



# Adaptation for multisensory relative timing

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Perception of relative timing for signals arising from different sensory modalities depends on the recent history of experienced asynchrony between the signals. Recent findings suggest that the changes in perceived relative timing following asynchrony exposure parallel the perceptual changes caused by adaptation to non-temporal attributes. In both cases, previous sensory stimulation changes discriminability and briefly presented adaptors are sufficient to produce perceptual changes that, functionally, can be consistent with repulsion and recalibration. Furthermore, a new class of after-effects in which reports are biased in the direction of the adaptor also occur for both temporal and non-temporal attributes. Computationally, the effects of previous sensory stimulation on behavior have been assessed using Bayesian and population code models.

## Addresses

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## Introduction

Determining the relative timing between two signals arising from different sensory modalities — whether the signals are simultaneous or the order in which they occur — might be an important perceptual operation to determine whether the two signals should be causally connected and integrated into a single perceptual event [1].

The perception of relative timing for multisensory signals has been studied since the origins of psychology (see [2]), but only about a decade ago was it discovered that relative

timing perception is not fixed, but depends on recently experienced asynchronies [3,4]. In such studies, audiovisual stimuli are repeatedly presented with a fixed asynchrony (e.g. vision leads audition by 235 ms). In subsequent test trials, presentations of a stimulus with a smaller asynchrony (e.g. vision leads audition by 100 ms) are apparently perceived as closer in time and more likely to be reported as having occurred simultaneously than they were before the period of exposure to a fixed asynchrony. (Figure 1a). A corresponding change in subjective simultaneity occurs after repeated exposure to an auditory signal leading a visual signal. The effect of asynchrony exposure on perceived relative timing, lag exposure effects for short, also occurs for other tasks and combinations of signals (Box 1).

Little is known about the mechanisms underlying lag exposure effects (Box 2), but recent studies indicate that lag exposure effects might have properties similar to the classic perceptual after-effects described for visual attributes such as lightness, contrast, color, spatial frequency, orientation, speed or motion direction [5,6]. Consequently, the effect of sensory history on temporal and non-temporal attributes may be described by similar principles.

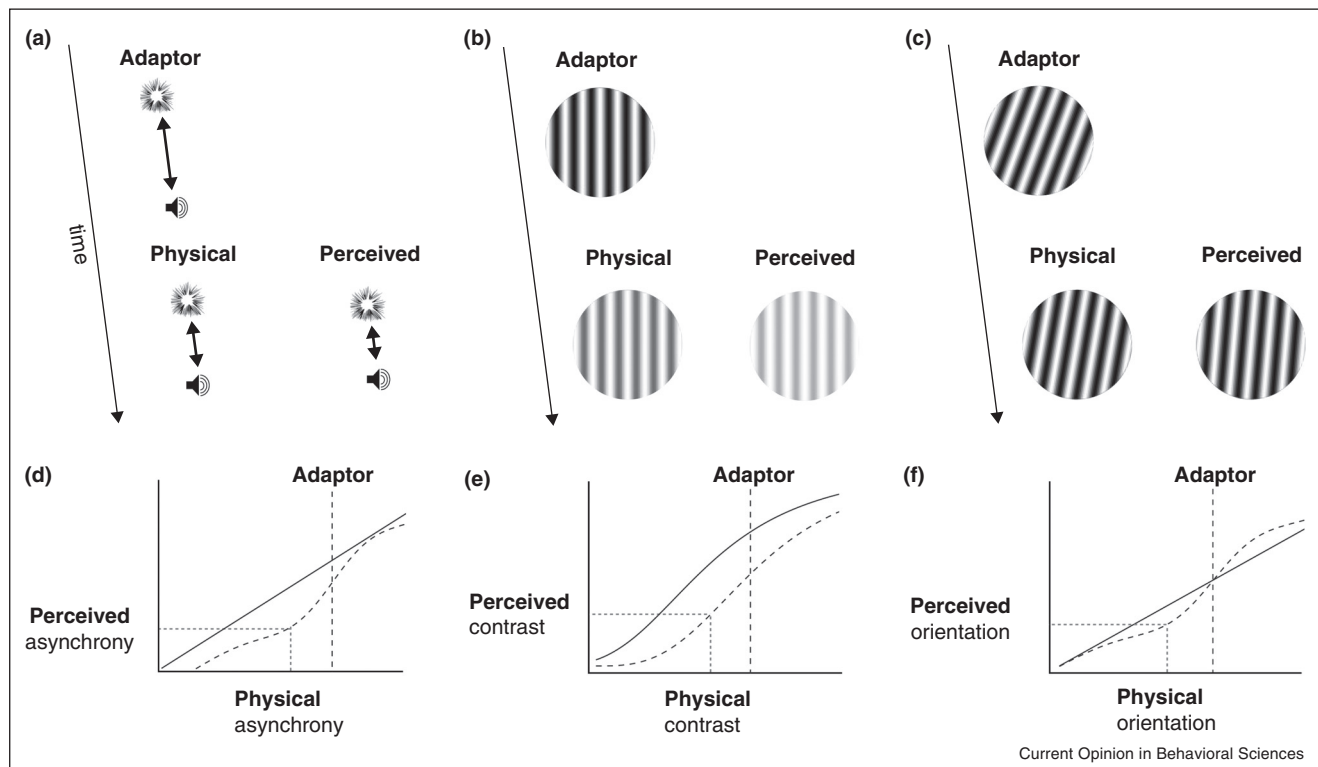
## Lag exposure effects are caused by adaptation

