# Visuotactile Temporal Recalibration Transfers Across Different Locations

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**Abstract**

Following prolonged exposure to audiovisual asynchrony, an observer's point of subjective simultaneity (PSS) shifts in the direction of the leading modality. It has been debated whether other sensory pairings, such as vision and touch, lead to a similar temporal recalibration, and if so, whether the internal timing mechanism underlying lag visuotactile adaptation is centralised or distributed. To address these questions, we adapted observers to vision- and tactile-leading visuotactile asynchrony on either their left or right hand side in different blocks. In one test condition, participants performed a simultaneity judgment on the adapted side (*unilateral*) and in another they performed a simultaneity judgment on the non-adapted side (*contralateral*). In a third condition, participants adapted concurrently to equal and opposite asynchronies on each side and were tested randomly on either hand (*bilateral opposed*). Results from the first two conditions show that observers recalibrate to visuotactile asynchronies, and that the recalibration transfers to the non-adapted side. These findings suggest a centralised recalibration mechanism not linked to the adapted side and predict no recalibration for the bilateral opposed condition, assuming the adapted effects were equal on each side. This was confirmed in the group of participants that adapted to vision- and tactile-leading asynchrony on the right and left hand side, respectively. However, the other group (vision-leading on the left and tactile-leading on the right) did show a recalibration effect, suggesting a distributed mechanism. We discuss these findings in terms of a hybrid model that assumes the co-existence of a centralised and distributed timing mechanism.

**Keywords**

Multisensory processing, temporal recalibration, adaptation, vision, touch, synchrony judgement

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## 1. Introduction

When observers are exposed to asynchronous audiovisual events for a prolonged period (e.g., a badly dubbed foreign movie), their perception of simultaneity changes in such a way that subsequent asynchronous audiovisual events are perceived as less asynchronous (the delay in the movie becomes less evident). In the experimental analogue, the point of subjective simultaneity (PSS) shifts toward the leading modality following audiovisual lag adaptation (Fujisaki *et al.*, 2004; Van der Burg *et al.*, 2015; Vroomen *et al.*, 2004). Far from existing only in artificial conditions, asynchronous audiovisual signals from a single external event are often encountered in the natural environment, as transmission times for distant auditory events exceed those of the more rapidly transmitted visual component (King and Palmer, 1985). Lag adaptation has therefore been suggested as a mechanism to flexibly compensate for the conditions our sensory systems have evolved in (for a more detailed discussion see, e.g., Sugita and Suzuki, 2003; Van der Burg *et al.*, 2013).

Differential delays in transmission of sensory signals can come from two sources, environmental and neural (Alais *et al.*, 2010). Neural processing times in audition and vision are relatively stable, however neural latencies for tactile signals are more variable and can differ by up to 30 ms between the face and foot (Harrar and Harris, 2005). In bimodal contexts, however, any event that produces a tactile signal must have occurred in peri-personal space and this limits the scope of environmental delays from any visual or auditory signal co-occurring with the tactile event to add further timing variance. As a result, the total temporal variation in sensory signals from environmental and neural sources is limited to a smaller range for audiotactile or visuotactile signals than for audiovisual signals, where the events can occur at large distances and thus contribute a substantial environmental delay. Therefore, if lag adaptation has evolved as a mechanism to compensate for environmental variance, it may not occur for inter-sensory pairings involving tactile signals (Miyazaki *et al.*, 2006). This notion has received support, for instance, from findings by Harrar and Harris (2008), in which only adaptation to audiovisual but *not* visuotactile and audiotactile asynchrony produced a shift in PSS. Similarly, Stetson *et al.* (2006) found that passive exposure to visuotactile asynchrony failed to produce a reliable shift in perceived timing, although shifts were observed after visuomotor adaptation. These findings suggest that recalibration is modality specific and does not operate across all senses in the same manner. However, there is also evidence to the contrary. Hanson *et al.* (2008) showed similar adaptation-induced PSS shifts for all three pairings (i.e., audiovisual, visuotactile and audiotactile) and Keetels and Vroomen (2008) also reported temporal recalibration after visuotactile lag adaptation.

In addition to questions of modality dependence there are also different mechanisms proposed for temporal recalibration. One suggestion is that timing is centralised so that the brain uses the same neural circuitry to determine the timing of auditory, visual or tactile stimuli (Mauk and Buonomano, 2004; see also Eagleman, 2008). This is supported by audiovisual adaptation studies showing recalibration is readily transferred to other stimulus contexts, as PSS shifts are maintained when the adapting and test stimuli, for example, change features (Fujisaki *et al.*, 2004; Navarra *et al.*, 2012).

However, other findings have suggested that instead of a centralised internal 'clock', there may be many distributed and modality-specific timing mechanisms, each of which can be varied independently. One such finding by Takahashi *et al.* (2008) shows that adaptation to visuo-haptic asynchrony is not transferrable from one hand to another, which implies that visuotactile lag adaptation may be particular to one location. In the audiovisual domain, Heron *et al.* (2012), found that adaptation to visual-leading asynchrony (henceforth VA) and auditory-leading asynchrony (AV) in different locations (e.g., left and right side) can occur simultaneously, as reflected in a shift in PSS toward the leading modality on each side.

These conflicting findings may be reconciled within a hybrid model, which assumes the co-existence of both global and local mechanisms that operate in a linked manner (e.g., Sugano *et al.*, 2014). In a recent study by Sugano *et al.* (2014), the authors observed that, during sensorimotor synchronisation (i.e., finger tapping with delayed auditory feedback), participants could adapt to different asynchronies (50 *vs* 150 ms lag) in each hand concurrently, giving rise to divergent recalibration effects, but that participants timing errors in one hand shifted further (towards that of the larger asynchrony presented to the other hand) during concurrent exposure than when the hand was exposed to the same asynchrony in isolation. This implies some crosstalk between the local recalibration mechanisms, and such crosstalk could possibly be mediated by a centralised system.

