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The rhythm aftereffect: Support for time sensitive neurons with broad overlapping tuning curves

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Abstract

Ivry [Ivry, R. B. (1996). The representation of temporal information in perception and motor control. *Current Opinion in Neurobiology*, *6*, 851–857.] proposed that explicit coding of brief time intervals is accomplished by neurons that are tuned to a preferred temporal interval and have broad overlapping tuning curves. This proposal is analogous to the orientation selective cells in visual area V1. To test this proposal, we used a temporal analog to the visual tilt aftereffect. After adapting to a fast auditory rhythm, a moderately fast test rhythm (400 ms between beats) seemed slow and vice versa. If the speed of the adapting rhythm was made too disparate from speed of the test rhythm the effect was diminished. The effect occurred whether the adapting and test stimuli were presented to the same or different ears, but did not occur when an auditory adapting rhythm was followed by a visual test rhythm. Results support the proposition that explicit time information is coded by neural units tuned to specific temporal intervals with broad overlapping tuning curves. In addition, it appears that there is a single timing mechanism for each incoming sensory mode, but distinct timers for different modes.

Keywords: Time; Duration; Aftereffect; Interval timer; Cerebellum; Adaptation; Rhythm

1. Introduction

It is clear that human behavior is affected by time across many different time scales. Long time scales include circadian rhythms (Czeisler et al., 1999; Wever, 1986) that operate over the scale of days. Intermediate time scales involve intervals from minutes to several hours (Buhusi & Meck, 2005) and information in this time range may be important for sequencing behaviors in complex tasks (Sohn & Carlson, 2003) and decision making (Ivry & Spencer, 2004). Very fine time scales, on the order of milliseconds to several seconds, are important for coordinating motor movements, and speech perception (Mauk & Buonomano, 2004) and production (Schirmer, 2004). Research investigating behaviors associated with these different time scales suggests that independent processes and distinct brain areas are responsible for processing time information for each time scale. While there is still some debate about whether timing information is explicitly coded for intermediate and longer time scales, there is growing consensus that there are structures which explicitly code time information for short time scales (Buhusi & Meck, 2005; Ivry & Spencer, 2004). In this paper we limit ourselves to the perception of short temporal durations, and investigate the organization of the neural units that explicitly code temporal information at this brief time scale.

Some of the earliest work indicating the existence of an independent neural mechanism for the encoding of brief temporal information came from Wing and Kristofferson (1973). In their experiments, subjects were asked to tap in unison with a metronome and to continue producing that rhythm after the metronome stopped. A careful examination of the variability between taps allowed Wing and Kristofferson to conclude that errors were caused by two independent sources of variability. One source was attributed to variability in executing a motor command, and a second source of variability was associated with a timing

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mechanism. This initial demonstration of an independent timing mechanism led to further research investigating both the processes and brain areas involved in explicitly coding temporal information.

A combination of lesion studies (Gerwig et al., 2003, 2005; Perrett & Mauk, 1995; Perrett, Ruiz, & Mauk, 1993; Spencer & Ivry, 2005) and functional magnetic resonance imaging studies (for review see Lewis & Miall, 2003), contribute to a growing consensus that the cerebellum is instrumental in the explicit coding of short duration temporal information (Buhusi & Meck, 2005; Ivry, 1996; Ivry & Richardson, 2002; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002). It is less clear whether the basal ganglia are also involved or only become involved when tasks require a less explicit coding of time associated with behaviors at intermediate time scales.

One model for how units within the cerebellum may code temporal information, the interval timer model (Keele, Nicoletti, Ivry, & Pokorny, 1989; Pashler, 2001), posits a bank of neural units each of which is tuned to a specific temporal duration. One indirect piece of evidence supporting this interval model comes from the observation of Fraisse (1963) who found that rhythm perception breaks down when the interval between beats exceeds a few seconds, suggesting that the precise timing associated with an explicit timing mechanism is limited in terms of the time frames to which it responds. In theory, the durations one could monitor under the interval timer model would be limited by the number of units within the bank and their tuning. The finding that rhythm perception breaks down when the interval between beats becomes too large is consistent with the interval timer model with temporally tuned units tuned to a limited set of durations.

