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The neural correlates of cognitive time management: a review

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Review

Abstract. Cognitive time management is an important aspect of human behaviour and cognition that has so far been understudied. Functional imaging studies in recent years have tried to identify the neural correlates of several timing functions, ranging from simple motor tapping to higher cognitive time estimation functions. Several regions of the frontal lobes, in particular dorsolateral prefrontal cortex (DLPFC), inferior prefrontal cortex (IFC), anterior cingulate gyrus (ACG) and the supplementary motor area (SMA), alongside non-frontal brain regions such as the inferior parietal lobes, the cerebellum and the basal ganglia have been found to be involved in tasks of motor timing and time estimation. In this paper we review and discuss the involvement of these brain regions in different tasks of cognitive time management, illustrating it with own findings on motor timing and time perception tasks using functional magnetic resonance imaging (fMRI). The review shows that the same brain regions are involved in both motor timing and time estimation, suggesting that both functions are probably inseparable and mediated by common neural networks.

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INTRODUCTION

Human behaviour is necessarily conducted in time and space, which makes cognitive time management an essential human function. Adequate timing of our behaviour and good time estimation skills are essential for normal social functioning and have an impact on a wide range of motor and cognitive functions such as movement, planning, speed of cognitive processing and speech.

In the timing literature, the distinction has been made between motor timing and time perception (Fuster 1990). In this article we use the term cognitive time management when we generalise across both forms of perceptive time estimation and motor timing. Motor timing refers to the timing aspects of the output of behaviour such as the temporal organisation of motor, speech or cognitive acts. Time perception refers to the more passive and perceptive aspects of cognitive time management such as perceiving temporal intervals and the ability to estimate temporal delays. In laboratory settings motor timing has so far been measured in tasks of finger tapping, rhythm production, rhythmic finger movements, sensorimotor synchronisation, and the temporal organisation of movements. The time range used with these methods range from the milliseconds' range to seconds and minutes. Time estimation has been measured in tasks of temporal estimation, where temporal intervals from milliseconds to minutes or even hours need to be estimated, in tasks of temporal production or reproduction, where subjects are told to (re)produce a time interval given to them in conventional time units, in time discrimination tasks, where two different temporal intervals need to be discriminated or in rhythm discrimination tasks.

Since cognitive time management is such an essential function of normal human behaviour, different behavioural pathologies have shown abnormalities in both motor timing and time estimation. Thus, abnormalities in time estimation have been observed in a wide range of pathologies including patients with brain lesions (Harrington et al. 1998, Rubia et al. 1997), attention deficit/hyperactivity disorder (Rubia et al. 1999a,b, 2001, 2003, Smith et al. 2002, Sonuga-Barke et al. 1998), antisocial personality disorder (Bauer 2001), dyslexia and dysphasia (May et al. 1988, Needham and Black 1970, Nicolson et al. 1995, Tallal et al. 1991), schizophrenia (Davalos et al. 2003, Rammsayer 1990, Ulferts et al. 1999, Volz et al. 2001), depression (Kuhs et al. 1991, Mundt et al. 1998, Rammsayer 1990), Parkinson's disease (Lange et al. 1995, Pastor et al. 1992, Riesen and Schnider 2001) and drug abuse (Mathew et al. 1998, Mintzer and Stitzer 2002, Solowij et al. 2002). Motor timing has been less extensively tested, but also been found to be abnormal in several psychopathologies such as attention deficit/hyperactivity disorder (Carte et al. 1996, Rubia et al. 1999a,b, 2001, 2003, Stevens et al. 1970), dyslexia (Denckla et al. 1985, Waber et al. 2000), Parkinson's disease (Elsinger et al. 2003, O'Boyle et al. 1996) and alcohol abuse (Parks et al. 2003).

