



Temporal Perceptual Learning

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Abstract

Our interaction with the environment and each other is inherently time-varying in nature. It is thus not surprising that the nervous systems of animals have evolved sophisticated mechanisms to not only tell time, but to learn to discriminate and produce temporal patterns. Indeed some of the most sophisticated human behaviors, such as speech and music, would not exist if the human brain was unable to learn to discriminate and produce temporal patterns. Compared to the study of other forms of learning, such as visual perceptual learning, the study of the learning of interval and temporal pattern discrimination in the subsecond range is relatively recent. A growing number of studies over the past 15 years, however, have established that perceptual and motor timing undergo robust learning. One of the principles to have emerged from these studies is that temporal learning is generally specific to the trained interval, an observation that has important implications to the neural mechanisms underlying our ability to tell time.

Keywords

Time, perceptual and motor learning

1. Introduction

Dancing, playing the piano or speaking are all challenging activities for our motor and sensory systems: these activities require the capacity to produce highly timed motor responses and at the same time to decode highly structured temporal patterns. Like many others perceptual and motor skills our capacity to produce and perceive time can be learned. In his seminal book ‘The Principles of Psychology’ (James, 1890, Vol. 2, Ch. XV, p. 618) William James wrote: “Like other senses, too, our sense of time is sharpened by practice”. James cites a work published in 1885 in which Max Mehner tested himself for two weeks on a perceptual interval dis-

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crimination task. Using auditory stimuli (empty intervals marked by the sound of a hammer attached to a hand-made clock), he measured discrimination thresholds across intervals ranging from 1 to 5 s. Based on his simple study with a single subject, he concluded that interval discrimination undergoes learning and that multiple days of practice were essential to improve timing (Mehner, 1885). This very early work anticipates what successive decades of systematic investigations confirm: training on temporal tasks improves temporal discrimination.

Here we review both psychophysical and neurophysiological literature on perceptual and motor temporal learning. Our focus is primarily on human literature in the subsecond time scale, however, in the context of the mechanisms underlying timing we also review some of the animal literature on temporal processing. Our aim is to offer a concise overview of empirical findings on temporal learning and to discuss these findings within the framework of current models of temporal processing.

2. Temporal Perceptual Learning

Temporal perceptual learning has been studied with two general approaches. Early work investigated the effect of temporal training by using a relatively small number of observations and by looking at behavioral changes within a single experimental session, usually conducted in a single day (Aiken, 1965; Goldstone & Goldfarb, 1966; Warm et al., 1975). These studies used durations mainly in the second range (Grondin et al., 2009; Kristofferson, 1980; Matthews & Grondin, 2012; Rousseau et al., 1983) and perceptual categorization and bisection tasks. Later studies made use of much longer training procedures, usually several days (see Table 1). These studies were most often based on temporal discrimination tasks in the subsecond range, and explored the generalization of temporal learning. In this section we focus on these later studies because they are primarily on timing in the subsecond range and because they systematically investigated generalization and specificity of temporal learning.

2.1. *The Tasks*

A large number of different tasks and procedures have been used to study temporal perceptual learning. However, the most commonly used temporal discrimination tasks ask subjects to compare stimuli of two different durations (Fig. 1A, B): a ‘standard’ and a ‘comparison’. Each stimulus can be defined as an empty interval or a filled duration, presented in the auditory, visual, or somatosensory modality. In the auditory domain a stimulus often consists of two brief tones (e.g., 25 ms) of a given pitch in which the time between the onset of each tone determines the interval of the stimulus. The duration of the standard stimulus is a fixed value (T) whereas the comparison can be either longer or shorter than the standard ($\pm \Delta T$). The sub-

Table 1. The psychophysics of perceptual temporal learning. Summary table of perceptual temporal learning studies in the subsecond range listed according to the task, the time range used, the days of training, the presence of learning and generalization to space and time. (AP) adaptive procedure, (CS) constant stimuli, (S) single stimulus presentation, (F) filled intervals, (E) empty intervals

Studies	Task	Time (s)	Interval	Days (trials)	Learning	Spatial Generalization	Temporal Generalization
Wright et al., 1997	AP	0.1	E	10 (9000)	Y	Y	N
Nagarajan et al., 1998	AP	0.075-0.125	E	10-16 (9000-14 400)	Y	Y	N
Westheimer, 1999	CS	0.5	F	1 (900)	Y	Y	-
Meehan et al., 2000	AP	0.3-0.5	E	5 (2500)	Y	Y	N
Karmarkar & Buonomano, 2003	AP-S	0.1-0.2	E & F	10 (7200)	Y	Y	N
Van Wassenhove & Nagarajan, 2007	CS	0.2	E	3 (2400)	Y	N	-
Planetta & Servos, 2008	AP	0.5-0.8	E	10-20 (5000-10 000)	Y	Y	N
Buonomano et al., 2009	AP	0.1	E	8 (5760)	Y	Y	N
Lapid et al., 2009	AP	0.1	E & F	5 (3000)	Y	Y	Y
Wright et al., 2010	AP	0.05-0.1	E	2, 4, 10 (1800, 3600, 9000)	Y	N, Y, Y	N, N, N
Grondin & Ulrich, 2011	CS-S	0.25	E	1 (2520)	N	N	-
Bratzke et al., 2012	CS-S	0.1-0.2	E	4 (2560)	Y	Y	N
Buetti et al., 2012	AP	0.1-0.4	E	4 (2880)	Y	Y	N

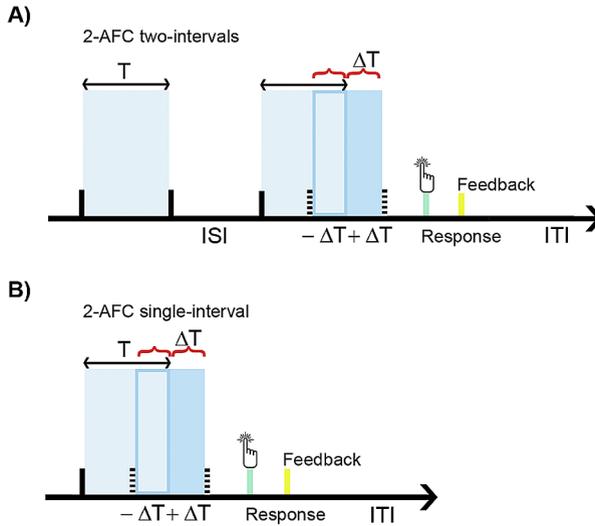


Figure 1. Temporal discrimination tasks. Two-interval alternative forced choice tasks (2AFC). (A) Schematic representation of a single trial where a standard (T) and a comparison duration ($T \pm \Delta T$) are sequentially presented. By pressing one of two response keys subjects have to decide which one of the two intervals lasted longer. After the response a feedback about performance accuracy is provided. In an alternate version of this 2AFC task, the comparison stimulus is equal to $T + \Delta T$, and the order of the standard and comparison are randomized. (B) Trial representation of a 2AFC task where only a single comparison duration ($T \pm \Delta T$) is presented in every trial. This figure is published in colour in the online version.

ject's task is to decide, by pressing one of two response keys, which one of the two stimuli was the longest.