In view of the above controversy, the present study sought to verify whether observers can adapt to visuotactile asynchrony as they adapt to audiovisual asynchrony and, if so, whether this temporal recalibration process is regulated by a global or local timing mechanism or a combination of both. To establish whether observers adapt to visuotactile asynchrony, we exposed participants to tactile-leading asynchrony (henceforth TV) to one side/hand (e.g., left) and visual-leading asynchrony (VT) to the other side/hand in separate blocks, and probed with a simultaneity judgement (SJ) on the adapted hand to determine whether participants' PSS had shifted following adaptation (*unilateral adaptation* condition). To test the hypothesis of a centralised recalibration mechanism, in a second condition (*contralateral transfer* condition), participants adapted to VT and TV asynchrony in separate blocks but were probed on

the non-adapted side with the same SJ task. If recalibration is regulated by a centralised timing mechanism, adaptation on one side should be transferable to the other side. In a third condition (*bilateral opposed* condition), we exposed participants concurrently to VT and TV asynchrony on opposite sides within the same block. If recalibration to visuotactile asynchrony is local, participants should show a PSS shift in each hand with opposite signs.

## 2. Methods

### 2.1. Participants

Eighteen participants (four male and one author), all right-handed, and between the ages of 19 and 33 years ($M = 22.89$, SD $= 4.25$) took part in the study. All naïve participants received payment ($AU 20 per hour) for their participation.

### 2.2. Stimuli

The stimuli comprised a brief flash from a red LED collocated over a small buzzer and a tactile vibration stimulating the index finger. Both stimuli lasted 100 ms, had a sampling rate of 48 kHz and were delivered *via* a custom-built audio-visuo-tactile apparatus (see Fig. 1). Stimulus presentation was controlled using the Datapixx hardware (VPixx Technologies, Saint-Bruno, QC)
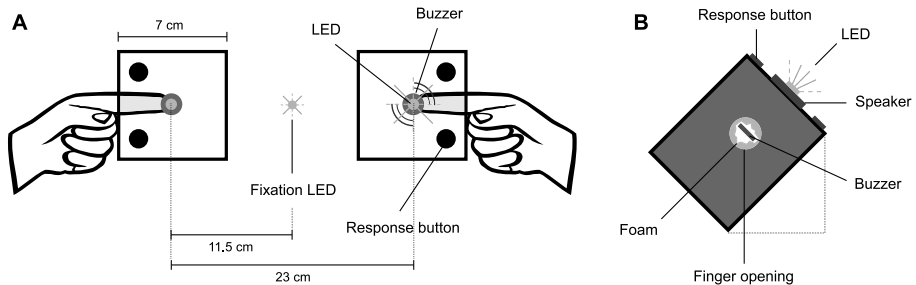


**Figure 1.** Schematic depiction of the audio-visuo-tactile apparatus. (A) The apparatus as seen from the participant's viewpoint. The participant reached inside a foam-filled cube with their index finger where a buzzer stimulated the finger pad. A small speaker was mounted on the cube surface facing the participant and a red LED was positioned over the speaker's centre. All three stimuli were collocated and the distance to the front surface of the cube was 30 cm from the participant's viewing position. A fixation LED was positioned between the cubes equidistant from each one. Two response buttons were located on each cube in the upper and lower outside corners and were easily reached with the thumb. (B) The cube seen from the outer side. The inside of the cube was filled with foam except for a narrow tubular opening allowing the finger to be inserted as far as the tactile buzzer. The apparatus was tilted back 45 degrees so that it squarely faced the participant and the whole apparatus was coloured black.

and a Mac Pro (Apple, Cupertino, CA) running Matlab 8.0 (The MathWorks, Natick, MA) with the Psychophysics Toolbox (Brainard, 1997).

## 2.3. Apparatus

As depicted in Fig. 1A, the audio-visuo-tactile apparatus consisted of two black card-board cubes (measuring $7 \times 7 \times 9.5$ cm in size) displaced horizontally by $\pm 11.5$ cm from midline, with each cube containing collocated auditory, tactile and visual stimuli. The cubes were located 30 cm from the viewing position and had an opening on their outer sides into which participants inserted their index fingers. The inside of the cubes was padded with foam and a small buzzer was embedded in the foam above the pad of the index finger. Each buzzer was collocated with a red LED mounted on top of a small speaker that was inserted into the surface of the cube that faced the participant. Two response buttons were situated beside each speaker on the outer side of the cube so that the thumb could comfortably reach them to respond. As shown in Fig. 1B, the whole apparatus was tilted upwards by approximately 45 degrees to squarely face the participant.

## 2.4. Procedure

The experiment took place in a dimly lit room. To mask the sound of the buzzer, white noise was played at a comfortable volume throughout the experiment. The noise was delivered binaurally *via* Sennheiser headphones (HD380 Pro; Sennheiser GmbH, Hanover, Germany). The participants' head position and viewing distance was kept steady by a chin-rest adjusted to a comfortable height. Participants could take a short break after each block.

## 2.5. Design

As illustrated in Fig. 2, each experimental block began with a long initial adaptation phase, followed by cycles of top–up adaptation and test trials. During the initial adaptation phase, participants were exposed to 50 pairs of asynchronous stimuli. The pairs consisted of the flash and vibration stimuli described above. Within each block, either the visual or the tactile stimulus led the other by a fixed stimulus onset asynchrony (SOA) of 100 ms. Participants were instructed to maintain their gaze on the central fixation LED and attend equally to the cubes. After the 50 pairs of adapting stimuli had been presented, two short beeps from the cube speakers signalled the end of the adaptation phase and indicated that the cycles of top–up and test were about to begin.