For non-temporal attributes, there is solid evidence that after-effects are indeed perceptual, caused by sensory adaptation, rather than changes in decision processes [7]. First, after-effects have neural correlates in sensory areas [6]. Second, after-effects are behaviorally associated with changes in the discriminability of the attribute [6,8,9]. For relative timing, to our knowledge only one study has examined the neural correlates of lag exposure effects [10], and until recently there was no evidence of changes in discriminability. In the absence of such evidence, it has been suggested that lag exposure effects could be caused entirely by decisional changes [11]. A recent study by Roseboom and colleagues [12\*\*], however, showed that exposure to audiovisual asynchronies changes asynchrony discrimination, supporting the idea that lag exposure effects are perceptual after-effects similar to those reported for non-temporal attributes and that asynchrony exposure causes adaptation.

## Function

As described in the introduction, lag exposure effects reduce the perceived asynchrony for relative timings in which the order of presentation of the signals matches the order of the adaptor (Figure 1a). Phenomenologically, this

Figure 1



**(a)** Lag exposure effects. Adapting to repeated presentations (only one presentation shown) of a visual signal leading an auditory signal reduces the perceived asynchrony between a visual and auditory signal making them to appear more simultaneous. **(b)** Contrast adaptation. Presenting a high contrast grating reduces perceived contrast. **(c)** The tilt after-effect. Adapting to a grating far from vertical makes a slightly tilted grating to appear more vertical. **(d)** Transduction of physical asynchrony, contrast **(e)**, and orientation **(f)** into perceived asynchrony, contrast and orientation. In each case, the continuous black line indicates transduction before adaptation (assuming linear transduction for asynchrony. See [12\*\*] for more realistic transducers for asynchrony) The dotted black lines show transduction following adaptation (assuming recalibration for asynchrony, [12\*\*]), recalibration for contrast, and repulsion for orientation. The blue dotted lines show the physical and the perceived asynchronies, contrasts and orientations illustrated in a, b, and c.

**Box 1** In addition to simultaneity judgments, lag exposure effects have been measured using other subjective tasks such as temporal order judgments [3,4], magnitude estimation [22], multisensory integration [3,17,69] and, more recently, an objective three-alternative forced choice task [12\*\*]. Lag exposure effects occur not only for audiovisual stimuli, but also for audiotactile [60], visuotactile [60,70,71], and even unimodal signal combinations [72–74]. Some studies, however, fail to find lag exposure effects for non-audiovisual stimuli [31,32\*,41,58,75].

