phase**	**Baseline phase**	**Delay phase**	**Post phase**
Experiment 1	−0.55 ± 2.5	21.73 ± 2.0	3.89 ± 2.8	1.18 ± 2.9	−4.57 ± 1.8	−3.69 ± 2.9
Experiment 2	−0.28 ± 4.4	19.09 ± 2.7	3.51 ± 4.4	0.95 ± 4.3	−1.72 ± 2.8	4.91± 4.2
Experiment 3	−33.88 ± 3.1	−12.16 ± 2.2	−31.48 ± 3.4	−33.06 ± 3.4	−37.93 ± 2.1	−38.19 ± 3.6
Experiment 4	21.01 ± 4.6	37.21 ± 3.3	24.39 ± 5.3	22.55 ± 4.9	23.35 ± 3.4	25.47 ± 5.6

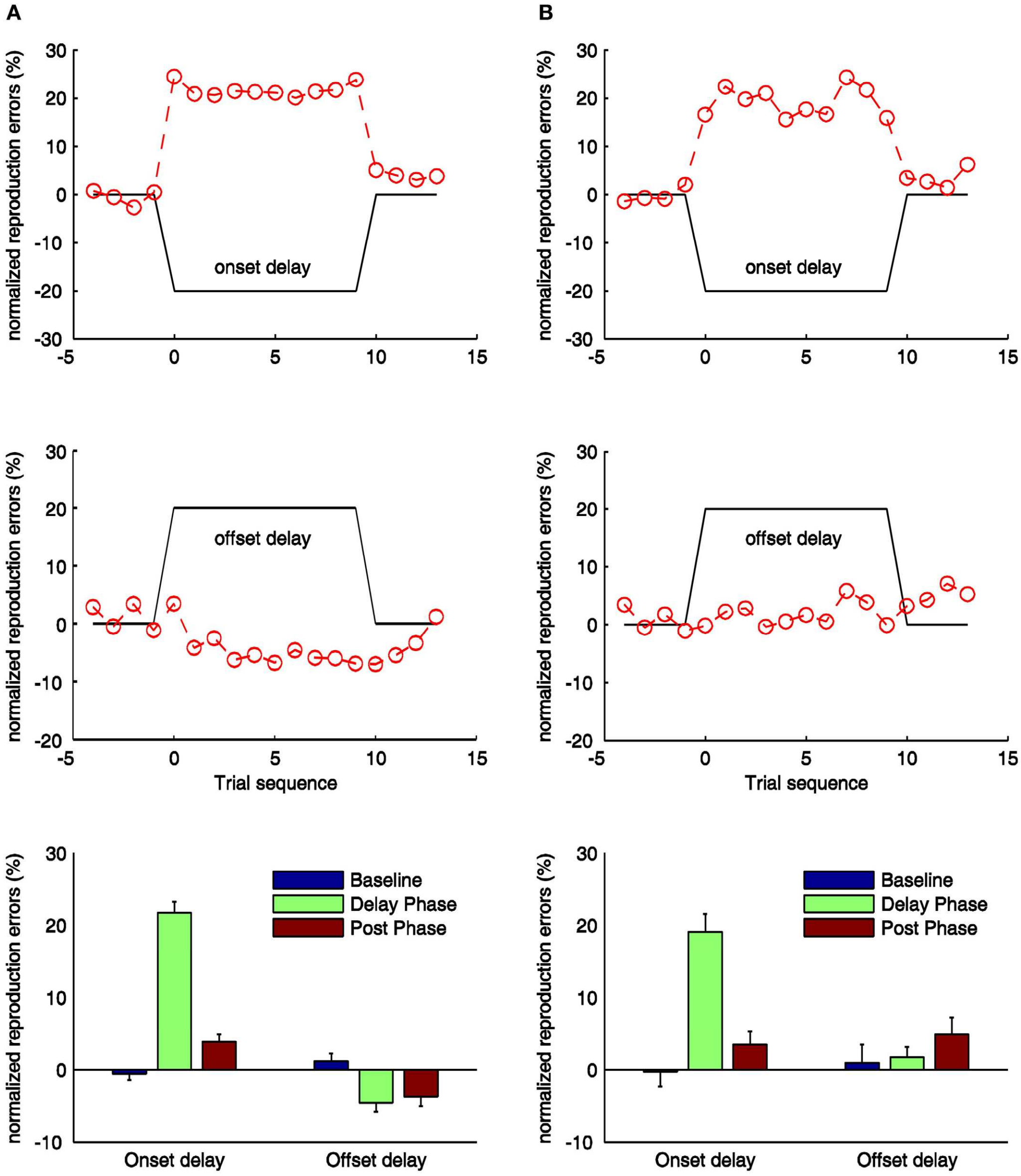

FIGURE 3 | Normalized reproduction errors [(subjective duration—physical duration)/physical duration] for the onset- and offset-delay condition of Experiment 1 (A) and Experiment 2 (B). In the upper and middle panels trial-wise dynamic changes of normalized reproduction are shown. Four trials from the synchronous block before the delay manipulation (baseline phase), delay block (delay phase), and four trials after the delay manipulation (post phase) are displayed. The black lines indicate the physical delay. The red dashed curves and circles depict mean normalized reproduction errors as a function of trial sequence and the onset-delay (up-panel) or offset-delay (middle panel). In the low-panels mean normalized reproduction errors (and associated standard errors) are plotted against baseline, delay and post phase for the onset- and offset-delay conditions.

in the post phase ($p < 0.05$); there was no difference between the latter two phases ($p = 1.00$). The increased underestimation due to the offset-delay manipulation is again comparable to the results of Experiment 1. Sequential-trial analysis revealed both the first and the second trial to differ significantly from the remaining trials in the delay phase [first: $t_{(13)} = 2.58$, $p < 0.05$; second: $t_{(13)} = 5.03$, $p < 0.01$]. In the post phase, normalized reproduction errors did not change over trials ($p > 0.1$). Trial-wise comparisons of delay- and post-phase reproduction errors yielded no significant differences (all $p > 0.1$). Thus, participants either needed more than four trials to readjust their reproduction performance to the synchronous-feedback, or normalized reproduction errors were too variable within trials. However, for the auditory-visual experiment, the offset-delay manipulation did not influence the reproduction performance, $F_{(2,\ 26)} = 0.95$, $p = 0.40$. None of the phases differed from any other (all $p > 0.1$). This result is similar to that obtained in Experiment 2.

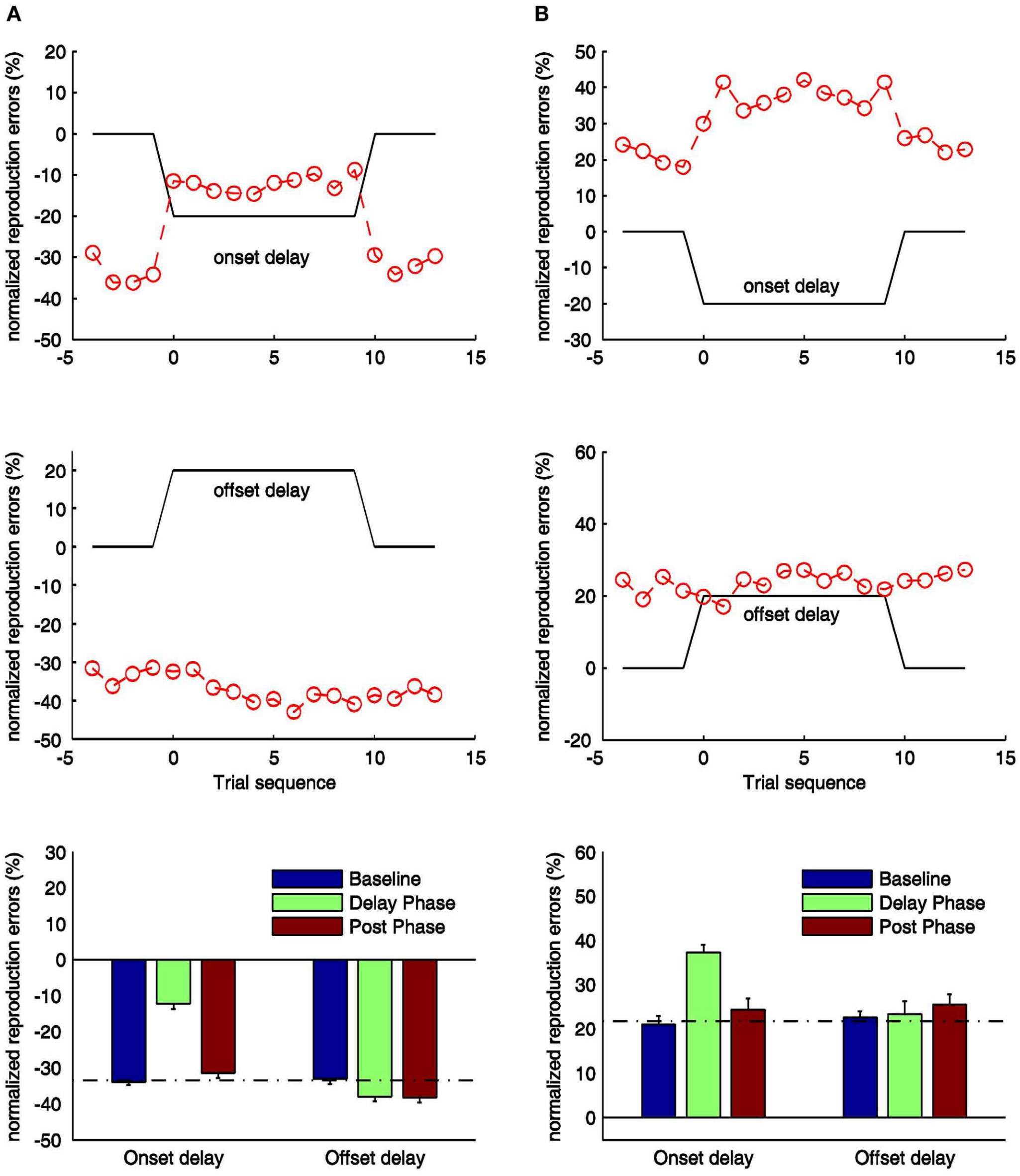

FIGURE 4 | Normalized reproduction errors for the onset- and offset-delay condition of Experiment 3 (A) and Experiment 4 (B). In the upper and middle panels trial-wise dynamic changes of normalized reproduction are shown. Four trials from the synchronous block before the delay manipulation (baseline phase), delay block (delay phase), and four trials after the delay manipulation (post phase) are displayed. The black lines indicate the physical delay. The red dashed curves and circles depict mean normalized reproduction errors as a function of trial sequence and the onset-delay (up-panel) or offset-delay (middle panel). In the low-panels mean normalized reproduction errors (and associated standard errors) are plotted against baseline, delay, and post phase for the onset- and offset-delay conditions. The dashed line indicates the mean normalized reproduction error in the baseline condition.

EFFECTS OF RANDOM ONSET- AND OFFSET-MANIPULATION ON THE DURATION REPRODUCTION

Figure 5 illustrates relationships between the reproduction error and the relative feedback onset (left panel) and offset (right panel) for a typical participant. For the onset-manipulation condition, there was a significant correlation between positive feedback delays and reproduction errors (correlation coefficient: 0.41, linear slope: 0.89, all $p < 0.05$). The steep slope indicates an about 89% compensation for the delayed onset in the duration reproduction, which was similar to the finding in Experiment 1. However, such correlation was broken down when the feedback was presented before participants' actions. There was no correlation [mean: 0.1, $t_{(12)} = 0.81$, $p = 0.43$] for those "preceded" feedback trials, and the mean slope (0.17) did not significantly differ from zero, $t_{(12)} = 0.90$, $p = 0.39$. For the offset-manipulation condition, the correlation between reproduction errors and random offsets was mildly related, mean correlation coefficient 0.31, $t_{(12)} = 6.53, p < 0.05$. The mean slope (0.3) was significant higher than zero, $t_{(12)} = 8.31, p < 0.05$, though it was significantly lower than the mean slope of the "delayed" onset

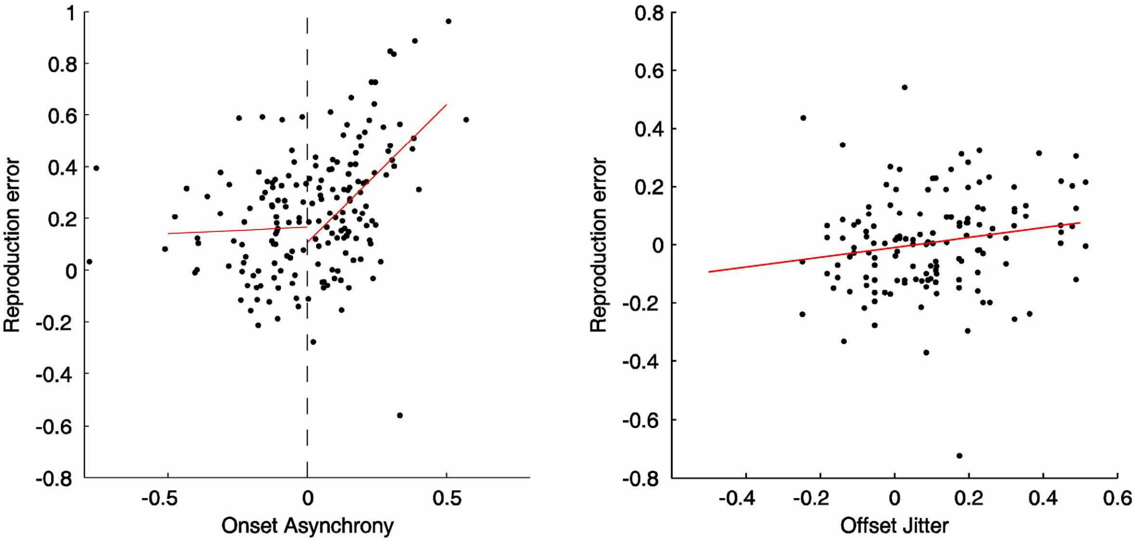

FIGURE 5 | Normalized reproduction errors and linear regression lines (red) for the onset (left side) and offset (right side) manipulation conditions from a typical dataset. In the onset-manipulation condition, the fitted slope for the feedback signal started before the action onset (0.06) is not significant different from zero, while the slope for the delayed feedback (1.07) is significant higher than zero. In the offset-manipulation condition the slope is 0.30, significantly higher than zero.

condition, $t_{(12)} = 3.83$, $p < 0.05$. The mild offset modulation confirmed the findings in Experiments 1 and 3.

DISCUSSION

The results of the present study illustrate how the onset- and offset-manipulation of the feedback signal influences the duration reproduction. In all experiments, we found an increase in duration reproduction for conditions with positive onset-delay feedback manipulation. The lengthening of the reproduced duration could almost compensate the onset-delay (about 90% for the auditory feedback and 75–90% for the visual feedback). The subjective lengthening started immediately with the first trial (or second in Experiment 4), and ended with the last trial of the delay phase. Despite our explicit instruction for reproducing the standard duration regardless the feedback signal, the reproduced duration was still heavily influenced by the onset of the delayed feedback. However, such influence was broken down when the feedback signal was presented before participant's button press.

The results suggest that the action-effect causal relationship may play a critical role in the duration reproduction. Through prior experience, we have learnt that the effect of an action is not always immediate (Pesavento and Schlag, 2006). For example, the response of a tap on the computer keyboard becomes visible as a letter on the screen only after a delay of some 20–50 ms, and the response of a remote control might even be slower (Rank et al., 2010; Shi et al., 2010a,b; Sugano et al., 2010). The action-effect causal relationship may lead to bind and recalibrate motor-sensory timing (Cunningham et al., 2001; Stetson et al., 2006), to attract a voluntary action toward its sensory effect (Haggard et al., 2002; Engbert et al., 2007, 2008), and to shift attention toward to the sensory feedback (Buehner and Humphreys, 2009). Such causal binding may well relate to the memory-mixing model (Gu and Meck, 2011). Due to limited capacity of working memory and the cause-effect relationship, motor timing, and *caused*-feedback timing may share the same representation, which pulls both onsets closer. Other studies have also shown similar binding and regression effects in the reproduction task (Teghtsoonian and Teghtsoonian, 1978; Lejeune and Wearden, 2009; Jazayeri and Shadlen, 2010). For example, participants are able to use temporal context (such as mean duration) to reduce variability of their performance by sacrificing accuracy during a reproduction task (Lejeune and Wearden, 2009; Jazayeri and Shadlen, 2010). However, when the causal relationship is violated (i.e., the feedback was prior to the action in Experiment 5), linkage between two events—the action and sensory feedback—becomes weak, which leads to less memory interference between the two representations. The causal binding and memory-mixing could also explain the quick adjustment to the onset-delay, since the binding and immediate adjustment of the reproduction can take place in the same trial.

In contrast to the effects of introducing feedback onset-delays, offset-delay manipulation appears to modulate duration reproduction in a modality-dependent manner, though with comparatively small effects. Duration reproduction for the auditory offset-feedback delay (Experiments 1, 3, and 5) was shortened by only some 25–30% of the delay manipulation, while there was no shortening effect for the visual offset-delay manipulation. The latter was probably due to sluggish visuomotor timing (Jäncke et al., 2000; Repp, 2005). With the auditory offset-delay manipulation, the shortening effect became manifested not on the first trial with a delay, but only on the second or third trial. Similarly, the shortening effect diminished more gradually after the removal of the delay (after one trial in Experiment 1 and probably more than four trials in Experiment 3). This dynamic adaptation is comparable to previously observed adaptive changes in synchrony perception (Fujisaki et al., 2004; Vroomen et al., 2004). Also, the amount of adaptation (25% of the auditory offset-delay manipulation) resembles previously reported shifts in PSEs for point-in-time calibration [e.g., 10% for multisensory adaptation (Fujisaki et al., 2004; Di Luca et al., 2009), and 29% for sensorimotor adaptation (Sugano et al., 2010)]. The partial compensation has been attributed to the fact that the brain takes into account a long history of "veridical" sensory inputs throughout lifetime, as compared to only a short adaptation phase during typical psychophysical experiments (Fujisaki et al., 2004). Similar in our study, the asynchrony between the end of an action and the end of the *auditory* feedback may be used as an error signal (Shadmehr et al., 2010) for sensorimotor adaptation to partially adjust future actions. As suggested by the memory-mixing account (Gu and Meck, 2011), participants may use the representation of previous experienced offset-delay for predicting a potential delay on a given offset-manipulation trial.

Mild partial compensation also suggests that participants trust their own stop signal more than the delayed offset signal. This may relate to the switch of the internal clock model (Gibbon, 1977; Gibbon et al., 1984), which consists of a pacemaker emitting pulses at a certain rate and a mode switch that can open and close to permit an accumulator to collect emitted pulses. When the switch closes, the number of pulses in the accumulator is compared against a reference time from memory. Larger amounts of accumulated pulses mean longer estimated durations. Recent striatal beat-frequency (SFB) model provides a neurobiological plausible model of interval timing and switch (Matell and Meck, 2004), which suggests timing is based on the coincidental activation of medium spiny neurons in the basal ganglia by cortical neural oscillators. At trial onset the synchronization of cortical oscillators is triggered by the dopaminergic burst, and at expected offset a burst is reflected on cortico-striatal transmission (see review Buhusi and Meck, 2005). It has been shown that neurons in the motor cortex increase their synchrony when animals are trained to expect an action (Riehle et al., 1997). The synchronization triggered by the expected stop-action might be considered as the more reliable switch-off signal than the offset of the external sensory feedback, leading to the offset-delay interval being largely neglected and to less memory-mixing than during the onset condition. This could also explain the findings in Experiment 5, where the feedback offset was random and unreliable.

In Experiments 3 and 4, in which the standard duration and the feedback signal were presented in different modalities, we observed a strong distortion of perceived durations: visual standard durations were strongly underestimated by presentation of auditory feedback signals during the reproduction, and this finding was mirrored by a strong overestimation of auditory standard durations when the feedback signal was a visual stimulus. The over- and underestimations across the audiovisual modalities are analog to previous findings. For example, Wearden et al. (1998) have provided evidence that the auditory pacemaker ticks faster than the visual pacemaker, as a result of which auditory durations are perceived as longer than physically equivalent visual durations. However, it remains an open question whether the observed audiovisual effects are mainly caused by the crossmodal memory-mixing. Nevertheless, recall that the overestimation (underestimation) was additive to the effects of delay manipulation, which suggests that the crossmodal standard-feedback signals comparison (i.e., presenting a standard stimulus in one modality and providing a feedback signal stimulus in another modality) is operating mainly on the perceptual level, relatively independent of sensorimotor adjustments.

CONCLUSION

In summary, the present study investigated the effects of feedback signal delay manipulation on active duration reproduction. When the onset of sensory feedback signals was delayed, reproduced durations lengthened immediately to compensate for the feedback signal delays in large proportion. The feedback before action onset was neglected. However, when the offset of sensory feedback signals was delayed, reproduced durations only shortened by about 25–30% of the delay with auditory feedback signals, while there was no compensation for visual feedback signals. These results suggest that active duration reproduction is heavily mixed with the delayed feedback onset and mildly influenced by the feedback offset. The results can be explained with causal binding and the memory-mixing accounts. Moreover, the observed under- and overestimation due to crossmodal manipulation of the standard and feedback signal stimuli is additive to the sensorimotor delay adaptation.

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REFERENCES

Angrilli, A., Cherubini, P., Pavese, A., and Manfredini, S. (1997). The influence of affective factors on time perception. *Percept. Psychophy.* 59, 972–982.

Brainard, D. H. (1997). The psychophysics toolbox. *Spat. Vis.* 10, 433–436.

Buehner, M. J., and Humphreys, G. R. (2009). Causal binding of actions to their effects. *Psychol. Sci.* 20, 1221–1228.

Bueti, D., and Walsh, V. (2010). Memory for time distinguishes between perception and action. *Perception* 39, 81–90.