Perhaps the best evidence supporting the existence of units tuned to specific durations comes from a study by Wright, Buonomano, Mahncke, and Merzenich (1997). In their study, participants were trained to discriminate whether a 1000 Hz tone was longer or shorter than 100 ms. During training, both the frequency of the tone and the time criterion were held constant and performance improved markedly. After training, either the time criterion was changed to a new interval (200 ms) or the tone was changed to a new frequency (4000 Hz). When the time interval was changed, the benefit due to training disappeared; however, when the tone's frequency changed and the time interval remained the same, the benefit of training transferred almost completely. These results suggest that the training was specific to a given temporal interval support the theory that there are different units specialized for encoding particular durations of time. Training one of these duration sensitive cells specifically affects temporal judgments at the trained interval without affecting duration judgments at untrained durations.

Given this evidence in favor of units that are tuned to specific temporal durations and the evidence suggesting that the cerebellum is the most likely site of these units, Ivry (1996) proposed a model of how these temporally sensitive units might be organized within the cerebellum. Ivry based this interval timing model on visual area V1. In area V1 there are cells which are tuned to lines of particular orientations. But, across these orientation tuned cells, there are a relatively limited number of preferred orientations with roughly 15 deg separating the preferred orientations between cells. Cells tuned to different orientations have broad tuning curves which overlap with the tuning curves of cells tuned to nearby orientations (Hubel & Wiesel, 1962). These tuning curves allow the precise orientation of lines to be determined by using distributed coding across a number of cells tuned to nearby orientations. This method of extracting orientation is extremely efficient, allowing a relatively small set of orientation selective cells to code a nearly infinite number of possible orientations.

Given the efficiency of this type of distributed coding and its prevalence for coding visual features (orientation, color, motion direction), Ivry speculated that a similar coding scheme could be used by the interval timer. Thus he suggested that the time sensitive units would be optimally tuned to a specific temporal delay but would have broad tuning curves that overlapped with other temporally sensitive neurons. Although Ivry's extension of the structure of V1 to the structure of the temporally sensitive cells in the cerebellum is logical, there is little direct evidence supporting this type of architecture within the cerebellum.

In the present experiments, we attempted to provide evidence for the broad overlapping tuning curves posited by Ivry. To do so we adopted a psychophysical technique that has been used to support the existence of broad tuning curves in area V1 and altered the method so that it was appropriate for investigating the structure of temporally tuned units in the cerebellum.

The broad overlapping tuning of orientation selective cells in area V1 is thought to cause the tilt aftereffect (TAE) in vision (Gibson & Radner, 1937; Jin, Dragoi, Sur, & Seung, 2005; Mitchell & Muir, 1976; Paradiso, Shimojo, & Nakayama, 1989). To produce the TAE, an observer stares for a number of seconds at an adapting display consisting of lines of a particular orientation and then views a test pattern that consists of lines of a nearby orientation. The effect is that the test pattern will be perceived as tilting away from the orientation of the adapting stimulus. For example, if one adapts to lines tilted just left of vertical, and then views a vertical test pattern, the lines of the test pattern will appear to be tilted to the right of vertical. The explanation of this effect is that adapting to a left tilting pattern will selectively reduce the firing rate of cells tuned to the left (Coltheart, 1971; Wainwright, 1999). When subsequently viewing a vertical pattern, the dampened response of the leftward tuned cells will result in a rightward shift in the overall pattern of activity, so that the vertical lines will appear to tilt rightward. This tilt aftereffect is a direct result of having a bank of orientation selective cells with broad overlapping tuning curves and distributed coding across those cells.