It has been suggested that motor timing as an executive function would be mediated by prefrontal brain regions while time perception as a perceptive function would be aided by the activation of more posterior brain regions such as the parietal lobes (Fuster 1990). Over the last decades, brain lesion and imaging studies using a wide range of timing tasks, from simple motor tapping to higher complex time estimation tasks, have attempted to specify the neural correlates associated with the various functions of motor and cognitive time management. Several regions in the frontal lobes such as dorsolateral and inferior prefrontal cortices, supplementary motor area, and anterior cingulate, but also non-frontal cortical regions such as the parietal lobes and subcortical brain areas including the cerebellum and the basal ganglia have been found to be implicated in motor timing and time estimation. Interestingly, it appears that strikingly similar brain regions seem to subserve both motor timing and time perception. This may reflect the fact that cognitively, both functions can not be clearly separated. Time estimation tasks that involve a button press, for example, will be confounded by motor timing functions and most motor timing tasks involve an element of perceptive time estimation such as estimating a temporal delay in order to make a perfectly timed move. It is the aim of this article to review and discuss the brain regions that have been found to be involved in both functions of motor timing and time perception. Furthermore, we hope to show with this review that the two functions are mediated by similar brain regions suggesting that they cannot be as clearly separated as previously thought.

A further important distinction in the timing literature is to be made between different temporal domains in which both time estimation or motor timing are being measured (Szelag et al. 2004 – this issue). As different cognitive functions are being co-measured, for example, in time estimation or reproduction of several seconds or minutes, sustained attention to time and working memory will be crucial basis functions to hold the time interval online. In reviewing the literature we will therefore clearly point out the time range that has been tested by the several studies.

DORSOLATERAL AND INFERIOR PREFRONTAL CORTICES

The prefrontal cortex was one of the first brain regions to be related to cognitive time management, based on animal and lesion studies of an involvement of the prefrontal cortex in planning and timing of behaviour and the perception of time (Fuster 1989). In recent decades, functional brain imaging studies using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) in combination with paradigms of motor timing and perceptive timing functions have confirmed the hypothesis of a predominant role of the prefrontal cortex in cognitive time management.

Lesion studies have shown that patients with lesions of right and left frontal brain regions appear to be impaired in their ability to estimate temporal durations of milliseconds, seconds and minutes (Casini and Ivry 1999, Harrington et al. 1998, Mangels et al. 1998, Nichelli et al. 1995, Rubia et al. 1997). In some of these studies, in particular the integrity of right DLPFC and right inferior parietal lobe has been shown to be critical for time discrimination and estimation deficits of several seconds (Harrington et al. 1998, Kagerer et al. 2002, Mangels et al. 1998, Rubia et al. 1997). Modern functional imaging studies using fMRI and PET have confirmed the role of DLPFC and IFC in mediating motor timing and time estimation. In most of these studies the prefrontal activation was in the right hemisphere. Thus, predominantly right hemispheric DLPFC, but also right IFC have shown to mediate time estimation of several seconds (Basso et al. 2003, Lewis and Miall 2002, Macar et al. 2002) and time discrimination of milliseconds (Maquet et al. 1996, Rao et al. 2001, Smith et al. 2003). DLPFC is also activated in motor timing tasks such as sensorimotor synchronisation of hundreds of milliseconds in finger tapping (Larsson et al. 1996) and of several seconds (Lejeune et al. 1997, Rubia et al. 1998, 2000). In our own studies of motor timing sensorimotor synchronisation was required for a stimulus that appeared every 5 s and contrasted to sensorimotor synchronisation of a 600 ms interval (Rubia et al. 1998, 2000). Sensorimotor synchronisation in the delay task of 5 s requires both adequate estimation of the

