Citation: Merchant, H. & Yarrow, K. (2016). How the motor system both encodes and influences our sense of time. Current Opinion in Behavioral Sciences, 8, pp. 22-27. doi: 10.1016/j.cobeha.2016.01.006

This is the accepted version of the paper.

This version of the publication may differ from the final published version.

This is an author-final version. The final (press-formatted) version of this article will be published by Elsevier in *Current Opinion in Behavioral Sciences* (DOI:10.1016/j.cobeha.2016.01.006).

How the motor system both encodes and influences our sense of time

Hugo Merchant [a,*&], Kielan Yarrow [b*&]

a. Instituto de Neurobiología, UNAM, campus Juriquilla

b. Department of Psychology, City University London

*Corresponding authors:

Dr. Hugo Merchant,

Phone: +52 442-238-1040

E-mail: hugomerchant@unam.mx

Dr. Kielan Yarrow,

Rhind Building, City University London,

Northampton Square, London EC1V 0HB, UK

Phone: +44 20 70408530

Email: Kielan.yarrow.1@city.ac.uk

[&]Equal contribution

Abstract

Several lines of evidence suggest that motoric brain structures may form the core amodal component of a neural network supporting a wide range of timed behaviours. Here, we review recent findings which elucidate the neural computations that occur within motor regions, and in particular the supplementary motor area, in order to support precisely timed actions. Although motor activity may help us represent time, it is also clear that action both enriches and complicates the interpretation of sensory inputs. Hence, in the second half of this review, we also consider the latest findings regarding the perceptual distortions that our actions can impose upon the subjective timeline.

Highlights

- The core timing mechanism resides within the motor system
- Interval tuning in SMA is a dynamic signal encoding time in different contexts
- The prediction of sensorimotor events is transmitted from motor to sensory areas
- Actions lead to highly selective distortions of perceived time
- Actions distort the subjective timeline before, during and after a movement

Introduction

Precise timing is an implicit component of all skilled actions, and often also an explicit requirement, as in musical production and dancing. It is possible to view such motor timing as a specific process generated by a dedicated timer. However, it is now clear that brain regions traditionally viewed as motoric form part of a core timing network which interacts dynamically with sensory regions to support a range of timing needs. Perception, meanwhile, is not merely a passive process; it is also an active one operating in tandem with the motor system. This implies that, just as for other aspects of perception, we should take account of our actions when interpreting the temporal meaning of sensory inputs. In this paper we provide a selective review of recent work in these two areas. First, we consider the neural mechanisms that support timed behaviours, with a particular focus on the role of the supplementary motor area (SMA), a key node in the cortico-thalamic-basal ganglia timing circuit (CTBGc). Second, we consider the ways in which temporal perception is affected by our ongoing actions.

Neural mechanisms for timed behaviours

Speech comprehension and articulation, as well as music appreciation and execution, depend on intricate loops linking the perception and execution of timed intervals. Hence, the timing mechanism engaged in these complex activities is multimodal and needs to extract temporal information from incoming stimuli and develop predictive signals about upcoming sensory and motor events. This scheme distinguishes time sensation (bottom-up) and time prediction (top-down). There is a vast functional-imaging literature that indicates that timing is based on a partially overlapping neural network that has two elements. The first is a core-timing network that resides in the motor system and includes the CTBGc, which emits predictive signals to the rest of the brain independently of the timing context. The second is a set of areas that are selectively engaged depending on the specific behavioural requirements of a task [1]. Thus, on one hand SMA and the basal ganglia of the CTBGc are activated during time production and perception tasks using both visual and auditory stimuli with various interval structures [2,3]. On the other hand, specific sensory and association areas are involved in interval timing, depending of the exact temporal paradigm [3,4].

Two basic features of interval timing are a linear increase in temporal variability as a function of interval duration, a phenomenon called the scalar property, and a systematic bias in estimated durations towards the mean of the input intervals. Using a Bayesian observer model it is possible to capture both features when the temporal context changes, creating a testable framework regarding how the core timing network represents the prior distribution of intervals and measures time in a scalar fashion [5]. Indeed, a scalar representation of time has been observed recently in the primate SMA [6**], as well as in the rodent striatum [7].