Before each test trial, participants received four top–up adaptation stimuli to each side with the same SOA as in the adaptation phase followed by a test trial. The test trial was a single asynchronous presentation with an SOA drawn randomly from a set of nine SOAs ($\pm 480, \pm 320, \pm 160, \pm 80$ and 0 ms), with negative SOAs indicating that the visual stimulus preceded the tactile
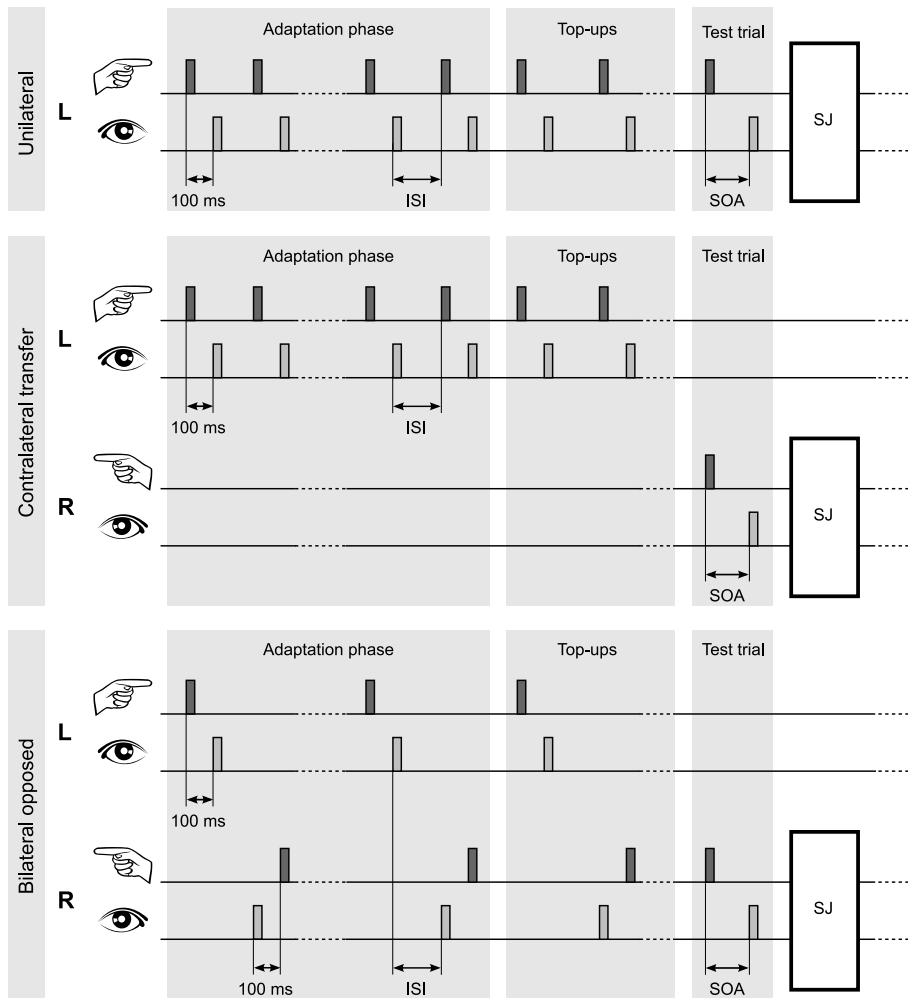
**Figure 2.** Experimental conditions. All blocks began with an extended adaptation phase of 50 stimulus pairs that were asynchronous by 100 ms, followed by cycles of top–up adaptation and test trials. The top–up before each test trial consisted of four repetitions of the adaptation stimuli and the task on the test trial was to judge whether the visual and tactile stimuli occurred synchronously or not. Stimulus onset asynchronies (SOAs) for test trials were drawn randomly from 9 SOAs: ±480, ±320, ±160, ±80, 0 ms, with negative SOAs indicating the visual stimulus occurred first. *Unilateral adaptation*: Participants adapted to visual-leading (VT) or to tactile-leading (TV) asynchrony one side (e.g., left, shown here) and were tested on the same side for six blocks (162 trials in total). Adaptation and test were then carried out on the other side (e.g., right, not shown) for another six blocks. *Contralateral transfer*: Participants adapted to VT or TV asynchrony on one side (e.g., left, shown here) and were tested on the other side for six blocks (e.g., right, shown here). In six additional blocks, adapt/test side was swapped (not shown). *Bilateral opposed*: One half of the participants (i.e., Group 1, shown here) adapted to VT asynchrony on the left side and TV asynchrony on the right side within the same block.

stimulus (TV). Following the test trial, participants made a simultaneity judgment (SJ) by pressing one of the buttons on the cube (see Fig. 1) from which the stimuli were delivered. The upper button indicated 'simultaneous' and the lower 'not simultaneous'. Participants were given 3 s to respond; responses beyond this time limit were not recorded (<1% of all trials). The inter-stimulus interval (ISI) varied randomly between 400 and 500 ms in both the initial adaptation phase and the subsequent top–up/re-test phase.

### 2.6. Groups

In all conditions, there were two groups of participants. For one half of the participants (Group 1), the visual stimulus was always leading in the left hand and the tactile stimulus was always leading in the right hand. That is, Group 1 adapted to the VT asynchrony in the left hand and TV asynchrony in the right hand. For the other half (Group 2), the association between hand and leading stimulus were reversed so that these participants adapted to the TV asynchrony in the left hand and VT asynchrony in the right hand.

### 2.7. Conditions

Participants were tested under three conditions in three separate sessions with at least one-hour break in between sessions. However, most participants completed each session on different days. In the *unilateral adaptation* condition (see Fig. 2), we tested whether they could adapt to visuotactile asynchronies on one and the same side. To this end, they were adapted to 50 presentations of TV asynchrony (i.e., tactile leading by 100 ms) one side and test trials were conducted on the same side for the first half of the test session (six blocks of 27 trials; three trials per SOA). In the second half of the same session (i.e., six additional blocks of 27 trials), participants were adapted to the opposite asynchrony (i.e., VT) on the other side and subsequently tested on that same side. One half of the participants started with TV adaptation and the other half with VT adaptation.