A critical component of temporal discrimination tasks relates to how the difference between the standard and comparison duration (ΔT) changes throughout the task. In an *adaptive* ('up-down') procedure this value is adjusted based on the subjects performance (therefore different subjects experience different values and ranges of comparison intervals). In the method of *constant stimuli* ΔT is randomly selected from a fixed set of values at each trial; therefore all subjects experience the same set of comparison values. Using the adaptive procedure, ΔT is varied in step-wise method that should ultimately converge to a psychophysical threshold (Levitt, 1971), whereas in the method of constant stimuli the percent of correct responses at each value of ΔT is used to fit a psychometric function and calculate the discrimination threshold (difference limen or just-noticeable different, Lapid et al., 2008). This threshold is often expressed as half of the value in milliseconds that spans the range in which subjects get between 25% and 75% of correct responses.

The presentation of both a comparison and standard stimulus on each trial represents a two-alternative forced choice task (Buetti et al., 2012; Nagarajan et al., 1998). However, tasks in which only the comparison stimulus is presented in each

trial can also be used (Fig. 1B). In these single-stimulus tasks subjects make a judgment based on comparison to the standard interval presented at the beginning of the block or to an evolving internal standard based on the continuous feedback over trials (Karmarkar & Buonomano, 2003).

2.2. *Perceptual Learning of Temporal Intervals*

One of the first systematic studies on temporal perceptual learning was performed by Wright and collaborators (Wright et al., 1997). In this work volunteers were trained for ten days (900 trials per day) on an interval discrimination task. The duration trained was a 100 ms empty interval marked by brief tones of 1 kHz frequency. Before and after-training volunteers were also tested with stimuli differing from the trained stimuli, including: 50 ms-1 kHz, 200 ms-1 kHz, and 100 ms-4 kHz. Training resulted in approximately a 50% decrease in the discrimination thresholds for the trained interval (100 ms-1 kHz), interestingly there was a similar improvement in the same interval-different pitch condition (100 ms-4 kHz). No improvement, however, was observed for the untrained intervals. These results were the first to establish that temporal training is interval specific, but can generalize across different stimulus dimensions. Similarly to subsequent studies (Bueti et al., 2012; Karmarkar & Buonomano, 2003), not all volunteers exhibited learning effects (two out of 14 subjects did not learn) and from the inspection of the Weber fractions over time it is clear that performance improved rapidly in the first few days of training and then reached a plateau, after which very little improvements were observed.

The learning-dependent improvement in interval discrimination of the trained interval and the absence of generalization to untrained intervals has since been replicated in numerous studies (Buonomano et al., 2009; Karmarkar & Buonomano, 2003; Meegan et al., 2000; Nagarajan et al., 1998; Wright et al., 2010). Table 1 summarizes many of the studies that have examined temporal perceptual learning of intervals in the subsecond range and interval specificity. At least one study failed to observe training related improvement in temporal discrimination thresholds (Rammsayer, 1994). In this study subjects were trained for 20 days on a temporal discrimination task of 50 ms auditory intervals. After the training none of the tested subjects ($N = 6$) exhibited a significant decrease in discrimination thresholds. A possible factor contributing to the lack of learning effects in this study was the use of only 50 trials per training day — all the studies reported in Table 1 used a minimum of 150 trials per day.

2.3. *Spatial and Temporal Generalization*

In this section we examine the critical question of generalization of temporal perceptual learning. There are at least two critical dimensions to the question of generalization, which we will refer to as spatial and temporal generalization. We will use the term spatial generalization to refer to the potential transfer of learning from the

trained stimulus to stimuli that arrive in the nervous system through different input pathways or channels (i.e., stimuli that are coded in different spatial locations). Thus spatial generalization would include a change in pitch of auditory tones (because of the tonotopic organization of the cochlea) or a change of sensory modality. Temporal generalization refers to changes from the trained interval in the absence of changes to the physical stimuli used (pitch, color, position, orientation, etc.).

Numerous studies have observed robust spatial generalization as reflected by improved timing to the trained interval presented with different sensory characteristics or in a different sensory modality (Karmarkar & Buonomano, 2003; Nagarajan et al., 1998; Westheimer, 1999; Wright et al., 1997; Wright et al., 2010). In the auditory modality, studies have shown that training to discriminate brief auditory intervals (e.g., 100 ms–1 kHz) led to a decrease of discrimination thresholds not only for the trained interval but also for intervals of equal length but different pitch (100 ms–4 kHz, Buonomano et al., 2009; Karmarkar & Buonomano, 2003; Wright et al., 1997; Wright et al., 2010). An equivalent result has been observed in the somatosensory modality, where training with brief tactile intervals (75 and 125 ms) produced generalization effects to the same intervals tested on different skin locations (i.e., different digits of the same hand and the same digit of the two hands, Nagarajan et al., 1998). Spatial generalization has also been shown in the visual modality for a 500 ms visual filled interval when presented from the trained (i.e., the left) to the untrained (i.e., right) visual field (Westheimer, 1999).

Generalization can also occur for the trained interval presented within an untrained sensory modality. This cross-sensory generalization has been observed from the somatosensory to the auditory modality (Nagarajan et al., 1998: 50 and 100 ms), from the visual to the auditory modality (Bueti et al., 2012: 200 ms) and vice-versa (i.e. from the auditory to the visual modality, Bratzke et al., 2012: 100 ms; but see Grondin & Ulrich, 2011; Lapid et al., 2009). Other forms of generalization concern the nature of the temporal interval, from empty to filled intervals (Karmarkar & Buonomano, 2003; Lapid et al., 2009), and from the sensory to motor modality (Meegan et al., 2000).

In contrast to the spatial generalization, as mentioned above, temporal generalization has rarely been reported, in other words temporal perceptual learning is mostly temporal specific (Fig. 2). None of the studies cited above observed generalization for intervals differing by more than 50% from the trained interval (but see Lapid et al., 2009 and Wright et al., 1997 concerning the generalization from 100 to 50 ms interval). Thus, as highlighted in Table 1, studies over the past 15 years have led to a clear picture relating to the generalization of temporal perceptual learning. Learning is highly specific in the temporal domain, but can generalize broadly — even across modalities — in the spatial domain.

The generalization signatures of temporal perceptual learning are of particular importance to one of the most significant questions in the timing field, specifically whether timing relies on a single ‘dedicated’ timing mechanism or whether tim-

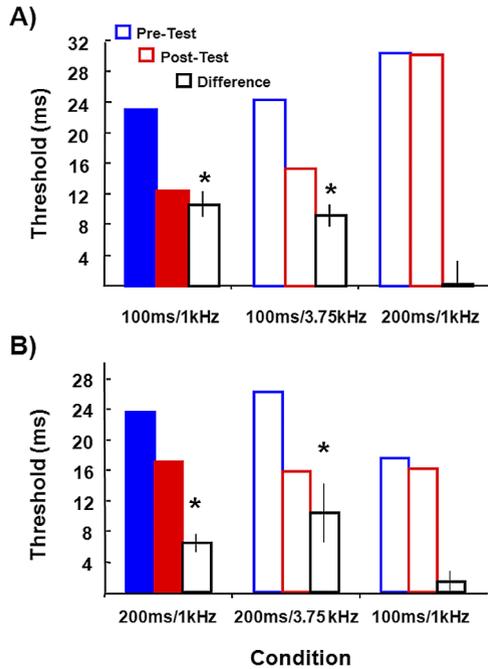


Figure 2. Interval specific learning and interval generalization. (A) Pretest and posttest interval discrimination thresholds for three different conditions: 100 ms standard interval bounded by a 1 kHz tone; 100 ms standard interval bounded by a 3.75 kHz tone; and a 200 ms interval bounded by 1 kHz tones. Between the pre- and posttests, subjects were trained for 10 days on the 100 ms/1 kHz condition (solid bars). In addition to the learning in the trained condition (solid bars), subjects demonstrated robust generalization to the same-interval-different-frequency condition (100 ms/3.75 kHz), but not to the novel interval. (B) Data from a separate experiment in which subjects were trained on the 200 ms/1 kHz condition (solid bars). Again, in addition to learning the trained condition (solid bars), there was robust generalization to the same-interval-different-frequency condition, but not to a novel interval. Modified from Karmarkar and Buonomano (2003). This figure is published in colour in the online version.