Lag exposure effects have also been reported for relative timings defined by a sensory signal and an action [45,68\*,76–82]. Such sensorimotor lag exposure effects may be equivalent to multisensory lag exposure effects as the critical signals for adaptation appear to be the sensory signal produced as a consequence of action — an auditory beep, for example — and the sensory feedback of the committed action — the tactile sensation of having pressed a button [83]. However, sensorimotor lag effects are generally larger in magnitude than other multisensory effects [76] and can exhibit a strong subjective phenomenology of illusory temporal reversal that is absent for other multisensory effects [76,77]. These results suggest that the mechanisms underlying sensorimotor and multisensory lag exposure effects may be distinct.

reduction is similar to the reduction caused by adaptation to non-temporal attributes such as color or contrast [5,6]. For example, adaptation to a high contrast grating causes a subsequently presented lower contrast grating to be perceived as even lower contrast (Figure 1b). These changes in appearance are descriptively consistent with a lateral shift of the transducer function in the direction of the adaptor ([12\*\*]; Figure 1e) and functionally associated with recalibration [5,6]. For non-temporal attributes, recalibration is associated with enhancement of sensitivity around the adaptor [5,6]. By contrast, for relative timing, the emphasis has been placed on how recalibration can reduce perceived asynchrony to facilitate the integration of signals that might have different perceptual latencies despite having a common source [3,4,13,14,30\*\*]. However, while some findings support the idea that perceptual integration depends directly on relative timing perception [1,3,15–17], other findings are at odds with this hypothesis [17–21]. Consequently, whether and how perceptual integration depends on perceived relative timing remains unclear at present.

**Box 2** Transfer manipulations can constrain the stage of processing at which adaptation occurs. For visual orientation, for example, perceptual after-effects occur when the adaptor is presented in one eye and the test in the other, which indicates that at least part of the adaptation is cortical [85]. For the perception of relative timing, recent studies have performed transfer manipulations for sensory modality, stimulus content, and body limb.

#### Transfer across sensory modalities

Adapting to asynchronies for a given modality pair, such as an audio and visual signal, changes not only the perceived timing for audiovisual asynchronies (as described in the main text), but can also change the perceived timing for other modality pairs as long as they include one of the adapting signals, such as an auditory signal ([55]; see also [56,57]; but see [58]). Transfer across modality pairs could be explained if adaptation affects the perceptual latency of one of the signals in the pair [55,59] or a supramodal mechanism that encodes relative timing ([60]; see also [61]).

#### Transfer across content

Several studies have found transfer of adaptation across content: adaptation to a given audiovisual stimulus, such as a male actor speaking, produces lag exposure effects in a different context, such as female actor speaking [3,33,42\*,62,63]. These findings support the existence of a mechanism that processes relative timing independently of stimulus content. However, other studies have found a lack of transfer, that is, concurrent and distinct lag exposure effects for different content [17,64,65], supporting the existence of a mechanism that processes relative timing at the level of multisensory objects. Part of the apparent inconsistency between studies may be attributable to different adaptation paradigms. For example, in some studies that report transfer across content, the adapting phase consists of repeated presentations of a given stimulus combination, such as a visual flash and a high-pitch auditory beep, and the subsequent test phase consist of the presentation of a different combination, such as a visual flash and a low-pitch auditory beep [3,63]. In studies that do not show transfer, during the adapting phase *both* stimulus combinations are presented, alternating between presentation of, for example, a male speaker for which audition leads vision and a female speaker for which vision leads audition [17,64,65]. However, this correspondence between paradigm and transfer does not always hold [33,62], indicating that other factors like task demands [65] and correspondence of temporal characteristics across sensory modalities [17] might also play a role.

#### Transfer across limbs

For sensorimotor lag exposure effects (Box 1), when concurrently adapting different limbs to distinct asynchronies, multiple concurrent lag exposure effects have been observed [66], possibly suggesting adaptation of peripheral motor mechanisms. When only a single limb is adapted and testing occurs in a different limb, some degree of transfer — although qualitatively different [67] — has been found [66,67], suggesting that central mechanisms might be also adapted. Alternatively, rather than being related to adaptation of peripheral versus central motor processes, this apparent difference may instead represent a sensorimotor version of the context-contingent effects for audiovisual discussed above (transfer across content).

