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Dissociating explicit timing from temporal expectation with fMRI

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Explicit timing is engaged whenever subjects make a deliberate estimate of discrete duration in order to compare it with a previously memorised standard. Conversely, implicit timing is engaged, even without a specific instruction to time, whenever sensorimotor information is temporally structured and can be used to predict the duration of future events. Both emergent timing (motor) and temporal expectation (perceptual) are forms of implicit timing. Recent fMRI studies demonstrate discrete neural substrates for explicit and implicit timing. Specifically, basal ganglia are activated almost invariably by explicit timing, with co-activation of prefrontal, premotor and cerebellar areas being more context-dependent. Conversely, implicit perceptual timing (or “temporal expectation”) recruits cortical action circuits, comprising inferior parietal and premotor areas, highlighting its role in the optimisation of prospective behaviour.

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Introduction

The cognitive neuroscience of interval timing (i.e. timing in the range of several hundred milliseconds to minutes) is plagued by several neuroanatomical dichotomies. Is there a left- or right-sided hemispheric lateralisation for timing [1,2]? Are there anatomical differences in the processing of subsecond versus suprasedond durations [3,4]? Do distinct neural systems subserve perceptual versus motor timing [4,5]? More generally, is there one ubiquitous task-independent timing network, or is timing represented locally in functionally specific areas [6–8]? We attempt to resolve some of these puzzles by deconstructing the monolithic term ‘timing’ and making clear the functional (and neural) distinction between explicit and implicit timing of stimulus duration or inter-stimulus intervals (Figure 1). Our aim is to show that some of the

apparent inconsistency, and consequent confusion, has arisen from a conflation of these processes. Specifically, we use results from the functional magnetic resonance imaging (fMRI) literature, highlighting those studies appearing within the past three years, to illustrate their discrete neural signatures. We restrict our discussion to *metrical* representations of time. The neural correlates of *ordinal* representations of time have recently been outlined by Battelli [9].

Functional definitions: explicit versus implicit timing

Explicit timing

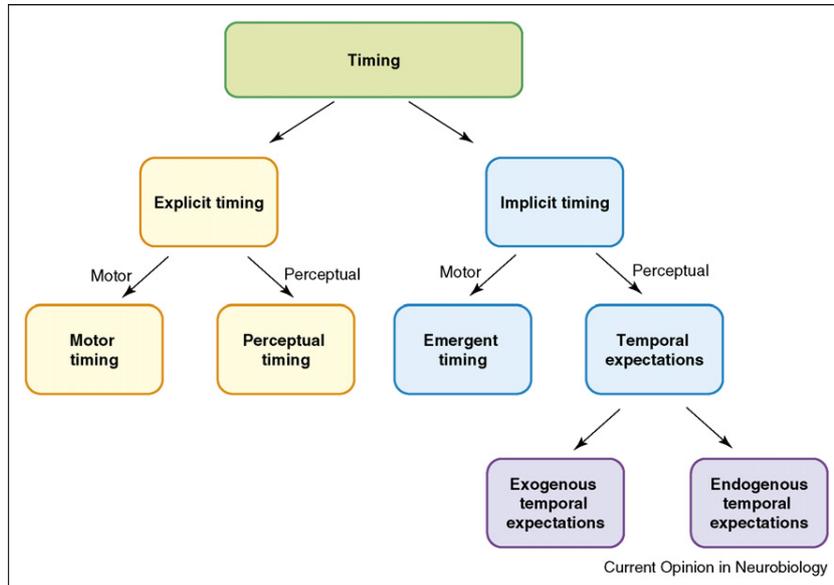
The crucial distinction between explicit and implicit timing is whether or not the task instructions require subjects to provide an overt estimate of duration. In tasks of explicit timing, estimates of stimulus duration or inter-stimulus interval (ISI) are given either in the form of a perceptual discrimination (‘perceptual timing’), in which subjects typically state whether one stimulus duration or ISI is shorter or longer than another (Figure 2a); or in the form of a motor response (‘motor timing’), in which subjects represent the timed duration or ISI with a sustained, delayed or periodic motor act (Figure 2b and c). In all cases, the ‘task goal’ for the subject is to provide an accurate estimate of elapsed time.