Buhusi, C. V., and Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nat. Rev. Neurosci.* 6, 755–765.

Burr, D., Banks, M. S., and Morrone, M. C. (2009). Auditory dominance over vision in the perception of interval duration. *Exp. Brain Res.* 198, 49–57.

Campbell, W. W., Ward, L. C., and Swift, T. R. (1981). Nerve conduction velocity varies inversely with height. *Muscle Nerve* 4, 520–523.

Chen, K.-M., and Yeh, S.-L. (2009). Asymmetric cross-modal effects in time perception. *Acta Psychol.* 130, 225–234.

Cunningham, D. W., Billock, V. A., and Tsou, B. H. (2001). Sensorimotor adaptation to violations of temporal contiguity. *Psychol. Sci.* 12, 532.

Di Luca, M., Machulla, T.-K., and Ernst, M. O. (2009). Recalibration of multisensory simultaneity: cross-modal transfer coincides with a change in perceptual latency. *J. Vis.* 9, 1–16.

Eagleman, D. M. (2008). Human time perception and its illusions. *Curr. Opin. Neurobiol.* 18, 131–136.

Eagleman, D. M., and Holcombe, A. O. (2002). Causality and the perception of time. *Trends Cogn. Sci.* 6, 323–325.

Engbert, K., Wohlschläger, A., and Haggard, P. (2008). Who is causing what? The sense of agency is relational and efferent-triggered. *Cognition* 107, 693–704.

Engbert, K., Wohlschläger, A., Thomas, R., and Haggard, P. (2007). Agency, subjective time, and other minds. *J. Exp. Psychol. Hum. Percept. Perform.* 33, 1261–1268.

Fujisaki, W., Shimojo, S., Kashino, M., and Nishida, S. (2004). Recalibration of audiovisual simultaneity. *Nat. Neurosci.* 7, 773–778.

Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychol. Rev.* 84, 279–325.

Gibbon, J., Church, R. M., and Meck, W. H. (1984). Scalar timing in memory. *Ann. N.Y. Acad. Sci.* 423, 52–77.

Gu, B.-M., and Meck, W. (2011). "New perspectives on Vierordt's law: memory-mixing in ordinal temporal comparison tasks," in *Multidisciplinary Aspects of Time and Time Perception, Vol. 6789,* eds A. Vatakis, A. Esposito, M. Giagkou, F. Cummins, and G. Papadelis (Berlin, Heidelberg: Springer), 67–78.

Haggard, P., Clark, S., and Kalogeras, J. (2002). Voluntary action and conscious awareness. *Nat. Neurosci.* 5, 382.

Hanson, J. V. M., Heron, J., and Whitaker, D. (2008). Recalibration of perceived time across sensory modalities. *Exp. Brain Res.* 185, 347–352.

Harrar, V., and Harris, L. R. (2008). The effect of exposure to asynchronous audio, visual, and tactile stimulus combinations on the perception of simultaneity. *Exp. Brain Res.* 186, 517–524.

Heron, J., Hanson, J. V. M., and Whitaker, D. (2009). Effect before cause: supramodal recalibration of sensorimotor timing. *PLoS ONE* 4:e7681. doi: 10.1371/journal.pone.0007681

Jäncke, L., Loose, R., Lutz, K., Specht, K., and Shah, N. J. (2000). Cortical activations during paced finger-tapping applying visual and auditory pacing stimuli. *Brain Res. Cogn. Brain Res.* 10, 51–66.

Jazayeri, M., and Shadlen, M. N. (2010). Temporal context calibrates interval timing. *Nat. Neurosci.* 13, 1020–1026.

Kennedy, J. S., Buehner, M. J., and Rushton, S. K. (2009). Adaptation to sensory-motor temporal misalignment: instrumental or perceptual learning? *Q. J. Exp. Psychol.* 62, 453–469.

King, A. J., and Palmer, A. R. (1985). Integration of visual and auditory information in bimodal neurones in the guinea-pig superior colliculus. *Exp. Brain Res.* 60, 492–500.

Klink, P. C., Montijn, J. S., and van Wezel, R. J. A. (2011). Crossmodal duration perception involves perceptual grouping, temporal ventriloquism, and variable internal clock rates. *Attent. Percept. Psychophys.* 73, 219–236.

Lejeune, H., and Wearden, J. (2009). Vierordt's the experimental study of the time sense (1868) and its legacy. *Eur. J. Cogn. Psychol.* 21, 941–960.

Matell, M. S., and Meck, W. H. (2004). Cortico-striatal circuits and interval timing: coincidence detection of oscillatory processes. *Cogn. Brain Res.* 21, 139–170.

Meck, W. H. (1996). Neuropharmacology of timing and time perception. *Brain Res. Cogn. Brain Res.* 3, 227–242.

Miall, R. C., and Jackson, J. K. (2006). Adaptation to visual feedback delays in manual tracking: evidence against the Smith Predictor model of human visually guided action. *Exp. Brain Res.* 172, 77–84.

Morrone, M. C., Ross, J., and Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. *Nat. Neurosci.* 8, 950–954.

Navarra, J., Vatakis, A., Zampini, M., Soto-Faraco, S., Humphreys, W., and Spence, C. (2005). Exposure to asynchronous audiovisual speech extends the temporal window for audiovisual integration. *Cogn. Brain Res.* 25, 499–507.

Park, J., Schlag-Rey, M., and Schlag, J. (2003). Voluntary action expands perceived duration of its sensory consequence. *Exp. Brain Res.* 149, 527–529.

Pesavento, M. J., and Schlag, J. (2006). Transfer of learned perception of sensorimotor simultaneity. *Exp. Brain Res.* 174, 435–442.

Purpura, K., Tranchina, D., Kaplan, E., and Shapley, R. M. (1990). Light adaptation in the primate retina: analysis of changes in gain and dynamics of monkey retinal ganglion cells. *Vis. Neurosci.* 4, 75–93.

Rank, M., Shi, Z., Müller, H. J., and Hirche, S. (2010). Perception of delay in haptic telepresence systems. *Presence Teleoper. Virtual Environ.* 19, 389–399.

Regan, D. (1989). *Human Brain Electrophysiology: Evoked Potentials and Evoked Magnetic Fields in Science and Medicine*. New York, NY: Elsevier.

Repp, B. H. (2005). Sensorimotor synchronization: a review of the tapping literature. *Psychon. Bull. Rev.* 12, 969–992.

Riehle, A., Grun, S., Diesmann, M., and Aertsen, A. (1997). Spike synchronization and rate modulation differentially involved in motor cortical function. *Science* 278, 1950–1953.

Shadmehr, R., Smith, M. A., and Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annu. Rev. Neurosci.* 33, 89–108.

Shi, Z., Chen, L., and Müller, H. (2010a). Auditory temporal modulation of the visual Ternus effect: the influence of time interval. *Exp. Brain Res.* 203, 723–735.

Shi, Z., Zou, H., Rank, M., Chen, L., Hirche, S., and Müller, H. J. (2010b). Effects of packet loss and latency on the temporal discrimination of visual-haptic events. *IEEE Trans. Haptics* 3, 28–36.

Shi, Z., Jia, L., and Mueller, H. J. (2012). Modulation of tactile duration judgments by emotional pictures. *Front. Integr. Neurosci.* 6:24. doi: 10.3389/fnint.2012.00024

Stetson, C., Cui, X., Montague, P. R., and Eagleman, D. M. (2006). Motor-sensory recalibration leads to an illusory reversal of action and sensation. *Neuron* 51, 651–659.

Sugano, Y., Keetels, M., and Vroomen, J. (2010). Adaptation to motor-visual and motor-auditory temporal lags transfer across modalities. *Exp. Brain Res.* 201, 393–399.

Takahashi, K., Saiki, J., and Watanabe, K. (2008). Realignment of temporal simultaneity between vision and touch. *Neuroreport* 19, 319–322.

Teghtsoonian, R., and Teghtsoonian, M. (1978). Range and regression effects in magnitude scaling. *Percept. Psychophys.* 24, 305–314.

van Wassenhove, V., Buonomano, D. V., Shimojo, S., and Shams, L. (2008). Distortions of subjective time perception within and across senses. *PLoS ONE* 3:e1437. doi: 10.1371/journal.pone.0001437

Vroomen, J., Keetels, M., de Gelder, B., and Bertelson, P. (2004). Recalibration of temporal order perception by exposure to audio-visual asynchrony. *Cogn. Brain Res.* 22, 32–35.

Walker, J. T., and Scott, K. J. (1981). Auditory–visual conflicts in the perceived duration of lights, tones, and gaps. *J. Exp. Psychol. Hum. Percept. Perform.* 7, 1327–1339.

Wearden, J. H., Edwards, H., Fakhri, M., and Percival, A. (1998). Why 'sounds are judged longer than lights': application of a model of the internal clock in humans. *Q. J. Exp. Psychol. B* 51B, 97–120.

Wenke, D., and Haggard, P. (2009). How voluntary actions modulate time perception. *Exp. Brain Res.* 196, 311–318.

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APPENDIX

INSTRUCTION

In this experiment your task is to reproduce the duration of a tone by pressing a button. For each trial, you will first hear a tone for a certain duration. Please try to memorize the temporal information as accurately as possible! As soon as the tone stops, you are asked to press the button in front of you for as long as you heard the tone before. It is important for the experiment that you reproduce the duration of the first tone as accurately as possible! While you press the button, another tone will be presented. This tone could be either dependent or independent of your button press. Therefore, please try to reproduce the duration of the first tone, regardless of the second tone! There will be a practice block in the beginning for familiarization with the task. After the practice block the actual experiment will be started automatically. There will be 10 blocks for the whole experiment, which lasts about 45 min.

2.2 Reducing bias in auditory duration reproduction by integrating the reproduced signal

2.2.1 Summary

Previous research has shown differences between sensory and motor temporal estimates. The first study, presented in this thesis (Chapter 2.1), left the question unanswered whether motor and sensory estimates are actually integrated in a sensorimotor reproduction task. Therefore, we investigated in the second study how differential motor reproduction and sensory estimates are integrated for reproducing a specific duration. We compared estimation biases and variances using three different duration estimation tasks: an auditory duration comparison task, a motor reproduction task, and an auditory reproduction task. The auditory duration comparison and the motor reproduction task were used to measure perceptual and action time processing, whereas the auditory reproduction task was a bimodal (i.e. perceptual and motor) task, which was used to investigate how perceptual and motor duration estimations are integrated together. In the motor and the sensorimotor auditory reproduction task we found consistent overestimation whereas the auditory comparison task provided a relative precise estimation. Interestingly, the overestimation in the auditory reproduction task was reduced, compared to the pure motor reproduction, due to the additional reproduced auditory signal. Similar findings could be shown in a subsequent experiment, which varied standard durations and varied signal-to-noise ratios in the compared/reproduced tones. We further compared reliability-based model predictions and observed behavioral results (considering perceptual and motor biases as two independent components), and found that the model successfully predicted the auditory reproduction biases. Our results thus provide behavioral evidence of how the brain combines perceptual and motor information together in order to reduce duration estimation biases and improve estimation reliability.

2.2.2 Author contributions

This work was carried out under the supervision of Zhuanghua Shi and Hermann J. Müller; S.G. and Z.S. conceived the idea and designed the research. SG performed research. Z.S. modeled the results. S.G. and Z.S. discussed the results and wrote the paper. H.J.M. commented on the manuscript. Z.S. and S.G. contributed equally to this work.

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Reducing Bias in Auditory Duration Reproduction by Integrating the Reproduced Signal

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Abstract

Duration estimation is known to be far from veridical and to differ for sensory estimates and motor reproduction. To investigate how these differential estimates are integrated for estimating or reproducing a duration and to examine sensorimotor biases in duration comparison and reproduction tasks, we compared estimation biases and variances among three different duration estimation tasks: perceptual comparison, motor reproduction, and auditory reproduction (i.e. a combined perceptual-motor task). We found consistent overestimation in both motor and perceptual-motor auditory reproduction tasks, and the least overestimation in the comparison task. More interestingly, compared to pure motor reproduction, the overestimation bias was reduced in the auditory reproduction task, due to the additional reproduced auditory signal. We further manipulated the signal-to-noise ratio (SNR) in the feedback/comparison tones to examine the changes in estimation biases and variances. Considering perceptual and motor biases as two independent components, we applied the reliability-based model, which successfully predicted the biases in auditory reproduction. Our findings thus provide behavioral evidence of how the brain combines motor and perceptual information together to reduce duration estimation biases and improve estimation reliability.

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Introduction

For everyday actions, we must be able to incorporate multiple sensory feedbacks for fine-tuned movement in space and time. Precise timing, especially in the sub-second range, is crucial for everyday activities like walking, speaking, or playing sports and making music [1]. However, research has revealed that our perception of time can be distorted in various ways, such as by a voluntary action [2,3], the emotional state of the observer [4,5], or repeated presentation [6]. Also, perceived durations in different modalities can vary substantially. For example, an auditory interval is often judged or produced longer than a visual interval with the same length [7–11]. Timing for action can also be different from timing for perception [12]. For instance, motor reproduction of an auditory duration relying only on kinesthetic information has been reported to be overestimated by about 12% [8], which is larger than the biases found in traditional perceptual comparison tasks. Moreover, not only the perceived time of an on-going action, but also the perceived time of an event that immediately follows an action can be distorted by the action. For example, the first second immediately after a saccadic or an arm movement is often perceived as longer than subsequent seconds, which is known as the chronostasis illusion [3,13,14]. Distortions induced by actions have also been shown in the opposite direction, such as compression of time during saccadic movements [2,15].

Given that perceived time is far from veridical and time estimation can be easily biased by various factors, our brain encounters challenges to integrate different sources of temporal information so as to enable accurate timing for multisensory or sensorimotor events. When inter-sensory biases are detectable (e.g., a longer auditory signal than a visual signal in an echo environment), it has been consistently found that the sensory system may recalibrate itself to maintain internal consistency (for a recent review, see [16]). How the sensory system recalibrates itself is still controversial. Some groups have proposed that the discrepancy in sensory estimates is recalibrated proportional to their reliabilities [17–19]. Based on developmental studies, on the other hand, Gori and colleagues [20] have argued that the recalibration depends on the robustness, rather than the reliability, of the senses. Other researchers have also proposed alternative accounts, for instance, that the calibration is based on prior knowledge about the probability of the signals being biased [16,21], or on fixed-ratio adaptation, whereby cues adapt toward one another at a fixed ratio regardless of cue reliability [22]. Rather than recalibrating the sensory input, the brain could also decide to primarily rely on one sense and ignore information from other senses, as suggested earlier by the modality dominance hypothesis [23]. Relying only on the estimate from one reliable modality could shield from noises and biases from unreliable or inaccurate senses. Note that recalibration or modality dominance in multimodal processing is needed mainly for maintaining an internal, consistent representation [16]. However, recalibration does not solve the bias problem because biases are inherited from individual sensory estimates. Thus, the system still faces the problem of having to reduce the bias. This is particularly true for large differences and biases in perceptual and motor estimates of the same time interval.

When estimation biases do not cause internal discrepancy, the question of how the brain deals with multiple temporal estimates is still poorly understood. In the spatial domain, reliability-based optimal integration models, such as Maximum Likelihood Estimation (MLE), have successfully predicted the effects of multimodal integration for various situations, including visual-haptic size estimation, audio-visual localization, etc. (for a recent review, see [24]). The optimal integration model assumes that our sensory system combines multiple unbiased estimates in a linear weighted fashion, with each weight set in proportion to the reliability of the corresponding sensory source. The integration is optimal since the weighted combination minimizes the estimation uncertainty, that is, maximizes the estimation reliability. However, with regard to the multimodal temporal domain, the findings are rather mixed. A study using temporal-order judgments (TOJ) has found that the MLE model could account well for performance in a bimodal, audio-tactile TOJ task [25]. However, using a temporal-bisection task, Burr, and colleagues [26] found that the MLE model only fitted roughly with their observed result pattern. Employing an apparent motion paradigm and an implicit measure of perceived time interval, Shi and colleagues [9] found that while audio-visual intervals were integrated in an optimal manner, the predicted reduction of the variability of the estimates in the audio-visual condition was not observed. A pattern of well predicted temporal estimates, but missing reductions of variability has also been confirmed by other studies using a temporal bisection task [27] or a visual-tactile reproduction task [28]. Thus, compared to spatial multimodal integration [29-31], the predictions of the reliability-based model are less consistent and inconclusive with regard to multimodal temporal integration. In particular, there is a lack of investigation of sensorimotor temporal integration.

Given this, the present study was designed to test the reliability-based cue integration model for sensorimotor temporal integration, in particular for auditory reproduction. According to the reliability-based MLE model, the estimate of the auditory reproduction ($\hat{D}_{ar}$) for a given standard auditory duration ($\hat{D}_S$) results from a linear weighted combination of the perceptual comparison ($\hat{D}_a$) and pure motor reproduction ($\hat{D}_r$). Assuming that the perceptual and motor estimates are statistically independent of each other, the MLE estimate of the auditory reproduction is given as follows:

$$\hat{D}_{ar} = w_a \hat{D}_a + w_r \hat{D}_r, \tag{1}$$

$$w_a = \frac{r_a}{r_a + r_r};\ w_r = 1 - w_a, \tag{2}$$

where w_a and w_r are the correspondent weights and r_a and r_r are the reliabilities of the estimates, where reliability is defined as the inverse of its respective variance, $r_i = 1/\sigma_i^2$. With these weights the variance of the auditory reproduction σ_{ar}^2 is given by

$$\sigma_{ar}^2 = \frac{\sigma_a^2 \sigma_r^2}{\sigma_a^2 + \sigma_r^2} \tag{3}$$

The variance is the minimum possible for any linear combination and is lower than the variances of the pure perceptual and motor estimates, σ_a^2 and σ_r^2. In other words, the reliability of the MLE estimate is the maximum. Note that minimizing variability (i.e., maximizing reliability) of the auditory reproduction does not guarantee reduction of the bias. Rather, derived from Eq. (1) and (2), the auditory reproduction bias, b_{ar}, becomes a weighted average of the perceptual bias b_a and motor bias b_r:

$$b_{ar} = w_a b_a + w_r b_r \tag{4}$$

If the system does not know where biases come from and if biases vary randomly around the true value, a linear weighted combination may, in general, reduce the bias, even though the combined sensorimotor estimate is not optimal in terms of accuracy.

Testing whether the sensory system uses a reliability-based integration to minimize variability and reduce biases in the auditory duration reproduction, we must compare the goodness of the predictions among the MLE, the auditory dominance, and the motor dominance models in the following aspects: (1) the predicted variances should be close to the observed variances; (2) the predicted estimates should be highly correlated with the observed estimates; (3) for an ideal prediction, the predicted estimates should be equal to the observed estimates. In other words, the slope of a linear regression (without an intercept) between the predicted and observed estimates should be close to 1; (4) the predicted errors measured by root mean square errors (RMSEs) should be smallest.

Thus, we conducted two experiments and compared duration biases and variances among three different tasks: motor reproduction, auditory duration comparison, and auditory reproduction (Figure 1).

The auditory comparison and motor reproduction tasks aimed to measure biases and variances for perceptual and motor timing, respectively. In the auditory comparison task, participants were

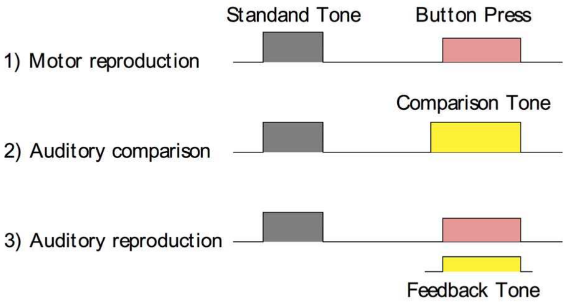

Figure 1. Schematic illustration of three estimation tasks, which all started with the presentation of an auditory standard duration. In the motor reproduction and auditory reproduction tasks, participants had to reproduce the standard duration by pressing a button. In the auditory reproduction task, the reproduced tone was synchronous with the button press. In the comparison task, an auditory comparison stimulus was presented and participants had to indicate which tone was perceived as longer.
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presented with two tones and had to indicate which one was longer. In the motor reproduction task, participants had to press a button as long as the duration of the (previously presented) standard auditory tone. The third, auditory reproduction task was a bimodal (i.e., perceptual and motor) condition: participants had to press a button to produce a tone of the same duration as the previously presented auditory standard. Note that in both reproduction tasks, there is kinesthetic and tactile (touch sense) feedback during the button press. A previous sensorimotor tapping study [32] has shown that blocking the peripheral feedback leads to an increase of the variability in synchronizing the pacing signal with the tap. Here, however, we consider motor action and peripheral touch feedback as one, unitary motor component. This does not compromise our aim of examining how reproduced auditory feedback influences time estimation. In Experiment 1, we compared estimations among the three tasks (duration comparison, pure motor reproduction, and auditory reproduction) for a single auditory standard duration (1 second). To vary the reliability of the signals, in Experiment 2, we manipulated comparison/reproduced tone signal-to-noise ratio (SNR) block-wise. In addition, we mixed two standard durations, 800 and 1200 ms, together to increase task uncertainty.

Results

Experiment 1

Figure 2 depicts the mean biases for three tasks (pure motor reproduction, auditory comparison, and auditory reproduction). Pure motor reproduction produced the largest overestimation (454±96.9 ms). For the auditory comparison task, on the other hand, the bias (60±9.5 ms) was the smallest, though it was still significantly greater than zero, $t(10)=6.69$, $p<0.01$. The overestimation in the comparison task was probably due to the low intensity of the comparison signal (46 dB) compared to the standard signal (68 dB), as shown previously [33]. Bonferroni corrected pairwise comparison revealed a significant difference between motor reproduction and auditory comparison ($p<0.01$), as well as one between auditory comparison and auditory reproduction ($p<0.01$). There was also a marginally significant difference between pure reproduction and auditory reproduction ($p=0.052$). Based on Equations (2) and (4), we then calculated the predicted mean bias of auditory reproduction according to the MLE model. The predicted bias did not differ from the observed bias ($p=0.88$).

