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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

on different stages of interactions between temporal frequency and duration. The duration dilation induced by the flicker is observed only when the flicker is perceived as flickering, while it is not observed when the temporal frequency of the flicker exceeds the flicker fusion frequency [28]. In contrast, the duration compression induced by flicker adaptation occurs even when the flicker exceeds the flicker fusion frequency and perceived to be stable [29]. This dissociation indicates that the temporal frequency of a stimulus affects the perceived duration of that stimulus at multiple processing stages. While the temporal frequency of the stimulus being perceived induces the flicker-induced time dilation, the temporal frequency that is coded at several neural levels before perception arises induces the duration compression by adaptation.

Some researchers have suggested that the neural basis of the adaptation-induced compression of the perceived duration is located in the early sensory areas, which is based on the observation that this aftereffect has retinotopic selectivity and does not exhibit dichoptic transfer [30,31]. In contrast, others have pointed out the involvement of higher-level mechanisms based on the observation that this effect occurs in environmental, rather than retinal, coordinates [32,33]. Studies in the multimodal domain could reconcile the apparent controversy regarding whether this adaptation is limited to the lower visual processing stages by investigating the existence of similar adaptation effects in other sensory modalities or whether they transfer across sensory modalities. Future research should address this issue.

Models: centralized or distributed timing mechanisms?
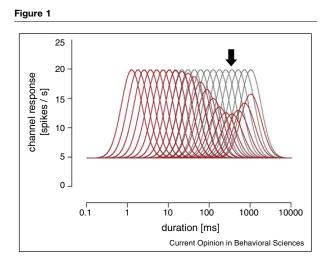
Channel-based adaptation model

In studies on sensory perception, computational modeling and phenomenological investigations have contributed to our understanding of the perceptual mechanisms. Computational modeling of temporal adaptation may help determine the components and stages of time perception. Several studies have tried to configure computational models that were developed for sensory perception to examine temporal adaptation, with one representative example being the channel-based model [5•,18••].

In sensory perception, the aftereffect induced by adaptation has been explained as follows: using spatial frequency as an example, the spatial frequency of a stimulus is coded by a population of channels that are tuned to various spatial frequencies; adaptation to a specific frequency selectively suppresses the activity of channels that are tuned around the adapted frequency. Then, a subsequently presented stimulus at another spatial frequency elicits the channels' activity, but the responses of the adapted channels are weakened. This distortion in

the activity distribution across channels generates the aftereffect induced by adaptation [34].

Recent studies on temporal adaptation also adopted the channel-based account for both temporal frequency [5•] and duration [18••]. Similar to spatial frequency channels, both temporal frequency and duration channels are activated in a selective manner by a stimulus with a particular temporal frequency or duration (Figure 1). It is important to note that the channel-based model of temporal frequency is different from the model for duration in terms of the modality specificity of the channels. As mentioned above, duration adaptation does not transfer across sensory modalities. Therefore, it is suggested that duration channels might be implemented in a distributed way for vision and audition and occur before multisensory integration during processing [19]. By contrast, Levitan et al. [5•] showed that temporal frequency adaptation transferred across sensory modalities, and interpreted this result as evidence of the existence of centralized supramodal channels that are tuned to the temporal frequency.

These channel-based models can explain the aftereffects induced by adaptation within each temporal attribute. However, it is unknown whether channel-based models can also account for the adaptation between temporal frequency and duration. Given the interaction between spatial frequency channels and temporal frequency channels [35], it is possible that temporal frequency channels and duration channels interact in a similar way, although no neurophysiological or psychophysical evidence of this

Figure 1

The channel-based model of temporal frequency and duration. Schematic showing the duration channel model, which has been adapted from Heron et al. [18••]. Each Gaussian distribution depicts the tuning curve of each duration channel. Normal responses of the duration channels are presented as gray lines. After adaptation to a specific duration (arrow), channel responses around the adapted duration are weakened (red lines), thereby distorting the group response to a subsequent test duration.

interaction has been reported to date. More research is needed to establish what types of computational models can explain the interaction between temporal frequency and duration, and to determine how existing models of time perception embed temporal frequency and duration in the psychological and neural mechanisms of temporal processing.