ing reflects a general and widespread computation that can be carried out in most neural circuits ('intrinsic timing', Buonomano & Karmarkar, 2002; Ivry & Schlerf, 2008; Ivry & Spencer, 2004). Temporal specificity seems to favor intrinsic timing mechanisms. But in contrast, spatial generalization seems to suggest the existence of a centralized temporal mechanism; one that, for example, processes/encodes time independently of the sensory modality and the spatial location of the temporal intervals (Allman et al., 2014; Meck & Church, 1982; Meck et al., 2008). These arguments however, rely on a number of assumptions, including that the spatial generalization relies on the same neural mechanisms subserving the learning of the trained stimulus, rather than an independent neural processes — such as improved encoding of the neural representations of temporal intervals. Interest-

ingly, the question of whether generalization and learning arise from either similar or distinct neural changes has been addressed in a recent psychophysical work (Wright et al., 2010). In this study different groups of volunteers were trained in a temporal discrimination task of brief auditory intervals (100 ms 1 kHz) for two, four or ten days. The results show that the time-course of learning on the trained interval was relatively rapid, with statistically significant improvement observed after two days of training (900 trials each). However, the time-course of generalization to an untrained frequency (100 ms-4 kHz) was considerably longer, only appearing after four days of training. The different time courses of these improvements indicate that perceptual learning and generalization have distinct neural substrates.

Further support to the notion that generalization may be dissociated from the mechanisms underlying perceptual learning is the observation that factors such as task difficulty and attention can influence generalizations processes. In orientation discrimination tasks in the visual domain, for example, it has been shown that the degree of learning specificity, and consequently the extent of generalization, depends on the difficulty of the trained condition (Ahissar & Hochstein, 1997). Consistent with this report is the result of a recent temporal learning study by Buonomano and colleagues (2009). In this work subjects were trained to discriminate two brief empty auditory intervals (100 ms) that could be separated by either a short (250 ms) or a long (750 ms) inter-stimulus-interval (ISI). Two groups of subjects were trained in either the long or the short ISI condition. In the absence of training, interval discrimination was impaired in the short ISI condition. After training a decrease of discrimination thresholds was observed in both groups. However, whereas the group that was trained with a long ISI showed generalization to stimuli with different pitches and to stimuli tested in the short ISI condition, the group trained with the short ISI did not exhibit generalization. These results are consistent with the notion that challenging training conditions produce less generalization. Additionally, as reviewed in Section 4, the idea that generalization and temporal learning are sustained by different neural mechanisms is supported by the recent observation that partially distinct brain regions are associated with cross-sensory (audio-visual) generalization and temporal learning of a short visual interval (Bueti et al., 2012).

Together, numerous studies suggest that learning and generalization may rely on distinct processes. Thus, we would argue that the spatial generalization observed in many temporal perceptual learning studies (Table 1), does not provide a strong argument for a shared centralized timing mechanism, particularly given data showing that significant improvements in interval discrimination can be observed in the absence of spatial generalization early in the learning process (Wright et al., 2010).

3. Learning of Temporal Motor Patterns

In addition to the perceptual temporal discrimination studies discussed above, temporal learning studies have focused on motor tasks. In this section we focus on the learning of motor timing tasks and the question of whether the learning of sensory and motor tasks relies on shared or distinct mechanisms. At the outset it is important to note that in many motor timing studies, the traditional distinction between perceptual and motor components is somewhat blurred, because in a typical reproduction task there is both a sensory and a motor component: subjects first experience an interval and then generate that interval using their fingers. Practice based improvements could thus include both a sensory component as well as a pure motor component.

3.1. *Learning of Motor Intervals and Patterns*

Motor studies of temporal learning have been based on a number of different tasks involving the reproduction of isolated intervals, or of periodic or aperiodic sequences. In an interval reproduction task, subjects hear or see a given interval and then reproduce that interval using a keyboard. In the context of periodic studies, the synchronization-continuation task is often used. In a typical version of this task subjects listen to a series of auditory tones presented at a given frequency, entrain their finger tapping to this sequence, and then continue to reproduce the target period once the sensory stimulus is turned off. Ivry & Hazeltine (1995) examined temporal motor learning in both interval reproduction and synchronization-continuation tasks based on intervals ranging from 325 to 550 ms. After four daily training sessions, they observed a decrease in the variance of the intervals produced in the interval task, but not in the periodic task — the absence of learning in the periodic task may have been related to the fact that there were effectively many more trials and feedback in the interval condition. Bartolo & Merchant (2009) also observed a training related reduction in the variance of an interval reproduction task. The subjects were trained on intervals of 450, 650, or 850 ms, and exhibited decreases of approximately 20 to 40% of the pre-training standard deviation (S.D). Consistent with the notion that temporal learning requires fairly extensive practice, the subjects in this study performed hundreds of interval specific trials over eight days of training.

Other studies in the motor domain have demonstrated learning of both periodic and aperiodic motor patterns. In one such study (Laje et al., 2011) subjects practiced the reproduction of either a periodic motor pattern, composed of a sequence of six repeating intervals of 500 ms, or an aperiodic pattern composed of a sequence of six different intervals in the range of 200 to 800 ms. The data from each daily training session was used to fit the generalized Weber function by plotting the variance of the response times of each event within a pattern, against absolute time squared (Getty, 1975). This analysis provides two sources of variance: a time-dependent variance source, related to the Weber fraction, and a time-independent

source often interpreted as motor noise. For both the periodic and aperiodic patterns robust learning effects were evident by a decrease in both variance terms after five days of training. The overall variance was significantly smaller in the periodic task, hinting at potential differences between the timing of periodic and aperiodic patterns.

The above studies, and numerous others, establish that timing of motor responses in the range of hundreds of milliseconds to a few seconds undergo learning (Ivry & Hazeltine, 1995; O'Reilly et al., 2008; Planetta & Servos, 2008; Ullen & Bengtsson, 2003). But, as with the perceptual temporal learning, a key question for the understanding of the neural basis of temporal motor learning, relates to whether motor learning leads to generalization to the production of different intervals and patterns.

3.2. *Temporal and Cross Sensory-Motor Generalization*

The issue of temporal specificity of motor timing learning has not been as carefully studied as in perceptual timing tasks, but was explicitly addressed in the learning of motor interval study by Bartolo & Merchant (2009). As mentioned above, in that study subjects were trained to produce intervals of 450, 650, or 850 ms, but before and after training they were also tested on their ability to reproduce a wide range of auditory intervals. There was significant generalization to neighbouring intervals as revealed by a decrease in the S.D. during the reproduction of untrained intervals. The generalization function was fairly well captured by a Gaussian function and the width of the generalization curve increased with the duration of the target interval — suggestive of a Weber-like generalization function.

Other studies have addressed generalization from the perspective of cross modal transfer from the learning of sensory interval discrimination to motor interval reproduction. Meegan and colleagues (2000) trained subjects on either a 300 or 500 ms two-forced-choice auditory interval discrimination task, after the training phase subjects performed 300 and 500 ms reproduction tasks. The subjects that were trained on the 300 ms perceptual task exhibited significantly larger reduction (compared to pretraining) of the S.D. during the reproduction of 300 ms interval compared to 500 ms interval. Conversely, subjects trained on the 500 ms discrimination task improved more on the 500 ms compared to the 300 ms motor reproduction task. A similar study replicated these findings by demonstrating that learning to discriminate 500 or 800 ms intervals in the somatosensory modality resulted in a significant SD decrease in a motor reproduction task of 500 or 800 ms, respectively (Planetta & Servos, 2008).