However, the pattern is different when looking at the estimation variability indicated by the standard deviations (SDs) (Figure 3).

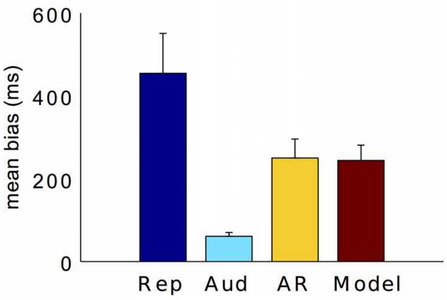

Figure 2. Mean biases (with±1 standard errors) for the pure motor reproduction (blue bar), auditory comparison (cyan bar), auditory reproduction (yellow bar), and predicted according to the MLE model (red bar) in Experiment 1.
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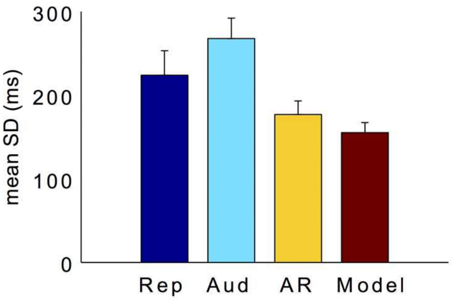

Figure 3. Mean SDs (with±1 standard errors) for the pure reproduction (blue bar), auditory comparison (cyan bar), auditory reproduction (yellow bar), and predicted according to the MLE model (red bar) in Experiment 1.
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The mean SDs differed significantly among the three tasks, as confirmed by a repeated measures ANOVA, $F(1.33,13.33)=219.33$, $p<0.05$ (Greenhouse-Geisser corrected). Bonferroni corrected pairwise comparisons revealed the variance to be significantly smaller in the auditory reproduction than in the auditory comparison task ($p<0.05$). More interestingly, the predicted mean variance according to the MLE model did not differ from the observed mean variance of the auditory reproduction ($p=0.09$).

We further compared the goodness of fit for three different models (MLE, auditory/motor dominance) using three additional measures: the slope of the linear regression (without an intercept) between the observed and predicted biases, the correlation between the predicted and observed biases, and the mean predicted error RMSE. Results are shown in Table 1. Both the MLE and the motor dominance model show a high correlation between the predicted and observed biases. However, only for the MLE model the slope was close to 1. In addition, RMSE was the smallest in the MLE model. Clearly, the prediction of the MLE model is better than that of the two dominance models.

Experiment 2

In Experiment 2, we increased task uncertainty by introducing two standard intervals (i.e., 800 and 1200 ms) and two signal-noise ratios (SNRs) in the compared/reproduced tones (High-SNR: 11 dB, Low-SNR: −14 dB). Figure 4 depicts the mean biases for Experiment 2. A three-way repeated measures ANOVA with length of duration, SNR, and task as factors revealed that the bias was significant influenced by all three factors: the length of duration, $F(1,9)=24.08$, $p<0.01$; SNR, $F(1,9)=23.31$, $p<0.01$; and task, $F(2,18)=15.43$, $p<0.01$. The low SNR increased the positive bias in the duration estimation. The higher overestimation for the short duration (800 ms) than for the long duration

Table 1. Goodness of predictions based on the slope (±95% confidence interval), correlation coefficient r (*p<0.05), and RMSE for the MLE, motor dominance, and auditory dominance models in Experiment 1.

Models	Slope±95% CI	r	RMSE
MLE	0.98±0.29	0.62 *	110
Motor dominance	0.48±0.16	0.66 *	305
Auditory dominance	3.14±2.01	−0.26	239

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(1200 ms) confirmed previously reported range and regression effects [34–37], which suggests that participants tend to be biased towards the center of the stimulus range. In our case, due to the random mixing of the short and long standard duration trials, estimation of the short duration was biased towards the long duration and vice versa. Further post-hoc Bonferroni multiple-comparison tests indicated that the biases differed significantly among the three tasks (all $p<0.05$), with the lowest bias in the comparison task and the highest in the motor reproduction task. There was also one (and only one) significant interaction between SNR and task, $F(2,18) = 10.49$, $p<0.01$. This was mainly due to the fact that there was no auditory and noise signals in the pure motor reproduction. Most interestingly, the predicted biases according to the MLE model did not differ from observed auditory reproduction biases (all $p>0.1$, Figure 4).

Similar to Experiment 1, we compared the goodness of fit for the three possible models (MLE, auditory/motor dominance) with three different measures. We pooled all data (conditions) together to make a strict test. Results are shown in Table 2. No correlation between the observed and predicted biases for the auditory dominance model clearly indicates its bad prediction. On the other hand, the correlation was highest in the motor dominance model, yet its regression slope was only half (0.47) and RMSE was the largest one. Taking three indicators together, the MLE model best predicted the data, which corroborated the finding in Experiment 1.

Further, we estimated weights for the different conditions. Figure 5 illustrates the systematic changes of motor weights with duration length and SNR. A repeated measures ANOVA revealed that both SNR and duration significantly influenced the weight adjustments, with greater reliance on motor timing for the long compared with the short duration, $F(1,9) = 22.17$, $p<0.01$, and higher weights on motor timing for the low SNR (−14 dB) than for the high SNR (11 dB) condition, $F(1,9) = 24.95$, $p<0.01$. This is because the long duration and, respectively, the low SNR auditory feedback exhibited larger variability than the short duration and, respectively, the high SNR auditory feedback. There was no interaction between the two factors, $F(1,9) = 1.2$, $p = 0.4$.

The pattern of variances indicated by the SDs is depicted in Figure 6, which shows that SDs are lower in the high compared to the low SNR conditions, and in the auditory reproduction compared to the pure motor reproduction condition. This pattern was confirmed by a three-way repeated measures ANOVA, which revealed significant effects for SNR, $F(1,9) = 21.94$, $p<0.01$, and task, $F(2,18) = 5.42$, $p<0.05$, but not for length of the standard duration, $F(1,9) = 0.15$, $p = 0.7$. Post-hoc Bonferroni tests indicated that the mean SD was lowest in the auditory reproduction task (all $p<0.05$). As in Experiment 1, we compared predicted variability based on the MLE model with observed variability, as additional confirmation criterion for reliability based integration. The observed variability and predicted variability did not differ for the long standard durations (both $p>0.1$), being in agreement with reliability based model predictions. However, for the short durations, there were significant differences between predicted and observed variability for high SNR, $t(9) = 5.70$; $p<0.05$, and for low SNR, $t(9) = 3.09$, $p<0.05$. This suggests that the integration was suboptimal for the short durations.

Discussion

We examined how the brain incorporates different sources of timing information in duration estimation. We compared estimation biases in an auditory comparison, motor reproduction, and auditory reproduction task. We found two major results: First, while perceptual comparison of two auditory tones was fairly accurate, reproduction of an auditory tone yielded consistent overestimation. The overestimation was reduced when the reproduction produced a tone feedback, though even then it remained larger compared to the auditory comparison task. Second, we fitted the results with the MLE optimal integration model, which yielded a good prediction for the estimation bias.

Our finding of a large difference between perceptual comparison and motor reproduction for the same physical duration clearly favors distributed timing mechanisms [38–42]. It is well

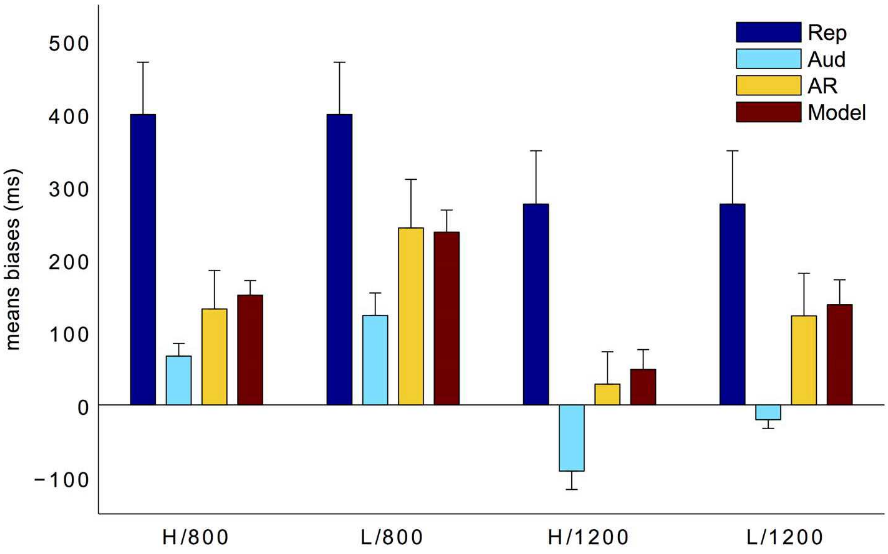

Figure 4. Mean biases (with±1 standard errors) for pure reproduction (blue bars), auditory comparison (cyan bars), auditory reproduction (yellow bars), and predicted according to the MLE model (red bars), as a function of the SNR and standard duration in Experiment 2. H and L denote the high and low SNR conditions, 800 and 1200 the short and long standard durations.
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Table 2. Goodness of predictions based on the slope (±95% confidence interval), correlation coefficient r (*p<0.05), and RMSE for the MLE, motor dominance, and auditory dominance models in Experiment 2.

Models	Slope±95% CI	r	RMSE
MLE	1.01±0.24	0.70 *	129
Motor dominance	0.47±0.09	0.81 *	242
Auditory dominance	0.57±0.65	0.21	217

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established that perceived duration in different modalities can vary, such that sounds are perceived as longer than lights or tactile vibrations of equal physical duration [7–9,43–45]. Some other recent studies have also pointed to different mechanisms for motor and sensory timing. For example, differences between perceptual and motor timing have been demonstrated by a delay manipulation prior to the task [12,46]. Also, an opposite temporal distortion pattern between perceptual and motor time estimations has been reported for novel versus repeated stimuli [47]. It should be mentioned that many other studies favor a common mechanism for motor and sensory timing [48–50]. Most of these studies, however, used slightly different tasks (e.g., rhythmic tasks) and often gap intervals. Unlike reproduction with a continuous button press, the perceptual task (defined by two brief stimuli) and the motor task (demarcated by two taps) with gap intervals are more "similar" to each other, as the gap information is likely modality-independent and processed by a common mechanism. In contrast to these paradigms, we used filled intervals for both perceptual comparison and motor reproduction. From this aspect, our findings of a strong difference between the motor reproduction and auditory comparison tasks argue in favor of a perception-action dichotomy in the timing mechanisms involved.

The strong over-reproduction in the motor task (about 38%) seems striking. Walker and Scott [8], some time ago, reported an overestimation of auditory durations by about 12%, though they did not provide any explanation for this finding. It has been suggested that motor reproduction might include an additional component of motor planning in time encoding [51]. Temporal reproduction has been thought to consist of two consecutive processes: waiting until the elapsed time is "close enough" to the standard, at which point a response is initiated, and then executing the response (i.e., button press), which again takes time (see also Wing and Kristofferson's model [52]). However, such an explanation cannot account for our finding of a pronounced overestimation, since the initiation and termination of a response in our *filled*-reproduction task could be both delayed and the delays might cancel each other. Even without any cancelation, the large over-reproduction is unlikely due to the motor planning time. However, the additional noise generated by the motor control and planning processes is most likely present, as indicated by the estimation variances.

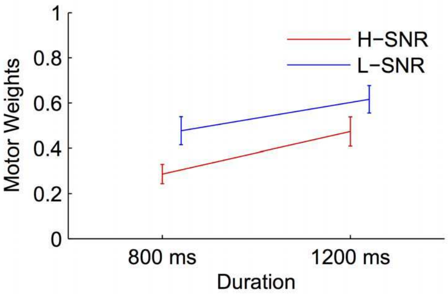

Figure 5. Mean predicted motor weights as a function of the duration length and SNR for the auditory reproduction task. H-SNR and L-SNR denote the high and low SNR conditions, respectively.
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Both estimation biases and variances were decreased in the auditory reproduction compared to the motor reproduction task. The reproduced auditory signal seems to contribute to the final reproduction by reducing the bias and variability. Using the reliability-based MLE model, we found that the quantitative model successfully predicted the auditory reproduction biases, and it performed far better than either a motor dominance or a perceptual dominance model.

It should be noted that most studies using MLE or a more general Bayesian approach employed physical measures as their integration cues for multimodal integration. Some small external discrepancies were often introduced during the experiments. The implicit assumption of optimal integration, using external physical measures, is that all sensory estimates are unbiased. Disregarding biases allows one to focus on minimizing variance as an optimality criterion [53]. As reviewed earlier, subjective and physical durations have been shown to be quite different and temporal biases are ubiquitous. If the quantitative model had considered only physical durations, it would not have provided any useful predictions in our case, because the physical durations were identical. In the present study, we explicitly modeled biases (see Equation 4). By integrating two (or more) estimates, the system can reduce the variability of the final estimate. This idea goes along with the recent memory-mixing account [54], which suggests that our brain might combine multiple signal durations together for time estimation. However, integrating or mixing multiple biased estimates may reduce the accuracy of the final estimate. For example, in our study, the bias in auditory reproduction was larger than that in the pure auditory comparison. Thus, the estimation would have been better in terms of accuracy if the system only trusted the auditory comparison. In this sense, the linear weighted integration is not optimal if estimates have biases. Of course, without any external feedback, the system does not know if the sensory or/and the motor estimate is biased. Using a weighted averaging method in this situation may reduce the variability of the estimate, though it may not lead to the best-unbiased estimate.

Integration of subjective estimates has also been tested recently with visual and tactile duration judgments [28], for which the bimodal duration was predicted successfully by the MLE model. However, the variability of the bimodal condition was far from "optimal", not showing the theoretically predicted improvement. Interestingly, several recent studies of multimodal temporal integration [9,26–28] confirmed that the MLE prediction of the bimodal variability was suboptimal: in general, the predicted variance was smaller than the observed one. This was also the case in our Experiment 2, in which the predicted variances for the short standard durations were significant lower than the observed variances. The reason for this suboptimal integration is not clear at present. It has been suggested that the assumption of Gaussian noise might not be appropriate for timing tasks [26]. Alternatively, variability in the auditory reproduction task may not be further reduced for the short standard durations, due to the accuracy limits of the motor system. It is also possible that time estimates from different sensory (motor) modalities are not completely distributed and statistically independent, as hinted at by the internal common time processing literature [49,50,55–58]. When

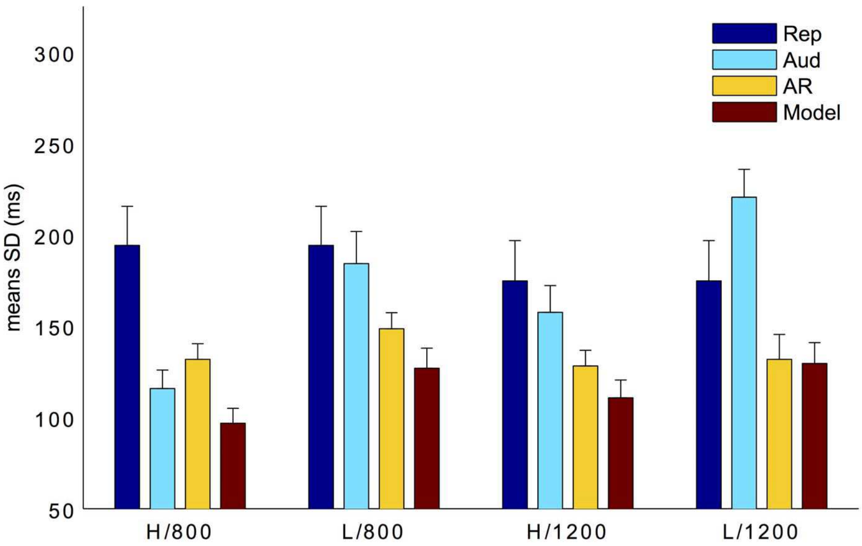

Figure 6. Mean SDs (with±1 standard errors) for pure reproduction (blue bars), auditory comparison (cyan bars), auditory reproduction (yellow bars), and predicted according to the MLE model (red bars), as a function of standard duration and SNR in Experiment 2. H and L denote high and low SNRs, 800 and 1200 short and long standard durations.
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sensory estimates are correlated, the optimal weights and reliability could dramatically deviate from independent optimal integration [59].

It should be mentioned, however, that the present study only investigated the integration of auditory reproduction. Several researchers have argued that there might be a privileged link between the auditory and the motor system in the time domain, allowing for a direct integration of auditory information into the motor system [39,60,61]. In an fMRI tapping study, for example, it has been shown that tapping to auditory stimuli is driven by a reliable internal movement rhythm. But during tapping to visual stimuli participants rather relied on an inefficient and computational demanding control network [61]. In a previous study, we have also found that while offset-delayed auditory feedback led to a decrease in duration reproduction, there was no effect of offset-delayed visual feedback [11]. Further, it has been shown that initiating an action during a temporal-bisection task could enhance auditory temporal sensitivity, while there was no effect of an action on visual temporal sensitivity [62]. Therefore, the integration of other-modality sensory feedback (visual or tactile) during duration reproduction might have different results, which is definitely intriguing for future studies.

In summary, the present study investigated subjective differences between perceptual and motor timing, and their integration mechanism. There was strong overestimation in the motor and auditory reproduction tasks. When a reproduced auditory signal was given during the reproduction, the overestimation bias was reduced, though it was still larger compared to the pure auditory comparison task. The reliability-based model successfully predicted the auditory reproduction bias for one and for multiple standard durations, as well as for the varying SNR conditions. The variability of the estimation was also reduced in the auditory reproduction task compared to the pure motor reproduction or perceptual comparison tasks. However, the observed variances did not reach the optimal level for the short duration conditions. To address this, the possibility of prior updates [34,63] ought to be investigated in future studies to quantify sensorimotor time estimation more precisely.

General Methods

Subjects

21 naive volunteers (16 females, mean age 25.3 years) participated in the two experiments for payment (11 and 10 participants for Experiments 1 and 2, respectively). All participants had normal or corrected-to-normal vision; none of them reported any history of somatosensory disorders.

Ethics Statement

All participants gave written informed consent in accordance with the Declaration of Helsinki (2008). Experiments were approved by the Ethics committee of the Psychology Department, LMU Munich.

Stimuli and apparatus

All experiments were conducted in a dimly lit cabin (0.21 cd/m^2). Auditory tones were the mainly used stimuli in the experiments. The standard tone was an 800 Hz, 68 dB tone presented for 1000 ms in Experiment 1; and an 800 Hz, 75 dB tone presented for 800 or 1200 ms in Experiment 2. The feedback and comparison tone was a 600 Hz, 46 dB tone in Experiment 1, and a 600 Hz, 74 dB and 49 dB tone for high and, respectively, low SNR conditions in Experiment 2. Additionally, pink noise was presented during the task (62 dB in Experiment 1 and 63 dB in Experiment 2). Thus the signal to noise ratio (SNR) of the comparison/feedback tone was 16 dB in Experiment 1, and 11 and -14 dB for the high- and, respectively, low-SNR comparison/feedback tones in Experiment 2. Stimulus presentation and data acquisition were controlled by a National Instrument PXI system, ensuring highly accurate timing (<1 ms). The experimental programs were developed using Matlab and Psychophysics Toolbox [64]. Tones and pink noise were delivered to participants via speakers imbedded in the monitor. The response button was placed on the table in-between the participant and the monitor. Reproduction times were measured using a response button, which participants pressed with their right-hand index finger. For the comparison task, left and right arrow keys were used for response acquisition.

Procedure

In both experiments, we tested three different tasks: pure motor reproduction, duration comparison, and auditory reproduction (Figure 1).

In the duration comparison task, each trial started with a standard tone, defining a standard duration (1000 ms in Experiment 1, 800 or 1200 ms in Experiment 2). After a variable inter-stimulus interval randomly selected from 650–800 ms, a second comparison tone was presented. The duration of the comparison tone was randomly selected from seven preselected intervals, which were centered on the respective standard duration: they were selected systematically from around the standard duration, separated by steps of 10% of the Weber fraction. Thus, for the 1000-ms standard, comparison durations were 700, 800, …, 1300 ms; for the 800-ms standard, 560, 640, …, 1040 ms; and for the 1200-ms standard, 840, 960,…, 1560 ms. Participants were asked to compare the duration of the two tones and indicate whether they perceived the first or the second tone as longer, by pressing the left or right arrow key, respectively. In Experiment 2, two comparison tones differing in loudness were presented in block-wise manner.

In the duration reproduction tasks, again each trial started with a standard tone (the same as in the duration comparison task). Following the presentation of the standard tone, participants were asked to reproduce the duration as accurately as possible by button press, with reproduction duration demarcated by the onset and offset of the press action. In the auditory reproduction task, pressing the button produced a synchronous tone. In Experiment 2, two feedback tones differing in loudness were presented during the auditory reproduction task, manipulated in blocked-wise manner.

The three tasks were presented in separate blocks, with block order randomized across participants. In Experiment 1, there were 4 blocks of the comparison task, 2 blocks of the motor reproduction task, and 2 blocks of the auditory reproduction task. Each block consisted of 49 trials. In Experiment 2, blocks were split into two sessions run on separate days, due to the large number of to-be-completed trials. There were 2 [days] $\times 7$ blocks of the comparison task, 2×2 blocks of the motor reproduction task, and 2×3 blocks of the auditory reproduction task. Each block consisted of 28 trials. Participants took a short break after every block. In addition, there was a short practice part introducing all three conditions, run prior to the formal experiment.

