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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.

Keywords: fMRI; Duration discrimination; Putamen; Supramarginal gyrus; Pre-SMA

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.

2.2. Design

The design of the fMRI experiment was a simple block design in which two task conditions, one experimental and one control, were alternated in blocks of 15 s. The cerebral activation was then directly compared between the two conditions. So that differences in activation could not be ascribed to stimulus differences, identical stimuli, varying in both duration and colour, were used for both blocks and only the task varied between blocks. The 'duration' condition involved discriminating the durations of two visual stimuli and the 'colour' (control) condition involved discriminating the colours of the same stimuli. The duration block was presented first. This design is similar to the approach taken by Coull et al. (2004) and ensures sustained processing during the control task as well as the timing task. It also allows controlled manipulation of task difficulty.

2.3. Stimuli

Computer-generated stimuli were projected onto a translucent screen mounted in the bore of the magnet 50 cm from the participant's head. The participant watched the screen by means of a mirror mounted on the headcoil. The stimulus for both tasks was a central, circular, uniform disk with a diameter of 10° of visual angle. During each stimulus presentation, the disk changed colour every 100 ms, each colour being selected from a pre-determined set of six very different colours. The stimuli were presented in pairs. One stimulus (first or second, chosen at random) had a longer duration (1.5 s) than the other (1.0 s) and one flashed red more frequently than the other. These differences formed the basis of the two tasks. In the intervals between stimuli, the disk was white. The order of presentation of the two durations was randomised and the order of the two types of colour sequence was independently randomised, giving four possible combinations of duration and colour.

2.4. Tasks

During each trial (presentation of one stimulus pair), the two stimuli were presented consecutively, the white disk appearing for 0.5 s before stimulus one and between stimuli one and two. After stimulus two finished, the white disk appeared once more, but with a question mark centred within the spot. This symbol indicated the end of the trial and prompted the participant to enter a response. The participant then had 1.5 s to respond before the next trial began. The total length of each trial was thus 5 s. To avoid speed/accuracy trade-offs, participants were told that they should respond at leisure (within the 1.5 s) and that reaction times would not be measured. Three consecutive trials of the same type were presented, in one 15 s block, before the task type altered.

2.4.1. Duration condition

In the duration condition, the participants were asked to attend to both stimuli before indicating which stimulus (first or second) had been presented for longer by pressing the corresponding button on a keypad. They were told to ignore the difference in colour between the stimuli. Because colour and duration were varied independently, colour provided no cue to the correct answer.

2.4.2. Colour condition

In the colour condition, the participants were again asked to attend to both stimuli. However, in this case the participants had to indicate which stimulus contained a greater proportion of red flashes, ignoring the difference in duration. This task was chosen for the control condition because, in common with the duration task, it requires sustained judgement, integrated over the whole stimulus duration. This feature, absent in some previous work, was intended to remove the possibility that the time task might cause greater activation simply because it engages the participant for a greater proportion of the total trial time.

The two durations (1.0 and 1.5 s) were chosen in the light of previous studies, most of which have used quite short intervals. This choice determined the difficulty of the time task. The level of difficulty of the control task was set following a pilot study, conducted outside the scanner with different participants, in which the relative frequency of red disks was varied, so as to vary the difficulty of the colour discrimination. Performance on the time discrimination task was also measured in the pilot study. Based on the results, a level of colour task difficulty was selected that gave higher performance, in terms of percent correct trials, than was achieved in the time condition, without being trivially easy.

Because the two tasks alternated between blocks with no change of stimulus, a cue was needed to tell the participant which task they should perform at any given time. The cue was a word that appeared above the coloured disk. The word *duration* appeared continuously throughout a block for the duration discrimination condition and the word *colour* appeared during colour discrimination blocks.

One run of the experiment consisted of 16 blocks of 15 s (total 4 min) and contained 48 trials (three trials per block). Six identical runs were completed for each participant in a single scan session.

2.5. Image acquisition

Images were acquired with a 3-T Siemens Magnetom Trio MR scanner equipped with an eight-channel array headcoil. Before functional imaging commenced, 3D anatomical images were collected (MP-RAGE, Siemens). Each functional time series consisted of 80 whole-brain, gradient-echo EPI scans (TR/TE = 3000/30 ms, flip angle = 90°, 3 mm isotropic voxel size, FOV = 192,192,126 mm, 42 axial slices) acquired with parallel imaging using GRAPPA (Griswold et al., 2002; acceleration factor = 2). This 4-min acquisition was repeated six times for each participant with a short break between runs. The participants' heads were lightly restrained using foam padding and the participants were instructed to keep their heads as still as possible.

2.6. Data analysis

The fMRI data were analysed using SPM2 (Wellcome Department of Imaging Neuroscience, London). Motion correction was performed by realigning each volume to the first volume of the first time series run, for each participant. The realigned images were then normalized to a template 3D brain (MNI-152, provided in SPM and originally produced by the Montreal Neurological Institute). Finally, in order to reduce spatial noise, the images were spatially smoothed using an isotropic Gaussian kernel (width at half height = 6 mm). The six repeated runs of the same type from each of the ten participants were analysed in a group analysis. The difference between the experimental (duration) and control (colour) task was tested by producing a t statistic for every voxel, using a fixed-effects GLM analysis. This choice was made because our purpose was to examine established timing areas, the existence of which is not in doubt, and we wished to identify all these areas with minimal losses from sensitivity issues. A correction for multiple comparisons (FDR; Genovese, Lazar, & Nichols, 2002) was applied using a corrected threshold level of $p < 0.01$.