The striatal beat-frequency (SBF) and entrainment model: from frequency to duration

One prominent computational model that incorporates temporal frequency and duration is the SBF model. Meck and colleagues [36,37[•]] have proposed a neural implementation of time perception, in which cortico-striatal circuits serve as the neural underpinnings of interval timing. The main outline of this model is shown in Figure 2a.

The SBF model is composed of cortical neurons that oscillate at different frequencies and striatal spiny neurons that detect a pattern of phases among the oscillating neurons. At the onset of an event to be timed, the phases of the cortical oscillators are reset, and then begin to oscillate again. Medium spiny neurons in the striatum receive inputs from the cortical oscillators and become active if a certain pattern of phases is observed from among the phases of the oscillators. Because the oscillators have different frequencies, different durations can be coded with different coincidence patterns among the oscillators.

Recently, Hashimoto and Yotsumoto [38[•]] proposed a computational model that explains flicker-induced duration dilation by assuming multiple oscillators with various intrinsic frequencies, as proposed in the SBF model, with the addition of neural entrainment. Specifically, the oscillators' frequencies are entrained to those of the flickering stimuli, resulting in changes in the oscillation phases and the time point at which coincidence patterns are detected (Figure 2b). The simulation by Hashimoto and Yotsumoto [38[•]] predicted the duration dilation effect, which systematically varied with the temporal frequency spectra of the flickering stimuli.

One of the advantages of the SBF model is that it contains both modality-specific and modality-independent components. The oscillators in the SBF model are assumed to be located in various parts of cortex based on physiological evidence indicating that medium spiny neurons in the striatum receive inputs from all parts of the cortex [39]. While the oscillators distributed in various cortical areas can be modulated in a manner that is modality dependent, the medium spiny neurons, as coincidence detectors, are centralized in the striatum and are modality independent. The striatum is known to be involved in multisensory integration [40]; therefore, the SBF model

can potentially explain the interaction of temporal information across sensory modalities.
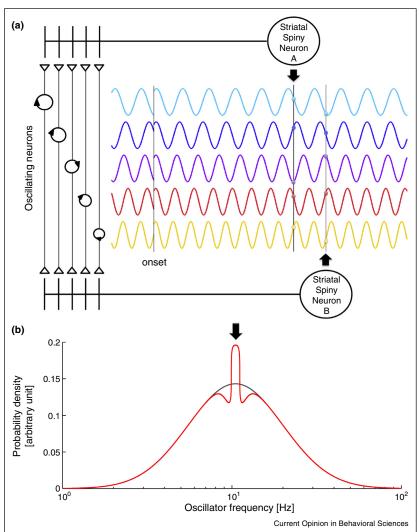
It will be important for future studies to investigate whether the SBF model can simulate temporal adaptation; in particular, such studies will need to (1) address the relationship between the temporal frequency and duration, and (2) develop a comprehensive model that incorporates both the modality-specific and modality-independent aspects of time perception.

Neural basis of temporal adaptation: relevant neuroimaging studies

Examining temporal adaptation using psychophysical and modeling studies has revealed the centralized and distributed mechanisms of time perception. The neural underpinnings of these mechanisms in humans have been explored by using various neuroimaging techniques. For instance, a number of studies have examined the multimodal interactions of temporal information. Harrington et al. [41] examined the underlying neural mechanisms of an audiovisual time distortion wherein an auditory stimulus is perceived to last longer than a visual stimulus of the same physical duration. By using functional magnetic resonance imaging (fMRI), the authors reported that the time distortion is generated by the connectivity between higher-level sensory areas (superior temporal, posterior insula, and middle occipital areas) and other areas such as the anterior insula or putamen [41]. Moreover, Kanai et al. [42] demonstrated asymmetric roles of the visual and auditory cortices in time perception by using transcranial magnetic stimulation. Specifically, the authors found that while disruption of the auditory cortex impaired the duration perception of both auditory and visual stimuli, disruption of the visual cortex impaired only the duration perception of visual stimuli [42].