Data analysis

For the duration comparison task, psychometric curves were fitted by cumulative Gaussian functions to each participant's responses. Points of subjective equality (PSEs) were then estimated from the 50% threshold points of the psychometric curves. The standard deviation (SD) was estimated from the cumulative Gaussian function [29,30]. Note that the standard tone was always presented first; thus, the perceptual standard deviation would have to be adjusted by a constant multiplier $\sqrt{2}$ (see [65,66]). However, since all three tasks started with the presentation of the standard tone (which participants would essentially memorize), this constant multiplier did not influence the model prediction. We therefore omitted it in the calculation. For the duration reproduction tasks, mean reproduced duration and standard deviation were calculated for each condition and individual participant. Extreme outliers, outside the upper 99% and lower 1% percentile, were removed from further analysis. The predicted biases and standard deviations were then calculated based on Equations (1) to (4).

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Author Contributions

Conceived and designed the experiments: ZS SG. Performed the experiments: SG ZS. Analyzed the data: ZS SG. Contributed reagents/materials/analysis tools: ZS SG. Wrote the paper: ZS SG HJM.

References

1. Buhusi CV, Meck WH (2005) What makes us tick? Functional and neural mechanisms of interval timing. Nat Rev Neurosci 6: 755–765.
2. Morrone MC, Ross J, Burr D (2005) Saccadic eye movements cause compression of time as well as space. Nat Neurosci 8: 950–954.
3. Park J, Schlag-Rey M, Schlag J (2003) Voluntary action expands perceived duration of its sensory consequence. Exp Brain Res 149: 527–529.
4. Angrilli A, Cherubini P, Pavese A, Manfredini S (1997) The influence of affective factors on time perception. Atten Percept Psychophys 59: 972–982.
5. Shi Z, Jia L, Müller HJ (2012) Modulation of tactile duration judgments by emotional pictures. Front Integr Neurosci 6: 1–9.
6. Pariyadath V, Eagleman DM (2008) Brief subjective durations contract with repetition. J Vis 8: 1–6.
7. Wearden JH, Edwards H, Fakhri M, Percival A (1998) Why 'sounds are judged longer than lights': Application of a model of the internal clock in humans. Q J Exp Psychol-B 51B: 97–120.
8. Walker JT, Scott KJ (1981) Auditory–visual conflicts in the perceived duration of lights, tones, and gaps. J Exp Psychol Hum Percept Perform 7: 1327–1339.
9. Shi Z, Chen L, Müller H (2010) Auditory temporal modulation of the visual Ternus effect: the influence of time interval. Exp Brain Res 203: 723–735.
10. Goldstone S (1968) Production and reproduction of duration: intersensory comparisons. Percept Mot Skills 26: 755–760.
11. Ganzenmüller S, Shi Z, Müller HJ (2012) Duration reproduction with sensory feedback delay: differential involvement of perception and action time. Front Integr Neurosci 6: 1–11.
12. Bueti D, Walsh V, Frith C, Rees G (2008) Different Brain Circuits Underlie Motor and Perceptual Representations of Temporal Intervals. J Cognit Neurosci 20: 204–214.
13. Yarrow K, Haggard P, Heal R, Brown P, Rothwell JC (2001) Illusory perceptions of space and time preserve cross-saccadic perceptual continuity. Nature 414: 302–305.
14. Yarrow K, Rothwell JC (2003) Manual chronostasis: tactile perception precedes physical contact. Curr Biol 13: 1134–1139.
15. Binda P, Cicchini GM, Burr DC, Morrone MC (2009) Spatiotemporal distortions of visual perception at the time of saccades. J Neurosci 29: 13147–13157.
16. Ernst MO, Di Luca M (2011) Multisensory Perception: From Integration to Remapping. In: Trommershäuser J, Körding KP, Landy MS, editors. Sensory Cue Integration. New York: Oxford University Press. pp. 224–250.
17. Burge J, Girshick AR, Banks MS (2010) Visual-haptic adaptation is determined by relative reliability. J Neurosci 30: 7714–7721.
18. Ghahramani Z, Wolpert DM, Jordan MI (1997) Computational models of sensorimotor integration. In: Morasso PG, Sanguineti V, editors. Self-organization, computational maps and motor control. Amsterdam: Elsevier Press. pp. 117–147.
19. Witten IB, Knudsen EI (2005) Why seeing is believing: merging auditory and visual worlds. Neuron 48: 489–496.
20. Gori M, Del Viva M, Sandini G, Burr DC (2008) Young children do not integrate visual and haptic form information. Curr Biol 18: 694–698.
21. Di Luca M, Machulla TK, Ernst MO (2009) Recalibration of multisensory simultaneity: cross-modal transfer coincides with a change in perceptual latency. J Vis 9: 7 1–16.
22. Zaidel A, Turner AH, Angelaki DE (2011) Multisensory calibration is independent of cue reliability. J Neurosci 31: 13949–13962.
23. Welch RB, Warren DH (1980) Immediate perceptual response to intersensory discrepancy. Psychol Bull 88: 638–667.

24. Alais D, Newell FN, Mamassian P (2010) Multisensory processing in review: from physiology to behaviour. Seeing Perceiving 23: 3–38.
25. Ley I, Haggard P, Yarrow K (2009) Optimal integration of auditory and vibrotactile information for judgments of temporal order. J Exp Psychol Hum Percept Perform 35: 1005–1019.
26. Burr D, Banks M, Morrone M (2009) Auditory dominance over vision in the perception of interval duration. Exp Brain Res 198: 49–57.
27. Hartcher-O'Brien J, Alais D (2011) Temporal ventriloquism in a purely temporal context. J Exp Psychol Hum Percept Perform 37: 1383–1395.
28. Tomassini A, Gori M, Burr DC, Sandini G, Morrone MC (2011) Perceived duration of Visual and Tactile Stimuli Depends on Perceived Speed. Front Integr Neurosci 5: Article 51.
29. Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415: 429–433.
30. Alais D, Burr D (2004) The Ventriloquist Effect Results from Near-Optimal Bimodal Integration. Curr Biol 14: 257–262.
31. Kording KP, Wolpert DM (2004) Bayesian integration in sensorimotor learning. Nature 427: 244–247.
32. Aschersleben G, Gehrke J, Prinz W (2001) Tapping with peripheral nerve block. a role for tactile feedback in the timing of movements. Exp Brain Res 136: 331–339.
33. Matthews WJ, Stewart N, Wearden JH (2011) Stimulus intensity and the perception of duration. J Exp Psychol Hum Percept Perform 37: 303–313.
34. Jazayeri M, Shadlen MN (2010) Temporal context calibrates interval timing. Nat Neurosci 13: 1020–1026.
35. Petzschner FH, Glasauer S (2011) Iterative Bayesian estimation as an explanation for range and regression effects: a study on human path integration. J Neurosci 31: 17220–17229.
36. Teghtsoonian R, Teghtsoonian M (1978) Range and regression effects in magnitude scaling. Percept Psychophys 24: 305–314.
37. Cicchini GM, Arrighi R, Cecchetti L, Giusti M, Burr DC (2012) Optimal encoding of interval timing in expert percussionists. J Neurosci 32: 1056–1060.
38. Takahashi K, Watanabe K (2012) Short-term memory for event duration: Modality specificity and goal dependency. Atten Percept Psychophys 74: 1–9.
39. Jantzen KJ, Steinberg FL, Kelso JAS (2005) Functional MRI reveals the existence of modality and coordination-dependent timing networks. NeuroImage 25: 1031–1042.
40. Gamache P-L, Grondin S (2010) Sensory-specific clock components and memory mechanisms: investigation with parallel timing. Eur J Neurosci 31: 1908–1914.
41. Bueti D, Bahrami B, Walsh V (2008) Sensory and Association Cortex in Time Perception. J Cognit Neurosci 20: 1054–1062.
42. Bueti D (2011) The sensory representation of time. Front Integr Neurosci 5: 34.
43. van Wassenhove V, Buonomano DV, Shimojo S, Shams L (2008) Distortions of Subjective Time Perception Within and Across Senses. PLoS One 3: e1437.
44. Chen K-M, Yeh S-L (2009) Asymmetric cross-modal effects in time perception. Acta Psychol (Amst) 130: 225–234.
45. Jones LA, Poliakoff E, Wells J (2009) Good vibrations: Human interval timing in the vibrotactile modality. Q J Exp Psychol 62: 2171–2186.
46. Bueti D, Walsh V (2010) Memory for time distinguishes between perception and action. Perception 39: 81–90.
47. Matthews WJ (2011) Stimulus Repetition and the Perception of Time: The Effects of Prior Exposure on Temporal Discrimination, Judgment, and Production. PLoS One 6: e19815.
48. Meegan DV, Aslin RN, Jacobs RA (2000) Motor timing learned without motor training. Nat Neurosci 3: 860–862.
49. Keele SW, Pokorny RA, Corcos DM, Ivry R (1985) Do perception and motor production share common timing mechanisms: A correlational analysis. Acta Psychol (Amst) 60: 173–191.
50. Ivry RB, Hazeltine RE (1995) Perception and production of temporal intervals across a range of durations: Evidence for a common timing mechanism. J Exp Psychol Hum Percept Perform 21: 3–18.
51. Wearden JH (2003) Applying the scalar timing model to human time psychology: Progress and challenges. In: Helfrich H, editor. Time and mind II: information processing perspectives: Hogrefe & Huber. pp. 21–40.
52. Wing A, Kristofferson A (1973) Response delays and the timing of discrete motor responses. Atten Percept Psychophys 14: 5–12.
53. Landy MS, Banks MS, Knill DC (2011) Ideal-Observer Models of Cue Integration. In: Trommershäuser J, Körding KP, Landy MS, editors. Sensory Cue Integration. New York: Oxford University Press. pp. 5–29.
54. Gu B-M, Meck W (2011) New Perspectives on Vierordt's Law: Memory-Mixing in Ordinal Temporal Comparison Tasks. In: Vatakis A, Esposito A, Giagkou M, Cummins F, Papadelis G, editors. Multidisciplinary Aspects of Time and Time Perception: Springer Berlin Heidelberg. pp. 67–78.
55. Treisman M (1963) Temporal discrimination and the indifference interval: Implications for a model of the 'internal clock'. Psychological Monographs: General and Applied 77: 1–31.
56. Gibbon J, Malapani C, Dale CL, Gallistel CR (1997) Toward a neurobiology of temporal cognition: advances and challenges. Curr Opin Neurobiol 7: 170–184.
57. Coull JT, Vidal F, Nazarian B, Macar F (2004) Functional Anatomy of the Attentional Modulation of Time Estimation. Science 303: 1506–1508.
58. Church RM (1984) Properties of the Internal Clock. Ann N Y Acad Sci 423: 566–582.
59. Oruc I, Maloney LT, Landy MS (2003) Weighted linear cue combination with possibly correlated error. Vision Res 43: 2451–2468.
60. Zatorre RJ, Chen JL, Penhune VB (2007) When the brain plays music: auditory-motor interactions in music perception and production. Nat Rev Neurosci 8: 547–558.
61. Jäncke L, Loose R, Lutz K, Specht K, Shah NJ (2000) Cortical activations during paced finger-tapping applying visual and auditory pacing stimuli. Cognitive Brain Res 10: 51–66.
62. Iordanescu L, Grabowecky M, Suzuki S (2013) Action enhances auditory but not visual temporal sensitivity. Psychol Bull 20: 108–114.
63. Petzschner FH, Glasauer S (2011) Iterative Bayesian Estimation as an Explanation for Range and Regression Effects: A Study on Human Path Integration. J Neurosci 31: 17220–17229.
64. Brainard DH (1997) The Psychophysics Toolbox. Spat Vis 10: 433–436.
65. Kuschel M, Di Luca M, Buss M, Klatzky RL (2010) Combination and integration in the perception of visual-haptic compliance information. IEEE Trans Haptics 3: 234–244.
66. Macmillan NA, Creelman CD (2005) Detection Theory - A User's Guide: Lawrence Erlbaum Associates, Inc.

2.3 Adapting the prior representation of the standard duration through feedback, loudness and delay manipulations in a sensorimotor reproduction task

2.3.1 Summary

Temporal context has been shown to easily distort subjective duration estimates. In the second study (Chapter 2.2) we found a non-optimal reduction in variability for auditory reproduction when different standard durations are presented randomly interleaved. On this ground, we hypothesize that the prior representation of a standard duration should affect the sensorimotor reproduction, and the prior itself is also updated on a trial-wise basis. So far, the dynamic prior representation of a standard duration is implicitly assumed, to come from the statistical properties of the stimulus distribution. In this third study, we used an adaptation-test paradigm to examine explicit changes to the prior distribution of the standard duration. We were interested in changes in the prior representation and in the changes of how much participants trusted the auditory information during the reproduction, observable during the test phase. In the adaptation phase, participants were asked to produce an auditory duration of the same length as the standard duration, but participants received a manipulated feedback of their accuracy, or generated a tone with different levels of signal-noise ratios (SNRs), or with manipulated onsets. In all experiments, we observed a change in prior representation of the standard duration in agreement with our predictions, based on a simple Bayesian model: an accuracy feedback range that is 100 ms shorter than the true feedback range, resulted in reduced reproduction durations in the test phase, when compared with a true accuracy feedback range; adaptation with a low SNR reproduced tone led to decreased reproduction times compared to adaptation with a high SNR reproduced tone; further adaptation to a delayed reproduced tone onset led to decreased reproduction times, but also to a reduction in auditory weights, compared to after adaptation with a synchronous tone onset. Trial-wise analysis during the test phase could show that the influence of the adapted prior diminished over time and reproduction times return towards a typically observed overestimation in auditory duration reproduction. The findings provide evidence that the reference memory can be explicitly changed by adaptation, as sensorimotor estimates are integrated with the history of duration estimates, building up a new prior representation of the standard duration.

2.3.2 Author contributions

This work was carried out under the supervision of Zhuanghua Shi and Hermann J. Müller; S.G. conceived the idea, designed the research and performed research. Z.S. modeled the results. S.G. and Z.S. discussed the results and wrote the paper. H.J.M commented on the manuscript. S.G. and Z.S. contributed equally to this work.

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Adapting the prior representation of the standard duration through feedback, loudness and delay manipulation in a sensorimotor reproduction task

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Abstract

Perceived duration can be easily distorted by temporal context and by prior information about target intervals. However, the mechanisms underlying the prior context influences are still not well understood. We examined whether the prior representation of a standard duration could influence an auditory duration reproduction by using an adaptation-test paradigm. In three experiments, we compared reproduced durations after adapting participants to two different priors of a standard duration. Here for, feedback, tone loudness and a delay was manipulated. We observed the dynamic influence of the prior knowledge on duration reproduction and, by introducing an onset-delay between reproduced tone and motor onset, how the prior influences the sensorimotor integration. Our results showed that manipulations of the correct feedback range (rewarding only reproduced durations 100 ms short of the standard duration), of the tone loudness (comparing reproduction after adaptation to low and high signal-to-noise reproduced tone), and of a delay (starting the reproduced tone independent of the button press), led to significant changes in the prior representation of the standard duration in the test phase. Data could be well predicted by a simple Bayesian model. Further, manipulating the reproduced tone onset during the adaptation phase caused participants to trust the auditory signal less during the reproduction in the test phase. Additional trial-wise analysis revealed diminishing prior effects over time and a return towards a typical overestimation in auditory reproduction. The results are discussed in terms of a Bayesian framework, predicting a dynamically updated prior representation of the standard duration in the reference memory, by integrating current sensorimotor estimates with the history of duration estimates.

Introduction

Subjective time has often been found to deviate from physical time, influenced by various contexts. For example, subjective duration of an auditory stimuli is generally judged longer than the same duration of a visual or haptic stimuli when these stimuli are tested inter-mixed in a session (Jones, Poliakoff, & Wells, 2009; Penney, Gibbon, & Meck, 2000; Wearden, Edwards, Fakhri, & Percival, 1998). Knowledge of stimulus durations could also influence subjective time, known as a central-tendency effect, in which short intervals are estimated as longer than they really are, whereas long intervals tend to be estimated shorter (Gu & Meck, 2011; Jazayeri & Shadlen, 2010; Lejeune & Wearden, 2009).

A traditional account explaining contextual influences in duration judgments, is the “memory-mixing” account (Gu & Meck, 2011). This account proposes that the memory distribution for a particular target interval is a mixture of an internal clock reading and the history of previous clock readings (Gu & Meck, 2011; Penney, Allan, Meck, & Gibbon, 1998). Other accounts, using quantitative Bayesian inference, argued that central tendency effects, as well as other temporal distortions, could be explained as an influence of prior knowledge (i.e. knowledge acquired from long- or short-term experience) or – more specifically – the influence of a prior representation of the to-be timed standard duration, on duration estimation. It has been suggested that incorporating the prior knowledge is beneficial for overall performance – that is, reducing overall errors (Burr, Rocca, & Morrone, 2013; Jazayeri & Shadlen, 2010). To achieve such optimal performance, humans have to rely more on the more reliable source (Berniker, Voss, & Kording, 2010). For example, a correlative relationship between the effect of an distractor, presented during a temporal comparison task, and the Weber fraction has been found (Burr, Rocca, & Morrone, 2013). If interval timing is more precise (i.e. low Weber fraction), as has been shown to be the case for long durations around 1 sec in comparison to short durations with less than 500 ms, the influence of a distractor interval, presented before or after a comparison interval is less strong, than if interval timing is less precise (i.e. high Weber fraction). The authors assume that a regularization mechanism, attempting to make the intervals for distractor and test equal, competes with the estimate of the physical duration of the interval. Combining the two estimates (i.e. regularization estimate and physical estimate) in a statistically optimal way (i.e. using Bayesian statistics) results in the systematic pattern of distorted perception observed during the experiments (Burr et al., 2013). Only recent studies have started to investigate effects of prior knowledge in time perception. Specifically addressing central tendency effects in a time reproduction task, Jazayeri and Shadlen could show that participants used the mean of the duration distribution as additional source of information to achieve a less variable reproduction performance. If the same duration was presented in different temporal contexts (i.e. different mean distributions) participants reproduced this duration significantly different depending on the distribution (Jazayeri & Shadlen, 2010). Note that in this study the authors implicitly assumed that participants can learn and use statistical properties of the stimuli’s distributions (i.e. uniform distribution from selected duration range). Another similar study demonstrated that participants are able to learn and built up an internal representation of various statistical features of simple and complex distributions of time intervals (Acerbi, Wolpert, & Vijayakumar, 2012).

Interestingly, it was generally accepted that prior knowledge about the environment is fairly stable across time (Beierholm, Quartz, & Shams, 2009; Dror, Willsky, & Adelson, 2004). However, the prior information about the statistical distribution of a given target stimulus may change dramatically in different situations, thus our brain must be able to flexible adapt to such changes. Thus, a mechanism that updates a prior on a trial-by-trial basis seems more reasonable. In a recent study, Taatgen & van Rijn demonstrated that if participants were asked to reproduce different intervals, the memory representation of one interval influenced the other (Taatgen & van Rijn, 2011). Even if only the duration of one interval was changed over trials, but the other was kept unchanged, the changing duration affected the representation of the unchanged interval. The authors suggested that the representation of one interval is not based on a single memory trace, but rather on a pool of recent experiences. Therefore, the model used also considers the built up of prior knowledge (i.e., the built up of a reference memory of the standard duration) as a dynamic process that changes estimations over time, based on previous experience and trials.

So far, most studies have implicitly assumed that the prior knowledge about the statistical distribution of a standard duration is acquired on a trial-by-trial basis (Acerbi et al., 2012; Jazayeri & Shadlen, 2010; Taatgen & van Rijn, 2011). However, it is generally assumed that in the same condition the prior for the first trial is the same as the prior for the last trial. Given that the prior must be formed through trial-wise acquisition, such a constant prior assumption will inevitably discard the dynamic nature of the prior. In this study, we used another approach, namely an adaptation-test approach. We first let participants explicitly adapt to a given prior of a standard duration during the adaptation phase in a sensorimotor duration reproduction task. We then investigated the dynamic influence of prior knowledge on auditory duration reproduction in the test phase. The adaptation-test paradigm allowed us to focus on the questions how manipulations of the feedback, the tone loudness and a delay would affect the prior representation, and subsequently how the prior influences the sensorimotor integration in the auditory reproduction. To investigate the second question, we introduced a temporal discrepancy during the auditory reproduction (i.e., by inserting a delay between the motor onset and the auditory tone onset) in the test phase.

In the three experiments, we manipulated the formation of the prior in different kind of ways: (1) shifting the correct feedback range; (2) changing the signal-noise ratio (SNR) on the reproduced auditory signal; (3) varying the onset of the reproduced auditory signal. In Experiment 1, we compared the duration reproduction with a correct feedback with a shifted feedback. In the shifted feedback condition, participant's reproduction was only rewarded as 'correct' when participants produced a duration, 100 ms less than the standard duration. We expected the prior representation to be shifted about 100 ms leftward, leading to shorter reproduced durations in the shifted feedback condition compared to the baseline. In Experiment 2, the signal-to-noise ratio (SNR) of the reproduced tone was manipulated. The idea here was that when the reliability of the reproduced auditory signal is changed, the sensorimotor integration in the auditory reproduction should also change. In addition, the perceived duration of the auditory signal of a low tone should be shortened compared to a loud tone (duration estimation is dependent on intensity, see for example Eagleman, 2008; Matthews, Stewart, & Wearden, 2011; Xuan, Zhang, He, & Chen, 2007). Therefore, we expected longer reproduced durations for the high SNR condition compared to the low SNR condition in the test phase. In Experiment 3, the onset of the reproduced auditory tone was manipulated. We compared synchronous-onset adaptation with randomized tone-onset adaptation. Here, we expected participants to trust the auditory signal after randomized tone-onset adaptation less, leading to less influence of the auditory delay, introduced during the test phase compared to the influence of delay after synchronous-onset adaptation.