The t-maps generated within SPM2 were then visualised using mri3dX (http://www.jiscmail.ac.uk/lists/mri3dX.html). The functional data obtained from the fixed-effects group analysis were overlaid on the standard 3D anatomical brain used for spatial normalization.

3. Results

3.1. Behavioural data

All participants attained greater than 70% correct but less than 100% in both tasks. The mean percentage of correct responses for the duration condition was 81.7% (S.D. = 4.8). For the colour condition it was 93.5% (S.D. = 5.2). This indicates that the level of task difficulty was indeed greater for the duration task, as intended. This difference was statistically significant [$t(9) = 11.65$, $p < 0.001$].

3.2. Imaging data

Several brain regions revealed significant differential activation during time perception (duration discrimination) relative to colour perception. These are shown in Fig. 1, in which active regions identified in the group analysis are superimposed on the

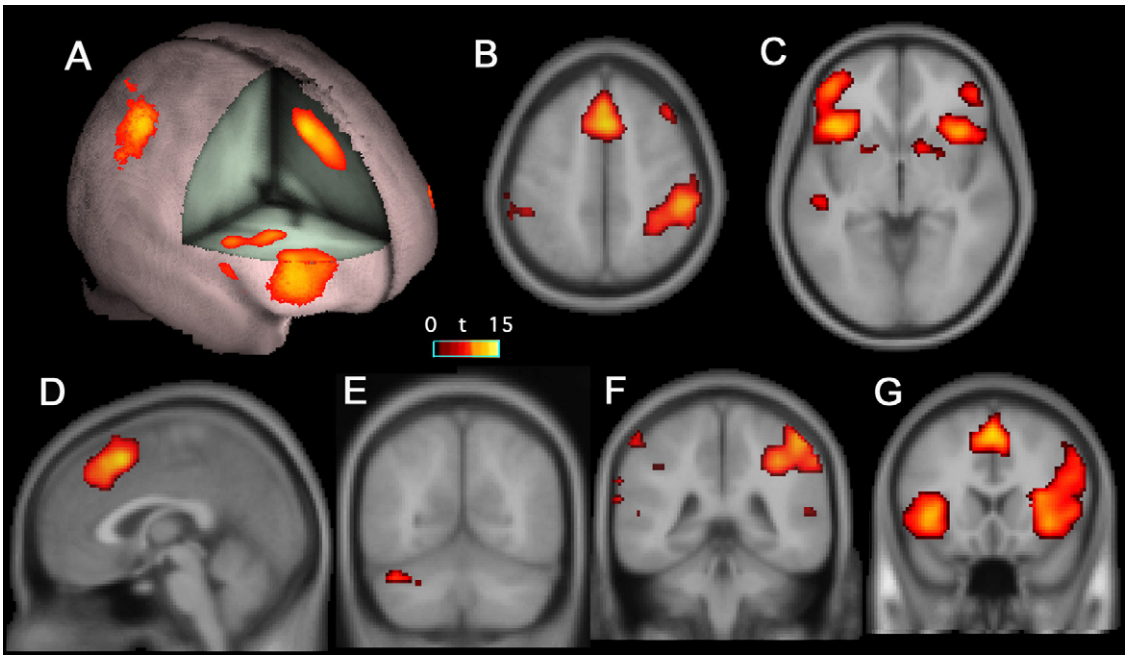

Fig. 1. Imaging data obtained from Experiment 1. The functional data reflect the *t*-map from a group analysis ($n = 10$) and are superimposed as a colour overlay (see key) on the average of 152 anatomical scans from different brains (Montreal Neurological Institute). Functional data are thresholded at $p < 0.01$ corrected for multiple comparisons using FDR. All slices are in neurological format (left on the left). (A) 3D rendered view of the brain, with a cutaway showing the lateral prefrontal areas of activation in the right hemisphere and the SMA complex in the left hemisphere. (B) Horizontal slice (in the Talairach plane $z = 43$) showing the pre-SMA and the inferior parietal activation bilaterally. (C) A more inferior horizontal slice ($z = -1$) showing activation in the frontal cortex and anterior insula bilaterally, together with the striatum. (D) A mid-sagittal section ($x = 0$), again showing the pre-SMA activation. (E) Coronal view ($y = -55$) showing activation in the left cerebellum. (F) A more anterior coronal view ($y = -35$) showing the active area in the right parietal lobe. (G) A coronal section through frontal cortex ($y = 19$) showing the prefrontal activity (laterally) and the pre-SMA (medially).

MNI-152 template brain used for spatial normalization. This template is the average of anatomical images of 152 brains and therefore appears quite blurred. The blurring gives an indication of the level of anatomical precision that can be attributed to activation sites in such a group analysis.

