

Time perception: Manipulation of task difficulty dissociates clock functions from other cognitive demands

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Abstract

Previous studies suggest the involvement in timing functions of a surprisingly extensive network of human brain regions. But it is likely that while some of these regions play a fundamental role in timing, others are activated by associated task demands such as memory and decision-making. In two experiments, time perception (duration discrimination) was studied under two conditions of task difficulty and neural activation was compared using fMRI. Brain activation during duration discrimination was contrasted with activation evoked in a control condition (colour discrimination) that used identical stimuli. In the first experiment, the control task was slightly easier than the time task. Multiple brain areas were activated, in line with previous studies. These included the prefrontal cortex, cerebellum, inferior parietal lobule and striatum. In the second experiment, the control task was made more difficult than the time task. Much of the differential time-related activity seen in the first experiment disappeared and in some regions (inferior parietal cortex, pre-SMA and parts of prefrontal cortex) it reversed in polarity. This suggests that such activity is not specifically concerned with timing functions, but reflects the relative cognitive demands of the two tasks. However, three areas of time-related activation survived the task-difficulty manipulation: (i) a small region at the confluence of the inferior frontal gyrus and the anterior insula, bilaterally, (ii) a small portion of the left supramarginal gyrus and (iii) the putamen. We argue that the extent of the timing “network” has been significantly over-estimated in the past and that only these three relatively small regions can safely be regarded as being directly concerned with duration judgements.

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1. Introduction

Time perception is an ability that is taken for granted, yet relatively little understood. Without it, other cognitive functions, especially motor actions and visual awareness, would be severely impaired. Basic tasks such as crossing the road would be near impossible.

Various models of time perception have been suggested, the most popular being the internal-clock model (Gibbon, 1977). Here a series of pulses are produced by an internal pacemaker; these pulses are collated, counted and then compared to stored representations in order to allow the brain to judge durations and produce time estimations. Such models have been extensively studied using behavioural paradigms (Thomas & Weaver, 1975; Block, 1990). However, our understanding of the neural

substrates of these functions is limited. Several neuropsychological studies and a growing number of neuroimaging studies have been conducted in this field, revealing the involvement of numerous brain areas in timing tasks, but the specific roles of these areas remain largely unclear.

The study of patients with neurological damage has revealed the importance of several brain structures in time processing. Early studies highlighted the cerebellum as a key component of the time processing network. Ivry and Keele (1989) demonstrated that patients with cerebellar lesions showed poor motor timing and time discrimination when comparing short intervals (less than 1 s), while Mangels, Ivry, and Shimizu (1998) found that patients with cerebellar lesions cannot discriminate longer intervals (4 s). These results suggest that the cerebellum has a fundamental role to play in both sub- and supra-second time perception. In recent years, the evidence from lesion studies has been greatly extended by imaging studies using fMRI and PET. Cerebellar activity has been reported in temporal discrimination tasks using intervals of various durations (Mathiak, Hertrich,

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Grodd, & Ackermann, 2004; Jueptner et al., 1995; Rao, Mayer, & Harrington, 2001) and also in time production tasks (Penhune, Zatorre, & Evans, 1998; Tracy, Faro, Mohamed, Pinsk, & Pinus, 2000).

More recently the notion of a central role for the cerebellum has been questioned (Harrington, Lee, Boyd, Rapcsak, & Knight, 2004), although this view still has its adherents (Ivry & Spencer, 2004). The advent of brain imaging has caused a shift in emphasis away from the cerebellum towards fronto-striatal pathways. Initial PET results suggested that the basal ganglia, particularly the striatum, and the cingulate cortex are active during time processing tasks (Jueptner et al., 1995; Lejeune et al., 1997). fMRI studies lead to similar conclusions. Rao et al. (1997) reported that generating a rhythm by finger-tapping causes differential activity for self-generated rhythms in the left putamen and left supplementary motor area (SMA). Rao et al. (2001) found similar results with a time perception task, and in addition showed that activity in the basal ganglia evolves earlier than that in the cerebellum, possibly suggesting a more fundamental role. Nenadic et al. (2003) found timing-related activity in the right putamen in a duration discrimination task, while Coull, Vidal, Nazarian, and Macar (2004) also reported timing-related activity in the striatum and showed that the activity increases with the level of attention paid to the timing task (as opposed to a competing control task). Also emphasised in the latter study are pre-SMA and the frontal operculum, which the authors see as parts of a fronto-striatal timing network. Other studies have also identified pre-SMA as important (e.g. Pastor, Day, Macaluso, Friston, & Frackowiak, 2004; Pouthas et al., 2005). Recent theoretical treatments of timing (e.g. Meck and Benson, 2002; Buhusi & Meck, 2005) give fronto-striatal circuits a key role, while evidence of disruption to timing processes in Parkinson's disease (Malapani et al., 1998), which involves degeneration of nigrostriatal dopamine systems, is consistent with such an account.