Implicit timing

Implicit timing, on the contrary, is engaged as a by-product of *non*-temporal task goals, when sensory stimuli or motor responses nevertheless adhere to a strict temporal framework. For example, task instructions may require subjects to make a perceptual judgement about stimulus features or to perform a specific motor act. Even though no overt estimates of stimulus or action duration are required, any temporal structure inherent in the rate of stimulus presentation or motor execution will engage timing mechanisms implicitly. For tasks in which implicit timing is indexed by the temporal regularity of a *motor output* timing is said to emerge as a by-product of the dynamics of motor control (‘emergent timing’) [10,11]. However, for tasks in which implicit timing is indexed by the temporal predictability of *perceptual input* timing is used to build an expectation of when the next stimulus will appear.

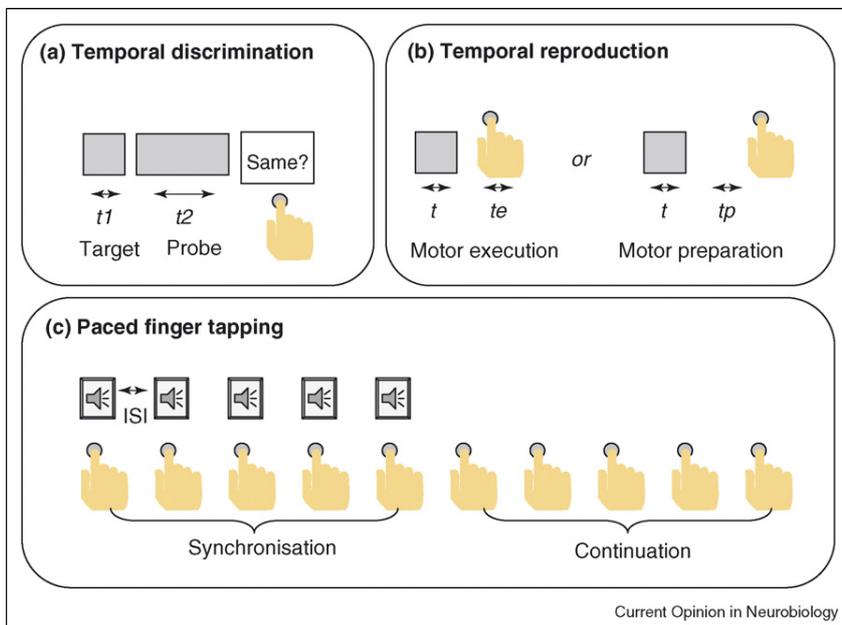
Moreover, the implicit use of timing to establish temporal expectations may be subconscious and unintentional (‘exogenous’) or conscious and deliberate (‘endogenous’) (see Figure 1). Exogenous temporal expectations are engaged incidentally as the by-product of a temporally regular stimulus structure (Figure 3a). Endogenous