The five main active areas were:

(i) A large, lateral frontal region (probably two discrete regions) comprising (a) parts of the middle frontal gyrus and inferior frontal sulcus together with (b) a portion of the nearby inferior frontal gyrus (IFG) and possibly anterior insula. This region is active bilaterally and overlaps the classical DLPFC (see Fig. 2a, c and g).
(ii) A medial frontal region corresponding to pre-SMA. Again, the activation is bilateral. Ventrally, this region borders (and may extend into) the cingulate sulcus but it does not appear to include any part of the cingulate gyrus (see Fig. 2a, b and g).
(iii) A portion of the inferior parietal lobule, activation being much stronger in the right hemisphere than the left (see Fig. 2a and f).
(iv) The striatum, including the putamen bilaterally and probably also the right caudate (see Fig. 2c).
(v) The superior cerebellum, the activation apparently being stronger in the left hemisphere than the right (see Fig. 2e).

Table 1 shows Talairach co-ordinates for these areas. The conversion from MNI to Talairach space was performed in *mri3dX*.

These areas have all previously been implicated in fMRI studies of time perception. The most obvious interpretation is therefore that they are differentially active in the 'duration' condition because they are specifically concerned with time judgements. But, in principle, some or all might be differentially activated by other cognitive components of the task, such as memory, attention or decision-making, given that the duration task was more difficult than the control task. These factors will be distinguished in Experiment 2.

4. Experiment 2: time perception with a harder control task

The areas that were differentially activated by the time perception task in Experiment 1 broadly correspond to those that have been identified previously in studies using time perception tasks. We now turn to the issue of the extent to which these areas were active because the difficulty of the time task was greater than that of the control task, rather than because they are concerned with measurement of time. To distinguish between activity related to time processing and that related to task difficulty, we repeated Experiment 1, using the same participants, with the control task manipulated so as to reverse the difference in task difficulty. With the control task harder than the timing task, areas reflecting cognitive demand should now be more active in the control condition, whereas true timing-related activity should still be greater in the duration condition.

4.1. Participants

The same ten participants who took part in Experiment 1 also took part in Experiment 2.

4.2. Design, stimuli and tasks

The design was identical to that of Experiment 1 except that the control task ("colour" condition) was made more difficult than the time perception task