As with the studies that observed spatial generalization above, the demonstration that training on sensory interval discrimination tasks generalized to the motor reproduction of the trained intervals, is suggestive of a centralized timing mechanisms, or at least that there may be shared mechanisms between sensory and motor timing. However, it should be noted that the transfer between sensory and mo-

tor tasks could be a result of the ability to store the reference interval, as opposed to shared sensory and motor timing mechanisms per se. Additionally, as with the study demonstrating that interval discrimination learning can be dissociated by spatial generalization early in training (Wright et al., 2010), it will be of relevance to see if the transfer to the motor domain is also dependent on the amount of training.

3.3. *Precision Versus Accuracy*

Motor timing tasks provide a particularly useful way to dissociate the learning of temporal precision and temporal accuracy. Precision refers to the reproducibility of the timed responses, and in motor tasks is generally measured by the standard deviation or coefficient of variation (the Weber fraction). Accuracy relates to how close the produced interval is to a target in absolute time. Precision and accuracy in motor tasks parallel the measure of the slope of the psychometric function (the difference limen) and the point of subjective equality, respectively (Lapid et al., 2008). However, most of the sensory studies discussed above have not carefully quantified changes in the difference limen and point of subjective equality because they were based on threshold measures determined from the adaptive procedure — which confounds precision and accuracy. The motor timing literature has often placed more emphasis on the question of precision, but it is necessary to consider both when addressing the psychophysical signature of timing and the potential underlying neural mechanisms. Indeed a fundamental question relates to whether the precision and accuracy of motor responses are independent or inseparable.

To date, motor timing learning studies seem to support a dissociation between the learning of precision and accuracy. For example, the two studies that reported an interval-specific transfer of perceptual interval discrimination learning to motor production, reported an improvement in the precision of the trained intervals but no significant improvement in accuracy (Meegan et al., 2000; Planetta & Servos, 2008). In other words, while training on the discrimination of a 300 ms interval resulted in subjects being less variable (more precise) during the reproduction of 300 ms intervals, there were not any more accurate.

Practice dependent changes in motor precision and accuracy have also been examined using a visual task with an implicit timing component (Sohn & Lee, 2013). In this study subjects were trained to predict the time at which an initially visible stimulus (moving at a constant speed) would reappear after disappearing behind an occlusion. In the different conditions of the study, the stimulus was occluded for intervals ranging from 0.5 to 3.5 s. Separate analysis of the temporal accuracy and precision revealed a dissociation between these components: the precision improved slowly and consistently across training days, while there was no consistent long-lasting improvement in accuracy (although there was a short lasting calibration effect in the presence of feedback). While the lack of accuracy learning could have been a result of low power (there were four subjects in the experiment), these

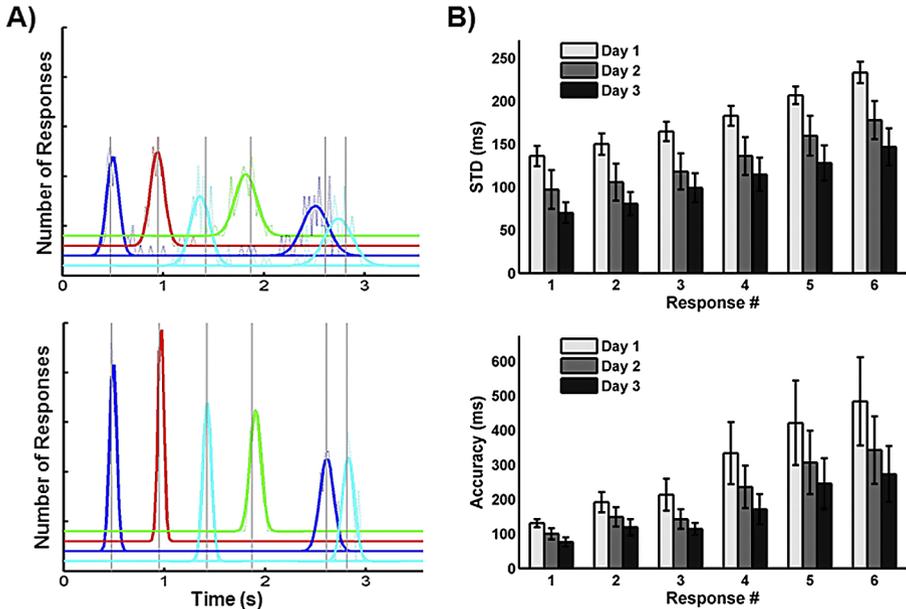


Figure 3. Improvements in precision and accuracy during learning of a complex motor timing task. Subjects learned to produce an aperiodic spatiotemporal pattern consisting of a sequence of six timed responses (six component intervals) using four fingers (upper inset in Panel A). (A) Single subject results from the first (upper graph) and the third (lower graph) day of training. Light dashed lines represent the response distributions, and the solid lines represent Gaussian fits of the data. (B) Average (12 subjects) precision (top) and accuracy (bottom) of each element of the pattern across three days of training. Both the precision ($F_{2,22} = 73$, $p < 10^{-6}$) and accuracy ($F_{2,22} = 7.2$, $p < 0.005$) exhibited a main effect of training across the three days. Modified from Experiment 2 from Laje et al. (2011). This figure is published in colour in the online version.

results provide further evidence for a mechanistic dissociation between the neural mechanisms underlying precision and accuracy of motor timing.

Although the above studies nicely demonstrate dissociations between the effects of training on precision and accuracy, it is clear that training can result in improvements in both. For example, Fig. 3 reproduces the results of a study in which subjects learned a spatiotemporal aperiodic task in which they used four fingers to reproduce a visually presented spatiotemporal pattern (Laje et al., 2011). Fitting the distribution of the response times of each of the 6 response events over a single day with a Gaussian function, revealed a decrease in the SD of the response times as well as the improvement in the accuracy — that is, the peak of the Gaussian curves are closer to the target times. Group data (Fig. 3B) demonstrates that there was a significant improvement in both the accuracy and precision across three days of training.

In addition to the above prospective learning studies, insights into the motor temporal learning and the precision versus accuracy issue, have been gleaned from

retrospective learning studies in which the performance of nonmusicians and musicians has been compared. As one might expect, it has been reported that musicians have better perceptual and motor timing performance than nonmusicians (Cicchini et al., 2012; Grondin & Killeen, 2009; Rammsayer et al., 2012). For example Cicchini and colleagues (2012) reported that in a reproduction task with intervals ranging from 500 to 1200 ms, percussionists exhibited superior motor timing and were less influenced by temporal context (i.e., the other intervals used in the same block of trials). Interestingly the accuracy of the percussionists was superior to that of both the nonmusician and string player musician groups, but the precision (as measured by the mean variation coefficient) of the string players was better than that of the percussionists. Another study contrasted motor timing of nonmusicians and musicians on the longer time scale of 6 to 24 s, and observed better timing as measured both by precision and accuracy in the musician group (Grondin & Killeen, 2009).

Although additional experiments are needed, the existing data strongly suggests that improvement in precision and accuracy of timed motor responses is dissociable, an observation that constrains the models of temporal processing (see below).