Figure 1



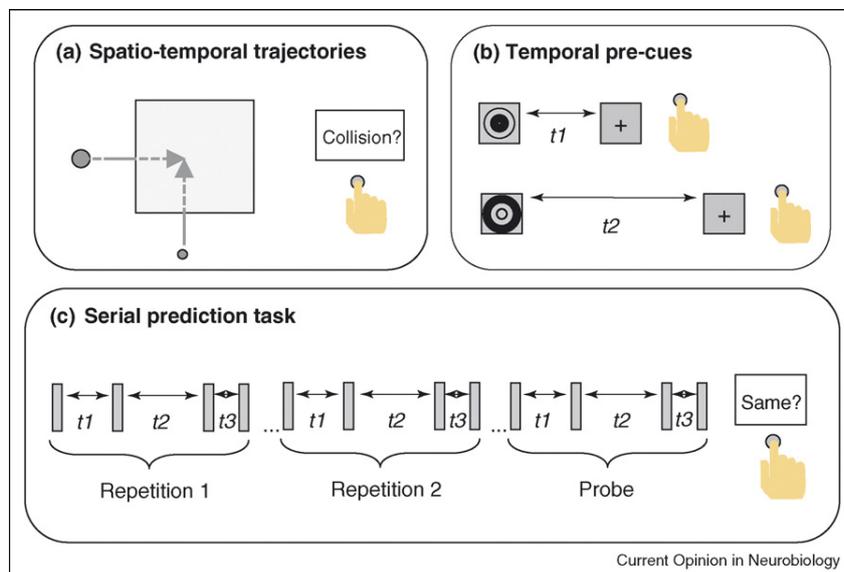
A functional taxonomy of timing. Explicit timing is engaged by tasks requiring either motor production (motor timing) or perceptual discrimination (perceptual timing) of a timed duration. Implicit timing is engaged as a by-product of the temporal regularity of either a motor output (emergent timing) or a perceptual input (temporal expectation). Temporal expectations may be established either incidentally via a temporally regular stimulus structure (exogenous temporal expectation) or deliberately via informative pre-cues (endogenous temporal expectation).

Figure 2



Explicit timing tasks. **(a)** Temporal discrimination. Subjects compare the duration (t_2) of a probe sensory stimulus with that (t_1) of a target stimulus previously stored in working or reference memory. Temporal estimates are measured with a delayed discriminatory response (e.g. same/different or shorter/longer). **(b)** Temporal reproduction. Subjects reproduce the duration (t) of a target sensory stimulus by producing a sustained motor response whose duration (t_e) corresponds to that of the target duration (motor execution) or by producing a brief motor response after an inter-stimulus interval (t_p) that corresponds to the target duration (motor preparation). **(c)** Paced finger tapping. During the synchronisation phase, subjects synchronise motor responses to a sensory (usually auditory) stimulus presented at regular inter-stimulus intervals (ISI). During the continuation phase, they use the temporal information acquired during the synchronisation phase to reproduce a motor representation of the timed ISI, in the absence of the sensory pacing stimulus. ISIs may be either isochronous or rhythmic.

Figure 3



Temporal expectation tasks. **(a)** Spatio-temporal trajectories. Subjects implicitly use temporal information inherent in the speed of a moving sensory stimulus to predict its eventual location. Responses generally take the form of a perceptual discrimination (e.g. will the moving stimuli collide). **(b)** Temporal pre-cues. Subjects learn temporal associations between symbolic cues and short (t_1) or long (t_2) inter-stimulus intervals (ISI). Subjects make deliberate use of this information in cued reaction-time tasks to predict when a target will appear and so speed its detection. **(c)** Serial prediction task. Subjects learn temporal patterns of target ISIs in order to estimate whether or not a probe sequence shows the same temporal pattern. Responses take the form of a perceptual discrimination.

temporal expectations are engaged when subjects make deliberate use of an informative pre-cue or regular temporal interval to predict stimulus onset (Figure 3b and c). In both the cases, temporal expectations are used to improve accuracy [12,13] and/or speed [1,14,15] of non-temporal task goals.

Explicit versus implicit timing

Behavioural studies have demonstrated a functional distinction between explicit and implicit timing. For example, Zelaznik *et al.* [10] reported no significant correlation in timing performance between the continuation phase of a paced finger-tapping task (explicit timing) and continuous circle drawing (implicit timing), suggesting engagement of discrete functional mechanisms. In this review, we investigate whether explicit and implicit timing engage discrete *neuroanatomical* substrates. While our distinction between explicit and implicit timing intersects empirically to some degree with Lewis and Miall's distinction between controlled and automatic timing [4], our functional criteria differ conceptually. Specifically, Lewis and Miall suggested that automatic timing is used to time a continuous series of subsecond motor acts, while cognitively controlled timing is used to measure discrete, suprasedond, non-motor stimuli. However, we believe the key discriminating feature is the temporal nature of the task goal (implicit or explicit) rather than the continuous or discrete nature

of the stimuli being timed. Note that our implicit/explicit distinction may also result in incidental empirical overlap with their sub/suprasedond distinction since the timing of very short durations is often measured in an implicit way [4]. However, subsecond durations *can* be timed in an explicit manner, in which case they actually activate many neural substrates in common with timing of suprasedond durations [16]. Finally, we prefer not to conflate the implicit/explicit nature of the task instructions with the perceptual/motor measure used to index timing and believe that perceptual and motor forms of both implicit and explicit timing can be uniquely identified (Figure 1).