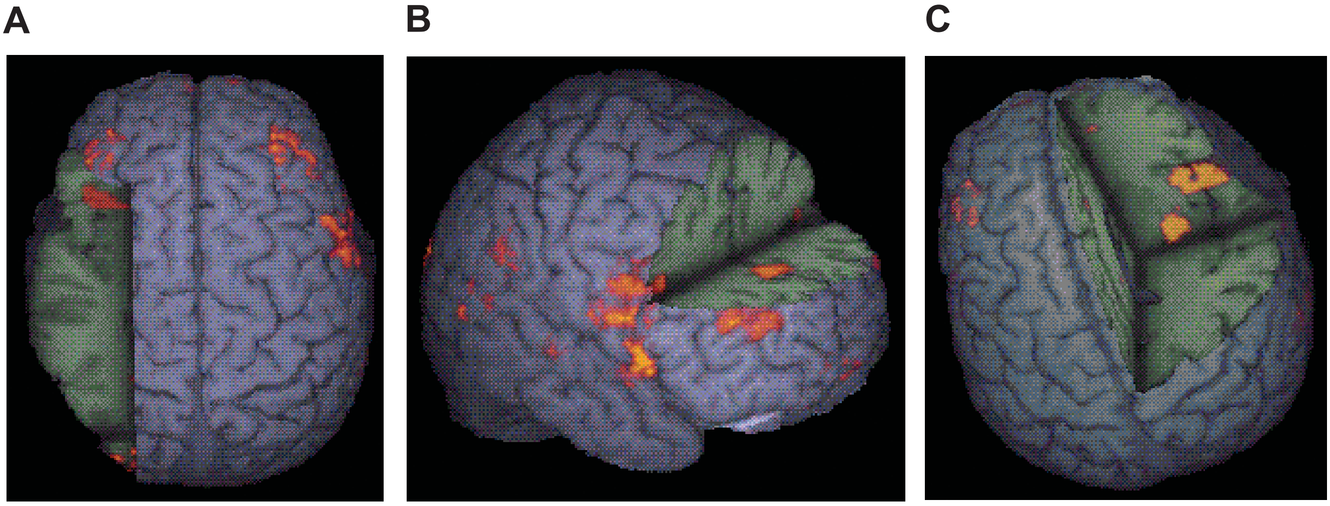

Fig. 1. Generic brain activation map of 8 right-handed male adults (aged 22 to 40 years; mean age 29 years) while performing a sensorimotor synchronisation task of 5 s, after contrasted with a sensorimotor synchronisation task (finger tapping) of 0.6 s in a block design fMRI study. Subjects were instructed to time their motor response to the regular appearance of the visual stimuli on the computer screen. For good sensorimotor timing subjects had to monitor the time interval elapsed since the presentation of the last visual stimulus. The long event rate condition imposes a higher load on time estimation and motor timing compared to the short event rate condition. Areas shown are brain regions that showed significant greater activation during the synchronisation task of 5 s in contrast to finger tapping, presumably reflecting both time estimation and motor timing (corrected $P<0.003$) (for further details see Rubia et al. 2000). (A) Activations in right and left dorsolateral (Brodmann area (BA) 46) and inferior prefrontal cortices (BA 45); (B) activation in anterior cingulate gyrus, right dorsolateral and inferior prefrontal cortices (BA 32) and right parietal lobe; (C) activation in right putamen and right inferior prefrontal lobe (BA 45).

5 s interval and accurate motor timing (see Fig. 1). In a posterior study we tested pure time estimation in a temporal discrimination task, where time intervals of about 1 seconds length differed by several hundreds of milliseconds; we observed a similar focus of right DLPFC and right IFC for pure time estimation (see Fig. 2).

A further distinction has been made between the neural correlates of long-term and short-term time estimations. Mangels et al. (1998) found that damage in lateral prefrontal cortex impaired the discrimination of long (4 s) but not short temporal durations (400 ms). This is in line with the studies of Rubia et al. (1998, 2000) where lateral prefrontal activation was only observed in the contrast of the longer synchronisation task with the tapping task, but not in the tapping task alone (see Fig. 1). These findings may suggest that regions of the prefrontal cortex have the function of a hypothetical accumulator within an internal clock model, which is required only with durations of more than several seconds. Indeed, prefrontal activation in timing tasks of durations of several seconds has often been related to other underlying functions besides pure timing processes, such as sustained attention to the time interval or working memory components (Macar et al. 2002, Maquet et al. 1996, Rao et al. 2001), based on the well-known role of DLPFC in working memory (Baker et al. 1996, Diwadkar et al. 2000, Manoach et al. 1997, Mull and Seyal 2001) and attention (Mazoyer et al. 2002, Posner and Peterson 1990, Sylvester et al. 2003). Thus, in some of the studies DLPFC activation was not only related to temporal discrimination but also to the attentional control conditions (Coull and Nobre 1998, Lejeune et al. 1997, Tracy et al. 2000). However, other studies have suggested that DLPFC may have a more primary role in time estimation processes (Constantinidis et al. 2002, Lewis 2002, Rubia et al. 1998, Zakay and Block 1996). Thus, studies using delay tasks with minimal working memory load have observed strong DLPFC and IFC activation (Rubia et al. 1998, 2000) (see Fig. 1). It has been argued that DLPFC activation often observed during working memory tasks such as the delayed response task (where a response is requested