Recent neurophysiological experiments have confirmed that the SMA is a crucial element in the core timing mechanism. The neural activity from this area in macaques was recorded during a synchronization-continuation task (SCT), where the tapping behaviour of monkeys was synchronized to a metronome of isochronous stimuli, followed by a period where animals internally temporalized their movements [8]. Monkeys use an explicit timing strategy to perform this task, tightly controlling the duration of the pauses (or dwell times) between movements, then making stereotyped pushing movements, across each produced interval in the rhythmic sequence [9].

Interestingly, SMA activity during the SCT indicates that the time-keeping mechanism is governed by different layers of neural clocks (Figure 1). At the bottom of the hierarchy is ramping activity that shows an instantaneous increase or decrease in response magnitude. This peaks at the time of the anticipated response, suggesting its involvement in the temporal construction of motor intentions and actions [10,11]. In fact, a tight interaction between the ramping cells computing elapsed time since the previous tap and a different set of cells encoding time remaining to the next tap generates a coordinated cycle of activation during the SCT that ends with the triggering of each tap [12].

On top of such climbing activity, there are SMA cells that are tuned not only to the duration of the produced intervals but also to the serial-order of elements within each reproduced sequence in the SCT. This suggests that the SMA uses a cell population signal that works rather like the notes of a musical score, representing both the duration and the rank order of the produced intervals in the sequence [13**]. Most importantly, a subgroup of these interval-tuned neurons showed similar preferred intervals across both auditory and visual modalities and during tasks involving the production of one or multiple intervals. This observation supports the notion that SMA is part of the core timing mechanism that uses interval tuning as an abstract signal across timing behaviours and modalities [13**].

The multiplexing of duration and serial order is a dynamic process, where discrete neural ensembles encode these parameters through small-time windows, so that the pattern of neural activity changes dramatically within each interval [6**]. Thus, the rapid activation of small groups of cells provides a strong synaptic drive to the next ensemble producing a neural avalanche across an interval [6**], which is repeated for every serial-order element of the SCT sequence [14*]. A recent study has shown that the activity of duration/serial-order tuned cells in SMA can be statistically linked to either the sensory or motor events of the SCT [14*]. Moreover, a substantial group of sensory-aligned cells predict the appearance of the next stimulus in the sequence instead of simply responding to the previous stimulus. Therefore, the activity of this neural subpopulation can act as a top-down predictive signal to create the indispensable sensory-motor coupling that permits an animal to execute the SCT.

Such predictive capabilities of the motor system seem well designed to sharpen perception in rhythmic contexts. When attention is allocated to auditory or visual events in a rhythmic sequence, delta oscillations of primary visual and auditory cortices of monkeys are entrained (i.e. phase-locked) to the attended modality [15]. Notably, however, the time-dependent processing of input stimuli can be further enhanced by using top-down signals coordinated by the motor system (Figure 1). A recent psychophysical study provides evidence for the existence of predictive signals associated with a rhythmic motor behaviour that are fed back to the sensory areas through a corollary discharge to enhance processing of incoming auditory signals at a particular cyclic phase [16**]. It seems that the motor system routinely generates strong dynamic signals in order to internally represent time, predict sensory events, and drive behaviour [17]. A possible mechanism for such active information distribution is through small pieces of spike-encoded data embedded in slow brain oscillations that can travel long distances [18]. Indeed, beta oscillations may be the channel for these top-down signals during rhythm perception and entrainment. The exact nature of the cell activity inserted into the beta oscillations is still unknown, but they have been associated with: (1) both the stimulus-driven and the endogenous interpretation of the beat in early auditory areas [19]; (2) the prediction of the onset of the next temporal event [20]; (3) the dynamical coupling between the motor and auditory areas [20], and (4) internally driven timing behaviour [21-23]. Such interactions between top-down information and perceptual processes provide a natural segue to our second area of focus: The tendency for action to bias temporal perception.

Time perception in the context of action

Actions induce distortions of the subjective timeline. Numerous distortions have been reported, affecting the events (and thus the intervals they define) occurring before, during, and after action (summarised in Figure 2). Here, we provide a brief update on classic findings.

In the chronostasis illusion, a new percept that is revealed by an action is experienced as longer than a control percept. For example, the target of a saccadic eye movement has a subjectively expanded duration, which may explain the commonly experienced stopped-clock effect (i.e. when we glance at a clock just after the second hand has advanced, and are surprised when it fails to advance again as quickly as we expect; [24]). A similar effect emerges when we reach to touch a vibrating stimulus [25].