Neuroanatomical substrates of explicit timing

Numerous fMRI studies of perceptual [16–23,24^{*}] or motor [26–30,31^{*},32^{••},33,34] timing have consistently identified several key 'timing areas': supplementary motor area (SMA), basal ganglia (BG), cerebellum and right inferior frontal and parietal cortices. The functional contribution, or necessity, of each to a timing network is still very much a matter of debate however.

Perceptual timing

In perceptual timing tasks, activity in a particular subset of these regions – the anterior portion of SMA (pre-SMA), the right inferior frontal cortex and BG – increases when the perceptual demands of a temporal discrimination task (Figure 2a) are increased, either by lengthening the

duration to-be-timed [17] or by reducing the temporal range within which two durations are to be compared [18]. Moreover, temporal discrimination tasks preferentially activate this core subset even when the control task to which it is compared is well matched for difficulty confounds and/or incidental motor demands [16,19–23]. Indeed, Livesey *et al.* [24^{*}] have shown that BG and inferior frontal cortex were selectively recruited during temporal discrimination even when the control task was made more difficult than the timing task.

Largely on the basis of animal work, Matell and Meck suggested BG act as a coincidence detector, comparing current neurophysiological representations of time to those previously experienced [25]. However, event-related fMRI studies [19,23] indicate that BG are selectively activated during the *encoding* phase of perceptual timing tasks, in which an initial representation of stimulus duration is stored for later recall. This suggests BG are activated during initial encoding of time, rather than at the later comparison stage as would be predicted by the coincidence detection model.

Motor timing

Distilling the results of these various perceptual timing studies down to a lowest common denominator invariably reveals activation of the BG. Indeed, BG are also routinely engaged when subjects produce *motor* representations of stimulus duration or interval. For example, BG are activated during motor reproduction tasks (Figure 2b) in which subjects are required to execute a discrete yet sustained motor response whose *duration* indexes the motor representation of the timed interval [26,27] or to prepare a discrete, brief motor response whose time of *onset* indexes the timed interval [27–29]. BG are also activated during the continuation phase of a finger-tapping task (Figure 2c) in which the time of onset of each element in a whole sequence of discrete motor responses indexes the timed interval [30,31^{*},32^{**}].

Whether BG co-activates with SMA (preSMA and/or SMA proper), inferior frontal cortex or cerebellum may depend, however, upon the task context. For example, reproduction of timed intervals previously specified by sensory stimuli [30,31^{*},32^{**}] or synchronisation to increasingly complex temporal rhythms [30,33] engages both BG and SMA (and sometimes inferior frontal cortex), but BG alone are activated when subjects produce their own internal representation of a variable time interval [28,34]. This suggests a differential role for BG and SMA in the representation of temporal intervals that are internally or externally specified, respectively¹. In

¹ The majority of timing studies probably engage a mixture of externally and internally specified temporal representations; often subjects time an externally specified interval then store (perceptual timing) or reproduce (motor timing) an internal representation of that interval.

line with this, Spencer *et al.* [11] recently showed lack of SMA activation in a motor timing task in which duration was internally rather than externally determined, although unfortunately BG were not imaged in this study. This experiment, however, did highlight the role of the cerebellum in explicit, rather than implicit ('emergent') motor timing [11]. In general, cerebellum is more often activated in motor studies of explicit timing (e.g. [26,27,32^{**}]) rather than perceptual ones and also appears to be more sensitive to subsecond rather than suprasedond intervals [4,16,18] (although see [26]). Indeed, recent TMS studies provide additional support for a specific role for the cerebellum in motor [35,36] or perceptual [37] timing of intervals in the subsecond range.