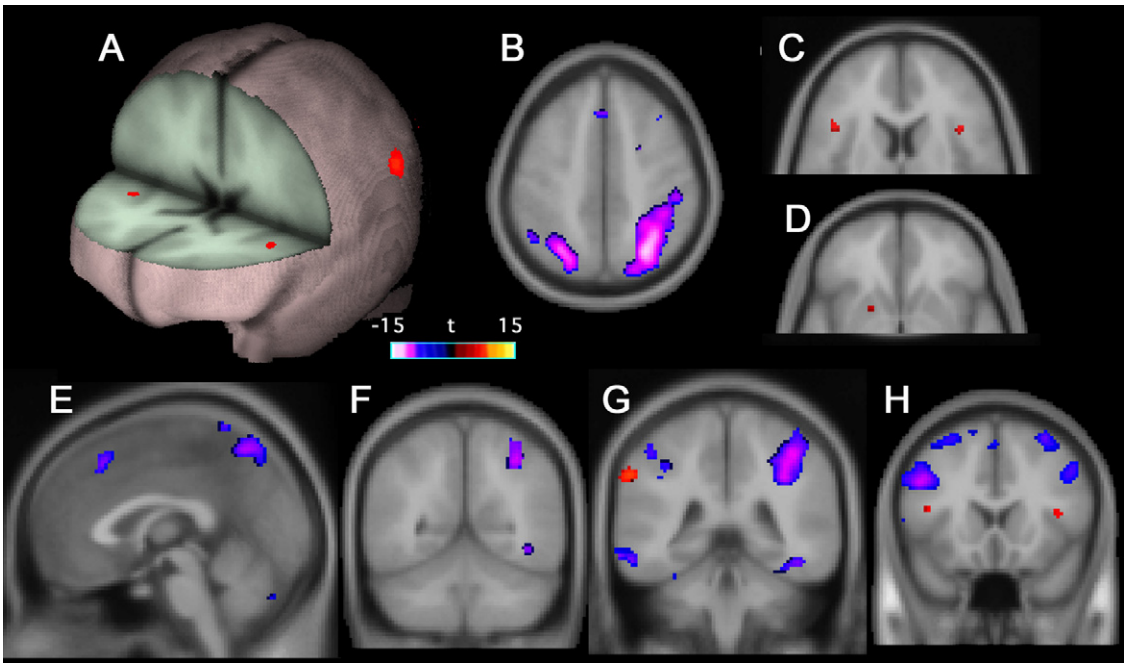

Fig. 2. Imaging data obtained from Experiment 2. The data are again from a group analysis and are thresholded at $p < 0.01$ (FDR corrected). The format is similar to Fig. 1 and in most cases the same slices are shown. Positive t values (red/yellow; see colour key) indicate greater activity during time perception than during the (more difficult) control task, as in Fig. 1. Negative t values (blue/purple) indicate greater activity during the control than the time perception task. (A) 3D rendered view of the template brain, with a cutaway showing the small portion of the inferior frontal gyrus bilaterally that is positively activated, along with an active region in the left inferior parietal cortex. (B) Horizontal slice (in the Talairach plane $z = 43$) showing negative activation (control > time) in the inferior parietal lobule bilaterally and also the pre-SMA. (C) Anterior portion of a more inferior horizontal slice ($z = 10$) showing timing-related activation in the inferior frontal cortex and/or anterior insula, bilaterally (D) Anterior portion of a horizontal slice ($z = -1$) showing timing-related activity in the left striatum. (E) A mid-sagittal section ($x = 0$) showing the negative activation in pre-SMA and parietal cortex. (F) Coronal view ($y = -55$) showing lack of timing-related activation in the left cerebellum. (G) A more anterior coronal view ($y = -35$) showing both timing-related activity in a portion of the left inferior parietal lobule and also negative activation in both right parietal lobes. (H) A coronal section through frontal cortex ($y = 19$) showing the same positive (timing-related) activation in the IFG/insula that is evident in panel C. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

("duration" condition). This was achieved by reducing the difference in the proportion of red disks between the two stimuli of each trial. Pilot studies conducted outside the scanner were used to set a level of difference that made the colour task possible but significantly more difficult (measured in terms of performance) than the duration task.

4.3. Image acquisition and data analysis

This was identical to Experiment 1 in all respects.

5. Results

5.1. Behavioural data

The mean percentage of correct responses for the duration condition was 78.2% (S.D. = 4.4), and for the colour task it was 69.5% (S.D. = 7.2). This indicates that, as intended, the participants found the time task easier than the colour

Table 1
Major areas of activation found in the two experiments, with the corresponding co-ordinates in Talairach space (Talairach & Tournoux, 1988)

Experiment 1: time perception (time task harder than control)		Experiment 2: time perception (time task easier than control)	
Cortical area	Talairach (x y z)	Cortical area	Talairach (x y z)
Prefrontal cortices (R)	41, 46, 3	Prefrontal cortices (R)	–
Prefrontal cortices (L)	−48, 44, 3	Prefrontal cortices (L)	–
Inferior parietal lobule (R)	51, −34, 54	Inferior parietal lobule (R)	–
Supramarginal gyrus (L)	–	Supramarginal gyrus (L)	−61, −39, 38
pre-SMA (R)	1, 20, 54	pre-SMA (R)	–
pre-SMA (L)	−1, 20, 54	pre-SMA (L)	–
Insula/IFG (R)	35, 23, 3	Insula/IFG (R)	40, 18, 9
Insula/IFG (L)	−36, 22, 3	Insula/IFG (L)	−43, 18, 13
Putamen (R)	13, 10, −2	Putamen (R)	–
Putamen (L)	−19, 6, −7	Putamen (L)	−15, 8, −5
Cerebellum (L)	−43, −63, −31	Cerebellum (L)	–

task. This difference was statistically significant [t (9) = 4.42, $p < 0.01$].

5.2. Imaging data

The results were strikingly different from those of Experiment 1, which differed only in the difficulty of the control task. Most of the activity seen in Experiment 1 was either absent (within the sensitivity limitations of the analysis) or else present but reversed in sign. That is, most areas that were previously more active during time perception than colour perception were now equally active or less active.

Fig. 2 shows the results of the group analysis in a similar format to Fig. 1 (Experiment 1). Taking the five regions previously identified as active in turn:

(i) The lateral prefrontal activation seen bilaterally in Fig. 1 is largely absent (see Fig. 2c and h). Indeed, there is patchy negative activity (control > time). However, a small frontal region is positively active bilaterally, in the inferior frontal gyrus (IFG) at its confluence with the anterior insula (Talairach co-ordinates −43, 18, 13 and 40, 18, 9 for left and right hemispheres, respectively) (see Fig. 2a, c and h).
(ii) The pre-SMA (medial frontal cortex) is negatively differentially activated (shown as blue; see Fig. 2e; also visible in b), in other words it is more active during the control (colour) condition than the duration condition. However, the size of this negative region appears smaller than the corresponding (positive) region in Experiment 1.
(iii) Much of the region of the inferior parietal cortex that is active in Experiment 1 is also negatively differentially activated in Experiment 2 (see Fig. 2b). As in Experiment 1, this activity is bilateral but more in evidence in the right hemisphere than the left. The correspondence between the active areas in the two experiments is imperfect; it extends more posteriorly/medially in Experiment 2.
(iv) The region of the putamen that is active in Experiment 1 is again positively active in Experiment 2 in the left hemisphere, but the activation is weaker and does not reach statistical significance in the right hemisphere (see Fig. 2d).
(v) The cerebellum shows no differential activation (see Fig. 2f and compare with Fig. 1e).

One new area, not identified in the results (Section 3) of Experiment 1, is positively active in Experiment 2. This is a small, ventral portion of the left inferior parietal cortex (supramarginal gyrus; Talairach co-ordinates −61, −39, 38), ventral to the parietal region that showed positive differential activation in Experiment 1 and now shows negative activation. It is clearly visible in Fig. 2a and g. The original, more dorsal region is stronger in the right than the left hemisphere in Experiment 1 (Fig. 1f) and so the new, more ventral area is on the side less strongly implicated in timing in Experiment 1. In fact, it may not be appropriate to regard the ventral left parietal region as 'new' (i.e. active only in Experiment 2), since re-examination of Fig. 1 shows that this region does show small spots of activation nearby.