The same general adaptation-test phase set up is used in all experiments, so that each experiment consisted of two phases: an adaptation and a test phase. The task was similar in both phases (see Figure 1): Participants had to press a button to produce a tone of the same duration as the immediately before presented auditory standard tone. During the adaptation phase participants always received a feedback after each trial, informing participants whether their produced duration was correct, too short or too long. In the test phase no feedback was given, which allowed us to investigate how the prior representation might influence reproduction without feedback and to observe the dynamic natural recover from the adapted prior. Second, as mentioned before, we introduced a random delay manipulation during the test phase; the onset of the reproduced auditory signal was delayed in respect to the motor onset. This delay manipulation allowed us to investigate changes in the associated motor and auditory weights. It has been shown that auditory duration reproduction can be described by the weighted sensorimotor integration of a motor and an auditory duration estimate (Shi, Ganzenmüller, & Müller, 2013). By introducing a delay between motor and reproduced tone onset, we could infer the actual weights of the auditory estimate in the reproduction from the amount of influence of the delay on the reproduction (see Supplementary Material).

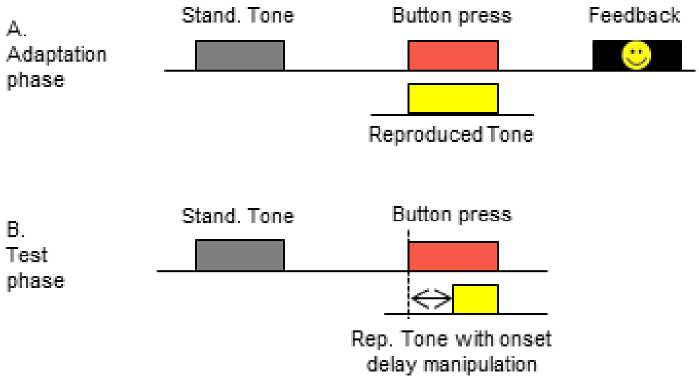

Figure 1. Schematic illustration of the general experimental design. A standard duration reproduction paradigm, with manipulation of feedback stimulus properties and delays during reproduction was used. An auditory standard tone is presented first. Participants reproduce the standard by pressing a button. Another auditory tone is fed back to participants based on the action. During the adaptation phase (A) participants receive a feedback in each trial after button release. In the test phase (B), the reproduced tone was onset delayed in respect to the action. No feedback was displayed.

Results

The effects of priors on auditory reproduction

In Experiment 1, we manipulated the range of "correct" feedback during the adaptation phase, so that in the baseline condition reproduction was only rewarded with a smiley if participants pressed the button for 720 to 880ms, while reproduction in the shifted-feedback condition was only rewarded for reproduction times from 620 to 780 ms. Figure 2 depicts the mean reproduced durations and variability of the two test phases for Experiment 1. The general over-reproduction (of about 100 ms) observed after baseline adaptation is consistent with previously reported over-reproduction of auditory intervals (Shi, Ganzenmüller, et al., 2013; Walker & Scott, 1981). A two-way repeated measures ANOVA with adaptation condition and delay as factors revealed that reproduction times were significantly influenced by adaptation, $F(1,11)=47.45$, $p<0.01$, and by delay, $F(2,22)=84.80$, $p<0.01$. Reproduction times in the baseline condition were longer (~90 ms) than compared to the shifted condition. Further, all reproduced durations increased with the three levels of delay (0, 100, 200 ms). We did not observe a significant interaction between adaptation condition and delay (p=.53).

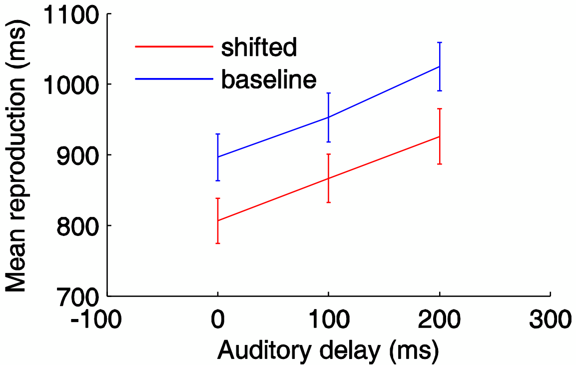

Figure 2. Mean reproduced durations and SDs (with +/- 1 standard error bars) in the test phase of Experiment 1. Duration estimates were significantly more overestimated for the baseline adaptation condition (blue line) and reproduction times increased for both adaptation conditions with delay duration.

In Experiment 2, the signal to noise ratio of the reproduced tone was manipulated (low: 55 dB tone, high: 75 dB tone), while during the test phase the loudness of the reproduced tone was always the same (independent of adaptation condition, 65 dB tone). In Figure 3 the mean reproduced durations and variability of the two test phases are shown. A two-way repeated measures ANOVA with adaptation condition (low SNR vs. high SNR) and delay (5 level of delays) as factors showed that reproduction times were significantly influenced by adaptation, *F*(1,11) = 12.05, *p*<0.01, and by delay, *F*(2,22) = 173.38, *p*<0.01. Compared to the low SNR condition participants pressed the response button longer in the high SNR condition (~ 45 ms). Again no interaction effect was observed (*p*=0.83).

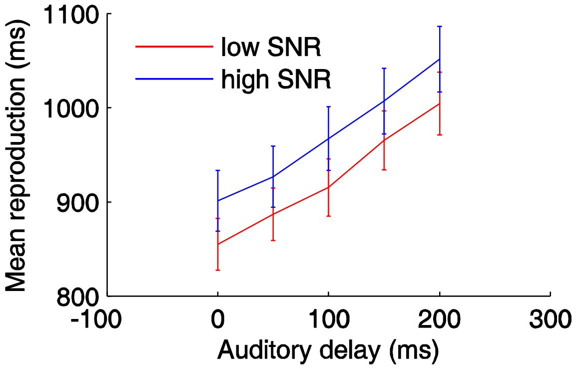

Figure 3. Mean reproduced durations and SDs (with +/- 1 standard error bars) in the test phase of Experiment 2. Duration estimates were significantly more overestimated for the high SNR adaptation condition (blue line) and reproduction times increased for both adaptation conditions with delay duration.

Figure 4 depicts the mean reproduction durations and variability for the two test phases (random tone-onset, synchronous-onset) and for five delay intervals (0-200ms) in Experiment 3. During the adaptation phase the onset of the reproduced tone in respect to the motor onset was manipulated; during the synchronous-onset condition the reproduced tone started immediately with the button press, while during the random tone-onset condition reproduced tone onset was completely independent of the button press. A two-way repeated measures ANOVA with adaptation condition (random tone-onset, synchronous-onset) and delay (0-200ms) as factors revealed that reproduced durations were significant influenced by both factors: the adaptation, *F*(1,11) = 42.02, *p*<0.01; and delay, *F*(2,22) = 49.12, *p*<0.01. After synchronous-onset adaptation, participants significantly overestimated the standard duration and pressed the button almost 90 ms longer than after the random-onset adaptation. Further, with increasing delay, reproduced durations increased in both conditions. Importantly, other than in the previous experiments, we found a significant interaction between adaptation and delay, *F*(2,22) = 4.00, *p*<0.01. After random tone-onset adaptation, the influence of delay was weaker then after synchronous-onset adaptation.

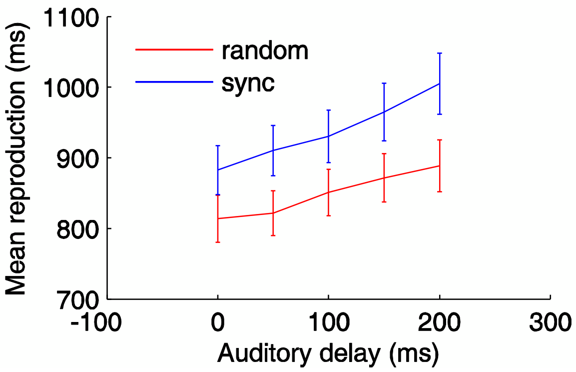

Figure 4. Mean reproduced durations and SDs (with +/- 1 standard error bars) in the test phases of Experiment 3. Duration estimates were significantly more overestimated for the synchronous-onset adaptation condition (blue line) and increased with delay duration. The observed increase after the random-onset adaptation (red line) was less strong than after the synchronous-onset adaptation.

Modeling the dynamic prior effects

That adaptation leads to significant changes of duration reproduction in the test phases, for which all parameters were kept the same, suggests that the internal representation (i.e., prior) of the standard tone was formed differentially due to the adaptation process. We propose here a simple Bayesian model to predict such changes in the prior representation and the auditory weights in the auditory reproduction due to the adaptation manipulation.

Shifts of reproduced duration by priors and sensorimotor duration integration

As shown in a previous study (Shi, Ganzenmüller, et al., 2013), auditory reproduction $\hat{D}_{AR}$ can be regarded as a statistical optimal estimation based on two sources of information: a motor $\hat{D}_R$ and an auditory $\hat{D}_A$ duration estimate. We assume that this reproduced duration $\hat{D}_{AR}$ is compared to the internal representation of the standard duration (i.e., prior) μ_P with a ratio rule (Penney, Gibbon, & Meck, 2008). Note the prior can be manipulated by different types of adaptation. When a delay Δ is introduced for the auditory onset in the auditory reproduction, we would expect to observe a change in $\hat{D}_R$, dependent on the introduced delay (see Supplementary material):

$$\hat{D}_R = \mu_P + w_A * \Delta \qquad (2)$$

where w_A is the auditory weight in the sensorimotor integration of auditory reproduction, which can be estimated from the slope of a linear regression. Thus, measuring the effect of the delay Δ on the reproduced duration will reveal how the auditory weights change due to the adaptation and how the adapted prior μ_P influences reproduction performance in general (for further model explanation see Supplementary Material). A summary of the results based on the above modeling are shown in Table 1.

Table 1. Overview over observed changes in the prior representation μ_P, changes in the auditory weights w_A and dynamic recovery.

	Shift in μ_P	**Auditory weights w_A**	**Dynamic recovery**
Exp1	90 ms	Shifted: $w_A = .60$ Baseline: $w_A = .65$	Faster recovery after shifted-feedback adaptation
Exp2	45 ms	Low SNR: $w_A = .76$ High SNR: $w_A = .77$	Similar recovery for both conditions
Exp3	90 ms	Random: $w_A = .40$ Synchronous: $w_A = .61$	Recovery after synchronous-onset adaptation, but no recovery after random tone-onset adaptation

As we expected, when we shifted the 'correct' feedback 100ms in the adaptation phase of Experiment 1, we observe a 90 ms change in $\hat{D}_R$, after shifting the prior distribution, compared to the reproduced durations after the baseline adaptation. However, the weights of the sensorimotor integration were not changed by the adaptation. We observed two parallel lines when the reproduction durations are regressed against the delay manipulation. A linear regression analysis, comparing actual reproduction times with predicted reproduction times (reproduction durations that were 100% adjusted for delay), failed to show a significant change in the auditory weight w_A for the shifted ($w_A = 0.60$) versus the baseline adaptation condition ($w_A = 0.65$), $t(11)=-0.88$, $p>0.05$. Therefore, the reproduction performance was influenced by the introduced delay in the shifted feedback condition by the same amount as in the baseline condition.

Convergent evidence suggests that subjective duration depends on the contrast intensity (Eagleman, 2008; Matthews et al., 2011; Xuan et al., 2007). Thus a low SNR auditory signal is perceived shorter than a high SNR auditory signal with the same physical length. When the correct feedback was kept the same for both low and high SNR conditions, we expected the prior representation for the standard duration in the low SNR condition to be shortened. This prediction is in agreement with the observed difference in the reproduced duration of about 45 ms. In addition, according to the MLE model, reducing the SNR should reduce the auditory weight (Shi, Ganzenmüller, et al., 2013). However, sensory weights in the test phase were not influenced by the formed weights during the adaptation phase. There was no interaction between adaptation and delay ($p>0.05$), indicating that the introduced delay had the same effect on reproduction behavior after both adaptation conditions. Also a linear regression analysis showed that there was no difference in the auditory weight w_A for the low SNR condition ($w_A = 0.76$) versus the high SNR condition ($w_A = 0.77$), $t(11) = -0.34$, $p>0.05$.

As revealed by a post-hoc analysis, the reproduced tone in the random tone-onset adaptation was on average delayed by about 270 ms. The delay was caused by the fact that participants started pressing the button earlier than expected based on data from pilot experiments. Due to this reason, the prior representation of the standard duration would be shortened for the random tone-onset adaptation condition. This prediction is confirmed by the behavioral results, which showed a decrease in reproduced duration of about 90 ms in the random tone-onset condition compared to the synchronous-onset condition. In Experiment 3, we again expected to observe a change in sensory weights, as the auditory weights should be reduced after random tone-onset adaptation. Other than in Experiment 2, we could confirm a transfer of sensory weights for the random tone-onset condition. The interaction between adaptation condition and delay was found to be significant, $F(2,22) = 4.00$, $p<0.01$. Additional regression analysis revealed that the auditory weight w_A for the random tone-onset condition ($w_A = 0.40$) was smaller than for the synchronous-onset condition ($w_A = 0.61$) and individual weights differed significantly for the two adaptation conditions, $t(11) = -2.40$, $p<0.05$.

Dynamic recovery from the adaptation phase

Based on the literature (Petzschner & Glasauer, 2011; Petzschner, Maier, & Glasauer, 2012; Taatgen & van Rijn, 2011), the adaptation is expected to influence the prior representation of the standard duration, and therefore, removing the feedback should result in a recovery of the adapted prior and the natural bias typically observed during an auditory reproduction task should be observable after some trials. As mentioned before, typically an overestimation has been shown for auditory reproduction (Ganzenmüller, Shi, & Müller, 2012; Shi, Ganzenmüller, et al., 2013; Walker & Scott, 1981). Therefore, we would expect that after removing the feedback, reproduced duration should increase over time.

Trial-wise analysis (see Supplementary material), depicted in Figure 5, revealed that reproduction during the test phase without feedback did change over time, indicating that the adapted prior representation diminished over the time and the typically observed over-reproduction bias is re-established.

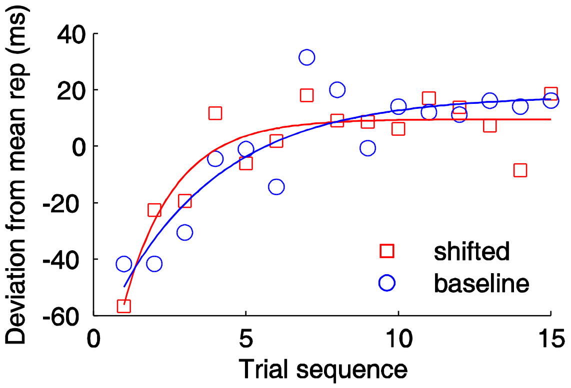

Figure 5. Trial-wise reproduction durations collapsed over all participants. For reproduction after shifted feedback range adaptation (red squares) faster decay of the adaptation can be observed (decay rate = -0.60, asymptotic level = 9.63, $R^2 = 0.83$) compared to reproduction after baseline adapation (blue circles, decay rate = -0.29, asymptotic level = 17.96, $R^2 = 0.79$).

In Experiment 2, we found a diminishing adaptation effect over trials. However, the trial-wise effects did not differ for the two conditions (see Table 2).

Table 2. Model parameters (decay rate a, saturation level C, model fit R^2) describing trial-wise reproduction performance. For the random tone-onset condition in Experiment 3, a linear model was used to describe trial-wise reproduction performance.

Experiments	Condition	Decay rate a (95% CI)	Saturation level C (95% CI)	Model fit R^2

Exp 1	Shifted	-0.60 (-0.98, -0.22)	9.63 (2.70, 16.55)	0.83
	Baseline	-0.29 (-0.52, -0.05)	17.96 (3.24, 32.68)	0.79
Exp 2	Low SNR	-0.16 (-0.27, -0.06)	24.63 (9.22, 40.03)	0.93
	High SNR	-0.21 (-0.43, 0.02)	17.27 (-0.83, 35.38)	0.76
Exp 3	Synchronous	-0.19 (-0.35, -0.03)	15.92 (2.94, 28.91)	0.86
	Random	Linear model: 0.57 (0.13, 1.01)	Linear model: -4.58 (-8.59, -0.57)	0.37

Interestingly, trial-wise analysis for Experiment 3 showed a different data pattern for the random tone-onset condition compared to the synchronous-onset condition (Figure 6). While during the synchronous-onset condition a similar diminishing adaptation effect can be observed as during Experiment 1 and 2, trial-wise analysis showed almost no change in reproduction durations during the random tone-onset condition (almost flat line, close to 0).

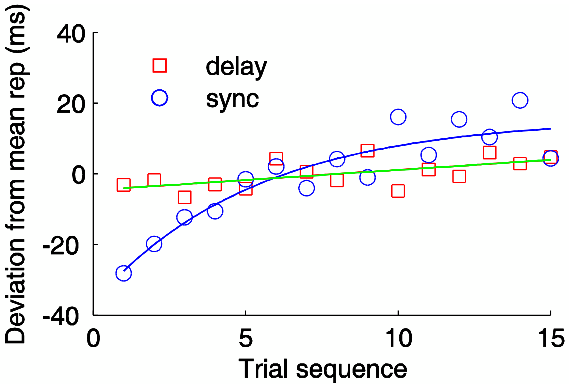

Figure 6. Trial-wise reproduction durations collapsed over all participants. For reproduction after synchronous-onset adaptation (blue circles) a diminishing adaptation effect can be observed (decay rate = -0.19, CI: -0.35, -0.03;

asymptotic level = 15.92, CI: 2.94, 28.91; $R^2 = 0.86$). Reproduction times after random tone-onset adaptation (red squares) did not change over time.

Discussion

In this study, we examined whether different adaptation conditions could affect the buildup of the prior representation of the standard duration in a sensorimotor temporal reproduction task. Therefore, we compared the effect of onset-delay during an auditory reproduction task, after different adaptation conditions. The prior representation of the standard duration was changed if the correct feedback range was shifted, leading to shorter reproduction times, after adaptation during which a "correct" feedback was only given for reproduction times that were 100 ms too short. Due to the fact that the low SNR tone is perceived as shorter than the high SNR tone, also the manipulation of the SNR changed the prior representation, in such a way that in the low SNR condition the prior representation is shortened compared to the high SNR condition, leading to shorter reproduction times after adaptation with a low SNR tone compared to a high SNR tone. Interestingly, auditory weights in the sensorimotor integration of the auditory reproduction were only changed when the reproduced tone onset was manipulated during the adaptation and the test phase. Here, after adaptation to a randomly starting reproduced tone we found lower auditory weights and a shortened prior representation of the standard duration, compared to the synchronous-onset condition. Additionally, we examined the trial-wise dynamic decay of the prior representation adaptation, when no feedback was given. Except for the random tone-onset condition in Experiment 3, we revealed that the adaptation effect always diminished over the course of 15 trials and reach a saturation level (i.e. the typically observed overestimation bias). However, there was no decay after random-tone onset adaptation.

That prior knowledge as additional cue can be formed dynamically by exposure and active learning has been shown previously. Berniker and colleagues (2010) demonstrated in a spatial sensorimotor task that the nervous system can efficiently learn a prior as the statistics of a task change over time. Also in a time reproduction task, participants could learn about the distribution of temporal intervals they encountered, enabling them to build up prior knowledge, which helped them to reduce uncertainty (Acerbi et al., 2012; Jazayeri & Shadlen, 2010). Influenced by this "temporal context", participants' reproduction times are drawn towards the mean of the standard durations. In our study, we demonstrated that reproduction times become consistently biased, because of an explicit experimental manipulation during the adaptation phase. In Experiment 1, participants learned the association between the 800 ms standard tone and an auditory reproduction around 700 ms. Therefore, if participants followed the feedback, the internal representation of the standard duration (μ_P) would be adjusted to 700 ms, leading to shorter reproduction times during the test phase after the shifted adaptation condition compared to the baseline condition. The results confirmed such an adapting process. In Experiment 2, the SNR manipulation had a significant influence on the perceived duration, consistent with previous findings that duration perception is dependent on stimulus contrast intensity (i.e. more intense stimuli are perceived as longer than less intense stimuli, Brown, 1995; Eagleman, 2008; Matthews, Stewart, & Wearden, 2011; Xuan, Zhang, He, & Chen, 2007). Given that the correct feedback range remains the same for both high and low SNR conditions, the perceived duration of the low SNR auditory signal would be shorter than compared to the high SNR auditory signal, leading participants to associate a perceptually shorter reproduced tone with the 800 ms standard tone and therefore to shorten reproduction times in the test phase after the low SNR adaptation compared to the high SNR adaptation. Also in Experiment 3 the prior representation of the standard duration was changed, due to the fact that the reproduced tone during the adaptation phase was delayed by about 270 ms. Participants associated the approximately 530 ms reproduced tone with the 800 ms standard tone, leading to shorter reproduction times in the test phase after random tone-onset adaptation compared to after the synchronous-onset adaptation.

Interestingly, we observed that the – through adaptation – built up prior representation diminishes once the feedback was absent. This finding is in agreement with the idea that prior representations are changed dynamically over trials (Petzschner & Glasauer, 2011). Our hypothesis that the memory representation of the standard duration is changed during the adaptation phase is also in agreement with the idea that recent experiences are pooled together and so influence the memory representation of the standard duration (Taatgen & van Rijn, 2011). Also the memory-mixing account proposes that memory distributions for a particular target duration is a mixture of the present duration estimations and of a history of estimations (Gu & Meck, 2011; Penney et al., 2000). In a recent paper, Shi et al. argued that the memory stage of the internal clock model (Church, 1984) is corresponding with the prior knowledge buildup of the Bayesian framework (Shi, Church, & Meck, 2013). In the classic internal clock model, three time processing stages have been proposed: in the clock stage, consisting of pacemaker, switch and accumulator, a to-be-timed duration is measured; in the memory stage the measured duration is transferred to the reference memory; in the third stage, the decision making stage, a decision is made whether the just measured duration is shorter, longer or equal to the memory representation of the standard duration (Church, 1984; Gibbon, Church, & Meck, 1984). The measurement in each trial is thought to be used to update the reference memory of a standard duration, meaning that prior knowledge of a reference (standard) duration is buildup and changed over trials (Shi et al., 2013). That the memory representation of a standard duration can be affected on a trial-wise basis was also shown by another related study demonstrating that sensitivity of duration judgments is often diminished, if the (trial-wise changing) comparison duration is presented prior to the standard duration, when compared to the reverse order (Dyjas, Bausenhart, & Ulrich, 2012). The framework can be used to explain our data, because a fixed standard-reproduced tone duration association is presented every trial during each adaptation phase. Participants should be able to learn these new associations over time and the internal reference memory should become stable so that the adapted association can even be observed once no feedback is provided anymore.