Centralised versus localised representations of time

Recent fMRI data have suggested that activation of cerebellum and preSMA in timing is context-dependant [31^{*}], thus supporting the notion of a localised [6], rather than centralised [7], representation of time. In other words, the temporal interval is represented directly by the pattern of local neural activity in the sensorimotor area recruited to process that interval, without recourse to a homuncular 'timer'. Mounting evidence suggests, however, that a more centralised representation of explicit timing may be found in BG. Bengtsson *et al.* [32^{**}], showed that timing-related BG activity was independent of the motor effector (left/right hand or speech) used to perform a rhythmic timing task; Buetti *et al.* [27] showed it was independent of the stage of motor processing (preparation or execution) being timed; Jantzen *et al.* [31^{*}] showed its independence from the sensorimotor context (synchronisation or syncopation) in which the timed interval was learned; and Jahanshahi *et al.* [26] demonstrated its activation for both subsecond (500 ms) and suprasedond (2 s) intervals.

However, a centralised representation of time in BG does appear to depend upon an explicit representation of temporal duration for a period of at least a few hundred milliseconds. While all of the aforementioned studies used durations of at least 300 ms, Pastor *et al.*'s [38] fMRI studies, which required temporal resolution of two very brief (<50 ms) consecutively presented stimuli rather than estimation of stimulus duration, observed selective activation of preSMA, not BG. Moreover, the proposal by Buonomano and colleagues [6,39] that time is represented in localised task-specific circuits applies only to brief intervals. Therefore, it is possible that the crucial temporal juncture for differential neural representation of time may not be the sub/suprasedond divide suggested previously [4], but rather the division between tens versus hundreds of milliseconds. This hypothesis remains to be tested formally.

In conclusion, we therefore suggest that explicit representations of time are instantiated in both task-invariant

and more functionally localised areas. Specifically, BG are routinely activated whatever the task requirements (e.g. manual/verbal responses [32^{••}]; perceptual/motor processing [5,27]; sub/suprasecond intervals [26]), as long as the duration being tested lasts at least a few hundred milliseconds. However, the involvement of other key areas (SMA, inferior frontal cortex, cerebellum) depends upon the specific temporal context. Context-dependent functional segregation among and within the various BG nuclei (putamen, caudate, accumbens) is entirely feasible and demands closer investigation in the future.

Neuroanatomical substrates of implicit timing: temporal expectations

We restrict our review to studies of implicit *perceptual* timing, or 'temporal expectations' (Figure 1), and refer the reader to Ivry *et al.* [40] for a discussion of implicit motor ('emergent') timing.

Responses to sensory stimuli that appear when expected are quicker and more accurate than those appearing at unexpected intervals [15]. Such temporal expectations (also referred to as implicit timing [14], anticipation of event timing [41,42] or future-oriented attending [12]) *make use* of timing information in order to optimise motor or perceptual performance. Temporal expectations can be established incidentally by the predictable temporal dynamics of the stimuli themselves (exogenous expectations), or voluntarily by informative pre-cues (endogenous expectations).

Exogenous temporal expectations

Electrophysiological recordings in monkeys show that neural firing varies dynamically as a function of the conditional probability that a target will occur at a particular time, given that it has not already occurred (the 'hazard function'). This firing pattern has been observed in visual [41] primary motor [43] and parietal cortices [42] for colour, motor and spatial tasks, respectively, indicative of context-dependent and functionally localised representations of temporal expectations. In support of this, magnetoencephalographic (MEG) recordings during a choice reaction-time (RT) task in humans showed increased activity in parietal cortex and cerebellum as a function of the hazard function [44], while increased phase synchronisation between parietal cortex, cerebellum and subcortical structures was evident during motor synchronisation to temporally predictable (isochronous) rather than random ISIs [45]. fMRI studies using both simple [46] and choice RT [14,47] have identified increased activity in left premotor and inferior parietal cortices for temporally predictable rather than random ISIs. In addition, synchronising motor responses to metrically salient (i.e. temporally predictable [12]) auditory rhythms increased activity in dorsal premotor cortex [48]. Premotor cortex, inferior parietal cortex and cerebellum form selective action circuits [49], and it appears that

temporal expectation simply modulates their motor-induced activity.