In the *contralateral transfer* condition (see Fig. 2), we probed whether adaptation to VT or TV asynchrony would transfer to the other side. For this purpose, participants were adapted to 50 presentations of TV asynchrony one side and subsequently tested on the other side in six consecutive blocks of 27 trials. Adaptation and test sides were then swapped and we tested for transfer

**Figure 2 (Continued).** The other half (i.e., Group 2, not shown) adapted to VT asynchrony on the right side and TV asynchrony on the left side within the same block. VT and TV adapting stimuli were delivered in alternation and test trials occurred randomly on either side (only a test trial on the right is shown here, however trials also occurred on the left). Participants completed six blocks of 54 trials (27 test trials on each side).

of adaptation to VT asynchrony in six additional blocks. As in the unilateral condition, one half of the participants started with TV adaptation and the other half with VT adaptation.

Finally, to test whether participants could adapt to a TV asynchrony one side and, at the same time, to an equal and opposite VT asynchrony on the other (*bilateral opposed* in Fig. 2), participants were exposed to 50 presentations of TV stimuli on one side and to 50 presentations of VT stimuli on the other (presented in alternation) during the adaptation phase (in total 100 stimulus pairs). They underwent six blocks of 54 test trials (27 trials on each side) in this condition. For all participants, the presentation of the adapting stimuli alternated left then right. All participants completed the three conditions in different random orders. They could take a break of maximum 15 min after each block. In total, each session lasted approximately an hour.

## 2.8. Data Analysis

The proportions of simultaneity responses to the nine test SOAs were computed for each participant, type of adaptation (TV and VT asynchrony), and condition (unilateral, contralateral transfer and bilateral opposed). The results were fitted with a Gaussian distribution with mean, width and height as free parameters. The mean of the best-fitting Gaussian was taken as the point of subjective simultaneity (PSS). In the *unilateral adaptation*, the two response distributions in Group 1 were VT (adaptation and testing on left) and TV (adaptation and testing on right) and in Group 2 were VT (adaptation and testing on right) and TV (adaptation and testing on left). In the *contralateral transfer*, the two response distributions fitted in Group 1 were VT (adaptation on left and testing on right) and TV (adaptation on right and testing on left) and in Group 2 were VT (adaptation on right and testing on left) and TV (adaptation on left and testing on left). In the *bilateral opposed*, the two response distributions fitted in Group 1 were VT (adaptation and testing on left) and TV (adaptation and testing on right) and in Group 2 were VT (adaptation and testing on right) and TV (adaptation and testing on left). However adaption and testing in each location occurred in the same testing block. Three separate repeated-measures ANOVAs were computed for each condition. Each ANOVA was conducted with one within-subject factor, Adaptation (TV and VT asynchrony), and one between-subject factor, Group (Group 1 and 2). The statistical analyses were carried out using R (R Core Team, 2013) in combination with RStudio (RStudio, 2013) and the package *ez* (Lawrence, 2014), which estimates effect sizes using generalized eta-squared $\eta_G^2$ (Bakeman, 2005).
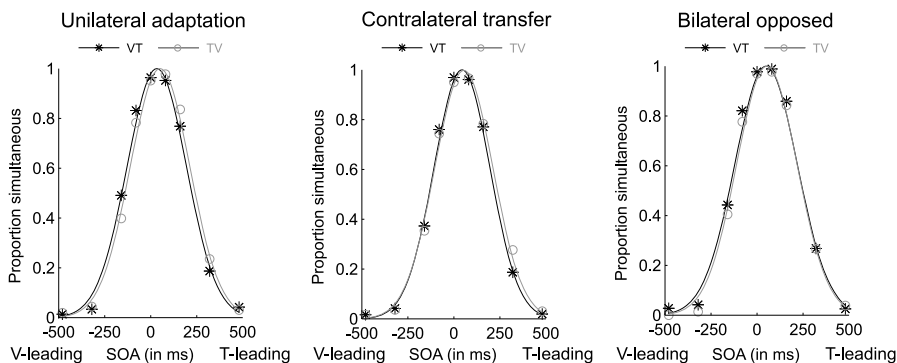
**Figure 3.** Group mean results from the *unilateral adaptation*, *contralateral transfer* and *bilateral opposed* conditions. The proportions of simultaneous responses were fitted with a Gaussian distribution. Negative SOAs indicate that vision was leading (VT) in these test trials. Positive SOAs indicate that touch was leading (TV) in these test trials. The black and grey lines represent the VT and TV adaptation conditions, respectively. These figures are for illustrative purposes only as all analyses were performed on individually fitted data.

## 3. Results

Proportions of simultaneity responses across the nine test SOAs were very well described by Gaussian distributions (mean $R^2 > 0.95$ for all conditions), as illustrated by the group mean data for the unilateral, contralateral transfer and bilateral opposed condition in Fig. 3. The mean, standard deviation and height parameters of the best fitting Gaussians are listed in Table 1 and also shown in Figs 4–6.

### 3.1. Point of Subjective Simultaneity (μ)

The mean PSS for both adaptation orders (i.e., TV and VT) is shown in Fig. 4 for the unilateral condition, in Fig. 5 for the contralateral transfer condition and in Fig. 6 for the bilateral opposed condition, Group 1 ($N = 9$) and Group 2 ($N = 9$) plotted separately and error bars indicating ±1 standard error. As Fig. 4 shows, exposing observers to TV or VT asynchrony during the adaptation phase in one hand caused the PSS to shift towards the leading modality in that same hand (unilateral adaptation). The statistical analysis confirmed that the PSSs in the TV and VT adaptation conditions were significantly different, $F(1, 16) = 17.16$, $p = 0.0008$, $\eta_G^2 = 0.16$. The between-subjects Group factor had no significant main effect, $F(1, 16) = 1.46$, $p = 0.25$, $\eta_G^2 = 0.07$, nor showed any significant interaction with Adaptation, $F(1, 16) = 0.25$, $p = 0.62$, $\eta_G^2 < 0.01$. Results from the contralateral transfer condition (Fig. 5) show that the PSS also shifted towards the leading modality when adaptation and testing were in different hands, suggesting that adaptation to TV or VT asynchrony in one hand can be transferred to the other. Confirming this,