These results suggest that while some of the activity in Experiment 1 relates specifically to timing functions, much of it relates to other cognitive task demands. The latter is suggested whenever positive activity is seen in Experiment 1 and negative activity is seen in Experiment 2. The extent to which this occurs is considered region-by-region in Section 6. The same suggestion arises when positive activity in Experiment 1 is paired with no activity in Experiment 2, but in this case the above interpretation is less compelling. Where time-related activity is seen in Experiment 1 but not Experiment 2, the absence could simply reflect sensitivity limitations. Likewise, there are various areas that are negative in Experiment 2 but absent in Experiment 1. For example, in Fig. 2g, negative differential activity (control > time) is seen bilaterally in the inferior temporal cortex. This presumably reflects colour processing and is not of interest in the context of time perception. Strong conclusions concerning distinction between timing activity and other cognitive demands can be drawn only where the sign of the activity reliably reverses between the two experiments.

In order to establish the areas that change polarity between the two experiments with precision and reliability, we performed a further analysis in which each voxel was tested with a logical AND operator (time > control in Experiment 1 AND control > time in Experiment 2), to identify areas that are reliably more active during the more difficult task in each case. Because the same participants were used in both experiments, this comparison is valid on a voxel-by-voxel basis despite the use of spatial normalization. The analysis was performed using FSL tools (http://www.fmrib.ox.ac.uk/fsl). It yielded a binary brain map of voxels that exceeded a threshold of $p < 0.01$ FDR corrected in both experiments.

Fig. 3 shows sections through all clusters of voxels that survive this test (shown in green). The most prominent area is the right inferior parietal lobule (Fig. 3b and d). The pre-SMA is also visible (Fig. 3a and b), although the area is small, reflecting the smaller area detected in Fig. 2e than in Fig. 1d. Finally, there are four patches (two on each side) in the middle frontal gyrus (Fig. 3c), extending to some extent into the inferior frontal gyrus (Fig. 3e). Note that within the extensive frontal activation found in Experiment 1, these patches of reversed activation are confined to the more superior portions (around $z = 28$) and they are largest in the more posterior portions (around $y = 7$). Note that the slice in Fig. 3e is more posterior than that in Fig. 1g.

6. Discussion

The objective of this study was to establish the extent to which previous studies may have associated particular brain regions with timing functions when in fact they are associated with other aspects of task-related cognitive activity.

6.1. Timing versus other cognitive functions

The results of Experiment 2 cast serious doubt on the notion that the brain regions identified in Experiment 1, and in previous studies of timing, are all directly involved in timing operations.

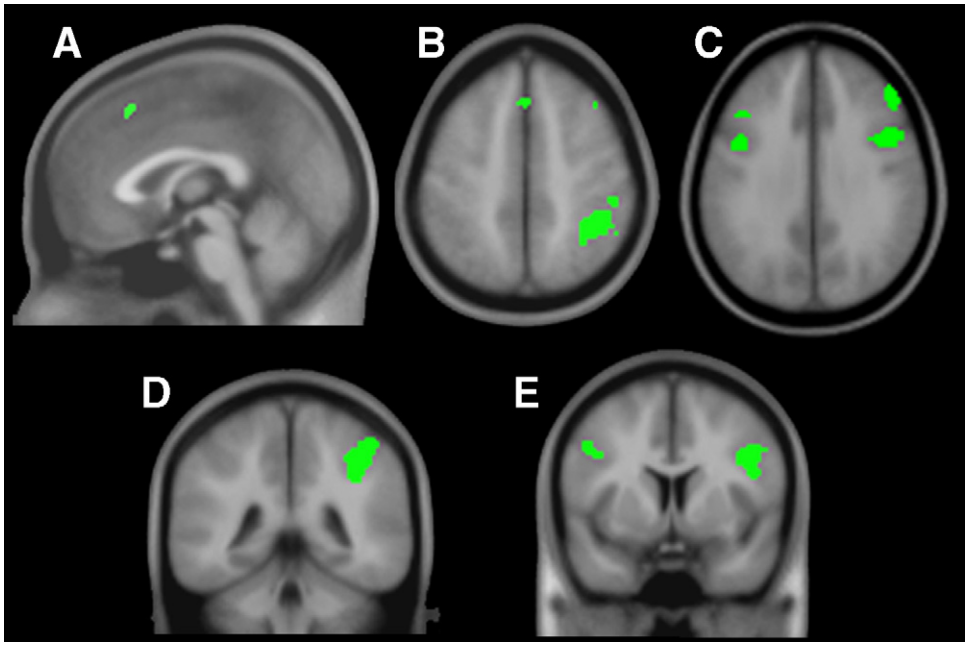

Fig. 3. Slices showing (in green) brain regions that are significantly positively active (time > control) in Experiment 1 and also negatively active (control > time) in Experiment 2. Only voxels that are significant at $p < 0.01$ (FDR corrected) in both experiments are included. (A) A mid-sagittal section ($x = 0$) showing the pre-SMA. (B) An axial slice ($x = 43$) showing pre-SMA and right inferior parietal cortex. (C) An axial slice ($z = 28$) showing frontal regions. (D) A coronal slice ($y = 35$) showing right inferior parietal cortex. (E) A coronal slice ($y = 7$) showing bilateral frontal regions.