4. Mechanisms and Location of Temporal Learning

4.1. *Models and Mechanisms of Temporal Processing*

Our goal here is not to provide a comprehensive review of the models and potential mechanisms underlying temporal processing, thus we refer the reader to previous reviews that have focused on the neural underpinnings of timing (Allman & Meck, 2012; Buhusi & Meck, 2005; Buonomano & Karmarkar, 2002; Buonomano & Laje, 2010; Coull et al., 2011; Goel & Buonomano, 2014; Mauk & Buonomano, 2004; Medina & Mauk, 2000). Nevertheless, any discussion of perceptual and motor temporal learning requires consideration of the potential mechanisms underlying timing, so we will briefly summarize the main theories of temporal processing in order to place the above studies in context.

As mentioned above a critical issue relating to the neural basis of timing and to temporal perceptual learning, is often posed as whether timing relies on what can be considered ‘dedicated’ or ‘intrinsic’ (distributed properties inherent to most cortical networks) mechanisms (Ivry & Schlerf, 2008). The term dedicated refers to highly specialized mechanisms — i.e., dedicated circuits would not be involved in other computations. Additionally, dedicated models are generally taken to be ‘centralized’ (see Buonomano & Karmarkar, 2002), meaning that in some sense a dedicated system would represent a ‘master’ clock. The terms ‘dedicated’ and ‘intrinsic’ are by necessity somewhat imprecise, however, they provide an extremely useful dichotomy to categorize different views regarding the mechanisms of timing.

The prototypical example of a dedicated model of timing is the concept of an internal clock (Creelman, 1962; Gibbon et al., 1984; Treisman, 1963). In its simplest form the internal clock framework suggests that some specialized neural circuitry is composed of an oscillator, and an accumulator that essentially counts the ‘ticks’ of the oscillator providing a linear metric of time. While there is little experimental support for the notion that timing relies on a centralized pacemaker-accumulator mechanism, the internal clock model continues to provide a valuable framework to study the neural basis of timing.

Intrinsic models propose that timing is a general computation of most neural network. The prototypical example of an intrinsic model of timing is the state-dependent network (SDN) model (Buonomano, 2000; Buonomano & Merzenich, 1995; Mauk & Buonomano, 2004). Within the SDN framework, timing is more analogous to the continuously changing dynamics produced by a pebble thrown into a pond, than to a conventional clock. Networks of neurons are very rich dynamical systems, and as such, changing patterns of activity can be set in motion. The time-varying nature of these patterns can provide a signature that can be used to tell time in the same manner that the expanding diameter of the ripples on a pond provides a measure of how much time has elapsed since the pebble was thrown in.

The first model to propose that timing may be encoded in dynamically changing patterns of activity was put forth by Mauk in the context of the Marr–Albus–Mauk model of the cerebellum (Mauk & Donegan, 1997). Specifically, it was proposed that a stimulus can trigger a dynamically changing pattern of neural activity as a result of negative feedback within the network (Buonomano & Mauk, 1994; Mauk & Donegan, 1997; Medina & Mauk, 2000). Such a timing mechanism has been referred to as a population clock because time is encoded in the changing population of active neurons within a network (Buonomano & Karmarkar, 2002; Buonomano & Laje, 2010). SDN models emphasize that in addition to the changing patterns of activity within a network, neurons and synapses have a large repertoire of naturally time-varying properties on the subsecond scale, perhaps most notably short-term synaptic plasticity — a form of plasticity in which the strength of synapses increases or decreases in a use-dependent manner on the time scale of hundreds of milliseconds. Thus the state of a network includes not only an ‘active state’ (which neurons are firing) but also a ‘hidden state’ (time-varying neural properties such as short-term synaptic plasticity). Indeed, experimental evidence suggests that short-term synaptic plasticity underlies some forms of neuronal interval selectivity (Carlson, 2009; Edwards et al., 2007; Goel & Buonomano, 2014; Kostarakos & Hedwig, 2012).

A number of experimental studies have reported that the dynamic changes in the activity pattern of neural networks can indeed encode time (Crowe et al., 2010; Jin et al., 2009; Lebedev et al., 2008). But it is important to note that while timing is proposed to be an inherent property of neural network dynamics in the SDN model, in order for these dynamics to be used to actually solve temporal problems,

the dynamics must be readout by downstream neurons that can fire at specific time points. In the context of the cerebellar model, this readout is accomplished by appropriately adjusting the synaptic weights from the dynamically changing population of granule cell to the ‘readout’ Purkinje cells (Buonomano & Mauk, 1994; Mauk & Donegan, 1997; Medina & Mauk, 2000). Similarly in the SDN model, the readout is achieved by adjusting the weights of excitatory neurons in the cortical circuits to downstream neurons that can then function as interval detectors (Buonomano, 2000; Buonomano & Merzenich, 1995). Under the framework of the SDN model, timing of different intervals within the same task — e.g., the discrimination of 100 or 250 ms auditory interval — would rely on different neurons within the same circuit. Thus learning-dependent improvements of the discrimination of a 100 ms interval, requires tuning downstream neurons to readout the relevant network states corresponding to the 100 ms interval — leading to temporally specific learning.

Numerous other mechanisms of timing have been proposed (Ahrens & Sahani, 2011; Allman et al., 2012; Buhusi & Meck, 2005; Fiala, Grossberg, & Bullock, 1996; Matell & Meck, 2004) including the proposal that at the onset of a stimulus, multiple oscillators that beat at different frequencies are engaged, and that time is readout from these oscillators by coincidence detectors that tell time through the beats among the oscillators (Allman & Meck, 2012; Coull et al., 2011; Matell & Meck, 2004; Miall, 1989). While this model does not fit neatly into a dedicated or intrinsic model framework, the multiple oscillator model is in a sense dedicated because it invokes a specialized array of independent oscillators of different frequencies. But the multiple oscillators model has also been placed in a more intermediate hypothesis in which timing mechanisms are neither entirely distributed nor fully centralized. This intermediate view hypothesizes the existence of a core-timing network represented by the basal ganglia-cortico-thalamic circuit that interacts with context-dependent brain regions, i.e., regions that are selectively engaged depending on the different task requirements (Merchant et al., 2011, 2013).

Another notion, one which has considerable experimental support, is that time may be encoded in the linear changes of neurons firing rate (Durstewitz, 2003; Leon & Shadlen, 2003; Quintana & Fuster, 1992; Rainer et al., 1999). Indeed, ramping activity has been observed in the neurons of a number of different areas during timing tasks (Brody et al., 2003; Janssen & Shadlen, 2005; Lebedev et al., 2008; Leon & Shadlen, 2003; Niki & Watanabe, 1979; Quintana & Fuster, 1992; Schneider & Ghose, 2012). Ramping models (Durstewitz, 2003; Reutimann et al., 2004; Simen et al., 2011) could potentially fit into either dedicated or intrinsic framework depending on the mechanisms responsible for such dynamics and on how ubiquitous these mechanisms are throughout the nervous system.

In the context of this review on temporal perceptual learning it is important to consider how the above models account for learning. While some of the models do not explicitly discuss learning, others explicitly or implicitly place the locus of

learning at the level of the readout units. For example, the state-dependent network and striatal beat frequency models share the property that output units must learn the specific patterns of activity of the timing networks/units (Buonomano & Mauk, 1994; Matell & Meck, 2004; Mauk & Donegan, 1997). This learning fits well into conventional neurocomputational frameworks in which unsupervised or supervised learning rules can be used to train output neurons to recognize the relevant patterns. The other option is that learning may occur at the level of the neural circuits that are actually doing the timing as opposed to reading out the temporal information (Haß et al., 2008; Laje & Buonomano, 2013). Indeed state-dependent network models assume there is plasticity also within the recurrent circuit — but this plasticity would be slower to develop and come into play only with extensive practice. Also in ramping models the rate of the change in firing rate can be tuned in a manner that reflect learning by potentially altering the behavior of the timer circuits themselves (Durstewitz, 2003; Reutimann et al., 2004; Simen et al., 2011).