The reduction of perceived asynchrony in lag exposure effects is not only consistent with recalibration, but also with a repulsive change in the transducer function near the adaptor [12\*\*,22]. Repulsion is commonly found following adaptation for non-temporal attributes such as spatial frequency, orientation, or motion direction [5,6]. For example, following exposure to a grating tilted

20 degrees from vertical, a test grating tilted 10 degrees will be slightly repulsed from the adaptor, making its orientation appear closer to vertical (Figure 1c,f). This increase in verticality is equivalent to the increase in simultaneity for lag exposure effects. In comparison with the lateral shift, which is consistent with the function of recalibration, repulsion predicts that asynchrony adaptation should cause non-uniform changes in relative timing perception such that perception of values nearby the adaptor is affected more strongly than those further away (Figure 1f) — a prediction that has been recently supported [22]. The changes in discriminability reported by Roseboom and colleagues are also consistent with repulsion, as long as a lateral shift of the transducer is also incorporated ([12\*\*]; Figure 1d). For non-temporal attributes, repulsion, like recalibration, is functionally associated with an enhancement of sensitivity around the adaptor [5,6,23–25]. For relative timing, it is not obvious how the non-uniform changes in appearance associated with repulsion might have functional benefits in terms of integration [22].

#### Rapid adaptation

Perceptual after-effects for non-temporal attributes are traditionally measured by presenting adaptors for a long time — on the order of seconds — before each test presentation [23,24]. However, some studies have also shown that adaptors presented for just tens or hundreds of milliseconds are sufficient to produce after-effects [26–29], a result consistent with the rapid changes in neural response caused by adaptation [6,28]. If the principles governing adaptation are similar for temporal and non-temporal attributes, brief adaptation might also induce perceptual after-effects for relative timing. Consistent with this idea, Van der Burg and colleagues [30\*\*,31,32\*,33] recently reported that a single exposure to audiovisual asynchrony was enough to produce lag exposure effects. At odds with previous studies that used repeated presentations of the adaptor, the lag exposure effects reported by Van der Burg and colleagues show a large asymmetry: the asynchrony reduction is very small when the adaptor consists of an auditory signal presented before a visual signal. This result might indicate that short and long adaptation operate on different mechanisms [30\*\*,32\*].

#### Attractive biases

For non-temporal attributes, a different class of perceptual after-effects have also been reported in which perception of the attribute is attracted toward the previously experienced value of the attribute, that is, biased in the direction opposite to classic after-effects [34–40]. Attractive biases have also been reported for relative timing [41,42\*]. In one study, for example, a series of pairs of tactile stimuli were delivered one to each hand with a distribution of relative timing in which, on average, the left stimulus preceded the right by 80 ms. When exposed

to a such biased distribution, smaller asynchronies, for example left-precedes-right by 50 ms, were apparently perceived as closer to 80 ms [41]. However, it remains to be determined whether the origin of these effects is perceptual as has been shown for non-temporal attributes. Processes pushing the system toward attractive biases and classic negative biases might co-occur; the final sign of the bias would depend on the balance between them [34,37,41,43]. For audiovisual relative timing, for example, it has been proposed that attractive biases are not generally observed because lag exposure effects are stronger [41,42], but can nevertheless be recovered by canceling out lag exposure effects [42].

### Mechanisms

Classic after-effects are often described by simple population codes in which adaptation reduces the gain of the neurons responding to the adaptor, and in which the decoder is unaware that adaptation has taken place [44]. Recalibration (for contrast, e.g.) and repulsion (for orientation, e.g.) effects could be obtained using band-pass and high-pass filters respectively [44]. A simple population code model with band-pass filters has been proposed to explain lag exposure effects in terms of repulsion [22]. A different kind of population code model has been proposed to explain sensorimotor lag exposure effects in terms of recalibration [45]. Roseboom and colleagues (2015), however, found evidence of both repulsion and recalibration. To the best of our knowledge, a population code model that can simultaneously predict both effects has not been developed. For non-temporal attributes, attractive biases have also been described using population codes, but with adaptation increasing rather than decreasing the gain of the neurons responding to the adaptor [37]. Whether attractive biases for relative timing [41,42] are also consistent with this sort of coding has not, to the best of our knowledge, been tested.