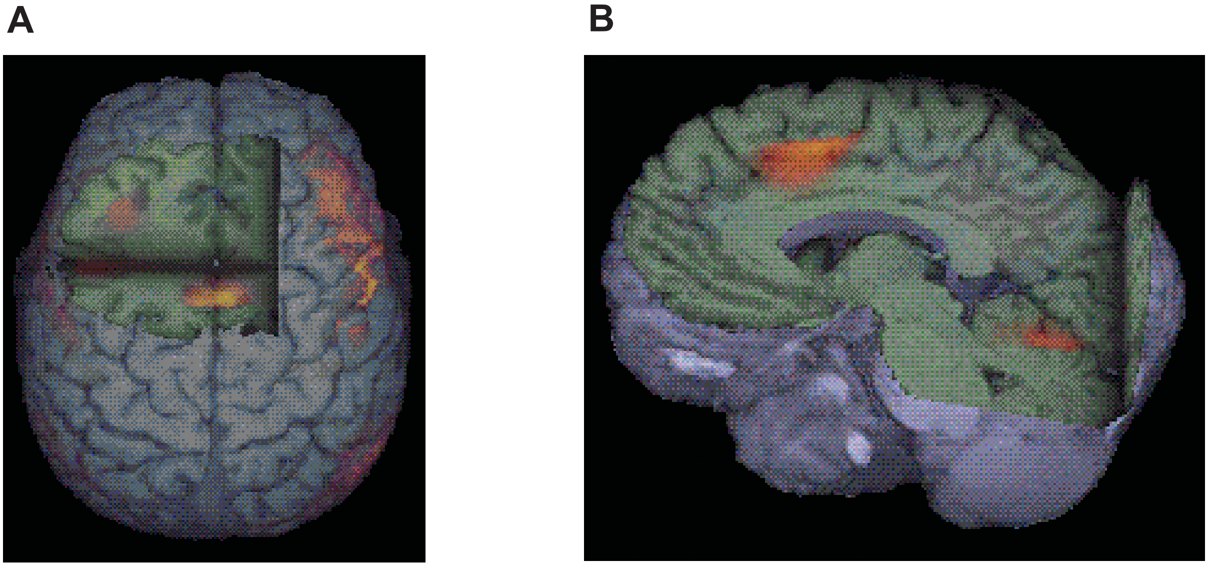

Fig. 2. Generic brain activation map of 20 healthy right-handed male adults (aged 22 to 42 years, mean age 29 years) while performing a time discrimination task after contrasted from an order discrimination task in block design fMRI. Subjects had to discriminate two time intervals. The standard interval lasted 1s, the comparison interval lasted either 1.3 s, 1.4 s, or 1.5 s. Both intervals were presented by a green or a red circle on a computer screen. Subjects had to decide which of the two circles that were presented consecutively on a computer screen lasted longer, the red of the green one (the standard and comparison intervals were counterbalanced in colour). The task was contrasted with an order discrimination task, where subjects had to indicate which of the two circles was presented first, the red or the green one (for details see Smith et al. 2003). Brain regions are shown of increased activation in relation to the temporal discrimination task when contrasted with the order judgement, thus representing areas responsible for pure perceptive temporal discrimination (corrected $P<0.05$) (A) Activation of right dorsolateral (BA 9/46) and inferior prefrontal (BA 45) cortices and the supplementary motor area (BA 6); (B) left hemispheric view: activation of left cerebellum and the supplementary motor area, that was activated bilaterally (see Fig. 2A).

after a certain temporal delay period), could in fact reflect underlying timing processes such as bridging the temporal gaps involved in these tasks or timing of the motor response (Rubia et al. 1998, 2000). Single cell recordings in prefrontal cortex in monkeys have been shown to be in line with this hypothesis. In an attempt to disentangle timing and working memory processes in delayed response tasks, Fuster (1973) found that different neurons in the DLPFC of monkeys were cue-coupled, presumably related to the mnemonic content, while others were showing sustained activity, presumably reflecting temporal processes. More recently, Constantinidis et al. (2002) studied cell pairs in DLPFC in primates and found that the firing of one of these paired neurons is then followed by inhibitory activity in the second cell of the pair. Temporally predictable decay curves in the first cell then determine the onset of activity of the second inhibited cell. These circuits could act as cortical oscillators and may even form the neural basis of a central clock mechanism (Lewis 2002). In support of this, an fMRI study found increasing activation in DLPFC with increasing delays in a working memory task, but not with increasing working memory load (Braver et al. 1997). Also, a study by Pochon et al. (2001) comparing a delayed matching task with a delayed response preparation task found that right-sided DLPFC activation was stronger for the response preparation than for the working memory task. Furthermore, there are also studies that have found DLPFC to be involved in shorter time estimation processes in the milliseconds' range, where sustained attention and working memory functions are less relevant (Larsson et al. 1996, Maquet et al. 1996, Ortuno et al. 2002, Rao et al. 2001 Smith et al. 2003). In our own study, the time intervals to be discriminated were about 1s long, but differed in hundreds of milliseconds (Smith et al. 2003). Thus, working memory or sustained attention demands were relatively small and well controlled by the control task and we still observed strong right-sided DLPFC and IFC activation (see Fig. 2).