Many recent studies suggested that through sensorimotor integration by incorporating multiple sources of information, the overall performance can be improved (Bays & Wolpert, 2007; van Beers, Sittig, & Van der Gon, 1996, 1999) - that is, combining sensory and motor information can result in a more precise and less variable estimate than could be obtained from either source alone. There is also evidence for temporal sensorimotor tasks. For example, auditory duration reproduction can be predicted by an optimal linear weighted integration of the motor and the auditory durations (Shi, Ganzenmüller, et al., 2013). In comparison to pure auditory estimation or pure motor reproduction, the bias and variability of auditory reproduction was reduced. Reducing tone loudness, as well as making the onset of the reproduced tone less predictable should lead to a decrease in auditory weights and an increase in motor weights (Bays & Wolpert, 2007; Ernst & Banks, 2002; Shi et al., 2013). Interestingly, even though we expected a change in auditory weights in Experiment 2 and 3, we only observed a transfer of sensory weights from the adaptation phase to the test phase in Experiment 3. Auditory weights are only reduced (compared to motor weights) in the test phase after random-tone onset manipulation.

After all other manipulations, the observed auditory weights were still dominant in comparison to the motor weights and were not different for the compared conditions.

As suggested by sensorimotor integration, assigning the weights is based on the sensory uncertainty (Ernst & Banks, 2002). However, the uncertainty of the stimuli is likely associated with a certain feature. This was partly confirmed by the three experiments. For example, in Experiment 2, the uncertainty was manipulated by auditory contrast intensity (i.e., signal noise ratio, as observed in Shi, Ganzenmüller, et al., 2013), however, this feature was absent in the test phase, as the reproduced tone here was always the same. In contrast to Experiment 2, in Experiment 3 the uncertainty of the auditory signal was manipulated, using random onsets and this onset manipulation partially remained in the test phase (i.e. the delay manipulation). Therefore, it seems possible that changes in the adaptation phase only transfer to other conditions, if the same features are manipulated. That weights are adjusted dynamically on a trial-by-trial basis could be shown in a study where participants could either rely on visual information about the position of a target stimulus or the prior knowledge about where the target has been over the last couple of trials. Participants relied more on the learned prior with variable visual information, but rather relied on the visual information in trials with more reliable sensory input (Berniker et al., 2010). One could argue that a transfer of weights in Experiment 2 is not to be expected as the actual sensory information, i.e. the reproduced tone is different in the test phase compared to the adaptation phase. However, in Experiment 3, participants are still confronted with the “same” unreliable reproduced tone onset as during the adaptation phase, leading to still reduced auditory weights. That auditory weights are only reduced to about 40% could be because the reproduced tone onset is not completely randomized in the test phase, but depended on the button press (always delayed in relation to the button press onset, while completely independent of button press onset during the adaptation phase). Further studies should investigate whether the same feature in adaptation and test enables a transfer of weights in comparison to a feature change.

Note, the slope effect observed in Experiment 3 could not only be explained by a reduction of the auditory weights due to the adaptation. It seems also reasonable that participants rather learned in the random-tone onset condition to segregate auditory and motor information. Additionally to the prior knowledge about the standard duration, participants might have built up prior knowledge about the causal action tone relationship (Berniker & Kording, 2011). That two (independent) priors can be learned at the same time is consistent with previous findings in the literature (Berniker et al., 2010; Nagai, Suzuki, Miyazaki, & Kitazawa, 2012). After the synchronous-onset adaptation, the causal action tone relationship would have been stronger than after the random tone-onset adaptation, leading participants to rely more on the reproduced tone rather than on their motor timing. An additionally learned prior about the action-tone relationship, might also be represented stronger and be less easily/dynamically changed, leading to the observed comparably minor trial-wise diminish of the adaptation effect in the random tone-onset condition of Experiment 3. Research is only beginning to investigate how prior interaction knowledge influences the way humans integrate multisensory or (as in our case) sensorimotor signals. Whether this prior consists of co-occurrence variability knowledge (Ernst & Di Luca, 2011) or of causal inference probability knowledge (Wei & Körding, 2011), predicting the true interaction is quite important for everyday life. For example, wrong causal attribution has been shown in schizophrenic patients, affecting their interpretation of common effects observed in their lives quite dramatically (Vilares & Kording, 2011). With the presented experimental setup, however, we cannot dissociate between a transfer of sensory weights or an additionally buildup knowledge about the common cause of the motor and auditory signal.

Conclusion

In summary, the present study investigated how the buildup of different internal representations of the standard duration, due to different adaptation conditions, influences on auditory reproduction. We observed a shift in the prior representation of approximately 90 ms by shifting the correct feedback range, a change of 45 ms in the reference prior due to a SNR (tone intensity) manipulation, as well as a reduction of about 90 ms in the internal representation due to manipulations of reproduced tone random onsets. These changes in prior representation were interpreted under a simple Bayesian model framework. Neither the correct feedback manipulation, nor the manipulation of the SNR could change the sensorimotor integration of auditory reproduction during the test phase. However, a transfer of reduced auditory weights from the adaptation to the test phase could be observed in the auditory reproduction after random tone-onset adaptation. This finding suggests that the auditory weight in the sensorimotor reproduction is specific tied to the onset uncertainty. Additionally, we revealed that the built up prior representation decays over time, once no feedback is given anymore. Only after the random tone-onset condition in Experiment 3, we did not observe a diminishing adaptation effect. We argue that the reference memory, as proposed by the internal clock model, can be explicitly changed by adaptation as current sensorimotor estimates, based on the provided feedback are integrated with the history of duration estimates, building up a new prior representation of the standard duration.

Methods

Subjects. Thirty-six naive volunteers (30 females, mean age 24.5 years) participated in the three experiments for payment (12 participants in each experiment). All participants had normal hearing; none of them reported any history of somatosensory disorders. All participants gave written informed consent in accordance with the Declaration of Helsinki (2008). All experiments were approved by the Ethics committee of the Psychology Department, LMU Munich.

Stimuli and apparatus. All experiments were conducted in a dimly lit cabin (0.21 cd/m2). The standard duration in all three experiments was 800 ms, generated by a 800 Hz 75 dB tone. The reproduced tones were 600 Hz 65 dB tones in Experiments 1 and 3, and 600 Hz tones, with loudness of 75 dB, 65 dB, and 55 dB for the high, medium and, respectively, low SNR conditions in Experiment 2. Additionally, pink noise (65 dB) was presented during the task. Stimulus presentation and data acquisition were controlled by a National Instrument PXI system, ensuring highly accurate timing (< 1ms). The experimental programs were developed using Matlab and Psychophysics Toolbox (Brainard, 1997). Tones and pink noise were delivered to participants via speakers imbedded in the monitor. The response button was placed on the table in-between the participant and the monitor. Motoric reproduced durations were measured by how long participants pressed the button with their right-hand index finger. In the adaptation phase, after each trial, a feedback was given on the screen, consisting either of the written text “too long”, “too short” or a smiley picture (2x2 degrees) displayed at the center of the monitor.

Procedure. All experiments were split up in an adaptation and a test phase for each condition (2 conditions per experiment) (Figure 1).

Experiment 1

Adaptation phase: Each trial started with a standard tone, defining a standard duration (800 ms). Following the presentation of the standard tone, participants were asked to reproduce the duration as accurately as possible by button press. Pressing the button produced immediately a tone. After button release, participants received a feedback signal on the screen, indicating whether they had pressed the button too short, too long or accurately. Here we manipulated the range of 'accuracy' by feedback: in the baseline condition, participants had to press the response button in the range between 720 to 880 ms in order to receive an "accurate" smiley. However, in the "shifted-feedback" condition, the range of 'accuracy' was shortened 100 ms (620 to 780 ms). Each participant had to do at least 50 trials of adaptation. After those obligatory trials, mean reproduced durations for the last 10 trials were measured. If the mean reproduced duration was within the 'accurate' range, the adaptation phase ended automatically. Otherwise 10 more trials were added until the above stopping criterion was reached.

Test phase: Again each trial was started with a standard duration and participants were asked to reproduce this duration as accurately as possible. However, other than in the adaptation phase, participants received a feedback only during the first five trials of each block (top-up trials). For the following 15 trials no feedback was presented. During the first five trials (top-up trials) the same feedback manipulation was applied as during the previous adaptation phase. For the following 15 trials without feedback, three levels of onset delay (feedback tone started after button press start) were introduced, ranging from 0 ms to 200 ms in 100 ms steps (0, 100, 200 ms). The test session consisted of 8 blocks with 20 trials per blocks. The order of phase-wise feedback manipulations was randomized across participants.

Experiment 2

Adaptation phase: The procedure was the same as in Experiment 1, except that the loudness of the reproduced tone was manipulated. Here, pressing the button produced immediately a high or low tone. Given that pink noise was presented as background noise, we referred to these two conditions as high and low signal-noise ratio (SNR) conditions respectively. A normal 'accuracy' range (i.e., 720 to 880 ms) was used for feedback.

Test phase: Again the procedure was generally the same as in Experiment 1. During the five top-up trials the loudness of the reproduced tone was the same as during the adaptation phase. For the following 15 trials without feedback, a medium tone was used as the reproduced tone (same as in Experiment 1), independent of conditions. Additionally, five levels of onset delay were introduced for these 15 trials, randomly selected from 0, 50, 100, 150, 200 ms. One test session consisted of 13 blocks with 20 trials per blocks. The condition order was randomized across participants.

Experiment 3

Adaptation phase: In Experiment 3 we compared a synchronous-onset condition (with reproduced tones always starting synchronized with the button press) with a random tone-onset condition. In the random tone-onset condition, a tone was started randomly 200 to 1200 ms after the offset of the standard tone, completely independent of the button press onset, and was stopped immediately when the button was released. Post-hoc analysis revealed that on average the tone was started 271 ms (±418 ms) later than the onset of the button press. Otherwise, the procedure was kept the same as in Experiment 1 and 2.

Test phase: We manipulated the onset of the reproduced tone in the first five top-up trials in accordance with the associated adaptation phase. For the following 15 trials without feedback, five levels of onset delay (same as in Experiment 2) were introduced randomly. One test session consisted of 13 blocks with 20 trials per block. The condition order was randomized across participants.

Data analysis. Mean reproduced duration and standard deviation were calculated for each test phase condition and individual participant. Extreme outliers, outside the upper 99% and lower 1% percentile were removed from further analysis. With repeated measures ANOVA we calculated differences in reproduced durations due to adaptation and introduced delay, as well as possible interactions. Linear regression analysis was used to compare the influence of the introduced delay on the adaptation conditions. Additionally, we included a trial-wise analysis to show whether and how fast adaptation effects diminish during the test phase (for more detail on the used model see Supplementary Material).

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References

Acerbi, L., Wolpert, D. M., & Vijayakumar, S. (2012). Internal representations of temporal statistics and feedback calibrate motor-sensory interval timing. *PLoS Computational Biology*, *8*(11), e1002771.

Bays, P. M., & Wolpert, D. M. (2007). Computational principles of sensorimotor control that minimize uncertainty and variability. *The Journal of Physiology*, *578*(2), 387–96.

Beierholm, U. R., Quartz, S. R., & Shams, L. (2009). Bayesian priors are encoded independently from likelihoods in human multisensory perception. *Journal of Vision*, *9*(5), 1–9.

Berniker, M., & Kording, K. P. (2011). Bayesian approaches to sensory integration for motor control. *Wiley Interdisciplinary Reviews: Cognitive Science*, *2*(4), 419–428.

Berniker, M., Voss, M., & Kording, K. P. (2010). Learning priors for Bayesian computations in the nervous system. *PLoS ONE*, *5*(9).

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–6.

Brown, S. W. (1995). Time, change, and motion: the effects of stimulus movement on temporal perception. *Perception & Psychophysics*, *57*(1), 105–16.

Burr, D., Rocca, E. Della, & Morrone, M. C. (2013). Contextual effects in interval-duration judgements in vision, audition and touch. *Experimental Brain Research*, *230*(1), 87–98.

Church, R. M. (1984). Properties of the Internal Clock. *Annals of the New York Academy of Sciences*, 566–582.

Dror, R. O., Willsky, A. S., & Adelson, E. H. (2004). Statistical characterization of real-world illumination. *Journal of Vision*, *4*, 821–837.

Dyjas, O., Bausenhart, K. M., & Ulrich, R. (2012). Trial-by-trial updating of an internal reference in discrimination tasks: Evidence from effects of stimulus order and trial sequence. *Attention, Perception, & Psychophysics*, *74*(8), 1819–1841.

Eagleman, D. M. (2008). Human time perception and its illusions. *Current Opinion in Neurobiology*, *18*(2), 131–6.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433.

Ernst, M. O., & Di Luca, M. (2011). Multisensory Perception : From Integration to Remapping. In M. S. Trommershäuser, K. P. Körding J. ; Landy (Ed.), *Sensory Cue Integration* (pp. 224–250). New York: Oxford University Press.

Ganzenmüller, S., Shi, Z., & Müller, H. J. (2012). Duration reproduction with sensory feedback delay: differential involvement of perception and action time. *Frontiers in Integrative Neuroscience*, *6*(10), 95.

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar Timing in Memory. *Annals of the New York Academy of Sciences*, *423*, 52–77.

Gu, B., & Meck, W. H. (2011). New Perspectives on Vierordt's Law : Memory-Mixing in Ordinal Temporal Comparison Tasks. In A. Vatakis, A. Esposito, M. Giagkou, F. Cummins, & G. Papadelis (Eds.), *Multidisciplinary Aspects of Time and Time Perception* (pp. 67–78). Berlin, Heidelberg: Springer.

Hartcher-O'Brien, J., & Alais, D. (2011). Temporal ventriloquism in a purely temporal context. *Journal of Experimental Psychology: Human Perception and Performance*, *37*(5), 1383–1395.

Jazayeri, M., & Shadlen, M. N. (2010). Temporal context calibrates interval timing. *Nature Neuroscience*, *13*(8), 1020–6.

Jones, L. A., Poliakoff, E., & Wells, J. (2009). Good vibrations: human interval timing in the vibrotactile modality. *Quarterly Journal of Experimental Psychology*, *62*(11), 2171–86.

Lejeune, H., & Wearden, J. H. (2009). Vierordt's The Experimental Study of the Time Sense (1868) and its legacy. *European Journal of Cognitive Psychology*, *21*(6), 941–960.

Matthews, W. J., Stewart, N., & Wearden, J. H. (2011). Stimulus intensity and the perception of duration. *Journal of Experimental Psychology: Human Perception and Performance*, *37*(1), 303–13.

Nagai, Y., Suzuki, M., Miyazaki, M., & Kitazawa, S. (2012). Acquisition of multiple prior distributions in tactile temporal order judgment. *Frontiers in Psychology*, *3*(8), 276.

Penney, T. B., Allan, L. G., Meck, W. H., & Gibbon, J. (1998). Memory mixing in duration bisection. In D. A. Rosenbaum & C. E. Collyer (Eds.), *Timing of behavior: Neural, psychological and computational perspectives* (pp. 165–193). MIT Press.

Penney, T. B., Gibbon, J., & Meck, W. H. (2000). Differential Effects of Auditory and Visual Signals on Clock Speed and Temporal Memory. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(6), 1770.

Penney, T. B., Gibbon, J., & Meck, W. H. (2008). Categorical scaling of duration bisection in pigeons (Columba livia), mice (Mus musculus), and humans (Homo sapiens). *Psychological science*, *19*(11), 1103–9.

Petzschner, F. H., & Glasauer, S. (2011). Iterative Bayesian estimation as an explanation for range and regression effects: a study on human path integration. *The Journal of Neuroscience*, *31*(47), 17220–9.

Petzschner, F. H., Maier, P., & Glasauer, S. (2012). Combining symbolic cues with sensory input and prior experience in an iterative bayesian framework. *Frontiers in Integrative Neuroscience*, *6*(8), 58.

Shi, Z., Church, R. M., & Meck, W. H. (2013). Bayesian optimization of time perception. *Trends in Cognitive Sciences*, (in press).

Shi, Z., Ganzenmüller, S., & Müller, H. J. (2013). Reducing Bias in Auditory Duration Reproduction by Integrating the Reproduced Signal. *PLoS ONE*, *8*(4), e62065.

Taatgen, N., & van Rijn, H. (2011). Traces of times past: representations of temporal intervals in memory. *Memory & Cognition*, *39*(8), 1546–60.

Tomassini, A., Gori, M., Burr, D. C., Sandini, G., & Morrone, M. C. (2012). Active movement restores veridical event-timing after tactile adaptation. *Journal of Neurophysiology*, (July), 2092–2100.

Van Beers, R. J., Sittig, A. C., & Van der Gon, J. J. D. (1996). How humans combine simultaneous proprioceptive and visual position information. *Experimental Brain Research*, *111*(2), 253–61.

Van Beers, R. J., Sittig, A. C., & Van der Gon, J. J. D. (1999). Integration of Proprioceptive and Visual Position-Information: An Experimentally Supported Model. *Journal of Neurophysiology*, *81*, 1355–1364.

Vilares, I., & Kording, K. (2011). Bayesian models: the structure of the world, uncertainty, behavior, and the brain. *Annals of the New York Academy of Sciences*, *1224*(x), 22–39.

Walker, J. T., & Scott, K. J. (1981). Auditory-visual conflicts in the perceived duration of lights, tones and gaps. *Journal of Experimental Psychology: Human Perception and Performance*, *7*(6), 1327–1339.

Wearden, J. H., Edwards, H., Fakhri, M., & Percival, A. (1998). Why"Sounds Are Judged Longer Than Lights": Application of a Model of the Internal Clock in Humans. *The Quarterly Journal of Experimental Psychology*, *51*(2), 97–120.

Wei, K., & Körding, K. P. (2011). Causal Inference in Sensorimotor Learning and Control. In M. S. Trommershäuser, K. P. Körding J. ; Landy (Ed.), *Sensory Cue Integration* (pp. 30–45). New York: Oxford University Press.

Xuan, B., Zhang, D., He, S., & Chen, X. (2007). Larger stimuli are judged to last longer — Journal of Vision. *Journal of Vision*, *7*(10), 2.1–5.

Supplementary Material

We used a Bayesian model to predict changes in the prior representation μ_P of the standard duration, due to training manipulation. As suggested by previous studies (Hartcher-O'Brien & Alais, 2011; Shi, Ganzenmüller, et al., 2013; Tomassini, Gori, Burr, Sandini, & Morrone, 2012), optimal auditory reproduction can be predicted by the linear-weighted integration of a motor $\hat{D}_M$ and an auditory $\hat{D}_A$ duration estimate

$$\hat{D}_{AR} = w_R \hat{D}_R + w_A \hat{D}_A \qquad (1)$$

where, w_R and w_A are correspondent weights of motor and auditory durations. According the Bayesian inference, w_R and w_A are proportional to the reliability (i.e., inverse variance) of their correspondent signals.

During the reproduction, the reproduced duration $\hat{D}_{AR}$ is compared with an internal prior representation of the standard duration μ_P with a ratio rule (Penney et al., 2008)

$$\left| \frac{\hat{D}_{AR} - \mu_P}{\mu_P} \right| < \varepsilon \qquad (2)$$

When a delay Δ is introduced in the auditory feedback onset, combined with Equation 2, Equation 1 will change to

$$\hat{D}_{AR} = w_R \hat{D}_R + w_A \hat{D}_A \qquad (3)$$

$$= (1 - w_A)\hat{D}_R + w_A(\hat{D}_R - \Delta) \qquad (4)$$

$$= \hat{D}_R - w_A \Delta \qquad (5)$$

that is,

$$\hat{D}_R = \hat{D}_{AR} + w_A \Delta \qquad (6)$$

$$= \mu_P + w_A \Delta + \varepsilon \qquad (7)$$

Equation 7 suggests that the weights of the auditory duration estimate in the reproduction can be inferred from the slope when the reproduced duration $\hat{D}_R$ is regressed against the delay time (Δ).

We fixed the standard duration to 800 ms in all experiments, but introduced various manipulations during the reproduction in the training phase. Therefore, we hypothesize that the prior representation of the standard duration during the training phase is:

$$\mu_P = 800 + bias \qquad (8)$$

The 'bias' was introduced by the different manipulations. The following predictions arise for the individual Experiments:

In Experiment 1, based on Equation 7, we expected the mean prior representation to be shifted about 100 ms leftward, leading to shorter reproduction durations in the shifted conditions compared to the true condition.

In Experiment 2, reliability of the reproduced auditory signal is changed and therefore the sensory weights should also be changed (Equation 9)

$$\mu_P = \tilde{w}_R \tilde{D}_R + \tilde{w}_A \tilde{D}_A \qquad (9)$$

where $\tilde{D}_R$ and $\tilde{D}_A$ are the estimated durations in the training phase, and $\tilde{w}_R$ and $\tilde{w}_A$ are their corresponding weights. During the training phase, a feedback was provided, informing participants if their reproduced duration was in the range of 720 – 880 ms, which means that $\tilde{D}_R$ was regulated in this range: $|\widetilde{D_R} - 800| < \varepsilon$.

When the SNR is low, the auditory signal would have high uncertainty. As a result, the weight $\tilde{w}_A$ is reduced according to the Bayesian inference. In addition, the perceived duration of the auditory signal is also shortened compared to the loud SNR condition (see for example Eagleman, 2008; Matthews et al., 2011; Xuan et al., 2007). Given that the correct feedback range remains the same, $\tilde{D}_R$ should be in that range. Thus the internal representation of the standard duration in the low SNR condition should be shortened. In contrast, the prior of the standard duration in the high SNR condition should be lengthened. Therefore, longer reproduction durations are expected for the high SNR condition compared to the low SNR condition based on Equation (7).