We have shown that by simply reversing the relative difficulty of the time and control tasks, the sign of the differential activation between the tasks can be reversed in some of these areas. This strongly suggests that activity in these areas is not related specifically to judging time intervals, but is associated in some way with cognitive effort or task difficulty. Specifically, right inferior parietal lobule (IPL) and bilateral pre-SMA show this behaviour (compare Fig. 3 with Fig. 2), as do some dorsal regions of the pre-frontal cortex. These areas are differentially activated by whichever task is more difficult and are not specifically concerned with timing. Other parts of the frontal cortex, and the cerebellum, do not show this reversal of differential activation, but they do show an absence of detectable timing-related activity when the control task is harder, casting at least some degree of doubt on the nature of their role in timing.

Where, then, are timing functions mediated? Notably, activity in the putamen survives (to some extent) the reversal of task difficulty (Fig. 2d). This is consistent with numerous other studies that suggest a fundamental role for this region in clock functions. In addition, a small portion of frontal cortex, bilaterally, at the confluence of the inferior frontal gyrus and the insula (Talairach co-ordinates −43, 18, 13 [L] and 40, 18, 9 [R]) also survives the reversal of task difficulty and is reliably activated in Experiment 2 (Fig. 2c). We suggest that this region may be of central importance. Finally, there is a small region in the left supramarginal gyrus (Talairach co-ordinates −61, −39, 38) that survives (Fig. 2g), suggesting that some of the more ventral parts of the IPL may have a specific role in timing even though the most prominent IPL activity appears to be related to task demands.

6.2. *Task difficulty in previous studies*

Since we are suggesting that some of the brain areas that have previously been associated with timing are in fact associated with other cognitive demands of the task, we now consider the extent to which this suggestion fits the results of previous studies, with particular reference to the difficulty of the control tasks in those studies.

At least four previous fMRI studies (Ferrandez et al., 2003; Nenadic et al., 2003; Lewis & Miall, 2003; Coull et al., 2004) have taken a similar approach to our experiments in the sense that a timing task was compared to a control task based on the same stimuli. In the Ferrandez et al. study, a duration task and a control task (judging the intensity of the stimulus) were performed in different scanning runs, but using identical visual stimuli. Contrasting the duration task with the control task revealed a pattern of activation that was quite similar to that found in our Experiment 1, including bilateral prefrontal cortex, the right insula, bilateral SMA and bilateral inferior parietal cortex. They did not measure task performance, except in terms of reaction times (which are not comparable across tasks, because intensity can be judged more rapidly than duration). But they comment that ". . .the duration task was perceived as more difficult." Our interpretation is that these areas of activation represent a mixture of true timing-related activity and activity related to other cognitive demands of the task. Coull et al. (2004) used a control task that was similar to ours (colour discrimination) and the two tasks were apparently well-balanced in terms of task difficulty, so there should not have been much activity that related to non-specific task demands. Nonetheless, it is hard to be sure that the balance was correct. Perhaps the best of these studies, in terms of balanc-

ing task difficulty, are those (Lewis and Miall, 2003; Nenadic et al., 2003), in which difficulty was varied according to an adaptive procedure based on the participant's own responses. This ensures that difficulty (or at least performance) is well matched for every participant, at least by the end of the run if not at the beginning. Nenadic et al. (2003) presented pairs of tones to participants who performed either duration discrimination or pitch discrimination. They found several clusters of activity when either task was contrasted with rest. But most of these (including DLPFC) were common to both tasks and dropped out when differential activity in the two tasks was examined, consistent with our hypothesis.

Although several previous fMRI studies have attempted to equate task difficulty between a timing and a control task, ours is the first to systematically manipulate task difficulty. There are clear advantages to the latter approach. Equating task difficulty accurately across different tasks is challenging and it is hard to be confident of success. Even if performance is successfully equated, it remains possible that related neural activity is not. The timing task may make greater (or lesser) demands on the brain than the control task, so that equivalent performance is achieved through greater cognitive and metabolic activity. Such uncertainty is removed if the control task is deliberately set to be first easier and then harder than the timing task and it is found that the pattern of activity reverses. Somewhere between the two, a null point must exist, where non-specific task-related activity is exactly equal in both cases, but it becomes unnecessary to find this point in order to draw safe conclusions.

6.3. Roles of the brain regions identified

We now consider the status of each of the brain regions differentially activated by a time discrimination task compared to a rather easier colour discrimination task, which broadly correspond to the areas associated with time perception in previous studies, and re-evaluate the status of each. We consider them in three groups: those that survive our more rigorous test of involvement in timing processes (positive activity independent of task difficulty), those which fail the test (sign of activity reverses with relative task difficulty) and those that do not pass the test but cannot be reliably assigned to the 'fail' category (activity disappears in Experiment 2 but does not reverse).