It could also be argued, on the other hand, that working memory, i.e., holding the temporal interval online, is an important underlying cognitive component of time estimation processes which would also explain DLPFC activation during temporal tasks. DLPFC could then be thought to act as an "accumulator", storing information about a passing time interval and making it the working memory component of a hypothesised internal clock (Gruber et al. 2000, Mangels et al. 1998).

A third theory, probably the most likely, would assume that different regions within DLPFC subserve both timing and working memory functions (D'Esposito et al. 2000, Rubia et al. 1998, Zarahn et al. 2000).

Right IFC is another prefrontal region that has commonly been found to be activated during motor timing and time estimation processes. Thus, IFC has shown to be activated during motor timing tasks such as finger tapping (Rao et al. 1997), rhythmic finger movement (Kawashima et al. 1999), rhythm reproduction (Penhune et al. 1998), and sensorimotor synchronisation (Lejeune et al. 1997, Rubia et al. 2000) (see Fig. 1). It has, however, also found to be involved in perceptive timing paradigms such as temporal discrimination of hundreds of milliseconds (Maquet et al. 1996, Pedersen et al. 2000, Pouthas et al. 2000, Smith et al. 2003) (see Fig. 2), simple attention to synchrony/asynchrony (Gruber et al. 2000), rhythm perception (Schubotz et al. 2000), timed counting of hundreds of milliseconds (Ortuno et al. 2002) and temporal production of several seconds (Brunia et al. 2000). In a study that combined event related potentials (ERPs) with PET increased activation was observed in right IFC and ACG during time discrimination trials compared with intensity discrimination and the timing of the ERPs associated with right prefrontal regions were aligned with the durations themselves (Pouthas et al. 2000). As mentioned above, we observed right IFC and DLPFC activation in a motor delay task, where subjects had to adjust the motor response to a stimulus appearing every 5 seconds, which required both motor timing and time estimation (Rubia et al. 2000) (Fig. 1). IFC and DLPFC were, however, not activated during a motor tapping task of 600 ms, when contrasted with the synchronisation task of 5 s (Rubia et al. 2000). Very similar right IFC and DLPFC activation was observed during a temporal discrimination task of hundreds of milliseconds (Smith et al. 2003) (see Fig. 2). In an elegant attempt to disentangle the involvement of different prefrontal brain regions in timing aspects, Brunia et al. (2000) could attribute IFC activation to the execution of an anticipated timed movement (the production of a 3 s interval) based upon feedback on previous performance, while DLPFC appeared to use internal cues for temporal programming of the motor output. Furthermore, Gruber et al. (2000) and Schubotz et al. (2000) found activation in IFC where subjects were instructed simply to attend to rhythm and where no movement was required. It thus appears that IFC may be related more to perceptive time estimation processes rather than to motor timing aspects of behaviour.

SUPPLEMENTARY MOTOR AREA (SMA) AND THE ANTERIOR CINGULATE GYRUS (ACG)