During Experiment 3, we expected to observe a change in sensorimotor weights due to the randomized tone-onset training. Further, due to the fact that on average the accompanied auditory signal was delayed by about 270 ms in the random tone-onset condition, the internal prior would be shortened according to Equation (8).

To analyze trial-wise reproduction performance we used an exponential decay model based on the fact that an adaptation effect should vanish after a certain amount of trials. We used a general exponential model $be^{-ax} + c$ to model the dynamic changes of auditory reproduction in the test phase, where a indicates the decay rate of the adaptation effect and c is the asymptotic level that describes the auditory reproduction without any adaptation. Further model fit (R^2) is provided to measure goodness of fit. For the random condition in Experiment 3 a linear model was used to get a better description of the trial-wise data.

Chapter 3: General Discussion

The aim of the present thesis was to investigate the effects of sensory feedback on reproduction timing. First, we looked at the effects of onset- and offset-delayed feedback on a sensorimotor reproduction task. Within and cross-modality effects were addressed here. In a second study, the influence of auditory feedback during a reproduction task was examined explicitly and a reliability-based model was applied to the results. The third presented study addressed the question, whether the prior representation of the standard duration could be explicitly manipulated experimentally in the same sensorimotor reproduction task, again using a Bayesian integration account to model the results.

3.1 Summary of findings

Introduction of an onset-delayed feedback during a reproduction task resulted in an increase in reproduced duration, and this increase could be observed immediately, on the first trial with the onset delay. In contrast, with offset-delayed feedback reproduction times decreased. However, this effect was weaker and could only be found for auditory feedback signals, not with visual feedback stimuli. The offset of the reproduction therefore seems to rely on the action stop signal. The findings suggest that during the sensorimotor reproduction task both perceptual and action time is integrated. However, participants rather rely on the feedback onset and on the action stop signal, in comparison to the action onset and the feedback offset.

Comparing perceptual timing and action timing explicitly showed that pure motor reproduction led to strong overestimations (about 40%), whereas in the comparison task relatively precise estimates were found. When an auditory feedback signal was presented during the reproduction, the overestimation bias was reduced, but was still larger than compared to the biases in the pure auditory comparison task. Reliability-based MLE predictions and observed behavioral results were compared and estimation biases for one and for multiple standard durations, as well as for varying SNRs could be predicted accurately. Further, it could be shown that the model fit (as indicated by correlation coefficient, regression slope without intercept and root-mean-squared errors) of the MLE model was better than fits for either the motor or auditory dominance models. Observed variance could be predicted well by the model; only the observed variance in one condition (short duration condition in Experiment 2) did not reach the optimal level predicted by the reliability-based model.

For the question whether the prior representation of the standard duration can be affected explicitly by different adaptation conditions, we could show significant changes in reproduction durations dependent on the previously presented adaptation condition. If the accuracy feedback range was shortened by 100 ms, we observed reduced reproduction times compared to after adaptation to a true accuracy range. Further, reproduction times after adaptation to a low SNR reproduced tone were shorter, than compared to reproduction times after adaptation to a high SNR reproduced tone. Interestingly, in this experiment, we did not observe a transfer of the weights (lower auditory weights for low SNR condition and higher auditory weights for high SNR condition) from the adaptation to the test phase. However, reduced auditory weights were transferred from the adaptation to the test phase, if participants were adapted with a random reproduced tone onset. Auditory weights were still significantly reduced in the test phase compared to the synchronous tone onset condition. Additional trial-wise analysis could show that the adaptation effect is diminished over time, when no accuracy feedback is given. The only exemption here is after random tone-onset adaptation. Here, reproduced durations in the test phase barely change over time. Overall, the observed results can be predicted by a simple Bayesian model.

3.2 Motor timing

Interestingly, we observed strong overestimations (of about 40%) for reproduction of auditory standard durations without any additional sensory feedback (see Chapter 2.2). Previously, overestimations for auditory durations of about 12% have been reported, however, the researchers did not provide any explanation for their findings (Walker & Scott, 1981). The observed strong bias cannot be explained by an additional motor planning process that might delay motor initiation and termination, as those two delays would cancel each other out in our filled duration reproduction paradigm. However, additional noise, probably due to the motor control and the planning processes involved in the action are present and were measured by the estimation variances. We still observed an overestimation bias for auditory standard durations if an auditory feedback tone is presented during the reproduction, compared to pure auditory comparison, (see Chapter 2.1, 2.2 and 2.3). Therefore, one might conclude that actions need to be carried out a little longer in order to match an auditory stimulus.

Additionally, we could observe that participants strongly depend on the action-stop signal during motor reproduction. The action-stop signal therefore, seems to be highly salient (see Chapter 2.1). This strong trust of the motor stop signal could be due to coincidental activation of medium spiny neurons, which has been observed in the motor cortex when animals are trained to expect an action (Riehle, Grün, Diesmann, & Aertsen, 1997). The stop signal of the reproduction, which might trigger a synchronization of neural activity, would therefore be more reliable than an external sensory feedback. On the other hand, the start signal of motor timing has been shown to be easily influenced by the onset of a sensory feedback signal, presented with some delay (Chapter 2.1). Importantly, not only auditory sensory feedback, which has been shown to be the dominant modality in time perception (Burr et al., 2009; K.-M. Chen & Yeh, 2009; Klink et al., 2011; Shi et al., 2010; Walker & Scott, 1981), but also delayed visual sensory feedback influences the perceived motor onset timing. This reduced trust of the motor onset timing might be due to intentional binding processes, which shift the attention away from the motor start signal towards the sensory signal. Intentional binding has been shown when a short action (button press) is followed by a delayed sensory feedback. This feedback is perceived to be earlier in time, when participants initiated the button press themselves rather than if somebody else pressed the button (Engbert et al., 2008, 2007; Haggard et al., 2002). Importantly, the studies on intentional binding never investigated whether the start or the release of a button is the critical point in time in order to observe intentional binding. Interestingly, motor start signals are not affected by a sensory signal that starts before the motor reproduction (Chapter 2.1), as no causal action-feedback relationship is expected. Overall, a strong influence of auditory feedback, presented during the reproduction, has been shown in all three studies.

3.3 Sensorimotor temporal integration as predicted by the Bayesian framework

Whether different temporal signals are combined in the brain comparably to spatial signals, has been a topic of discussion for the last decade. While theoretically it has been argued for comparable mechanisms in time and spatial perception (Walsh, 2003), findings from studies using Bayesian approaches to model multisensory temporal integration are rather mixed (Burr et al., 2009; Hartcher-O'Brien & Alais, 2011; Shi et al., 2010; Tomassini et al., 2011). Mainly, a pattern of well predicted multisensory estimates, but sub-optimal reduced variability has been reported (Hartcher-O'Brien & Alais, 2011; Shi et al., 2010). Considering the often observed differences between subjective temporal estimations and physical durations (Morrone et al., 2005; Pariyadath & Eagleman, 2008; Shi et al., 2012; Walker & Scott, 1981), we have used estimation biases rather than physical durations to model our sensorimotor integration results. Only considering these estimation biases, we could demonstrate that auditory reproduction bias is well predicted by auditory estimation bias and pure motor reproduction bias (Chapter 2.2). Using different temporal estimation biases, rather than physical discrepancies (which is usually used in a more general Bayesian approach, see for example Ernst & Banks, 2002), it could be shown that results from the two cue (sensorimotor) condition could be quantitatively predicted by a reliability-based integration account. That biased estimates can be integrated in the brain and that the integration of biased estimates can still be beneficial for observers has also been shown in a recent study investigating shape estimations from biased motion and stereo cues (Scarfe & Hibbard, 2011).

Further, as predicted by the MLE model, variability in the sensorimotor estimate has been shown to be reduced (Chapter 2.2). Only for one condition (short duration and high SNR) the sensorimotor variability was not decreased in comparison to the auditory estimation variability. While this pattern is in agreement with previously observed patterns in multisensory temporal integration, as reported above, (Hartcher-O'Brien & Alais, 2011; Shi et al., 2010; Tomassini et al., 2011), one might argue that either this sub-optimal result might be dependent on accuracy limits in the motor system or on the inappropriate assumption of Gaussian noise for temporal estimation tasks (Burr et al., 2009). On the other hand, it seems to be also important to consider that the MLE approach assumes that the prior information is uninformative and can be neglected. This assumption is partly based on previous findings that prior knowledge stays fairly stable within an experiment (Beierholm et al., 2009). Only recent studies have highlighted the importance of prior knowledge in reproduction tasks (Jazayeri & Shadlen, 2010; Petzschner & Glasauer, 2011). We could also demonstrate a strong influence of prior knowledge in sensorimotor reproduction (Chapter 2.3). The prior knowledge was explicitly introduced by specific experimental manipulations during an adaptation phase, and was strong enough to raise the point about the need of considering the influence of prior knowledge during multisensory temporal processing or sensorimotor reproduction. Small and subtle effects of prior knowledge might have led to the sub-optimal behavior found in temporal integration studies to some degree.

3.4 Sensorimotor timing and the internal clock model

An important implication that can be drawn from all studies of this thesis is that all results support the idea of distributed timing mechanisms, which are only gradually accepted in time research recently (Bueti, 2011; Buhusi & Meck, 2005). Convergent evidence has been shown that a single-timer account cannot explain modality-specific pacemaker rates (Droit-Volet, Meck, & Penney, 2007; Penney et al., 2000; Wearden et al., 1998), and separate brain regions are devoted to visual, auditory or action duration processing separately (Bueti, Bahrami, et al., 2008; Bueti, Walsh, et al., 2008; Ghose & Maunsell, 2002). In agreement with the distributed timing account, we could show significant overestimates in a motor reproduction task, compared to a fairly accurate auditory comparison task (Chapter 2.2). Also the fact that an onset-delayed feedback signal influences motor reproduction in a different way than an offset-delayed feedback signal, rather speaks for two separate temporal estimates that might get mixed together in the memory representation and influence each other dependent on the experimental condition (Chapter 2.1). Neurologically, modality-specific timing could be achieved by climbing neural activation within modality specific brain areas (Wittmann, 2013). Theoretically, the idea of modality-specific timing is still in agreement with the internal clock model (Church, 1984; Gibbon et al., 1984), if one includes the assumption of modality dependent pacemakers and maybe even modality dependent accumulators. Given the good predictability of the internal-clock model and the fact that the basic structure of the model is easy to understand, it seems preferable to rather change a well-established model by simply adding the assumption of a modality specific clock stage.

It is also interesting that the Bayesian framework can be used to provide quantitative new perspectives on the internal clock model (Shi, Church, & Meck, 2013). Shi et al. (2013) suggest that the essential components of the Bayesian framework (i.e. the likelihood function, the prior and the loss function for optimization) can be easily mapped onto the three stages of the internal-clock model (i.e. clock stage, memory stage and decision stage). If one considers the prior knowledge to be equivalent to the memory reference that is built up over trials, one would expect "bad" timers to trust more on the prior representation (i.e. the memory representation of previous trials rather than the estimate of the actual trial) and "good" timers more on the actual sensory estimate. In agreement with the Bayesian predictions, it has been shown that good timers, in this case experienced drummers show less strong central tendencies (tendency to perceive "short durations longer, and "long" durations shorter) compared to normal, non-musician participants (Cicchini et al., 2012). On the other hand, bad timers, here Parkinson's disease (PD) patients off their medication show stronger central tendencies compared to PD patients on medication (Malapani et al., 1998). An equivalent pattern of result has been shown in a sensorimotor spatial task, where participants were shown to rely rather on prior knowledge about the target location if the sensory input is more variable and more on the sensory input if the visual information is clear (Körding & Wolpert, 2004). Also our study (Chapter 2.3) describes a process of how current estimates are integrated with the prior knowledge in the memory and how this dynamic updating process affects estimations of further durations. Different effects on the sensorimotor estimates and individual weights could be demonstrated through different training manipulations. The results are in agreement with an internal clock with a modality specific clock stage and a dynamically updated memory stage that can be described in a Bayesian framework.

3.5 Conclusion and Outlook

The focus of this cumulative doctoral thesis is on temporal processing of sensorimotor information. It could be shown that when a sensory feedback delay is introduced during a sensorimotor estimation task, the reproduced duration then heavily relied on the onset of the feedback, as well as the offset of the motor action. Further, it could be shown that auditory reproduction can be described as a weighted integration of motor and perceptual time estimates. The weights of perceptual and motor time depend on the variances of the correspondent estimates. Using reliability-based integration models, crossmodal temporal integration has been shown to follow the MLE model with some modifications. The main modification is that biases are explicitly acknowledged in sensory time estimates and in motor reproduction. Incorporating biases explicitly in the model shows high prediction of MLE for sensorimotor duration reproduction. In addition, it could be demonstrated that the prior representation of the standard duration in sensorimotor reproduction, could be affected by adaptation. These results give first insights on how prior knowledge might influence temporal sensorimotor integration.

The findings of the research work also raised various further research questions. One constrain is that results reported here are mainly based on auditory-motor integration. Visual-motor or tactile-motor integration in the temporal domain might be different, as several researchers have shown less efficient processing for visual-motor and tactile-motor information than for auditory-motor timing (Jäncke et al., 2000; Jantzen et al., 2005; Zatorre et al., 2007). Also the temporal sensitivity in these senses (i.e. visual and tactile) have been shown to be inferior compared to auditory temporal sensitivity (Chen, Shi, & Müller, 2010; Chen & Yeh, 2009; Jones et al., 2009; Klink et al., 2011; Shi et al., 2010). Therefore, it would be a future interesting and important research issue how visual or tactile information is integrated in sensorimotor reproduction and what the differences compared to auditory-motor reproduction are. The sub-optimal reduction of the variability observed in the second study (Chapter 2.2, Experiment 2) for short durations, and also the effect that additional to the change in auditory weights, another independent causal relationship prior could explain the results observed in the third experiment of study 3 (Chapter 2.3), highlights the importance of further investigating the influence of prior knowledge on temporal integration. Last but not least, we would consider the question about what actually happens in the brain during sensorimotor temporal integration, an important one as well. Currently, there is hardly any connections between Bayesian theories and implementations in neural circuits (for one exemption see Vilares, Howard, Fernandes, Gottfried, & Kording, 2012, see also Shi et al., 2013). An important problem here is probably the fact that researchers cannot even agree on how temporal processing is achieved in the brain (Wittmann, 2013). Future experiments using a wide range of technologies including behavioral, electrophysiology, transmagnetic stimulation, and imaging studies will hopefully shine light on these issues.

References

Acerbi, L., Wolpert, D. M., & Vijayakumar, S. (2012). Internal representations of temporal statistics and feedback calibrate motor-sensory interval timing. *PLoS Computational Biology*, *8*(11), e1002771.

Alais, D., & Burr, D. C. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology*, *14*(3), 257–62.

Alais, D., Newell, F. N., & Mamassian, P. (2010). Multisensory processing in review: from physiology to behaviour. *Seeing and Perceiving*, *23*(1), 3–38.

Angrilli, A., Cherubini, P., Pavese, A., & Mantredini, S. (1997). The influence of affective factors on time perception. *Perception & Psychophysics*, *59*(6), 972–82.

Aschersleben, G., Gehrke, J., & Prinz, W. (2001). Tapping with peripheral nerve block. *Experimental Brain Research*, *136*(3), 331–339.

Battaglia, P. W., Jacobs, R. A., & Aslin, R. N. (2003). Bayesian integration of visual and auditory signals for spatial localization. *Journal of the Optical Society of America. A, Optics and image science*, *20*(7), 1391–1397.

Bays, P. M., & Wolpert, D. M. (2007). Computational principles of sensorimotor control that minimize uncertainty and variability. *The Journal of Physiology*, *578*(2), 387–96.

Beierholm, U. R., Quartz, S. R., & Shams, L. (2009). Bayesian priors are encoded independently from likelihoods in human multisensory perception. *Journal of Vision*, *9*(5), 1–9.

Berniker, M., Voss, M., & Kording, K. P. (2010). Learning priors for Bayesian computations in the nervous system. *PLoS ONE*, *5*(9).

Bertelson, P., & Aschersleben, G. (1998). Automatic visual bias of perceived auditory location. *Psychonomic Bulletin & Review*, *5*, 482–489.

Brouwer, A.-M., & Knill, D. C. (2009). Humans use visual and remembered information about object location to plan pointing movements. *Journal of Vision*, *9*(1), 1–19.

Bueti, D. (2011). The Sensory Representation of Time. *Frontiers in Integrative Neuroscience, 5*(8), 1–3.

Bueti, D., Bahrami, B., & Walsh, V. (2008). Sensory and association cortex in time perception. *Journal of Cognitive Neuroscience*, *20*(6), 1054–62.

Bueti, D., & Walsh, V. (2010). Memory for time distinguishes between perception and action. *Perception*, *39*(1), 81–90.

Bueti, D., Walsh, V., Frith, C., & Rees, G. (2008). Different brain circuits underlie motor and perceptual representations of temporal intervals. *Journal of cognitive neuroscience*, *20*(2), 204–14.

Buhusi, C. V, & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience*, *6*(10), 755–65.

Burle, B., & Bonnet, M. (1999). What' s an internal clock for? From temporal information processing to temporal processing of information. *Behavioural Processes*, *45*(1-3), 59–72.

Burr, D. C., Banks, M. S., & Morrone, M. C. (2009). Auditory dominance over vision in the perception of interval duration. *Experimental Brain Research*, *198*(1), 49–57.

Chen, K.-M., & Yeh, S.-L. (2009). Asymmetric cross-modal effects in time perception. *Acta Psychologica*, *130*(3), 225–34.

Chen, L., Shi, Z., & Müller, H. J. (2010). Influences of intra- and crossmodal grouping on visual and tactile Ternus apparent motion. *Brain Research*, *1354*, 152–162.

Chen, Y.-C., & Yeh, S.-L. (2009). Catch the moment: multisensory enhancement of rapid visual events by sound. *Experimental Brain Research*, *198*(2-3), 209–19.

Church, R. M. (1984). Properties of the Internal Clock. *Annals of the New York Academy of Sciences*, 566–582.

Cicchini, G. M., Arrighi, R., Cecchetti, L., Giusti, M., & Burr, D. C. (2012). Optimal encoding of interval timing in expert percussionists. *The Journal of Neuroscience*, *32*(3), 1056–60.

Coull, J. T., Vidal, F., Nazarian, B., & Macar, F. (2004). Functional anatomy of the attentional modulation of time estimation. *Science*, *303*(5663), 1506–8.

Davis, R. (1962). Time uncertainty and the estimation of time-intervals. *Nature*, *195*, 311–312.

Di Luca, M., Machulla, T.-K., & Ernst, M. O. (2009). Recalibration of multisensory simultaneity: cross-modal transfer coincides with a change in perceptual latency. *Journal of Vision*, *9*(12), 7.1–16.

Dixon, N., & Spitz, L. (1980). The detection of auditory visual desynchrony. *Perception*, *9*(6), 719–721.

Droit-Volet, S. (2003). Alerting attention and time perception in children. *Journal of Experimental Child Psychology*, *85*(4), 372–384.

Droit-Volet, S., Meck, W. H., & Penney, T. B. (2007). Sensory modality and time perception in children and adults. *Behavioural Processes*, *74*(2), 244–50.

Droit-Volet, S., & Wearden, J. (2002). Speeding up an internal clock in children ? Effects of visual flicker on subjective duration. *The Quarterly Journal of Experimental Psychology*, *55B*(3), 193–211.

Dror, R. O., Willsky, A. S., & Adelson, E. H. (2004). Statistical characterization of real-world illumination. *Journal of Vision*, *4*, 821–837.

Dyjas, O., Bausenhart, K. M., & Ulrich, R. (2012). Trial-by-trial updating of an internal reference in discrimination tasks: Evidence from effects of stimulus order and trial sequence. *Attention, Perception, & Psychophysics*, *74*(8), 1819–1841.

Eagleman, D. M. (2008). Human time perception and its illusions. *Current Opinion in Neurobiology*, *18*(2), 131–6.

Eagleman, D. M., & Holcombe, A. O. (2002). Causality and the perception of time. *Trends in Cognitive Sciences*, *6*(8), 323–325.

Engbert, K., Wohlschläger, A., & Haggard, P. (2008). Who is causing what? The sense of agency is relational and efferent-triggered. *Cognition*, *107*(2), 693–704.

Engbert, K., Wohlschläger, A., Thomas, R., & Haggard, P. (2007). Agency, subjective time, and other minds. *Journal of Experimental Psychology: Human Perception and Performance*, *33*(6), 1261–8.

Ernst, M O, & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433.

Ernst, M. O., & Bülthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences*, *8*(4), 162–9.

Ernst, M. O., & Di Luca, M. (2011). Multisensory Perception : From Integration to Remapping. In M. S. Trommershäuser, K. P. Körding, J. Landy (Ed.), *Sensory Cue Integration* (pp. 224–250). New York: Oxford University Press.

Fendrich, R., & Corballis, P. M. (2001). The temporal cross-capture of audition and vision. *Perception & Psychophysics*, *63*(4), 719–25.

Franz, A., Ivry, R. B., & Helmuth, L. L. (1996). Reduced Timing Variability in Patients with Unilateral Cerebellar Lesions during Bimanual Movements. *Journal of Cognitive Neuroscience*, *8*(2), 107–118.

Fujisaki, W., Shimojo, S., Kashino, M., & Nishida, S. (2004). Recalibration of audiovisual simultaneity. *Nature Neuroscience*, *7*(7), 773–8.

Gamache, P.-L., & Grondin, S. (2010). Sensory-specific clock components and memory mechanisms: investigation with parallel timing. *The European journal of neuroscience*, *31*(10), 1908–14.

Gerardin, P., Kourtzi, Z., & Mamassian, P. (2010). Prior knowledge of illumination for 3D perception in the human brain. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(37), 16309–14.