**Table 1.**

Parameters from the best-fitting Gaussians fitted to the proportions of simultaneity responses across the nine test SOAs for all conditions. The point of subjective simultaneity is estimated by the mean ($\mu$) of the best-fitting Gaussian. The bandwidths ($\sigma$) and amplitudes ($a$) of best-fitting Gaussians are also shown. All values are group averages across all participants ($N = 18$). TV and VT refer to the stimulus order during adaptation, either touch leading (TV) or vision leading (VT). Group 1 participants adapted to VT asynchrony in the left hand and TV asynchrony in the right hand, while the adaptation-hand association was reversed for Group 2 participants
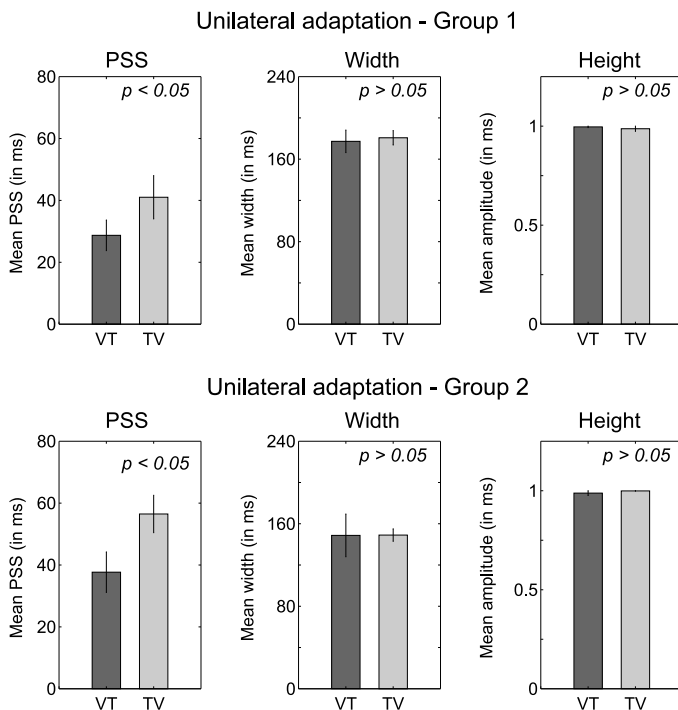
| Condition | Group | VT | | | TV | | |
|---|---|---|---|---|---|---|---|
| | | $\mu$ | $\sigma$ | $a$ | $\mu$ | $\sigma$ | $a$ |
| Unilateral | 1 | 27.47 | 175.03 | 1.00 | 41.81 | 182.7 | 0.99 |
| | 2 | 35.77 | 139.48 | 0.99 | 54.08 | 142.39 | 1.00 |
| Contralateral transfer | 1 | 39.62 | 171.93 | 1.00 | 45.59 | 168.06 | 0.98 |
| | 2 | 41.7 | 129.95 | 0.98 | 53.48 | 142.41 | 1.00 |
| Bilateral opposed | 1 | 41.53 | 196.84 | 1.00 | 51.64 | 175.47 | 1.00 |
| | 2 | 53.96 | 138.91 | 1.00 | 50.59 | 140.99 | 1.00 |

the ANOVA revealed that the PSSs for TV and VT adaptation were significantly different, $F(1, 16) = 5.62$, $p = 0.03$, $\eta_G^2 = 0.05$. As in the unilateral condition, the between-subjects Group factor had no significant main effect, $F(1, 16) = 0.28$, $p = 0.60$, $\eta_G^2 = 0.01$, nor showed any significant interaction with Adaptation, $F(1, 16) = 0.60$, $p = 0.44$, $\eta_G^2 < 0.01$.

The bilateral opposed condition tested whether participants could adapt simultaneously to TV asynchrony in one hand and VT asynchrony in the other. Participants in Group 1 adapted to the VT asynchrony in the left hand and TV asynchrony in the right hand. This was reversed for Group 2 participants, that is, Group 2 adapted to the TV asynchrony in the left hand and VT asynchrony in the right hand. The ANOVA yielded a non-significant main effect of Adaptation, $F(1, 16) = 2.07$, $p = 0.17$, $\eta_G^2 < 0.01$, and a non-significant main effect of Group, $F(1, 16) = 0.32$, $p = 0.58$, $\eta_G^2 = 0.02$, however, the interaction between these two factors was statistically significant, $F(1, 16) = 8.29$, $p = 0.01$, $\eta_G^2 = 0.03$. Inspecting Fig. 6 shows that only Group 1 displayed an effect of adaptation, which a subsequent $F$-test confirmed was significant, $F(1, 8) = 15.54$, $p = 0.004$, $\eta_G^2 = 0.07$. In contrast, Group 2 showed no reliable PSS difference between the TV and VT condition, confirmed by the $F$-test showing no significant difference, $F(1, 8) = 0.74$, $p = 0.41$, $\eta_G^2 < 0.01$.

### 3.2. Width ($\sigma$) and Height ($a$)

The widths and heights for all conditions and adaptation orders were also analysed in repeated-measures ANOVAs with the same factors as the PSS analysis: Adaptation (TV and VT) and Group (Group 1 and 2). For the unilat-

**Figure 4.** Results from the *unilateral adaptation* condition. Group 1 participants first adapted to VT asynchrony on the left and were tested on the left. Subsequently, they adapted to TV asynchrony on the right and were tested on the right. Group 2 participants first adapted to VT asynchrony on the right and were tested on the right. Subsequently, they adapted to TV asynchrony on the left and were tested on the left. The point of subjective simultaneity (PSS) was estimated using the mean of the best-fitting Gaussian to the distribution of each individual's responses for each adaptation session (either VT or TV asynchrony). Also plotted are the Gaussian width and height estimates. Both groups showed a significant shift in PSS. Error bars indicate standard errors ($N = 9$).