Research conducted in the noughties suggested that saccadic chronostasis reflects an active mechanism compensating for sensory degradation during a saccade. The post-saccadic image may be being *antedated*, to stitch up the temporal gap induced by saccadic suppression and masking [24,26-29]. An active mechanism is implied because chronostasis emerges over and above any time dilation induced in passive control conditions, which simulate the visual effects of a saccade. A recent paper, however, included a very realistic passive control condition, and found temporal distortion similar to that obtained using real saccades (albeit in a very small sample of observers; [30*]). As we will see, action-induced timing illusions are often challenged on the basis that the fundamental cause is some *correlate* of action, rather than the action per se. For saccadic chronostasis, this issue bears further scrutiny.

A similar effect, intentional binding, arises when an action causes a punctate event (such as a beep) to occur after a short delay [31]. Typically, the time of both the action and the beep are evaluated against a rapidly rotating clock in separate blocks. Judgements are made in a condition when the action causes the beep, but also in control conditions when each occurs alone. Generally, the time of the action is perceived relatively later, and the beep relatively earlier, when the action causes the beep; hence they are “bound.” The logical implication, that the interval from action to beep is perceptually compressed, has been verified directly via interval judgements (e.g. [32]).

How central is action to this illusion? The effect is eliminated (even reversed) when the hand movement is triggered by magnetic brain stimulation, removing the sense of agency [30]. However, recent findings suggest that causality (rather than agency or intentionality) may be the critical factor inducing binding effects. For example, a binding-like effect can emerge between the “action” of an intentionless machine and a consequent flash [33]. It is important to keep in mind that this emphasis on causality stands against a backdrop of several studies emphasizing the importance of intentionality in this illusion [34]. Interestingly, while the focus of the effect has always been the interval between the action and the resulting sensory event, one recent study suggests that a similar temporal binding can occur between an imperative stimulus and an action, i.e. for the interval *prior* to action [35*]. The relative contributions of intentionality and causality to this new illusion are yet to be fully explored.

Shortly after intentional binding was described, a possible alternative account emerged in the form of motor-sensory temporal recalibration [36]. Here, an action causes an event, but only after a short lag (in baseline conditions the event occurs almost immediately). Participants adapt to these temporal relationships over multiple trials. On test trials, various timings are used and the time of the sensory consequence is judged relative to the time of the action. Compared to baseline, lag adaptation recalibrates the perceived temporal relationship, so that delayed events are now more likely to be judged synchronous with (or even preceding) the action. Now recall intentional binding. Because that effect is measured in a situation that might be expected to generate recalibration, it could be recast as a consequence of adaptation. However, at least one recent study suggests that these are actually independent effects [37].

Regardless of whether motor-sensory temporal recalibration explains intentional binding, it is interesting in its own right. Recent work shows that recalibration emerges when correlated events consistently lead (as well as lag) tapping actions ([38]; c.f. [35*]) and can also be induced by delayed-feedback tracking tasks [39]. Transfer of recalibration occurs when the stimulus changes ([40,41]; but see [42]). This, along with the details of the transfer observed between hand and foot tapping [43] and the (partial) capacity to adapt the two hands independently [44] suggests that recalibration mainly induces an *effector-specific* change in the perceived time of *actions*.

The studies described so far focus mainly on the interval after the action. What happens before and during an action? The answers may depend upon which aspect of the subjective timeline we assess. For example, Morrone and colleagues briefly flashed two lines before or during a saccadic eye movement, and found a compression of the interval between them [45,46]. The effect was most pronounced when both lines appeared just before the saccade, and could even result in subjective order reversals, but was not found for auditory stimuli. However, as with other illusions considered here, there are some questions about whether these effects are fundamentally motoric in nature, or arise from correlated changes in visual sensitivity [47].

A recent paper has now found analogous compression for *manual* actions [48*]. Specifically, an interval defined by two brief tactile stimuli was subjectively compressed immediately prior to and during a reach when the taps were applied to the reaching hand, but not when they were applied to the non-reaching hand. This effect also occurred during static (isometric) force production, but not in a passive control experiment when stimulus intensity was adjusted to approximate the reduced percept occurring during action (as a result of tactile sensory suppression).