6.3.1. Areas truly concerned with timing

We have identified three small brain regions that show clear involvement in time perception, irrespective of task difficulty. These are the IFG/insula, the left supramarginal gyrus and the left putamen (red areas in Fig. 2). Of these, all have previously been associated with timing but the one most commonly documented is the putamen, which has been repeatedly implicated (Rao et al., 1997, 2001; Nenadic et al., 2003; Coull et al., 2004). The activity is sometimes in left putamen (e.g. Rao et al., 1997) and sometimes right (e.g. Nenadic et al., 2003), so presumably there is bilateral involvement. Indeed, we find bilateral activation in Experiment 1, so the fact that it survives only unilaterally in Experiment 2 may simply reflect limited sensitivity. Other parts of the basal ganglia are not prominent in Experiment 2 but there is no sign that activity here reflects task difficulty. In view of the strong theoretical and experimental underpinnings of the involvement in this area (e.g. Meck & Benson, 2002; Matell & Meck, 2004), the weak nature of its activation is again probably best attributed to sensitivity limitations.

The bilateral frontal region (IFG/insula) that is clearly involved in timing irrespective of task difficulty constitutes a small volume relative to the total frontal activation in Experiment 1. In other words, much of the lateral prefrontal cortex belongs in section 6.3.3 below, rather than here. It is therefore necessary to take the view that different frontal regions are concerned with different aspects of the task.

The other two regions are less strongly emphasised in the literature than the putamen and prefrontal cortex. In the study of Nenadic et al. (2003), the principal area showing differential timing activity was the right putamen but, notably, they also found differential activity in the IFG/insula region in the right hemisphere, at (36, 30, 2). Similarly, Ferrandez et al. (2003) found a cluster at (36, 21, 6), which they referred to as right insula, that is very close (see Table 1) to the co-ordinates of the area we have described (bilaterally) at the confluence of the anterior insula and the inferior frontal gyrus. Lewis and Miall (2003), in a study with good control of task difficulty, also report differential activity in the anterior insula, and the co-ordinates given suggest that it is the same as the IFG/insula area we have identified. Notably, this area was active bilaterally, whereas Nenandic et al. and Ferrandez et al. found activity only in the right IFG/insula. Another study in which this region is associated with timing is that of Pouthas et al. (2005), although the control condition in this study was passive so the evidence for specific timing processes is weaker than in earlier studies. All these studies are therefore consistent with the notion that the IFG/insula plays a special role in timing functions.

At least two studies have documented a ventral region of the left inferior parietal cortex (supramarginal gyrus) in connection with time perception. Assmus et al. (2003) employed a task involving collision judgements. Participants had to judge whether two objects would collide, which depended on timing. In a control task, the sizes of the two objects had to be compared. Only a single area gave differential activation: the left supramarginal gyrus. The co-ordinates (−60, −36, 34) are very close to those of our supramarginal region. Although the collision task is rather different from interval judgements, what they have in common is a requirement for judging time intervals. The same group also activated the left supramarginal gyrus with a synchrony judgement task (Lux, Marshall, Ritzl, Zilles, & Fink, 2003).

6.3.2. Areas concerned with other demands of the task

We have identified three regions that have been implicated in time processing several times but which our manipulation of task difficulty suggests are in fact involved with other aspects of the task demands (green areas in Fig. 3). These are the pre-SMA, the (right) inferior parietal lobule (IPL) and some dorsal portions of the lateral prefrontal cortex.

We use the label 'IPL' to refer to the cortical region shown in Figs. 1f, 2g and 3d and centred at around (50, −34, 53),

in the right postcentral sulcus. It may include a much smaller corresponding region in the left hemisphere but it excludes the more inferior region of left parietal cortex discussed above and referred to as supramarginal gyrus. Harrington et al. (1998) studied a group of stroke patients and found that those with inferior parietal lobule lesions showed markedly impaired timing in comparison to control lesion patients. However, the variability of their cases makes it difficult to assess exactly which region is crucial. The IPL of the right hemisphere, at least, has been implicated in time processing by several imaging studies (e.g. Basso, Nichelli, Wharton, Peterson, & Grafman, 2003; Ferrandez et al., 2003). In our Experiment 1 there is also a strong right hemisphere bias in IPL activation (Fig. 1), and the portion that survives the AND test (green in Fig. 3) is unilateral. Our Experiment 2 suggests strongly that this region of right IPL is not concerned specifically with timing but more with other task demands. In the parietal lobes, only the supramarginal region appears genuinely to be associated with timing. Additionally, a PET study (Maquet et al., 1996) of duration discrimination identified the right inferior parietal lobule as active, but in the same study this region was found to be active when an intensity discrimination task was performed. This again suggests that it is not specific for timing functions, but reflects other task demands.