eral and contralateral transfer conditions (Figs 4 and 5), the ANOVA yielded no significant main effects or interactions for width or height (all $p$'s $> 0.05$). For the bilateral opposed condition (Fig. 6), no significant main effects or interactions were found in the analysis of height (all $p$'s $> 0.05$), however, the width analysis yielded a significant main effect of Adaptation, $F(1, 16) = 5.87$, $p = 0.03$, $\eta_G^2 = 0.01$, and interaction between Adaptation and Group, $F(1, 16) = 8.67$, $p = 0.01$, $\eta_G^2 = 0.02$. Subsequent $F$-tests revealed that Group 1 displayed a significantly different width between the VT and TV adaptation, $F(1, 9) = 8.99$, $p = 0.02$, $\eta_G^2 = 0.06$, while Group 2 did not, $F(1, 9) = 0.34$, $p = 0.56$, $\eta_G^2 < 0.01$. This can be seen in the width plots in Fig. 4 where for Group 1 the width of the Gaussian for the VT condition
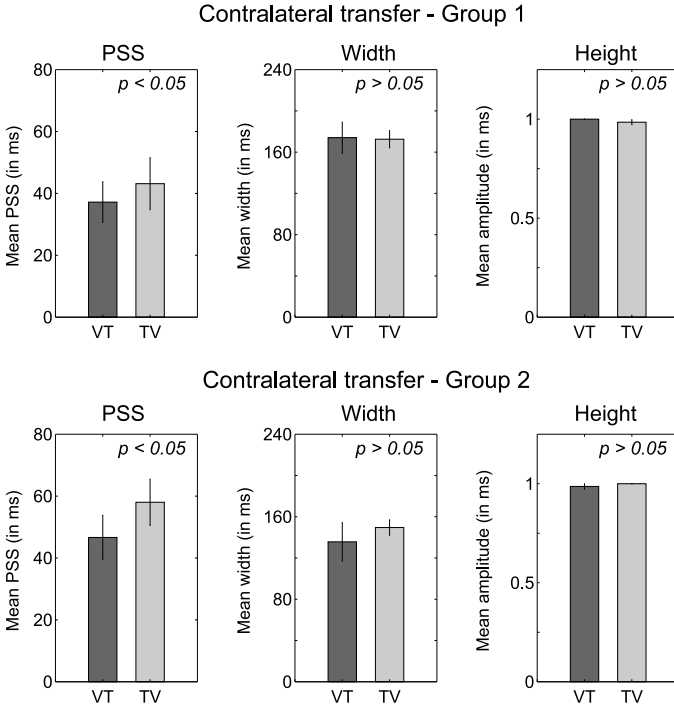
**Figure 5.** Results from the *contralateral transfer* condition. Group 1 participants first adapted to VT asynchrony on the left and were tested on the right. Subsequently, they adapted to TV asynchrony on the right and were tested on the left. Group 2 participants first adapted to VT asynchrony on the right and were tested on the left. Subsequently, they adapted to TV asynchrony on the left and were tested on right. The point of subjective simultaneity (PSS) was estimated using the mean of the best-fitting Gaussian to the distribution of each individual's responses for each adaptation session (either VT or TV asynchrony). Both groups showed a significant shift in PSS. Error bars indicate standard errors ($N = 9$).

is markedly greater than for the TV condition while for Group 2 the order is reversed and the difference is smaller.

## 4. Discussion

In the present study we investigated whether observers recalibrate to visuo-tactile asynchrony and whether any such recalibration is maintained across locations. We also tested whether observers can recalibrate to opposite asynchronies (i.e., VT and TV) at the same time on different sides. The results of the unilateral adaptation condition showed that the PSS shifted after prolonged adaptation to visuotactile asynchrony in both groups (see also Hanson *et al.*, 2008; Keetels and Vroomen, 2008) contradicts the notion that temporal recalibration is unique to AV asynchrony (Miyazaki *et al.*, 2006). Additionally,
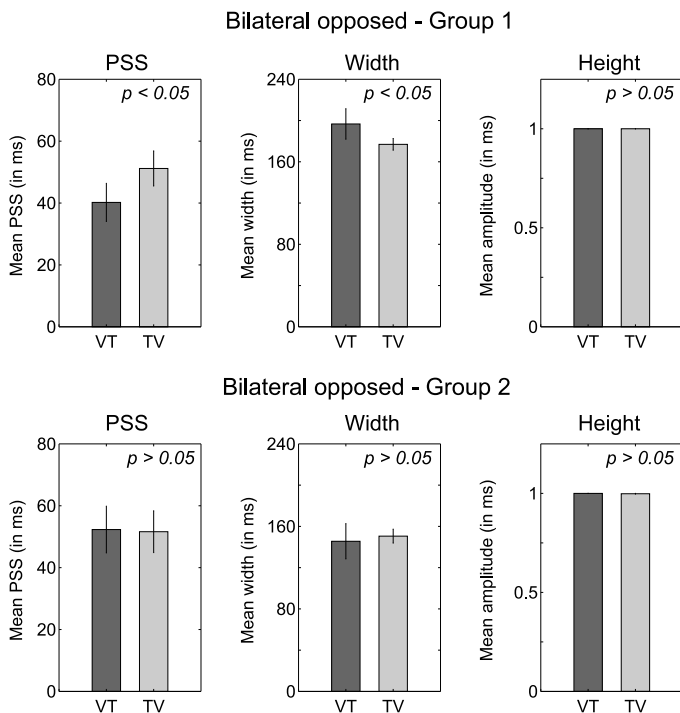
**Figure 6.** Results from the *bilateral opposed* condition. Group 1 participants adapted to VT asynchrony on the left and TV asynchrony on the right in the same session. Group 2 participants adapted to VT asynchrony on the right and TV asynchrony on the left in the same session. Both groups were tested on the left and right during the session. The point of subjective simultaneity (PSS) was estimated using the mean of the best-fitting Gaussian of each individual's responses to each side (which were exposed to either VT or TV asynchrony). Also plotted are the Gaussian width and height estimates. Only Group 1 participants showed a significant shift in PSS. Error bars indicate standard errors ($N = 9$).

we found that adaptation to TV or VT asynchrony on one side (e.g., left hand side) was transferable to the other side (i.e., right hand side) in both groups. This supports a centralised timing mechanism operating over different spatial locations. In our third condition (bilateral opposed), however, the evidence for a central timing mechanism is equivocal. While one group (exposed to TV asynchrony on the left side, VT on the right) failed to show recalibration, consistent with cancellation of equal and opposite PSS shifts, the other group (TV asynchrony on the right side, VT on the left) did show concurrent adaptation to VT and TV asynchronies presented on opposite sides. The latter result points to multiple distributed timing mechanisms that are location-specific. These apparently contradictory findings may be reconciled within a hybrid model that assumes the co-existence of a centralised and distributed recalibration mechanisms (Sugano *et al.*, 2014).