This manual illusion is intriguing, but also puzzling, because it appears to be at odds with another recent report [49*]. Here, participants lifted either their index or middle fingers. When a vibrotactile stimulus was applied to the active finger, its perceived duration *increased,* but this did not occur for a stimulus applied to the static finger. This result is opposite to that described previously, despite a similar setup. This increase was also observed when visually judging the duration of the same action on a computer screen. It occurred regardless of exact viewing perspective and spatial alignment.

It is difficult to know what procedural differences gave rise to these apparently opposite effects, but we might speculate that dilated (filled) intervals generate simultaneous contrast effects affecting the empty intervals that they subsume. At first glance, a similar contradiction seems to emerge when the interval just prior to an action is considered. As already described, when assessed using two taps to the active hand, compression occurs just before movement [48*]. This is broadly in line with the bias to perceive a visual imperative stimulus (a change in the colour of a fixation dot) as later (assessed via comparison with a rotating clock) when it triggers an action [35*]. However, another recent report found that time (assessed visually) is *expanded* during the preparatory period preceding action [50]. In this case, however, the period in question was earlier, coming prior to the imperative stimulus triggering movement. Hence expansion of that interval is broadly consistent with a delayed perception of the imperative stimulus, and thus contraction of the interval from imperative stimulus to action onset.

Conclusions

In this brief review, we have highlighted how time is represented within core motor areas and translated into meaningful predictions and actions. Balancing the roles of core and dedicated timing systems in order to provide a more complete mechanistic explanation of their interactions and interdependencies will provide a key challenge for the future. We have also provided a concise update regarding the many ways in which time can be distorted by our actions. Researchers should focus on nailing down the functional relevance of these curious effects, in order to provide a concrete contribution to our understanding of active temporal perception.

Acknowledgements

We thank Raul Paulín and Luis Prado for their technical assistance. Hugo Merchant was supported by the grants CONACYT: 236836 and PAPIIT: IN201214-25.

References

[1] Merchant H, Harrington DL, Meck WH: **Neural basis of the perception and estimation of time.** *Annu Rev Neurosci* 2013, **36**:313-36.

[2] Macar F, Coull J, Vidal F: **The supplementary motor area in motor and perceptual time processing: fMRI studies.** *Cogn Process* 2006, **7**(2):89-94.

[3] Harrington DL, Castillo GN, Fong CH, Reed JD: **Neural underpinnings of distortions in the experience of time across senses.** *Front Integr Neurosci* 2011, **5**:32.

[4] Jantzen K, Steinberg F, Kelso J: **Functional MRI reveals the existence of modality and coordination-dependent timing networks.** *Neuroimage* 2005, **25**(4):1031-42.

[5] Jazayeri M, Shadlen MN: **Temporal context calibrates interval timing.** *Nat Neurosci* 2010, **13**(8):1020-6.

[6] ** Crowe DA, Zarco W, Bartolo R, Merchant H: **Dynamic representation of the temporal and sequential structure of rhythmic movements in the primate medial premotor cortex.** *J Neurosci* 2014, **34**(36):11972-83.

This paper describes a neural correlate of the scalar representation of time, as well as the properties of the dynamic mechanism governing the flux of encoding information across small SMA cell populations that represent the temporal and sequential structure of a rhythmic tapping task.

[7] Mello GB, Soares S, Paton JJ: **A scalable population code for time in the striatum.** *Curr Biol* 2015, **25**(9):1113-22.

[8] Zarco W, Merchant H, Prado L, Mendez JC: **Subsecond timing in primates: comparison of interval production between human subjects and rhesus monkeys.** *J Neurophysiol* 2009, **102**(6):3191-202.

[9] Donnet S, Bartolo R, Fernandes JM, Cunha JP, Prado L, Merchant H: **Monkeys time their pauses of movement and not their movement-kinematics during a synchronization-continuation rhythmic task.** *J Neurophysiol* 2014, **111**(10):2138-49.

[10] Renoult L, Roux S, Riehle A: **Time is a rubberband: neuronal activity in monkey motor cortex in relation to time estimation.** *Eur J Neurosci* 2006, **23**(11):3098-108.

[11] Knudsen EB, Powers ME, Moxon KA: **Dissociating movement from movement timing in the rat primary motor cortex.** *J Neurosci* 2014, **34**(47):15576-86.