After-effects can also be modeled using probabilistic frameworks in which the perception of a given attribute  $s$ , given some measurements  $I$ , is treated as an inference problem that combines probabilistic knowledge of previously acquired information, the prior  $p(s)$ , with current sensory information, the likelihood  $p(I|s)$ , to give the posterior probability distribution  $p(s|I)$  which the observer can use to estimate  $s$  [46,47]. Independently of the attribute considered, the posterior distribution is calculated by multiplying the prior by the likelihood (according to Bayes' rule; [46]). Attractive biases can be described by a shift of the posterior toward the prior. The precise value of the bias depends on the shape of the prior and likelihood [46]. For non-temporal attributes, attractive biases that match the Bayesian prediction have been reported using models in which the prior is centered statically taking into account all trials [47,48], or is updated on a trial-by-trial basis [39,40,49,50] to account for the biases that depend more strongly on the stimulation presented

on the immediately previous trial. Attractive biases have also been found and quantitatively predicted for time intervals in the order of hundreds of milliseconds — interval timing [51–54,84]. For relative timing, attractive biases have been found for unimodal [41] and multisensory signal combinations [42], although the quantitative predictions have not yet been confirmed.

Although attractive biases may be described by changes in the prior, such changes cannot account for classic after-effects, which are biases of perception in the opposite direction [25]. Instead, it has been proposed that classic after-effects could be better captured by changes in the likelihood function. Specifically, following adaptation, the likelihood narrows nearby the adaptor, increasing the reliability of the measurement,  $I$ . This change is counterbalanced by a broadening beyond the immediate region of the adaptor, thus conserving total resources [25]. Changes in the likelihood have been incorporated in a model of adaptation for audiovisual relative timing that also incorporates changes in the prior, potentially accounting for both attractive and lag exposure effects [43]. The model, in which both the prior and the likelihood are updated on each trial, predicts that whether an attractive or lag exposure effect is observed depends on the statistical properties of the presented stimuli. For example, compared to repeated exposures of a single value of asynchrony — such as is the case in typical lag exposure studies — exposure to asynchronies drawn from wider distributions should push the system toward exhibiting attractive biases. Although tested in different studies with different stimuli, audiovisual asynchronies drawn from wide distributions [41,42], produce lag exposure effects that are even larger than those found using exposures of a single value of asynchrony [3,4]. This observation is inconsistent with the extended Bayesian framework of Sato and Aihara [43].

### Conclusions

Audiovisual and sensorimotor lag exposure effects have been the subject of many recent investigations. Although it remains unclear whether different mechanisms underlie their operation, and whether they differ from those for other multisensory combinations, the results of recent studies suggest that the associated perceptual changes are similar to those caused by adaptation to non-temporal attributes.

For relative timing, it is often proposed that the function of adaptation is the alignment of multisensory signals to enhance multisensory integration. An alternative is that adaptation occurs to enhance the discriminability of recently experienced percepts, one of the proposed functions of adaptation for non-temporal attributes [6]. For both the perception of relative timing and non-temporal attributes, the function of adaptation is still unclear [6,12].

As for non-temporal attributes, adaptation for relative timing has been modeled using population codes and Bayesian approaches. To date, the simple population code models examined cannot concurrently account for all of the components of lag exposure effects, and have not been tested for attractive biases. Bayesian models capable of reproducing both lag exposure effects and attractive biases have been proposed, although they require further empirical investigation to be validated.

## Conflict of interests statement

Nothing declared.

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- Typically, perceptual after-effects are measured using two types of stimulus presentation. Some stimuli — called the adaptors — are presented for a long time or repeatedly, kept constant across trials, and do not require observers to respond. Other stimuli — called the tests — are presented for a short time or just once, change from trial to trial, and require observers to respond. In this study the distinction between adaptors and tests was removed; all stimuli changed from trial to trial and required the response of observers. Hence, all stimuli potentially caused adaptation and functioned as tests to measure perceived simultaneity. Lag exposure effects were revealed by estimating the point of subjective simultaneity for different groups of trials, selected according to the temporal relationship between audio and visual signals on the previous trial. Using this method, they found that the distribution of simultaneity responses for trials in which the previous trial contained a vision-leading-audio relationship was shifted in the direction of vision leading audition.

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