However, temporal expectations modulate activity in action-related areas even when task demands are perceptual rather than motor. For example, metrically salient rhythms were associated with activation of ventral areas of prefrontal/premotor cortex (as well as BG) in a perceptual discrimination task [50]. And when subjects used temporal information inherent in the spatio-temporal trajectory of a dynamic visual stimulus (Figure 3a) to predict its final position, activations were reported in left-lateralised inferior parietal cortex [51[•]], sensorimotor regions of premotor and parietal cortices [52] and cerebellum [53]. Although fMRI has relatively poor temporal resolution compared with electrophysiological recordings, it does have the advantage of whole-brain coverage, thus allowing identification of potential neuroanatomical overlap across methodologically diverse studies. Consistent activation of action-related areas across motor and perceptual studies is suggestive of a rather more task-independent representation of temporal expectation, at least at the macroscopic scale.

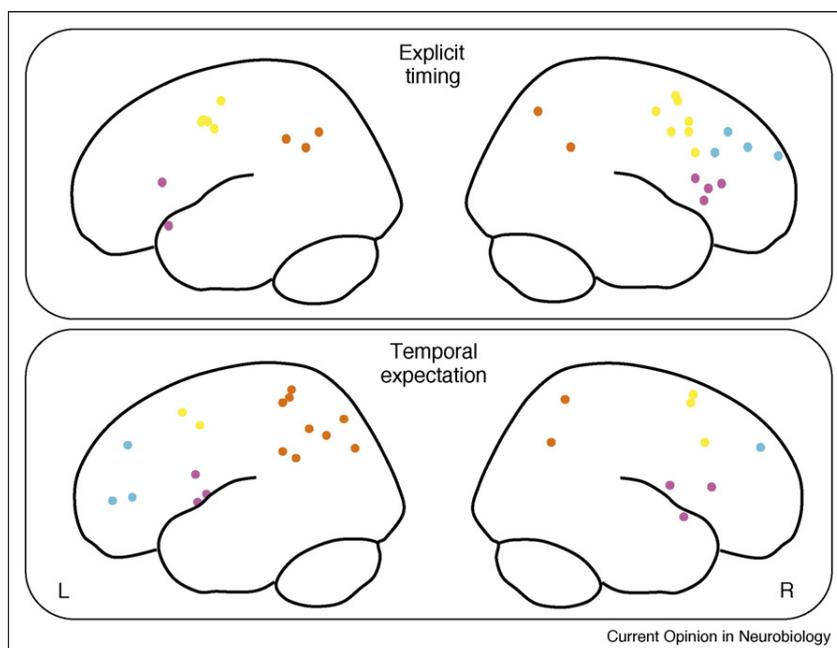
Endogenous temporal expectations

When subjects are asked to make explicit use of temporal information in order to optimise performance, a similar set of motor-association regions are engaged. Left inferior parietal cortex and cerebellum were activated when subjects deliberately used temporally predictable ISIs to improve motor speed in a sequence-learning paradigm [54]. Moreover, left inferior parietal cortex and ventral premotor cortex were activated when subjects used informative attentional pre-cues (Figure 3b) to predict stimulus onset and so improve motor speed [1,55]. And Schubotz and colleagues have shown that temporally predictable inter-stimulus intervals in a serial prediction task (Figure 3c) activate ventral premotor cortex even though the task is purely perceptual [56,57].