Several other brain regions have been identified as being active during time processing. In particular, the right dorsolateral prefrontal cortex (DLPFC) has been implicated in time discrimination studies (Rao et al., 2001; Macar et al., 2002; Lewis & Miall, 2003), although one lesion study suggests that the DLPFC is only important for longer durations (Mangels et al., 1998). A final region that has been implicated in several studies is the inferior parietal cortex. Both lesion studies (Harrington, Haaland, & Knight, 1998) and fMRI studies (Lewis & Miall, 2003; Pastor et al., 2004) implicate the right inferior parietal lobule, in particular, and there is some evidence for involvement of the left supramarginal gyrus (Assmus, Marshall, Ritzl, Noth, & Fink, 2003).

1.1. Outstanding problems

A recurring problem in the interpretation of neuroimaging studies of time perception is that activation seen during timing tasks may be related to cognitive functions other than pure timing functions. Consider, for example, the case of the DLPFC. Working memory has been linked to the DLPFC (e.g. MacDonald, Cohen, Stenger, & Carter, 2000) and the possibility of working

memory components being involved in timing tasks is plausible. But not all researchers take this view. Zakay and Block (1996), Rubia et al. (1998) amongst others argue for a more primary role for the DLPFC in the time estimation process. Smith, Taylor, Lidzba, & Rubia, 2003 specifically investigated the role of the DLPFC and also concluded that it may play a more central and specific role in time processing than simply providing working memory.

In this context, the choice of control task is a concern in several previous studies. Ideally, the experimental and control tasks should use identical stimuli. In addition, and perhaps more crucially, the two tasks should impose the same cognitive demands apart from timing, which should be absent in the control. This means that the control task should involve sustained cognitive activity during the period of the trial and have a similar level of difficulty. In some previous studies, different stimuli were used for the time task and the control task. In others, the stimuli were the same but the control task was easier, perhaps just requiring a button press at the end of a time period. If the timing task is more difficult or requires more sustained attention than the control task, differential activation may reflect these factors rather than timing activities. Several studies have, in fact, included careful attempts to equate task difficulty (see Section 6). However, no study has systematically varied task difficulty in order to dissociate pure time functions from other cognitive demands. To do so is the purpose of the present investigation.

We have conducted two experiments that are identical apart from the difficulty of the control task. The same group of participants was used for both experiments. Within each experiment, we compared activity elicited by a duration discrimination task with that found in a control task (colour discrimination) that used identical stimuli. The control task required a judgement based on information integrated over the entire duration of the stimulus, to ensure that cognitive demand was imposed throughout the duration of the control trial. In Experiment 1, the difficulty of the control task was set to be slightly easier than the time task, whereas in Experiment 2 it was slightly harder. In areas that are truly concerned with timing, differential activity should be found in both experiments. In any areas where activity reflects general task demands, rather than time perception *per se*, the polarity of activation should reverse, from timing > control in Experiment 1 to control > timing in Experiment 2.

2. Experiment 1: time perception with an easier control task

2.1. Participants

Ten participants (seven female) completed the experiment. Their ages ranged from 18 to 29 years (mean = 21.4). None of the participants had any history of neurological damage or disease and all had normal acuity and colour vision. The study was approved by the relevant ethics committee and each participant completed standard screening and consent procedures.

Participants were given an instruction sheet and the experimenter explained any aspect that the participant did not understand. A 4-min practice run was completed before scanning, to familiarise the participant with the task. A second practice run was performed in the scanner, whilst an anatomical scan was carried out, at the start of the MRI session.

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