The SMA forms part of fronto-striatal pathways. It has projections to and from the basal ganglia *via* the thalamus, and is also connected to frontal and parietal cortical attention areas (Schell and Strick 1984). Focal lesions in the SMA have shown to produce deficits in the timing of movements as tested in rhythm reproduction (Halsband et al. 1993). Activation of the SMA has consistently been found in motor timing tasks, including tasks of finger tapping and rhythm tapping of hundreds of milliseconds, and motor preparation, temporal production and temporal synchronisation of several seconds (Brunia et al. 2000, Lang et al. 1990, Penhune et al. 1998, Rao et al. 1997, Riecker et al. 2003, Rubia et al. 1998, 2000) (see Fig. 1). However, despite its postulated role in motor aspects of timing, the SMA has also been activated in tasks of pure perceptive time estimation. Thus, some studies have observed increased SMA activation during estimation of longer time intervals of seconds as opposed to milliseconds (Fernandez et al. 2003, Pouthas et al. 2001, Rubia et al. 1998, 2000) (see Fig. 1) and in time production of several seconds (Lewis and Miall 2002). However, SMA activation has also been found in studies of discrimination of short intervals in the milliseconds' range (Macar et al. 2002, Rao et al. 2001), of second intervals that differed by hundreds of milliseconds (Smith et al. 2003) (see Fig. 2), in rhythm discrimination involving milliseconds (Gruber et al. 2000, Schubotz et al. 2000), timed counting (Ortuno et al. 2002) and in temporal orienting to brief temporal intervals of hundreds of milliseconds (Coull and Nobre 1998). Indeed, Macar et al. (2002) found SMA activation in both short (milliseconds) and long time (seconds) interval discriminations. We observed a similar focus of the SMA in sensorimotor timing of 5 s (Rubia et al. 2000) (see Fig. 1) and in temporal discrimination of seconds intervals that differed by hundreds of milliseconds (Smith et al. 2003) (see Fig. 2). It thus appears that, while earlier studies have postulated a strong role of the SMA in motor timing processes, more recent studies have shown that the timing functions of the SMA also include purely perceptive timing.

The closely adjacent anterior cingulate gyrus (ACG) has also found to be activated in motor timing tasks such as sensorimotor synchronisation of seconds (Rubia et al. 1998, 2000) and sensorimotor synchronisation of hundreds of milliseconds (Lejeune et al. 1997, Rubia et al. 1998). It has, however, also been found to be activated in studies of time estimation such as time production and reproduction of seconds (Lewis and Miall 2002, Macar et al. 2002), temporal discrimination (Maquet et al. 1996) and timed counting (Ortuno et al. 2002) in the milliseconds range. Unlike the study of Maquet et al. (1996) we did not observe ACG activation when subjects had to discriminate time intervals that differed by hundreds of milliseconds (Smith et al. 2003) (see Fig. 2), but we observed ACG activation during sensorimotor synchronisation of hundreds of milliseconds and seconds (Rubia et al. 1998, 2000) (see Fig. 1). It has been suggested that ACG, rather than being specifically related to cognitive time management per se, might be related to motor attention functions. Thus, ACG has been found to show a biphasic activation in both a motor tapping task of 600 ms and a delay task of 5 s and has been suggested to play a role in switching and attention allocation (Rubia et al. 1998). The ACG forms part of the midline attention system and has therefore been attributed a role in attention to action as well as an evaluative comparator role assisting executive control (Carter et al. 1999, 2000, Gehring and Knight 2000, McDonald et al. 2000, van Veen et al. 2000), both important functions that are necessary for motor timing and distinguishing time intervals, respectively.