### 4.1. Observers Recalibrate to Visuotactile Asynchronies

While we observed a shift in PSS following exposure to VT and TV asynchronies in the unilateral condition, a similar study by Harrar and Harris (2008) did not. Both studies presented visual and tactile information using a 'multisensory cube' that ensured the collocation of the signals (see Fig. 1), as collocation has been shown to be important in previous recalibration studies with AV stimuli (Di Luca *et al.*, 2009, although see Keetels and Vroomen, 2007, for counter-evidence). One key difference, however, between studies that have successfully demonstrated visuotactile recalibration and those that have not is the time between synchrony judgements and re-exposure to asynchrony. In the present study, as in Hanson and colleagues (2008), four repetitions of top–up adaptation were presented after every test judgment. Keetels and Vroomen (2008) presented ten top–up repetitions after every third judgment. All three studies found significant visuotactile recalibration. In contrast, Harrar and Harris (2008) presented top–up adaptation only after eight judgements. When piloting the present study, we discovered that four top–up repetitions were needed after every judgement to obtain a reliable recalibration effect and that two was not sufficient. This suggests that adaptation to visuotactile asynchrony may decay quickly and require frequent re-adaptation to be maintained (however, see Takahashi *et al.*, 2008, for a different opinion). In addition to re-exposure, prolonged initial exposure is likely to be important and may explain Stetson and colleagues' (2006) failure to find a visuotactile recalibration effect. In their study, participants did not undergo an extended adaptation phase but were immediately required to judge temporal order following every stimulus presentation. A recent study by Van der Burg *et al.* (2015) is consistent with these findings. Building on a new finding showing that audiovisual recalibration can occur very rapidly, after exposure to only a single asynchronous stimulus pair (Van der Burg *et al.*, 2013), Van der Burg *et al.* (2015) compared audiovisual and visuotactile conditions within the same rapid adaptation paradigm. Their results showed that there was no significant visuotactile recalibration when perceivers did not undergo an extended adaptation phase (Van der Burg *et al.*, 2015).

### 4.2. Transfer of Visuotactile Recalibration Across Hands

Stetson and colleagues (2006) were, however, able to show recalibration to visuomotor asynchrony using the same experimental paradigm as their visuotactile paradigm. In the visuomotor condition, participants were cued to press a key triggering a flash. In the visuotactile condition, the key automatically pushed up to touch the participants' finger. Stetson and colleagues' (2006) results suggest that cross-sensory recalibration and sensorimotor recalibration differ in their underlying mechanisms. In particular, visuomotor

recalibration appears to be achieved with less adaptation exposure than visuotactile recalibration. Further support for visuomotor and visuotactile recalibration operating differently comes from the conflict between Takahashi and colleagues' (2008) findings and our own. In Takahashi and colleagues' (2008) study, participants' index finger was stimulated with a haptic object that *deformed* synchronously or asynchronously with a virtual object. While Takahashi and colleagues (2008) failed to find a manual transfer of their visuohaptic recalibration effect, our results in the contralateral transfer condition show that visuotactile recalibration is maintained even if perceivers switch from the adapted to the non-adaptive side. In another sensorimotor study, in which participants tapped with either their hand or foot, triggering an auditory stimulus with constant delay of 0–150 ms, Yarrow *et al.* (2013) observed a transfer of audiomotor recalibration across limbs but argued this effect was largely due to a criterion shift rather than a perceptual one. Taken together, the results from sensorimotor and cross-sensory recalibration suggest that the PSS readily shifts following adaptation to sensorimotor asynchrony but is localised and not transferable across limbs, whereas cross-sensory recalibration appears to be more difficult to achieve, yet once established it is maintained across different locations and stimulus features (Fujisaki *et al.*, 2004; Navarra *et al.*, 2012).

### 4.3. Concurrent Adaptation to the Opposite Visuotactile Asynchronies

The above findings corroborate the notion of a centralised internal timing mechanism underlying cross-sensory adaptation to asynchrony. On this view, adapting observers to VT asynchrony on one side and TV asynchrony on the other side *simultaneously* should cause the recalibration effects to cancel each other out. Our results from the *bilateral opposed* condition only partially support this prediction. In Group 2, which adapted to VT asynchrony on the right hand-side and TV asynchrony on the left, no shift in PSS on either side was observed. Yet, in Group 1, which adapted to TV asynchrony on the right and VT asynchrony on the left, we found separate recalibration effects on each side (see Fig. 6). This latter finding fits with previous studies showing concurrent adaptation to opposite asynchronies (AV and VA) in different locations (Heron *et al.*, 2012) and with concurrent adaptation at the same location to different stimuli (male and female speakers) (Roseboom and Arnold, 2011). Our latter finding, then, is inconsistent with a centralised internal timing mechanism and instead points to multiple local recalibration mechanisms operating in parallel.

### 4.4. Co-existence of a Centralised and Multiple Distributed Timing Mechanisms?

These seemingly conflicting observations may be reconciled within a hybrid model that assumes the co-existence of both a centralised internal 'clock'

and multiple timing mechanisms distributed more peripherally. In Sugano and colleagues' (2014) view, multiple local timing processes may occur simultaneously, but not necessarily independently from each other. The local timing mechanisms may be linked *via* a centralised timing mechanism, in the sense that observers recalibrate to the asynchronies on each side or hand separately but there is 'crosstalk' (i.e., exchange of information) between these local mechanisms. Given our findings, we propose that the interaction between the local mechanisms may not be all encompassing or bi-directional. In fact, the role of the centralised timing system may be to regulate the flow of information between the local processes. Indeed, this would be important in the case that inconsistent or even opposite temporal information arises in separate locations, where a central inhibition of information transfer would prevent confusion. This notion aligns with Sugano and colleagues' (2014) idea that the global mechanism in temporal recalibration corresponds to the 'cognitively controlled' mechanism in interval timing (Buhusi and Meck, 2005; Lewis and Miall, 2003; Repp and Su, 2013). Crucially, this cognitively controlled timing system is thought to be susceptible to attentional modulations, among other factors, and to be interconnected with a second, automatic timing system that may correspond to the local mechanisms in temporal recalibration (Sugano *et al.*, 2014).