It remains far from clear how the brain tells time, thus it is an open question whether dedicated or intrinsic frameworks best capture the neural mechanisms of temporal processing. Nevertheless, given the diversity of areas (see below) and mechanisms that have been implicated in timing, it is highly unlikely that a single well-defined brain area is universally responsible for all forms of timing. We favor the view that timing is an intrinsic computation of neural circuits, and that the circuits underlying timing can be distinct (but possibly shared) depending on the task and modality being invoked.

4.2. Neurophysiological Correlates of Temporal Learning in Humans

In humans, the neurophysiological changes associated with temporal learning remain unclear. This is due in large part because, to the best of our knowledge only two studies have explicitly looked at brain plasticity induced by temporal learning performing pre- and post-training measurements: a magnetoencephalography (MEG) and a magnetic resonance imaging (MRI) study (Bueti et al., 2012; van Wassenhove & Nagarajan, 2007).

In the first of these studies human volunteers were trained for three days (for a total of 2400 trials) in a temporal discrimination task of auditory stimuli (trains of four tones separated by 200 ms) while MEG recordings were acquired. Temporal training led to improvements of discrimination thresholds only for the trained condition and was associated with amplitude changes of early auditory evoked responses (i.e., m100, Van Wassenhove & Nagarajan, 2007). This result suggests that plasticity in an auditory timing task can occur locally in early auditory cortices.

A similar result but in the visual domain was reported in a recent MRI study showing an increase of the hemodynamic response in bilateral mid-occipital gyri after training with a visual temporal interval (Bueti et al., 2012). In this study healthy volunteers were trained for four days (one hour per day, 570 trials) to discriminate 200 ms visual temporal intervals. Before and after training structural

as well as functional MRI data were acquired while participants were tested with stimuli of the trained (vision) and untrained sensory modality (audition) and with the trained (200 ms) and untrained temporal intervals (100, 400 ms). Consistent with previous psychophysical results, temporal learning was found to be duration specific and to partially generalize from the visual to the auditory modality. At neurophysiological level the hemodynamic response to the trained interval was greater in post compared to pre-training session, in visual areas for the visual intervals (i.e., trained sensory modality) and in the insular cortex for both the visual and the auditory (i.e., untrained modality) intervals (see Fig. 4A). Generalization to the auditory stimuli was associated with the activation of the left inferior parietal cortex (Fig. 4B). Training-related changes were also observed in grey-matter volume and white-matter connectivity of the right cerebellar cortex (cerebellar lobules VIIa and VIIIa, see Fig. 4C). Moreover both structural and functional changes correlated with changes in behavioral performance.

These findings show, first, that a relative short temporal training could produce both functional and structural changes not in a single region but in a network of brain areas. Some of these regions are modality specific others are modality independent. Second, that the brain changes correlated with the trained interval can be dissociated from those correlated with the cross-sensory generalization. This neurophysiological dissociation is in line with previous behavioral studies showing that learning of the trained interval and spatial generalization represents an early and a late stage of the learning process, respectively (Burk & Humes, 2007; Wright et al., 2010). Concerning this particular MRI finding we can hypothesize that learning-related activations observed for the trained visual modality (i.e., insula and visual cortices) reflect time-specific processes associated with perceptual learning, while the activation of the parietal cortex specific for audition may relate to ‘intermodal transfer’ and generalization. More generally we can also speculate that similarly to the motor learning domain, where different learning stages engage distinct brain regions (Hikosaka et al., 1999; Hikosaka et al., 2002), the temporal training of a specific interval requires the involvement of local/modality specific temporal mechanisms (e.g., visual or auditory regions) whereas spatial generalization engages high-level/amodal cores of timing networks (e.g., parietal and premotor cortices).

In accord with the finding that parietal cortex is activated during generalization of temporal learning across sensory modalities is the observation that transcranial stimulation of the parietal lobe paired with a behavioral training, leads to improvements in both the trained (i.e., numerosity discrimination) and the untrained tasks (i.e., temporal and spatial discrimination; Cappelletti et al., 2013). This result has been interpreted as suggesting the existence in the parietal cortex of a neural substrate that is shared between numerical (i.e., the trained task), temporal and spatial abilities (i.e., the untrained tasks). The key question not only of this particular study but in general of all learning studies is the following: what is actu-

A) fMRI Results - Temporal Learning

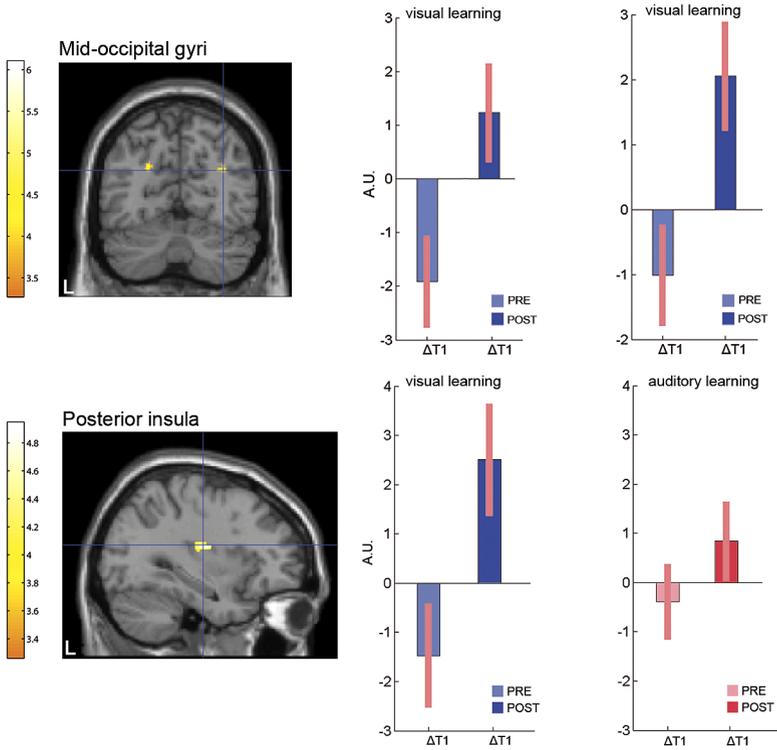
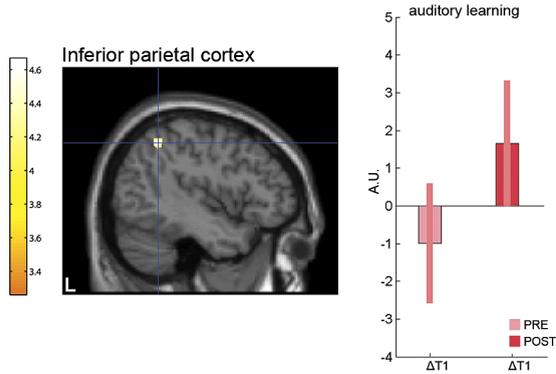