[12] Merchant H, Zarco W, Perez O, Prado L, Bartolo R: **Measuring time with different neural chronometers during a synchronization-continuation task.** *Proc Natl Acad Sci U S A* 2011, **108**(49):19784-9.

[13] ** Merchant H, Perez O, Zarco W, Gamez J: **Interval tuning in the primate medial premotor cortex as a general timing mechanism.** *J Neurosci* 2013, **33**(21):9082-96.

This study shows that neurons in SMA are tuned to both the intervals and serial order elements of the SCT, and demonstrates that a subgroup of interval-tuned neurons show similar preferred intervals across both auditory and visual modalities and during tasks involving the production of one or multiple intervals, supporting the notion of a core timing mechanism.

[14] * Merchant H, Pérez O, Bartolo R, Méndez JC, Mendoza G, Gámez J, Yc K, Prado L: **Sensorimotor neural dynamics during isochronous tapping in the medial premotor cortex of the macaque.** *Eur J Neurosci* 2015, **41**(5):586-602.

This paper is the first to show that the activity of duration/serial order tuned cells in SMA can be statistically linked to either the sensory or motor events of the SCT, and that a substantial group of sensory aligned cells predict the appearance of the next stimulus in the sequence.

[15] Lakatos P, Karmos G, Mehta AD, Ulbert I, Schroeder CE: **Entrainment of neuronal oscillations as a mechanism of attentional selection.** *Science* 2008, **320**(5872):110-3.

[16] ** Morillon B, Schroeder CE, Wyart V: **Motor contributions to the temporal precision of auditory attention.** *Nature communications* 2014, **5**:5255.

This exciting paper shows that the predictive signals derived from rhythmic motor behaviour are send back to sensory areas through a corollary discharge to enhance processing of incoming auditory signals.

[17] Laje R, Buonomano DV: **Robust timing and motor patterns by taming chaos in recurrent neural networks.** *Nat Neurosci* 2013, **16**(7):925-33.

[18] Buzsáki G, Draguhn A: **Neuronal oscillations in cortical networks.** *Science* 2004, **304**(5679):1926-9.

[19] Iversen JR, Repp BH, Patel AD: **Top-down control of rhythm perception modulates early auditory responses.** *Ann N Y Acad Sci* 2009, **1169**(1):58-73.

[20] Fujioka T, Trainor LJ, Large EW, Ross B: **Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations.** *J Neurosci* 2012, **32**(5):1791-802.

[21] Bartolo R, Prado L, Merchant H: **Information processing in the primate basal ganglia during sensory-guided and internally driven rhythmic tapping.** *J Neurosci* 2014, **34**(11):3910-23.

[22] Kononowicz TW, van Rijn H: **Single trial beta oscillations index time estimation.** *Neuropsychologia* 2015, **75**:381-9.

[23] Bartolo R, Merchant H: **Beta Oscillations are Linked to the Initiation of Sensory-Cued Movement Sequences and the Internal Guidance of Regular Tapping in the Monkey.** *J Neurosci* 2015, **35**(11):4635-40.

[24] Yarrow K, Haggard P, Heal R, Brown P, Rothwell JC: **Illusory perceptions of space and time preserve cross-saccadic perceptual continuity.** *Nature* 2001, **414**(6861):302-5.

[25] Yarrow K, Rothwell JCE: **Manual chronostasis: Tactile perception precedes physical contact.** *Curr Biol* 2003, **13**:1134-9.

[26] Yarrow K, Whiteley L, Haggard P, Rothwell JC: **Biases in the perceived timing of perisaccadic perceptual and motor events.** *Percept Psychophys* 2006, **68**(7):1217-26.

[27] Yarrow K, Johnson H, Haggard P, Rothwell JC: **Consistent chronostasis effects across saccade categories imply a subcortical efferent trigger.** *J Cogn Neurosci* 2004, **16**(5):839-47.

[28] Yarrow K, Haggard P, Rothwell JC: **Action, arousal, and subjective time.** *Conscious Cogn* 2004, **13**(2):373-90.

[29] Yarrow K: **Temporal dilation: the chronostasis illusion and spatial attention.** In *Attention and time*. Edited by Nobre AC, Coull JT. . Oxford University Press; 2010: 163-176.

[30] * Knöll J, Morrone MC, Bremmer F: **Spatio-temporal topography of saccadic overestimation of time.** *Vision Res* 2013, **83**:56-65.