CEREBELLUM

Two important subcortical brain structures have been related to motor and cognitive time management, namely the cerebellum and the basal ganglia. The importance of the cerebellum in timing processes has been postulated long time ago (Braitenberg 1967) and is now fairly well established (Harrington and Haaland 1999). Lesion studies have shown that patients with cerebellar lesions display poor performance on both motor tapping and time estimation tasks such as velocity perception and temporal discrimination, both in the range of hundreds of milliseconds (Ivry and Diener 1991, Ivry and Keele 1989, Ivry et al. 1988). In one of the studies the poor performance of cerebellar patients on motor tapping and time discrimination contrasted with the performance of patients with cortical lesions, who showed deficits in a finger tapping but not a discrimination task, and patients with basal ganglia damage, whose performance did not differ from that of controls in either task (Ivry and Keele 1989, Ivry et al. 1988). Since temporal discrimination is often thought to be the purest measure of time perception (Rubia et al. 1999a), this study was interpreted as evidence for a central role of the cerebellum in temporal perception. Other studies of cerebellar patients have shown them to be poor at time discrimination in both long (seconds) and short (hundreds of milliseconds) intervals (Casini and Ivry 1999, Mangels et al. 1998, Nichelli et al. 1996) and, in contrast with patients with prefrontal lesions, the temporal discrimination deficits of cerebellar patients were not alleviated by counting strategies and the use of short durations (Mangels et al. 1998). The above evidence, derived from focal lesion studies is supported by functional imaging studies where cerebellar activation has been found in temporal discrimination of short intervals of hundreds of milliseconds (Dupont et al. 1993, Jueptner et al. 1995, Maquet et al. 1996, Rao et al. 2001, Smith et al. 2003), temporal orienting of under a second intervals (Coull and Nobre 1998), rhythm discrimination (Schubotz et al. 2000), rhythm reproduction of hundreds of milliseconds (Penhune et al. 1998) and time production of several seconds (Lewis and Miall 2002, Tracy et al. 2000). Furthermore, apart from perceptive time estimation functions, the cerebellum has also been found to be activated in functional imaging studies on motor timing functions such as sensorimotor synchronisation of short intervals in the milliseconds' range (Inui and Hatta 2003, Larsson et al. 1996, Penhune et al. 1998, Rao et al. 1997) and longer time intervals of several seconds (Lejeune et al. 1997, Riecker et al. 2003). We observed activation in the left cerebellar hemisphere during a fine-temporal discrimination task of hundreds of milliseconds (Smith et al. 2003) (see Fig. 2a). Most imaging studies have found an involvement of the lateral portions of the cerebellar hemispheres in timing processes. It has therefore been suggested that motor execution may be subserved by medial regions of the cerebellum, while internal clock processes or temporal management may be subserved by lateral regions of cerebellum (Ivry et al. 1988). In line with this functional division is the difference in the connectivity of these two regions of cerebellum – the lateral cerebellum projects to premotor cortex and DLPFC, important for motor and perceptive timing, while medial cerebellum is connected with the spinal cord, affecting motor implementation (Middleton and Strick 1994, 2000). Two PET studies, however, found that besides the lateral portions of the cerebellar hemispheres also the vermis of the cerebellum was involved in temporal discrimination of hundreds of milliseconds (Jueptner et al. 1995, Maquet et al. 1996). In conclusion, based on the findings in the literature of an involvement of the cerebellum in motor timing and time perception tasks, it has been speculated that the cerebellum might be especially relevant to event timing (Ivry et al. 2002).

THE BASAL GANGLIA

Although basal ganglia lesion patients were not impaired in time discrimination in the study of Ivry and Keele (1989), the basal ganglia have been observed to be involved in time estimation and motor timing in several other studies. Thus, lesions in the right supralenticular white matter, presumably consisting of fronto-striatal pathways, have been found to be associated with impaired time estimation and production of several seconds in patients with brain lesions (Rubia et al. 1997). We observed right putamen activity in a sensorimotor task of 5 s in healthy adults using fMRI (Rubia et al. 2000) (see Fig. 1). Left and right putamen (Lejeune et al. 1997) and left putamen, globus pallidum and caudate nucleus (Riecker et al. 2003) have been found to be activated during other sensorimotor synchronisation tasks of several seconds and left putamen has been found to be activated during a finger tapping task of hundreds of milliseconds (Larsson et al. 1996, Rao et al. 1997) and left and right putamen during rhythm reproduction in the milliseconds range (Penhune et al. 1998). Furthermore, caudate and putamen have been also found to be activated in perceptive time estimation tasks. Thus, caudate and putamen have been found to be activated in time discrimination tasks in the milliseconds range (Dupont et al. 1993, Jueptner et al. 1995, Rao et al. 2001), in rhythm discrimination of hundreds of milliseconds (Schubotz et al. 2000), and in time production of several seconds (Lewis and Miall 2002). The role of the basal ganglia in time estimation and motor timing functions corroborates studies in patients with Parkinson's disease showing deficits in motor timing and time perception that can be ameliorated with dopaminergic treatments (Lange et al. 1995, O'Boyle et al. 1996, Pastor et al. 1992, Riesen and Schnider 2001). Furthermore, dopaminergic agents have also shown to have an effect on time estimation and motor timing functions in healthy subjects (Rammsayer 1993, 1997, Rammsayer and Vogel 1992). Animal studies show disruptions in response timing after focal lesions or drugs targeting the dopaminergic functions in the basal ganglia (for review see Meck 1996).