Figure 4. Timing-related plasticity in the human brain. (A, B) Brain areas showing training-related plasticity as measured by fMRI. In both panels the contrast tested is: (trained duration–untrained duration) PRE > (trained duration–untrained duration) POST. Statistical threshold was set to $p_{\text{FWE}} < 0.05$ corrected for multiple comparisons. Activations are overlaid on the single subject $T1$ -MNI template. For all cluster of voxels we plot the parameter estimates for the $\Delta T1$ condition (i.e., the actual discrimination threshold) in pre (light shade) and post-training (dark shade) fMRI sessions. A.U. is arbitrary unit. (A) Upper row shows left and right mid-occipital regions activated during the visual task (dark bars). The lower row shows the left posterior insula activated in both the visual (dark) and the auditory (light) task. (B) Left inferior parietal cluster activated only in the auditory task (light). (C) Training-related plasticity as measured by grey and white-matter structural indexes. The panel shows right cerebellar clusters where grey matter volume (GM) and fractional anisotropy (WM) were greater in post compared to pre-training session. Statistical threshold was set to $p_{\text{FWE}} < 0.05$ corrected for multiple comparisons. For both clusters we also show the correlations between the structural indexes (i.e., $T1$ post– $T1$ pre/ $T1$ pre and FA post–FA pre/FA pre) and the behavioral performance. Clusters are overlaid on the single subject $T1$ MNI template. Modified from Figures 2 and 3 from Buetti et al. (2012). This figure is published in colour in the online version.

ally shared between trained and untrained conditions (different tasks or different stimulus dimensions) and what is transferred during generalization? Are core cognitive abilities shared, e.g., a common representation? Or are secondary aspects of the tasks shared, like the response selection or the strategy used? The answer to

B) fMRI Results - Intersensory Generalization



C) Structural Results - Learning Related Changes in Cerebellum

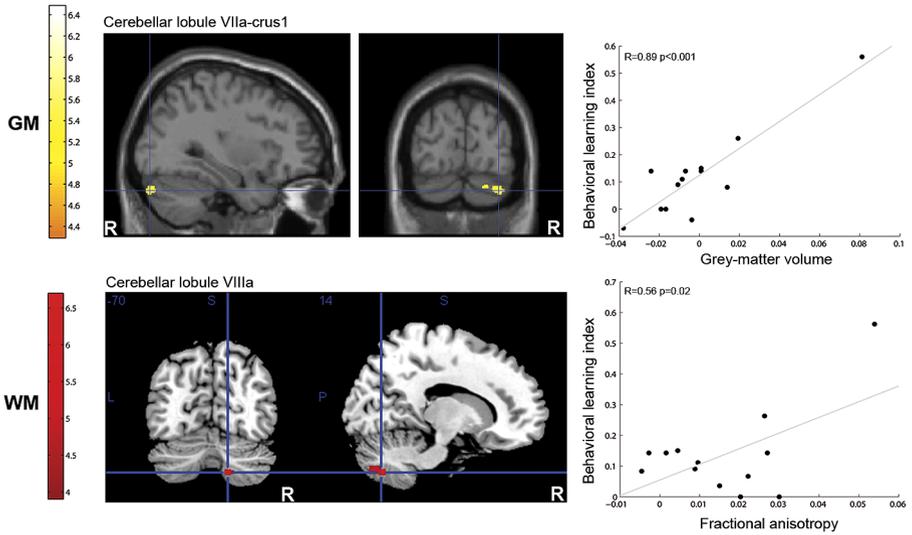


Figure 4. (Continued.)

these questions remains unknown. However these considerations relative to the object of the generalization have to be taken into account when interpreting spatial generalization in temporal learning studies. In the temporal learning context, spatial generalization can be interpreted as reflecting the existence of a common timing network only if the transfer during generalization concerns the duration representation. However, if the transfer is about the strategy used to perform the task or other non-temporal components of it, then its presence cannot be used to make claims about the neural substrate of temporal representations.

Finally, a related issue in interpreting the findings of both neurophysiological and behavioral temporal learning studies concerns the specificity of learning. Perceptual and motor timing tasks are characterized by the presence of non-temporal components (e.g., memory, decision and motor components) and behavioral training could, in principle, affect any of them. To overcome this interpretational issue fMRI studies should always compare conditions that are matched across cognitive components (i.e., attention, memory and motor responses) or alternatively compare groups that are trained on different stimulus features (e.g., time and pitch).

4.3. Neurophysiological Correlates of Temporal Learning in Animals

Our knowledge of the neurophysiological changes associated with temporal learning derives mainly from animal studies. Some of the earliest of these studies explored temporal motor learning in the cerebellum as revealed by eyelid conditioning. In eyelid conditioning a neutral stimulus such as a tone (CS) is repeatedly paired with an unconditioned stimulus (US) such as a puff of air to the eye, which evokes a reflex eyelid response. The repeated pairing of the tone and unconditioned stimuli leads to the acquisition of a conditioned response, i.e., the tone stimulus elicits eyelid closure. Importantly, the timing of the eyeblink response is strongly dependent on the time interval between the CS and US, for example if the CS-US interval is 500 ms, the timing of the learned eyeblink response is a bit under 500 ms (Mauk & Buonomano, 2004; Mauk et al., 2000). Lesions of the cerebellar cortex have been shown to spare the conditioned responses but to abolish response timing (Medina et al., 2002; Perrett et al., 1993). In the Marr–Albus–Mauk model of the cerebellum, the timing is hypothesized to arise from the time-varying patterns of granule cell activity and the temporally specific decrease in the activity of the Purkinje neurons. This decrease is mediated by depression of the granule to Purkinje cell synapses that are activated at the time of the reinforcing unconditioned stimulus (Mauk & Donegan, 1997).

More recently animal studies have explicitly examined the neural correlates of temporal learning. In one of such studies, rats were trained to associate the stimulation of one of the two eyes with either a early (approximately 1 s) or a late (approximately 2 s) reward (the two rewards were actually a function of a low or high number of licks, which resulted in early or late rewards; Shuler & Bear, 2006). The firing pattern of V1 neurons after visual stimulation was modulated by these two different reward delays (43% of the recorded neurons). For example, some neurons showed sustained firing rate to a stimulus, and the duration of the firing reflected the interval between that stimulus and the reward. Reward timing neurons in V1 were not observed in naïve rats. This last result has led to the conclusion that timing activity in primary visual cortex is a consequence of a learning process. In a more recent work this research group demonstrated that it was possible to observe 'learned' timed responses by pairing electrical stimulation and acetylcholine in visual cortex slices (Chubykin et al., 2013). This finding is consis-

tent with another *in vitro* study showing that the chronic presentation of a specific interval to cortical circuits in culture, alters the temporal profile of evoked activity in a manner that reflects the experienced interval (Johnson et al., 2010). These two studies demonstrate that *in vitro* cortical circuits can in a manner of speaking learn temporal intervals, and provide some of the most compelling evidence that timing is a local and intrinsic computation of neural circuits.

In the last part of this review we focus on animal works that did not explicitly study temporal learning because they did not, for example, contrast pre- and post-training neural responses, but made extensive use of training. These studies often focused on the neural basis of timing in animals that were trained for several months before electrophysiological recording. In the majority of cases it is difficult to establish the extent to which these electrophysiological findings reveal mechanisms that are independent from learning. Despite these caveats, these studies provide valuable insights to our understanding of the neural mechanisms underlying temporal learning (Table 2).

As discussed in Sections 2 and 3 both perceptual and motor temporal learning in the subsecond range are duration selective, i.e., training increases duration sensitivity and reduces performance variability exclusively for the trained interval. This selectivity seems to suggest the existence of neurons tuned to specific temporal intervals and indicate duration-sensitive tuning as a possible mechanism underlying the active encoding of time in the millisecond/second range.