In accord with the above view, our findings suggest that when observers are exposed to only one asynchrony at a time (as in the *contralateral transfer* condition), temporal recalibration readily transfers to the other side. However, when observers are faced with two opposite asynchronies at the same time (as in the *bilateral opposed* condition), temporal recalibration is kept local (Group 1). Nevertheless, under certain circumstances, some uni-directional crosstalk between the local processes may occur (Group 2). In the present study, only the right hand that underwent VT adaptation (i.e., the condition in which the time shift occurred) appeared to be receptive to temporal information from the left hand, which results in a cancellation of the local recalibration effect. As all participants in the present study were right-handed, *hand dominance* may be a factor that contributes to the information transfer. However, assuming that the dominant hand receives more attention, it may be attention that is the driving factor and several findings show that selective attention influences temporal recalibration (Heron *et al.*, 2010; Ikumi and Soto-Faraco, 2014).

### 4.5. Increase in Width Following VT Adaptation in the Left Hand

The findings from the *bilateral opposed* condition need to be interpreted with caution. In addition to a PSS shift, participants in Group 1 exhibited a significant difference in width (i.e., the width of the response distribution) that was not observed in Group 2 (see Fig. 6 and Table 1). Similar width differ-

ences have also been reported by Roseboom and Arnold (2011) in a study on feature-specific audiovisual recalibration with male and female speakers following concurrent adaptation to opposite asynchronies. Specifically, a greater increase in the width was found following VA than AV adaptation. In the present study, the width was greater following VT adaptation (on the left hand side) than TV adaptation (on the right hand side) in Group 1. One possible interpretation is that the 'recalibration' effect may not reflect an actual perceptual shift but a shift in criterion at the decision level (Yarrow *et al.*, 2013). Given that all participants in the present study were right-handed, their tactile sensitivity in their left hand (adapted to VT) was likely to be inferior to their right hand (adapted to TV). However, in this case, a similar width effect should have been observed in Group 2 but was not. Another possible interpretation is that the larger width shown by participants in Group 1 reflects greater predisposition to recalibration, as previous studies have shown a positive correlation between width and the recalibration shift in PSS (Van der Burg *et al.*, 2013).

Roseboom *et al.* (2013) successfully adapted observers to opposite audiovisual asynchronies (i.e., AV *vs* VA) simultaneously using both complex (i.e., male and female speakers) and simple stimuli (i.e., gabor patch and auditory pulse), yet found no significant difference in widths between conditions. This shows that PSS shifts following adaptation to opposite feature-specific asynchronies need not produce increases in width. Nevertheless, Roseboom *et al.* (2013) proposed that their results could be explained in terms of a decision-level effect, noting that a reliable shift was only found when participants were explicitly informed beforehand about which visual and auditory signal formed a pair in an experimental condition. In contrast, when naïve participants were merely instructed to attend to the temporal relationship of visual and auditory signals, no reliable PSS shift following feature-specific adaptation occurred. This latter observation is consistent with Heron and colleagues' (2012) results showing that simultaneous adaptation to opposite audiovisual asynchronies led to respective PSS shifts if the AV and VA stimuli were spatially segregated. However, if spatial segregation was replaced by stimulus feature (e.g., pitch and spatial frequency), no recalibration occurred unless participants were explicitly informed about the audiovisual pairing, as in Roseboom *et al.*'s (2013) study. Taken together, Heron *et al.*'s (2012) and Roseboom *et al.*'s (2013) findings suggest that temporal recalibration is a local, low-level process, which may be influenced by top–down factors, such as expectancy and attention. Under which exact conditions these factors exert influence on the local recalibration process (e.g., with less complex or non-ecologically valid stimuli) may be a question of interest for future research.

## 5. Conclusion

To summarise, the present study shows that PSS shifts occur following adaptation to visuotactile asynchrony (*unilateral adaptation* condition), which provides further evidence that temporal recalibration is *not* unique to audiovisual synchrony perception. In addition, we found that visuotactile recalibration is maintained even when perceivers switch from one side/hand to another between adaptation and testing (*contralateral transfer* condition). This points to a centralised internal timing mechanism underlying lag adaptation. However, when adapting observers to opposite visuotactile asynchronies (i.e., VT on left and TV on right, or *vice versa*) at the same time (*bilateral opposed* condition, Group 1), we observed a shift in PSS following VT adaptation on the left side and TV adaptation on the right, suggesting multiple local recalibration processes rather than one centralised timing mechanism. No recalibration effect occurred when observers were exposed to VT and TV asynchronies on the right and left side, respectively (*bilateral opposed* condition, Group 2). These conflicting bilateral results may be reconciled within a hybrid model that assumes the co-existence of a centralised and multiple local recalibration mechanisms (Sugano *et al.*, 2014). However, the PSS shift shown by Group 1 in the *bilateral opposed* condition was accompanied by a significant difference in the width of simultaneity judgments, which may be indicative of a shift at the decision level rather than at a sensory level. The present study was not designed to separate whether temporal recalibration to visuotactile asynchrony reflects a sensory change or a criterion shift and future studies will be needed to address this. Equally important is the general question of whether the mechanisms underlying temporal recalibration across all modalities are better characterised by a hybrid model rather than the 'centralised clock' or 'distributed clocks' dichotomy. Studies investigating the effects of selective attention and expectancy on recalibration across visuotactile, audiovisual, and audiotactile perception will be needed to answer this.

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