This study revisits the saccadic chronostasis illusion using several methodological innovations. It shows spatial as well as temporal dependencies for the effect, and casts doubt on the active/motoric interpretation developed in the original series of papers.

[31] Haggard P, Clark S, Kalogeras J: **Voluntary action and conscious awareness.** *Nat Neurosci* 2002, **5**(4):382-5.

[32] Moore JW, Wegner DM, Haggard P: **Modulating the sense of agency with external cues.** *Conscious Cogn* 2009, **18**(4):1056-64.

[33] Buehner MJ: **Understanding the past, predicting the future: causation, not intentional action, is the root of temporal binding.** *Psychol Sci* 2012, **23**(12):1490-7.

[34] Moore JW, Obhi SS: **Intentional binding and the sense of agency: a review.** *Conscious Cogn* 2012, **21**(1):546-61.

[35] * Yabe Y, Goodale MA: **Time flies when we intend to act: temporal distortion in a go/no-go task.** *J Neurosci* 2015, **35**(12):5023-9.

Here, an interesting new component of the intentional binding illusion is revealed by focussing on the imperative stimulus that precedes the action.

[36] Stetson C, Cui X, Montague PR, Eagleman DM: **Motor-sensory recalibration leads to an illusory reversal of action and sensation.** *Neuron* 2006, **51**(5):651-9.

[37] Cravo AM, Haddad H, Claessens PM, Baldo MV: **Bias and learning in temporal binding: Intervals between actions and outcomes are compressed by prior bias.** *Conscious Cogn* 2013, **22**(4):1174-80.

[38] Rohde M, Ernst MO: **To lead and to lag–forward and backward recalibration of perceived visuo-motor simultaneity.** *Front Psychol* 2012, **3**:599.

[39] Rohde M, van Dam LC, Ernst MO: **Predictability is necessary for closed-loop visual feedback delay adaptation.** *J Vis* 2014, **14**(3):4.

[40] Heron J, Hanson JV, Whitaker D: **Effect before cause: supramodal recalibration of sensorimotor timing.** *PLoS ONE* 2009, **4**(11):e7681.

[41] Sugano Y, Keetels M, Vroomen J: **Adaptation to motor-visual and motor-auditory temporal lags transfer across modalities.** *Exp Brain Res* 2010, **201**(3):393-9.

[42] Sugano Y, Keetels M, Vroomen J: **The Build-Up and Transfer of Sensorimotor Temporal Recalibration Measured via a Synchronization Task.** *Front Psychol* 2012, **3**:246.

[43] Yarrow K, Sverdrup-Stueland I, Roseboom W, Arnold DH: **Sensorimotor Temporal Recalibration Within and Across Limbs.** *J Exp Psychol Hum Percept Perform* 2013, **39**:1678-1689.

[44] Sugano Y, Keetels M, Vroomen J: **Concurrent sensorimotor temporal recalibration to different lags for the left and right hand.** *Front Psychol* 2014, **5**:140.

[45] Morrone MC, Ross J, Burr D: **Saccadic eye movements cause compression of time as well as space.** *Nat Neurosci* 2005, **8**(7):950-4.

[46] Binda P, Cicchini GM, Burr DC, Morrone MC: **Spatiotemporal distortions of visual perception at the time of saccades.** *J Neurosci* 2009, **29**(42):13147-57.

[47] Terao M, Watanabe J, Yagi A, Nishida S: **Reduction of stimulus visibility compresses apparent time intervals.** *Nat Neurosci* 2008, **11**(5):541-2.

[48] * Tomassini A, Gori M, Baud-Bovy G, Sandini G, Morrone MC: **Motor commands induce time compression for tactile stimuli.** *J Neurosci* 2014, **34**(27):9164-72.

In this paper, a temporal compression between visual events occurring before or during a saccade is generalised to manual actions by applying tactile taps around the time of movement onset.

[49] * Press C, Berlot E, Bird G, Ivry R, Cook R: **Moving time: The influence of action on duration perception.** *J Exp Psychol: Gen* 2014, **143**(5):1787.

These authors demonstrate selective temporal dilation for both tactile and visual intervals with close spatial correspondence to a current action.

[50] Hagura N, Kanai R, Orgs G, Haggard P: **Ready steady slow: action preparation slows the subjective passage of time.** *Proc Biol Sci* 2012, **279**(1746):4399-406.