The existence of duration tuning has been hypothesized by theoretical models (Ivry & Richardson, 2002; Matell & Meck, 2004), suggested by behavioral findings in humans (Heron et al., 2012), but only recently has been supported by neurophysiological observations. In monkey pre-supplementary motor area (pre-SMA) neurons selectively firing for specific temporal intervals have been observed (Mita et al., 2009). In this experiment, monkeys were trained to hold down a response key for 2, 4 or 8 s. The holding time was signaled by a color cue. During the presentation of the color cue, two main classes of neurons were described in pre-SMA: neurons selectively responsive to the different holding times ('time selective', 35% of neurons responsive to the color cue) and neurons with ramping activity proportional to the different time intervals (47% 'time graded neurons', Mita et al., 2009). Premotor neurons selective to different temporal intervals but in the subsecond range (range tested 450–1000 ms) and across different motor tasks (i.e., finger tapping and interval reproduction) and sensory modalities (visual and auditory) have also been recently described by Merchant and colleagues (Merchant et al., 2013). In this study the authors trained monkeys in two distinct motor timing tasks. In the synchronization-continuation task, monkeys had to synchronize a finger movement (a button press) with the presentation of a visual or an auditory sound; after a few synchronized movements the stimuli driven the movements stopped and monkeys continued tapping at the same stimulus rate. In the reproduction task, monkeys had to reproduce with two successive finger presses the

Table 2.

The neurophysiology of temporal learning. Summary of human and animal studies investigating the neural basis of temporal processing by using temporal learning protocols (human studies) or investigating time behavior after learning (animal studies). Studies are listed according to the task used, the time range tested and the brain regions involved in time computations. TD = temporal discrimination, (cs) = constant stimuli, (ap) = adaptive procedure, CC = classical conditioning, OCDt = orientation change detection task, DEMt = delayed eye movement task, REX = reward expectation, P = production, SST = sequential saccade task, FT = finger tapping, STS = self timed saccades, 2ITG = 2 intervals temporal generalization, DMt = delay memory task

Studies	Task	Time (s)	Areas
Humans			
Van Wassenhove & Nagarajan, 2007	TD (cs)	0.2	auditory
Bueti et al., 2012	TD (ap)	0.1-0.4	visual, insula, premotor; cerebellar cortex
Animals			
<5 s			
Perret et al., 1993	CC	0.15, 0.75	cerebellar cortex
Medina et al., 2000	CC	0.25-0.75	cerebellar cortex
Ghose & Maunsell, 2002	OCDt	1-3	V4
Leon & Shadlen, 2003	TD (cs)	0.3, 0.8	LIP
Jassen & Shadlen, 2005	DEMt	1-2	LIP
Shuler & Bear, 2006	Rex	1-2	V1
Lebedev et al., 2008	P	2.5, 4.5	motor-premotor
Genovesio et al., 2009	TD (cs)	0.2-1.2	prefrontal
Jin et al., 2009	SST	0.4-0.8	prefrontal, striatum
Mita et al., 2009	P	2-8	pre-SMA and SMA
Merchant et al., 2011	FT	0.45-1	medial premotor
Schneider & Ghose, 2012	STS	1	LIP
Chubykin et al., 2013	Rex	1-2	V1
Merchant et al., 2013	P, FT	0.45-1	premotor
>5 s			
Matell et al., 2003	2ITG	10, 40	striatum
Pastalkova et al., 2008	DMt	10, 20	hippocampus

duration of a presented visual or auditory interval. The results show that a proportion of the recorded premotor neurons fired selectively for different temporal intervals. Interestingly this ‘interval selectivity’ was invariant across the two tasks and the sensory modalities used to drive the timing behavior. This result suggests the existence in premotor cortex of an abstract representation of duration. Based on these findings we can further speculate that duration sensitive neurons in premotor cortex reflect an active reconstruction, i.e., a read-out mechanism, of explicit duration codes from relevant temporal signal sources that comes from elsewhere in brain (perhaps sensory regions). While most of the above primate studies did not

explicitly study temporal learning it is fair to assume that many of the observed responses are likely a result of the training.

As summarized in Table 2, timing-related activity and plasticity has been observed in many brain regions: in visual cortices (Chubykin et al., 2013; Ghose & Maunsell, 2002; Shuler & Bear, 2006) in the lateral intraparietal area (LIP, Janssen & Shadlen, 2005), in the premotor cortex (Lebedev et al., 2008; Merchant et al., 2013; Mita et al., 2009), in the prefrontal cortex (Genovesio et al., 2009; Jin et al., 2009), in the striatum (Jin et al., 2009; Matell et al., 2003) and also in the hippocampus (Kim et al., 2012; Pastalkova et al., 2008). Thus these studies, together with the studies in the two previous sections, suggest that temporal learning engages a number of different brain areas including sensory, motor and associative cortices and relies at least in part on the emergence of temporally-tuned neurons.

5. Conclusions

Here we have reviewed the literature on temporal perceptual learning in humans focusing primarily on the subsecond time scale. The studies reviewed allow us to formulate two general conclusions:

1. In both the sensory and motor domains timing undergoes robust learning. Temporal learning, however, generally requires relatively long practice periods as evidenced by the fact that the majority of learning studies have trained subjects over multiple days.
2. Temporal perceptual learning is generally temporally specific, that is, the improvements produced by training are often limited to the trained (or nearby) intervals.

This second point is perhaps the single most important principle to be derived to date from the studies of temporal perceptual learning, as it provides key insights into the potential mechanisms underlying timing and temporal perceptual learning. For example, twenty years ago one might have hypothesized that temporal perceptual learning was a result of the increased precision (and accuracy) of a centralized timing circuit. Using a stopwatch analogy, such a mechanism would essentially correspond to creating a better stopwatch, and thus be expected to improve timing across a wide range of intervals. The studies reviewed above strongly argue against such a scenario, and suggest that whatever the underlying mechanisms, temporal perceptual learning is generally interval specific. This temporal specificity likely relies primarily on improvements on ‘reading out’ the relevant temporal signatures (e.g., the neural dynamics) generated by the neural circuits that actually mark time.

A third point that emerges from the literature is that the benefit of learning can be transferred from a trained stimulus to an untrained condition (i.e., spatial gen-

eralization). This can be a stimulus of a different sensory modality, pitch, spatial position, and even a different task. However, it is also evident that generalization can be dissociated from temporal learning (Wright et al., 2010). Thus generalization and temporal learning appear to be different stages of the learning process and may be associated with different neural substrates.

The field of the neural basis of temporal processing remains in its infancy as even the most basic questions regarding timing remain unanswered. The unanswered questions include which parts of the brain are involved in timing and temporal learning. Although it is still too early to answer these questions, based on the findings reviewed here and on the fact that more brain areas than not (Table 2) have been implicated in timing, we favor the view that timing is a distributed and intrinsic property of the brain. Thus, which parts of the brain are responsible for temporal learning will depend in part on the modality, task, and time-scale of interest.

Temporal learning studies will continue to provide an essential approach to constrain and study how the brain tells time, and future work should further emphasize the need to study the generalization of temporal perceptual learning and characterize its psychophysical signatures (Shi et al., 2013). Lastly, we emphasize that elucidating how timing improves as a function of experience will be a necessary step toward understanding some of the most important computational tasks the brain performs, because the ability to discriminate and produce temporal patterns allows us to communicate, appreciate and play music, anticipate events in our environment, and execute complex spatiotemporal motor patterns.

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