Ghose, G. M., & Maunsell, J. H. (2002). Attentional modulation in visual cortex depends on task timing. *Nature*, *419*(6907), 616–20.

Gibbon, J, Malapani, C., Dale, C. L., & Gallistel, C. (1997). Toward a neurobiology of temporal cognition: advances and challenges. *Current Opinion in Neurobiology*, *7*(2), 170–84.

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar Timing in Memory. *Annals of the New York Academy of Sciences*, *423*, 52–77.

Grondin, S. (1993). Duration discrimination of empty and filled intervals marked by auditory and visual signals. *Perception & Psychophysics*, *54*(3), 383–94.

Grondin, S. (2010). Timing and time perception: a review of recent behavioral and neuroscience findings and theoretical directions. *Attention, Perception, & Psychophysics*, *72*(3), 561–82.

Gu, B., & Meck, W. H. (2011). New Perspectives on Vierordt's Law: Memory-Mixing in Ordinal Temporal Comparison Tasks. In A. Vatakis, A. Esposito, M. Giagkou, F. Cummins, & G. Papadelis (Eds.), *Multidisciplinary Aspects of Time and Time Perception* (pp. 67–78). Berlin, Heidelberg: Springer.

Haggard, P., Clark, S., & Kalogeras, J. (2002). Voluntary action and conscious awareness. *Nature Neuroscience*, *5*(4), 382–5.

Hanson, J. V. M., Heron, J., & Whitaker, D. (2008). Recalibration of perceived time across sensory modalities. *Experimental Brain Research*, *185*(2), 347–52.

Harrar, V., & Harris, L. R. (2008). The effect of exposure to asynchronous audio, visual, and tactile stimulus combinations on the perception of simultaneity. *Experimental Brain Research*, *186*(4), 517–24.

Hartcher-O'Brien, J., & Alais, D. (2011). Temporal ventriloquism in a purely temporal context. *Journal of Experimental Psychology: Human Perception and Performance*, *37*(5), 1383–1395.

Helmuth, L. L., & Ivry, R. B. (1996). When two hands are better than one: reduced timing variability during bimanual movements. *Journal of Experimental Psychology: Human Perception and Performance*, *22*(2), 278–93.

Heron, J., Hanson, J. V. M., & Whitaker, D. (2009). Effect before cause: supramodal recalibration of sensorimotor timing. *PLoS ONE*, *4*(11), e7681.

Hillis, J. M., Ernst, M. O., Banks, M. S., & Landy, M. S. (2002). Combining sensory information: mandatory fusion within, but not between, senses. *Science*, *298*(5598), 1627–30.

Hinton, S. C., & Meck, W. H. (2004). Frontal-striatal circuitry activated by human peak-interval timing in the supra-seconds range. *Brain Research. Cognitive Brain Research*, *21*(2), 171–82.

Ivry, R. B. (1996). The representation of temporal information in perception and motor control. *Current Opinion in Neurobiology*, *6*(6), 851–7.

Ivry, R. B., & Hazeltine, R. E. (1995). Perception and production of temporal intervals across a range of durations: evidence for a common timing mechanism. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(1), 3–18.

Ivry, R. B., & Keele, S. W. (1989). Timing Functions of The Cerebellum. *Journal of Cognitive Neuroscience*, *1*(2), 136–152.

Ivry, R. B., & Schlerf, J. E. (2008). Dedicated and intrinsic models of time perception. *Trends in Cognitive Sciences*, *12*(7), 273–80.

Ivry, R. B., & Spencer, R. M. C. (2004). The neural representation of time. *Current Opinion in Neurobiology*, *14*(2), 225–32.

Izawa, J., & Shadmehr, R. (2008). On-line processing of uncertain information in visuomotor control. *The Journal of Neuroscience*, *28*(44), 11360–8.

Jacobs, R. A. (1999). Optimal integration of texture and motion cues to depth. *Vision Research*, *39*(21), 3621–9.

Jäncke, L., Loose, R., Lutz, K., Specht, K., & Shah, N. J. (2000). Cortical activations during paced finger-tapping applying visual and auditory pacing stimuli. *Brain Research. Cognitive Brain Research*, *10*(1-2), 51–66.

Jantzen, K. J., Steinberg, F. L., & Kelso, J. A. S. (2005). Functional MRI reveals the existence of modality and coordination-dependent timing networks. *NeuroImage*, *25*(4), 1031–42.

Jazayeri, M., & Shadlen, M. N. (2010). Temporal context calibrates interval timing. *Nature Neuroscience*, *13*(8), 1020–6.

Johnston, A., Arnold, D. H., & Nishida, S. (2006). Spatially localized distortions of event time. *Current Biology*, *16*(5), 472–9.

Jones, L. A., Poliakoff, E., & Wells, J. (2009). Good vibrations: human interval timing in the vibrotactile modality. *Quarterly Journal of Experimental Psychology*, *62*(11), 2171–86.

Kaneko, S., & Murakami, I. (2009). Perceived duration of visual motion increases with speed. *Journal of Vision*, *9*(7), 1–12.

Keele, S. W., Pokorny, R. A., Corcos, D. M., & Ivry, R. (1985). Do perception and motor production share common timing mechanisms: A correlational analysis. *Acta Psychologica*, *60*(2-3), 173–191.

Keetels, M., & Vroomen, J. (2008). Temporal recalibration to tactile-visual asynchronous stimuli. *Neuroscience Letters*, *430*(2), 130–134.

Kennedy, J. S., Buehner, M. J., & Rushton, S. K. (2009). Adaptation to sensory-motor temporal misalignment: instrumental or perceptual learning? *Quarterly Journal of Experimental Psychology*, *62*(3), 453–69.

King, A. J., & Palmer, A. R. (1985). Integration of visual and auditory information in bimodal neurons in the guinea-pig superior colliculus. *Experimental Brain Research*, *60*, 492–500.

Klink, P. C., Montijn, J. S., & van Wezel, R. J. A. (2011). Crossmodal duration perception involves perceptual grouping, temporal ventriloquism, and variable internal clock rates. *Attention, Perception, & Psychophysics*, *73*(1), 219–36.

Knill, D. C., & Saunders, J. A. (2003). Do humans optimally integrate stereo and texture information for judgments of surface slant? *Vision Research*, *43*(24), 2539–2558.

Koekkoek, S. K. E., Hulscher, H. C., Dortland, B. R., Hensbroek, R. A, Elgersma, Y., Ruigrok, T. J. H., & De Zeeuw, C. I. (2003). Cerebellar LTD and learning-dependent timing of conditioned eyelid responses. *Science*, *301*(5640), 1736–9.

Kononowicz, T. W., & van Rijn, H. (2011). Slow potentials in time estimation: the role of temporal accumulation and habituation. *Frontiers in Integrative Neuroscience*, *5*(9), 48.

Körding, K. P., & Wolpert, D. M. (2004). Bayesian integration in sensorimotor learning. *Nature*, *427*(6971), 244–7.

Lebedev, M. A, O’Doherty, J. E., & Nicolelis, M. A L. (2008). Decoding of temporal intervals from cortical ensemble activity. *Journal of neurophysiology*, *99*(1), 166–86.

Lejeune, H., & Wearden, J. H. (2009). Vierordt’s The Experimental Study of the Time Sense (1868) and its legacy. *European Journal of Cognitive Psychology*, *21*(6), 941–960.

Leon, M. I., & Shadlen, M. N. (2003). Representation of time by neurons in the posterior parietal cortex of the macaque. *Neuron*, *38*(2), 317–27.

Levitin, D. J., MacLean, K., Mathews, M., & Chu, L. (2000). The perception of cross-modal simultaneity. *International Journal of Computing and Anticipatory Systems*, 323–329.

Lewis, P. A., & Miall, R. C. (2003). Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging. *Current Opinion in Neurobiology*, *13*(2), 250–255.

Ley, I., Haggard, P., & Yarrow, K. (2009). Optimal integration of auditory and vibrotactile information for judgments of temporal order. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(4), 1005–19.

Malapani, C., Levy, R., Meck, W. H., Deweer, B., Dubois, B., & Gibbon, J. (1998). Coupled Temporal Memories in Parkinson ' s Disease : A Dopamine-Related Dysfunction. *Journal of Cognitive Neuroscience*, *10*(3), 316–331.

Meck, W. H. (1983). Selective adjustment of the speed of internal clock and memory processes. *Journal of Experimental Psychology. Animal Behavior Processes*, *9*(2), 171–201.

Meck, W. H. (1996). Neuropharmacology of timing and time perception. *Brain Research. Cognitive Brain Research*, *3*(3-4), 227–42.

Meck, W. H., & Malapani, C. (2004). Neuroimaging of interval timing. *Brain Research. Cognitive Brain Research*, *21*(2), 133–7.

Meegan, D. V, Aslin, R. N., & Jacobs, R. A. (2000). Motor timing learned without motor training. *Nature Neuroscience*, *3*(9), 860–2.

Mirsky, S. (2002). Einstein's Hot Time. *Scientific American*, *287*, p.102.

Morein-Zamir, S., Soto-Faraco, S., & Kingstone, A. (2003). Auditory capture of vision: examining temporal ventriloquism. *Cognitive Brain Research*, *17*(1), 154–163.

Morrone, M. C., Ross, J., & Burr, D. C. (2005). Saccadic eye movements cause compression of time as well as space. *Nature Neuroscience*, *8*(7), 950–4.

Pariyadath, V., & Eagleman, D. M. (2008). Brief subjective durations contract with repetition. *Journal of Vision*, *8*(16), 11.1–6.

Park, J., Schlag-Rey, M., & Schlag, J. (2003). Voluntary action expands perceived duration of its sensory consequence. *Experimental brain research*, *149*(4), 527–9.

Penney, T. B., Gibbon, J., & Meck, W. H. (2000). Differential Effects of Auditory and Visual Signals on Clock Speed and Temporal Memory. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(6), 1770.

Penton-Voak, I. S., Edwards, H., Percival, a, & Wearden, J. H. (1996). Speeding up an internal clock in humans? Effects of click trains on subjective duration. *Journal of Experimental Psychology. Animal Behavior Processes*, *22*(3), 307–20.

Petzschner, F. H., & Glasauer, S. (2011). Iterative Bayesian estimation as an explanation for range and regression effects: a study on human path integration. *The Journal of Neuroscience*, *31*(47), 17220–9.

Rammsayer, T. H., & Lima, S. D. (1991). Duration discrimination of filled and empty auditory intervals: cognitive and perceptual factors. *Perception & Psychophysics*, *50*(6), 565–74.

Repp, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. *Psychonomic Bulletin & Review*, *12*(6), 969–992.

Riehle, A., Grün, S., Diesmann, M., & Aertsen, A. (1997). Spike Synchronization and Rate Modulation Differentially Involved in Motor Cortical Function. *Science*, *278*(5345), 1950–1953.

Scarfe, P., & Hibbard, P. B. (2011). Statistically optimal integration of biased sensory estimates. *Journal of Vision*, *11*(7), 1–17.

Schubotz, R. I., Friederici, A. D., & von Cramon, D. Y. (2000). Time perception and motor timing: a common cortical and subcortical basis revealed by fMRI. *NeuroImage*, *11*(1), 1–12.

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error Correction, Sensory Prediction, and Adaptation in Motor Control. *Annual Review of Neuroscience*.

Shams, L., Kamitani, Y., & Shimojo, S. (2000). Illusions. What you see is what you hear. *Nature*, *408*(12), 788.

Shi, Z., Chen, L., & Müller, H. J. (2010). Auditory temporal modulation of the visual Ternus effect: the influence of time interval. *Experimental Brain Research*, *203*(4), 723–35.

Shi, Z., Church, R. M., & Meck, W. H. (2013). Bayesian optimization of time perception. *Trends in Cognitive Sciences*, (in press).

Shi, Z., Jia, L., & Müller, H. J. (2012). Modulation of tactile duration judgments by emotional pictures. *Frontiers in Integrative Neuroscience*, *6*, 24.

Shimojo, S., Scheier, C., Nijhawan, R., Shams, L., Kamitani, Y., & Watanabe, K. (2001). Beyond perceptual modality: Auditory effects on visual perception. *Acoustical Science and Technology*, *22*(2), 61–67.

Simen, P., Balci, F., de Souza, L., Cohen, J. D., & Holmes, P. (2011). A model of interval timing by neural integration. *The Journal of Neuroscience*, *31*(25), 9238–53.

Stetson, C., Montague, P. R., & Eagleman, D. M. (2006). Motor-sensory recalibration leads to an illusory reversal of action and sensation. *Neuron*, *51*, 651–659.

Stone, J. V., Hunkin, N. M., Porrill, J., Wood, R., Keeler, V., Beanland, M., … Porter, N. R. (2001). When is now? Perception of simultaneity. *Proceedings Biological sciences / The Royal Society*, *268*(1462), 31–8.

Sugano, Y., Keetels, M., & Vroomen, J. (2010). Adaptation to motor-visual and motor-auditory temporal lags transfer across modalities. *Experimental Brain Research*, *201*(3), 393–9.

Taatgen, N., & van Rijn, H. (2011). Traces of times past: representations of temporal intervals in memory. *Memory & Cognition*, *39*(8), 1546–60.

Takahashi, K., Saiki, J., & Watanabe, K. (2008). Realignment of temporal simultaneity between vision and touch. *NeuroReport*, *19*(3), 319–22.

Tassinari, H., Hudson, T. E., & Landy, M. S. (2006). Combining priors and noisy visual cues in a rapid pointing task. *The Journal of Neuroscience*, *26*(40), 10154–63.

Tomassini, A., Gori, M., Burr, D. C., Sandini, G., & Morrone, M. C. (2011). Perceived duration of Visual and Tactile Stimuli Depends on Perceived Speed. *Frontiers in Integrative Neuroscience*, *5*, 51.

Treisman, M. (1963). Temporal Discrimination and the Indifference Interval: Implications for a Model of the "Internal Clock." *Psychological Monographs: General & Applied*, *77*(13), 1–31.

Van Beers, R. J., Sittig, A. C., & Van der Gon, J. J. D. (1996). How humans combine simultaneous proprioceptive and visual position information. *Experimental Brain Research*, *111*(2), 253–61.

Van Beers, R. J., Sittig, A. C., & Van der Gon, J. J. D. (1998). The precision of proprioceptive position sense. *Experimental Brain Research*, *122*(4), 367–77.

Van Beers, R. J., Sittig, A. C., & Van der Gon, J. J. D. (1999). Integration of Proprioceptive and Visual Position-Information: An Experimentally Supported Model. *Journal of Neurophysiology*, *81*, 1355–1364.

Van Wassenhove, V. (2009). Minding time in an amodal representational space. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences*, *364*(1525), 1815–30.

Van Wassenhove, V., Buonomano, D. V, Shimojo, S., & Shams, L. (2008). Distortions of subjective time perception within and across senses. *PLoS ONE*, *3*(1), e1437.

Vilares, I., Howard, J. D., Fernandes, H. L., Gottfried, J. a, & Kording, K. P. (2012). Differential representations of prior and likelihood uncertainty in the human brain. *Current Biology*, *22*(18), 1641–8.

Vilares, I., & Kording, K. (2011). Bayesian models: the structure of the world, uncertainty, behavior, and the brain. *Annals of the New York Academy of Sciences*, *1224*, 22–39.

Vorberg, D., & Wing, A. M. (1996). Modeling variability and dependence in timing. *Handbook of Perception and Action*, *2*, 181–262.

Vroomen, J., & Keetels, M. (2010). Perception of intersensory synchrony: a tutorial review. *Attention, Perception, & Psychophysics*, *72*(4), 871–84.

Walker, J. T., & Scott, K. J. (1981). Auditory-visual conflicts in the perceived duration of lights, tones and gaps. *Journal of Experimental Psychology: Human Perception and Performance*, *7*(6), 1327–1339.

Walsh, V. (2003). A theory of magnitude: common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, *7*(11), 483–488.

Walter, R., Hoffman, P. L., Church, a C., Flexner, J. B., & Flexner, L. B. (1982). The cyclized C-terminal dipeptide of arginine vasopressin: metabolic stability and antagonism of puromycin-induced amnesia. *Hormones and Behavior*, *16*(2), 234–44.

Wearden, J. H. (2003). Applying the scalar timing model to human time psychology : Progress and challenges. In J. H. Helfrich, Hede, Wearden (Ed.), *Time and mind II: Information processing perspectives* (pp. 21–39). Gottingen, Germany: Hogrefe & Huber Göttingen, Germany.

Wearden, J. H. (2004). Decision processes in models of timing. *Acta Neurobiologiae Experimentalis*, *64*(3), 303–17.

Wearden, J. H., Edwards, H., Fakhri, M., & Percival, A. (1998). Why''Sounds Are Judged Longer Than Lights": Application of a Model of the Internal Clock in Humans. *The Quarterly Journal of Experimental Psychology*, *51*(2), 97–120.

Welch, R. B., & Warren, D. H. (1980). Immediate perceptual response to intersensory discrepancy. *Psychological Bulletin*, *88*(3), 638–667.

Wenke, D., & Haggard, P. (2009). How voluntary actions modulate time perception. *Experimental Brain Research*, *196*(3), 311–8.

Wing, A. M. (1977). Perturbations of auditory feedback delay and the timing of movement. *Journal of Experimental Psychology: Human Perception and Performance*, *3*(2), 175.

Wing, A. M., & Kristofferson, A. B. (1973). Response delays and the timing of discrete motor responses. *Perception & Psychophysics*, *14*(1), 5–12.

Wittmann, M. (2009). The inner experience of time. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *364*(1525), 1955–67.

Wittmann, M. (2013). The inner sense of time: how the brain creates a representation of duration. *Nature Reviews Neuroscience*, *14*(March), 217–223.

Wittmann, M., Simmons, A. N., Aron, J. L., & Paulus, M. P. (2010). Accumulation of neural activity in the posterior insula encodes the passage of time. *Neuropsychologia*, *48*(10), 3110–20.

Yarrow, K., Haggard, P., Heal, R., Brown, P., & Rothwell, J. C. (2001). Illusory perceptions of space and time preserve cross-saccadic perceptual continuity. *Nature*, *414*(6861), 302–5.

Zakay, D., & Block, R. A. (1996). Time, Internal Clocks and Movement. *Advances in Psychology*, *115*, 143–164.

Zatorre, R. J., Chen, J. L., & Penhune, V. B. (2007). When the brain plays music: auditory-motor interactions in music perception and production. *Nature Reviews Neuroscience*, *8*(7), 547–58.

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Shi, Z.*, Ganzenmüller, S.*, & Müller, H.J. (2013). Reducing bias in auditory duration reproduction by integrating the reproduced signal. *PLoS ONE 8*(4):e62065.

Ganzenmüller, S., Shi, Z., Taylor, P.C.J., & Müller, H.J. (in preparation). V5/MT+ TMS affects Ternus apparent motion.

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Jia, L., Shi, Z., Ganzenmüller, S., & Müller, H.J. (in preparation). Benefits of biased audiovisual estimates in duration judgment.

Eidesstattliche Erklärung / Affidavit

Ich versichere hiermit an Eides statt, dass die vorliegende kumulative Dissertation „Effects of Sensory Feedback on Duration Reproduction - A Bayesian Approach to Characterize Sensorimotor Temporal Estimation“ selbstständig angefertigt habe, mich außer der angegebenen keener weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

I hereby confirm that the cumulative dissertation „Effects of Sensory Feedback on Duration Reproduction - A Bayesian Approach to Characterize Sensorimotor Temporal Estimation“ is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

München,

Stephanie Ganzenmüller

Die Beiträge zu den Manuskripten waren wie folgt:

Die Erstellung der Veröffentlichung

> Ganzenmüller, S., Shi, Z., & Müller, H.J. (2012). Duration reproduction with sensory feedback delay: differential involvement of perception and action time. *Frontiers in Integrative Neuroscience, 6,* 1-11.

wurde unter der Supervision von Zhuanghua Shi und Hermann J. Müller durchgeführt; S.G. und Z.S. entwickelten das Forschungsprojekt; S.G. führte die Experimente durch und analysierte die Daten; S.G. und Z.S. diskutierten die Ergebnisse; S.G. und Z.S. schrieben das Paper. H.J.M. überarbeitete und kommentierte das Paper.

Die Erstellung der Veröffentlichung

Shi, Z.*, Ganzenmüller, S.*, & Müller, H.J. (2013). Reducing bias in auditory duration reproduction by integrating the reproduced signal. *PLoS ONE 8*(4):e62065.

wurde unter der Supervision von Zhuanghua Shi und Hermann J. Müller durchgeführt; S.G. und Z.S. entwickelten das Forschungsprojekt; S.G. führte die Experimente durch und analysierte die Ergebnisse; Z.S. modellierte die Daten; S.G. und Z.S. diskutierten die Ergebnisse; S.G. und Z.S. schrieben das Paper. H.J.M. überarbeitete und kommentierte das Paper. Z.S. und S.G. trugen zu gleichen Teile bei der Erstellung dieses Paper bei.

Die Erstellung des Manuskriptes

Ganzenmüller, S.*, Müller, H.J., & Shi, Z.* (in preparation). Adapting the prior representation of the standard duration through feedback, loudness and delay manipulations in a sensorimotor reproduction task.

wurde unter der Supervision von Zhuanghua Shi durchgeführt. S.G. und Z.S. entwickelten das Forschungsprojekt; S.G. führte die Experimente durch und analysierte die Ergebnisse; Z.S. modellierte die Daten; S.G. und Z.S. diskutierten die Ergebnisse; S.G. und Z.S. schrieben das Manuskript. H.J.M. überarbeitete und kommentierte das Manuskript. S.G. und Z.S. trugen zu gleichen Teilen bei der Erstellung des Manuskriptes bei.

Hiermit bestätigen die Mitautoren die von Frau Ganzenmüller angegebenen Beiträge zu den einzelnen Publikationen.

München,

Hermann J. Müller Zhuanghua Shi