The role of the cerebellum and the basal ganglia in cognitive time management and timing of movements is not surprising giving the important role these two structures have in fine-modulation of the behavioural output and of movement in particular. Both the basal ganglia and the cerebellum have important reciprocal connections with the motor areas of the frontal lobes (Middleton and Strick 1994, 2000, Picard and Strick 1996), but also receive input from sensory brain regions such as the parietal lobes. Their role in fine-modulation of the motor and cognitive output makes them well suited to regulate the timing aspects of behaviour.

PARIETAL LOBES

Other cortical brain regions that have commonly been associated with time estimation, but less with motor timing, are the inferior parietal lobes. Focal lesion studies have found time estimation deficits of several seconds in patients with predominantly right parieto-occipital brain lesions (Harrington et al. 1998, Petrovici and Scheider 1994). Inferior parietal lobes have found to be activated during a sensorimotor synchronisation task of several seconds, which involved both time estimation and time estimation functions (Rubia et al. 2000) (see Fig. 1), during synchronisation of an interval of several seconds (Lejeune et al. 1997), during finger tapping (Larsson et al. 1996) and rhythm reproduction (Penhune et al. 1998) of hundreds of milliseconds, during time estimation tasks of several seconds (Basso et al. 2003, Lewis and Miall 2002, Macar et al. 2002), and in temporal discrimination (Dupont et al. 1993, Maquet et al. 1996, Pedersen et al. 2000, Rao et al. 2001), rhythm discrimination (Schubotz et al. 2000) and timed counting (Ortuno et al. 2002) of hundreds of milliseconds. It has been argued that the role of the parietal lobes in time estimation tasks could be related to aspects of sustained attention to time (Ortuno et al. 2002, Pardo et al. 1991). In our time discrimination task that was well controlled for sustained attention by a control task, we did not observe any parietal lobe activation (Smith et al. 2003) (see Fig. 2). Sustained attention to time intervals is certainly a necessary basis function for time estimation processes. Furthermore, the inferior parietal lobes are interconnected with the frontal lobes, the basal ganglia and the cerebellum (Cavada and Goldman-Rakic 1991, Schmahmann and Pandya 1990), all of which have shown to be important in time estimation. The parietal lobes with their connections to fronto-striatal and fronto-cerebellar circuits are thus strategically well placed to support cognitive time management processes by assisting them with sustained attention to time.

CONCLUSIONS

In conclusion, this review on the neural correlates of cognitive time management shows that predominantly right hemispheric dorsolateral and inferior prefrontal cortices, anterior cingulate, the SMA, the basal ganglia and the lateral cerebellar hemispheres appear to be involved in both functions of motor timing and time estimation.

Furthermore, the review shows that the dichotomy between motor and perceptive timing functions may be artificial. Both functions appear to be mediated by identical neural networks and may be inseparable.

There could be several reasons for the fact that motor timing and time perception are mediated by the same brain regions. The most likely reason is that the two timing functions are cognitively inseparable and therefore mediated by identical brain areas. This argument would suggest that timing a movement, for example, is not possible without good temporal perception functions, and, on the other hand, many time perception tasks involve elements of motor timing such as for example tasks of temporal and rhythm production and reproduction.

Another argument would be that third cognitive basic functions are underlying time estimation and motor timing such as sustained attention and working memory that would be responsible for the findings of common neural substrates. Several imaging studies, however, have controlled for sustained attention and working memory and it is therefore unlikely that the activation in timing tasks is due to timing-unspecific working memory or attention functions. It rather appears that each of these different brain regions has their specific role in contributing to cognitive time management.

Right dorsolateral and inferior prefrontal cortices – possibly in connection with their role in working memory – appear to play a special role in holding temporal intervals online which is essential for most time estimation and motor timing functions. The SMA, traditionally been related to motor timing, but, as the review shows, with recent involvement in purely perceptive temporal estimation, appears to be a crucial brain area to process temporal intervals in order to adjust movement in the temporal domain. The anterior cingulate has been suggested to have a more generic role in attentional components necessary for both motor timing (attention to action) and time estimation (evaluative comparator). This area thus contributes to cognitive time management as comparator of temporal intervals in time estimation tasks or by assisting motor timing with allocation of motor attention. The cerebellum and the basal ganglia, known to be fine-modulators of emotional, cognitive and motor behaviour, appear to be crucial also for the fine-modulation of the temporal aspects of behaviours at both the motor and perceptive levels. Last, not least, the parietal lobes seem to contribute to time estimation and motor timing through allocation of sustained attention to time.

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