In contrast to the neural basis of the modality specificity in time perception, the neural basis of temporal adaptation itself is still largely unknown. Using an fMRI adaptation paradigm, Hayashi et al. [43] demonstrated that the right inferior parietal lobule (IPL) exhibited an activation pattern tuned for specific durations of visual stimuli. Further studies should address how this adaptation in BOLD responses affects the perceptual adaptation in time and how modality-specific these duration-tuned BOLD responses are.

The neural basis of several temporal illusions has also been studied to investigate the neural mechanisms of time perception. Wittmann et al. [44] measured the brain activity of participants by using fMRI while the participants experienced a temporal illusion in which the duration of a deviant stimulus within a stream of standard events is overestimated. They reported that the perception of the illusion was correlated with activity patterns in medial cortical structures, which collectively are referred

Figure 2

Diagrams showing the general striatal beat-frequency (SBF) model and the SBF and entrainment model. **(a)** Schematic showing the SBF model, which has been adapted from the works by Meck and his colleagues [1,34,35]. At the onset of an event to be timed, the phases of cortical oscillating neurons are reset, and then begin to oscillate again. Oscillators with various frequencies project to medium spiny neurons (A and B) in the striatum, which detect specific coincidence patterns among the oscillators' phases. Striatal spiny neuron A and B detect different coincidence patterns, indicating that these spiny neurons code different durations. **(b)** A computational model of neural entrainment. Distribution in gray indicates a hypothetical distribution of cortical oscillators in the SBF model. When a flickering visual stimulus at a specific frequency (arrow) is presented, neurons oscillating around the flickering frequency are entrained to this frequency, resulting in an alteration in the distribution of oscillator frequencies (red distribution).

to as the default mode network [44]. Herbst and colleagues [28,45] investigated the neural correlates of flicker-induced dilation of duration using electroencephalography. They reported that the duration dilation effect was correlated with flicker perception, but was not correlated with steady-state visual evoked potentials induced by flicker [28], or with the magnitude of the contingent negative variation [45], which has been identified as a potential candidate for the neural basis of time perception ([46,47]; but see [48]).

Insights into the neural mechanisms of time perception might also be found in neuroimaging studies on number perception, as number perception shares various common features with time perception. A number is a supramodal perceptual attribute and has features in common with sensory perception. Number perception is also susceptible to adaptation [49]. Moreover, an association between time and number perception has been indicated [50,51], and recent neuroimaging studies have revealed that number and time perception share neural processes to

some extent [52,53]. In addition, Harvey *et al.* [54] reported the existence of a topographic representation for numerosity in the posterior superior parietal cortex, which showed channel-like numerosity tunings. These studies might shed light on the potential outcomes of neuroimaging studies on temporal adaptation.

Neuroimaging studies on time perception are associated with interpretation difficulties in terms of the magnitude or latency of time-related brain activity because the duration of a stimulus sometimes co-varies with the amount of sensory input or the latency of neuronal activity induced by the stimulus. Researchers will need to address this problem by carefully manipulating various temporal parameters; thus, identifying the neural basis of temporal adaptation will be a challenging issue.

Concluding remarks

We reviewed psychophysical, modeling, and neuroimaging studies of time perception, with a focus on temporal adaptation. Temporal adaptation has features in common with sensory adaptation in terms of the selective adaptation to a specific temporal frequency or duration, or the applicability of the channel-based model for adaptation effects. Through this phenomenon, both the centralized and distributed mechanisms of time perception have been revealed. Studies on duration adaptation revealed that separate mechanisms are involved in processing duration for the visual and auditory domains, while there is evidence to suggest that temporal frequency adaptation can be transferred across sensory modalities, thus indicating the existence of a supramodal mechanism for temporal frequency perception. Despite a growing body of behavioral literature, the computational model or neural correlates that explain these phenomena remain unclear, and await further research.

Conflict of interest statement

Nothing declared.

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contrast, some intrinsic models emphasize the temporal representation in early sensory areas.

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