Figure Legends

Legend to Figure 1.

A flux diagram for time processing using auditory stimuli, ranging from the extraction of temporal features (time sensation) in early sensory areas, to time perception, time production and time prediction (green characters) in the motor system. In turn, time prediction is fed back as a top-down signal to enhance the processing of incoming stimuli in sensory areas. The colored squares on the right highlight the tentative neural signals involved at each processing level of time quantification [6,7,10-22].

Legend to Figure 2

Schematic overview illustrating the contextual effects of action upon perceived time. Temporal distortions are placed along a timeline, beginning with the imperative stimulus that instructs action and ending with the consequences of that action. Widened clocks indicate subjectively expanded intervals, contracted clocks represent subjectively compressed intervals, and arrow shapes indicate subjective shifts of the events demarcating different intervals. Matched shading is used to indicate the event biases that belong with different interval biases. **A.** Visually defined intervals dilate during action preparation [50]. **B.** Visual events are perceived later when they trigger actions [35]. **C.** Vibrotactile and visual filled intervals dilate when they overlap action [49]. **D.** Empty intervals between pairs of visual/tactile markers are compressed before and during saccades/manual actions respectively [45,48]. **E.** Tactile (visual) information revealed at the end of a manual action (saccade) is temporally dilated (and antedated) [24-26]. **F.** Actions and their delayed consequences seem compressed in time [31] and adapting to delayed feedback induces a recalibration of the perceived timing between action and its sensory correlates [36].