Our results also suggest that a portion, at least, of the SMA/pre-SMA complex is activated by some aspect of cognitive task demand other than the timing function itself. Several studies have reported activity in SMA proper (e.g. Macar, Anton, Bonnet, & Vidal, 2004), whereas we find it in pre-SMA, as did Lewis and Miall (2003). There is therefore some uncertainty as to which region is implicated in what circumstances. Both areas also feature in studies of rhythm production (e.g. Schubotz, Friederici, & von Cramon, 2000). Lewis and Miall (2003) found activity in pre-SMA in an interval discrimination task, despite task performance being apparently well equated in the timing and control tasks. However, we show (Experiment 2) that pre-SMA, or at least some of it, is activated during the more demanding task, whether this is the timing task or the control task. We can only speculate on the reason for the difference; possibly the matching of task difficulty was imperfect in the former study, despite the use of an adaptive procedure. The time perception literature is quite mixed on the involvement of pre-SMA. Coull et al. (2004) and Pouthas et al. (2005) also reported time-related activity there. Coull et al. provided a demanding control task, but it is unclear how well equated for difficulty it was. Pouthas et al. found that pre-SMA was differentially activated by discrimination of long versus short intervals, but did not use a control task. On the other hand, two studies in which a well-equated control task was used (Nenadic et al., 2003; Ferrandez et al., 2003) both failed to find differential time-related activity in pre-SMA, consistent with our interpretation.

Finally, portions of the lateral pre-frontal activity in Experiment 1 appear to mediate functions other than timing *per se* (Fig. 3c). But larger portions merely drop out in Experiment 2, rather than reversing polarity, and so the prefrontal cortex will be considered in the next section.

6.3.3. Areas of uncertain involvement

We have identified two areas that have repeatedly been associated with time perception (amongst other functions), which we suspect may be involved in aspects of time judgements other than the timing function *per se* (because activity is lost when the control task is harder) but which do not permit such strong statements as the pre-SMA and IPL. These are the dorsolateral cerebellum and the lateral prefrontal cortex.

In Experiment 1, large portions of prefrontal cortex were differentially activated by the time task. The active region encompasses parts of both dorsolateral and ventrolateral prefrontal cortex (DLPFC and VLPFC). The area is extensive in both anterior–posterior (Fig. 1c) and dorsal–ventral (Fig. 1g) dimensions. Yet this activity is completely absent in Experiment 2, strongly suggesting that it is more related to task difficulty than to timing. A stronger case can be made for DLPFC than for VLPFC, since only in dorsal regions does the sign of the activity reverse between experiments (and then only patchily; see Fig. 2h and Fig. 3c).

Smith et al. (2003) have specifically considered the role of the DLPFC in time perception. They argue that because their experimental and control tasks were expected to make similar demands on memory and attention, the resulting prefrontal activity is likely to reflect true timing functions. But their own performance data showed that of their two tasks, duration discrimination (89% correct) was somewhat harder than temporal order (97%). If cognitive demands are considered in the round, rather than in terms of specific components such as working memory, their argument becomes questionable. Our Experiment 2 suggests that much of their prefrontal (and other) activity may after all reflect differences in task demands rather than timing functions. One other study (Lewis & Miall, 2003) has reported timing activation in DLPFC, despite task performance again being (apparently) well equated with the control task. Interestingly, these authors report timing-related activity at bilateral co-ordinates close to the more anterior regions shown in Fig. 3c that reverse polarity in our Experiment 2. Our conclusion is that even a careful attempt to equate task difficulty between tasks may not suffice, because of the difficulty of achieving a perfect balance, and the safer approach employed here raises substantial doubt about the role of DLPFC in clock functions *per se*. Several other previous studies have also implicated lateral prefrontal cortex in timing function (e.g. Rao et al., 2001; Macar et al., 2002; Basso et al., 2003), but none of these manipulated task difficulty or evaluated the relative difficulty of the timing task and (where present) control task.

The lateral cerebellum has been identified as active during timing tasks in several previous studies (Penhune et al., 1998; Tracy et al., 2000; Rao et al., 2001; Mathiak et al., 2004; Harrington et al., 2004). Penhune et al. were concerned with motor timing and it could be that the cerebellum is involved in motor but not sensory timing. Harrington et al. found cerebellar activation related to the encoding (as opposed to decision-making) phase of a time judgement task and attributed a central timing role to the cerebellum (along with the striatum). In contrast, Rao et al. take the view that timing is handled in the striatum while the cerebellum is involved in other aspects of the task.

Tracy et al. compared interval generation with a timing task while Mathiak et al. compared discrimination of two durations with categorization (long or short) of the gap between them; in neither case was task difficulty controlled with precision. The role of the cerebellum in timing remains uncertain and, indeed, controversial (Buhusi & Meck, 2005; Ivry & Spencer, 2004). Our study argues against a key role in timing, but not strongly. In lateral cerebellum, activity did not reverse polarity with reversed task difficulty but was merely absent in Experiment 2, leaving open the possibility that the cerebellum is indeed involved specifically in timing but that for some reason activity failed to be reliably detected in Experiment 2. A counter-argument to this, of course, is that activity may equally well have reversed in polarity, as in pre-SMA and IPL and parts of DLPFC, but failed to be detected. A strong conclusion is possible only for the latter areas, in which activity followed the more difficult task in a straightforward way. But the absence of timing activity in lateral cerebellum when the control task was harder is sufficient at least to cast some doubt on their involvement.

7. Conclusion

We conclude that the extent of the timing "network' has been significantly over-estimated in the literature. When activity associated with time perception is pitted against that produced by a cognitively more demanding control task, three small regions are active (the confluence of the inferior frontal gyrus and insula bilaterally, a portion of the left supramarginal gyrus and the putamen) and only these can truly be regarded as concerned with time processing.

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