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# The centralized and distributed nature of adaptation-induced misjudgments of time

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Whether the neural representation of time is modality-independent or modality-specific is still under debate. However, temporal adaptation has recently been shown to induce perceptual misjudgments of time, which can transfer across sensory modalities for some temporal features. Indeed, recent psychophysical studies indicate that temporal frequency adaptation transfers across sensory modalities, whereas duration adaptation does not. We reviewed two neural timing models, the channel-based model and the striatal beat-frequency model, from the perspective of temporal adaptation and multisensory integration of temporal information. This paper highlights the recent developments in understanding time perception and proposes future research directions for the field.

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## Sensory adaptation and temporal adaptation: similarities and differences

Temporal information is vital for various kinds of behavior in animals and humans [1]. However, whether temporal processing is modality-independent and centralized or modality-specific and distributed is still being debated [2••]. The centralized framework of time perception is based on the supramodal nature of time perception. For example, we can compare the durations of stimuli presented using different modalities. In contrast, the distributed framework assumes that time is represented in a distributed manner among the sensory modalities.

Time perception has features in common with primary sensory perception. For instance, the variability of perceived time is proportional to the physical time, preserving Weber's law. However, some differences between time perception and sensory perception exist. Time is a supramodal perceptual property, and no specific brain area is dedicated to time perception, unlike sensory perception, which does have dedicated brain areas, for example, the visual and auditory cortices. Instead, temporal information is processed by broad networks comprised of multiple brain areas [3].

The focus of this review is to discuss recent research on temporal adaptation. Adaptation techniques have been widely used in sensory perception research [4] with the finding that adaptation within a band-limited region around a test stimulus produces a rebound effect in the perceived magnitude of the test. Recent studies have revealed that adaptation to various temporal features induces perceptual misjudgments of time, and that the adaptation effect may transfer across sensory modalities for some temporal attributes [5•]. Thus, temporal adaptation is an ideal method for studying time perception because one can examine both the similarities between time and sensory perception, as well as the uniqueness of time perception, which is not encaptured within a sensory modality.

This review discusses adaptation in two temporal attributes: temporal frequency and duration. Recent psychophysical studies have reported that these two distinct temporal attributes are closely related in temporal processing networks, and several biologically plausible computational models have been proposed. Through these phenomena and models, we discuss how temporal information is processed and integrated across sensory modalities.

## Phenomena: adaptation-based temporal illusions and their modality specificity

### Frequency adaptation alters frequency perception

We can perceive various temporal properties of events, such as their temporal frequency and duration. Neurophysiological studies have reported the existence of neurons that selectively respond to the temporal frequency in both the visual [6] and auditory cortices [7], and psychophysical studies have also investigated temporal frequency-selective systems in each sensory modality [8,9].

It is well known that adaptation to temporal frequency alters the perceived temporal frequency of subsequently presented stimuli. For example, after exposure to a high temporal frequency, a frequency in the medium range is perceived to be slower, while exposure to a low temporal frequency causes a frequency in the medium range to be perceived as being faster. These adaptation-induced misjudgments of temporal frequency have been reported in both the visual [10] and auditory [11] domains.

Recently Levitan *et al.* [5•] reported that adaptations in temporal frequency transfer across sensory modalities. In their study, the temporal frequency of a visual adaptor affected the perceived temporal frequency of the subsequently presented auditory test and vice versa. As in sensory adaptation, when the temporal frequencies between the adaptor and the test were very different, no aftereffect was observed. The authors proposed that temporal frequency perception could be modeled by the population activity of crossmodal temporal frequency channels, which is described later in the section on models. However, their method involved rate estimation in the absence of an explicit comparison rate, requiring observers to retain an internal standard. This type of 'single-presentation' method has received considerable criticism in the timing literature [12]. Given the importance of their finding, confirmatory evidence would be useful, perhaps using a methodology of rate reproduction.

### Duration adaptation alters duration perception

We can also judge the elapsed time of sensory events from hundreds of milliseconds to seconds. Similar to the findings for temporal frequency, neurophysiological studies have reported the existence of duration-selective neurons in both the visual [13] and auditory [14] systems. Duration perception also tends to be affected by the duration of a previously presented stimulus through adaptation [15,16] or perceptual anchoring [17]. For instance, if participants are adapted to a shorter duration stimulus, then a medium duration stimulus will seem longer; if participants are adapted to a longer duration stimulus, then the same medium duration stimulus will seem shorter.

In contrast to temporal frequency adaptation, Heron *et al.* [18••] reported that duration adaptation does not transfer across sensory modalities. In their adaptation paradigm, participants adapted to a specific duration defined by either visual or auditory stimuli, and then were instructed to compare the durations of the test stimulus in the adapted modality to that of a reference stimulus in the non-adapted modality. If the adaptation in duration transfers across sensory modalities, both the test and reference stimuli would be adapted equally, thus no difference in the perceived duration of the test and reference stimuli would occur. In their study, Heron *et al.* [18••] found that only the test duration was affected by the adaptation, indicating that duration adaptation occurs only within the adapted modality.

The same authors then investigated whether the duration adaptation occurs based on the physical or perceived duration [19]. The perceived duration of a visual stimulus illusorily becomes close to the duration of a concurrently presented auditory stimulus. The authors used this distorted visual duration as an adapting duration and found that duration adaptation occurs based on the physical rather than the perceived duration. This result suggests that adaptation occurs at the processing stages that occur before multisensory information is integrated and duration perception arises.

A recent study by Li *et al.* [20] confirmed the modality-specific nature of duration adaptation using a clever technique in which observers adapted simultaneously to different durations in the two senses (e.g. vision short, audition long). The subsequent effect on a medium duration test stimulus was opposite depending on whether the test was vision or audition. This demonstrates that modality-specific adaptation mechanisms can operate in parallel.

Duration adaptation and its modality specificity have only been investigated for durations in the sub-second range. Shima *et al.* [21] quite recently demonstrated that duration adaptation occurs also in the supra-second range. Several studies have revealed that sub-second and supra-second durations involve different neural mechanisms [22,23]. In the future, it will be important to investigate the modality specificity for duration adaptation in the supra-second range.

### Frequency adaptation alters duration perception

Although temporal frequency and duration are distinct temporal attributes, they are not processed by completely separate mechanisms and have been shown to interact. A number of psychophysical studies have indicated that the temporal frequency of a stimulus modulates its perceived duration; for instance, the temporal frequencies of visual flicker [24], visual motion ([24]; but see [25]), and auditory flutter [26,27] systematically dilate the perceived duration. These interactions between temporal frequency and duration have also been observed in the adaptation effect. Johnston *et al.* [10] reported that the perceived duration of a 10-Hz visual motion or flicker stimulus was compressed after exposure to a 20-Hz visual motion or flicker stimulus. In their study, adaptation also induced changes in the perceived temporal frequency. Johnston *et al.* [10] also demonstrated that duration compression occurred regardless of the change in the perceived temporal frequency. Therefore, temporal frequency adaptation has a different effect on the perception of temporal frequency and on the perception of duration.

The motion-induced or flicker-induced duration dilation and the adaptation-induced duration compression are similar to the extent of the duration misjudgment induced by the temporal frequency modulation. It has been further demonstrated that these two phenomena are based