Action circuits code for perceptual temporal expectation

Both exogenous and endogenous temporal expectations are represented within areas traditionally associated with action, notably premotor or inferior parietal cortices. Moreover, action circuits are activated whether the task is motor *or* perceptual, although there may be some functional specialisation within discrete zones of this action circuit. For example, dorsal areas of premotor cortex are generally activated when temporally predictable stimuli require a speeded motor response [14,46–48], whereas more ventral premotor areas are associated with perceptual discrimination of these stimuli [50,56,57]. Activation of action-related areas by perceptual temporal expectations is consistent with the observation that motor areas can code for perceptual representations of action as well as their actual execution [58] and, furthermore, suggests that the primary purpose of temporal expectation

Figure 4



Fronto-parietal hemispheric lateralisation for explicit timing versus temporal expectation. Each dot represents the site of peak amplitude of an activation cluster in prefrontal (cyan), dorsal premotor (yellow), ventral premotor/frontal operculum (magenta) or parietal cortices (orange). Activations are plotted on the left (L) and right (R) lateral surfaces of a template brain. We considered only those studies in which task difficulty was strictly controlled. Therefore, the activations shown here are taken from studies in which performance of the explicit timing [11,17,19–21,24*,28,31*,32**] or temporal expectation task [1,48,50,52–54,57] was not significantly worse than that of the control task, or in which the timing parameter was parametrically modulated [30,33,51*]. Although these studies also reported activations in supplementary motor area (SMA), basal ganglia, temporal cortex or cerebellum, these clusters are not illustrated here for reasons of parsimony.

(i.e. perceptual implicit timing) is to optimise prospective motor behaviour.

Hemispheric lateralisation for explicit timing and temporal expectation

Recently, Geiser *et al.* [59**] have directly compared implicit perceptual timing (i.e. temporal expectation) with explicit timing of a verbal rhythm task. They identified a clear-cut hemispheric lateralisation, with right-sided temporo-parietal areas being activated by explicit timing of temporally predictable rhythmic speech patterns, while their left-sided homologues were activated by implicit temporal processing of the same stimuli. This experiment exemplifies, at least for perceptual timing studies, the general pattern of hemispheric lateralisation that can be observed in the literature (Figure 4): more right-sided activity for explicit timing but more left-sided activity for temporal expectation (i.e. implicit perceptual timing). Since motor prediction is also predominantly left-lateralised [60], these data indicate yet another neural overlap between implicit timing and prospective motor control.

In a review of the hemispheric lateralisation of movement control [61], Serrien *et al.* suggested that the left hemisphere specialises in feedforward specification of future

movement dynamics, whereas the right hemisphere uses sensory feedback to compare current limb position to its intended goal. We propose a parallel hemispheric lateralisation for temporal processing. Implicit perceptual timing, or temporal expectation, relies on previously learned timing information to predict future stimulus onset or duration and is generally lateralised to the left hemisphere. Conversely, explicit timing, which is generally lateralised to the right hemisphere, uses sensory feedback to compare perception (or production) of current stimulus duration to a target duration held in working memory.

Conclusions

We aimed to imbue some clarity into the disparate findings in the timing literature by re-classifying it into those studies in which timing is the explicit task goal versus those in which timing is conducted implicitly in order to achieve a motor or perceptual goal. Explicit timing almost invariably engages BG, while activation of SMA, inferior frontal cortex and cerebellum, although common, depends more upon the specific task-context. Implicit perceptual timing activates a different set of regions, most consistently left-lateralised premotor and parietal cortices. This pattern of activation may represent local modulation of action-related processing areas that are necessary for producing a speeded

manual response at the expected time. However, Schubotz [62**] has recently suggested that the feedforward characteristics of motor association areas can be used to predict future *perceptual*, as well as motor states. This theory recasts what we have traditionally thought of as a 'motor' system into a prediction system, suggesting that activation of premotor and parietal areas during temporal expectation may index engagement of a temporal prediction network, rather than temporal tuning of action-related areas. We are currently investigating the neural substrates of temporal prediction in motor versus perceptual tasks, and in motor tasks that engage different response effectors. Neuroanatomical overlap across distinct experimental paradigms would support the existence of a task-independent temporal prediction network.

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