Figure 1

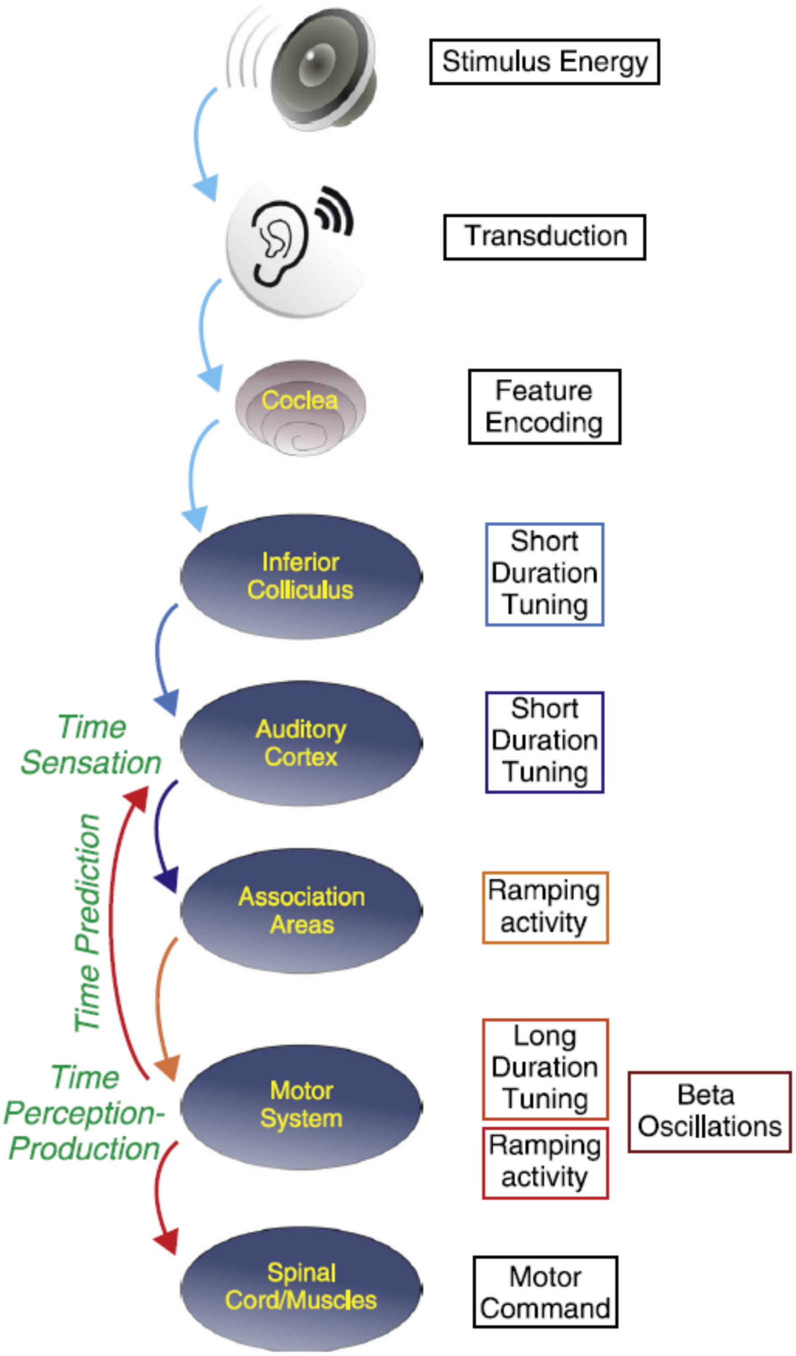
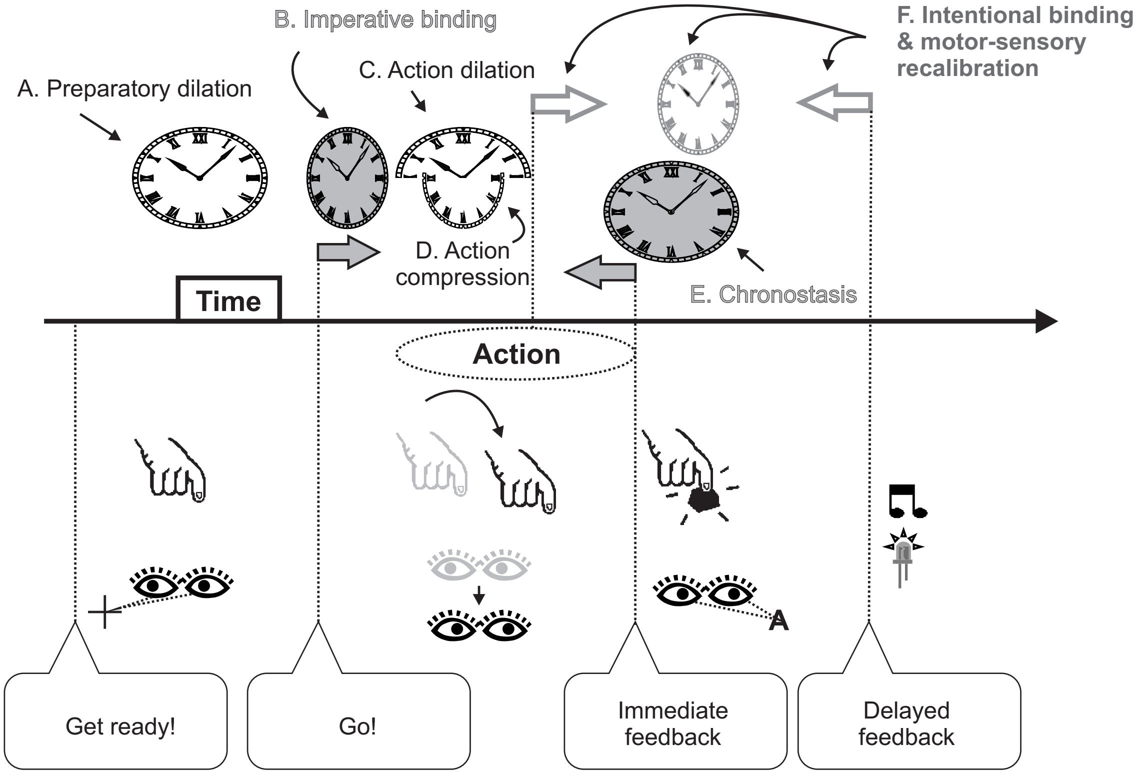

Stimulus Energy
Transduction
Coclea
Feature Encoding
Inferior Colliculus
Short Duration Tuning
Time Sensation
Auditory Cortex
Short Duration Tuning
Time Prediction
Association Areas
Ramping activity
Time Perception-Production
Motor System
Long Duration Tuning
Ramping activity
Beta Oscillations
Spinal Cord/Muscles
Motor Command

Figure 2


B. Imperative binding
F. Intentional binding & motor-sensory recalibration
C. Action dilation
A. Preparatory dilation
D. Action compression
E. Chronostasis
Time
Action
A
Get ready!
Go!
Immediate feedback
Delayed feedback