

## Unconscious determinants of free decisions in the human brain

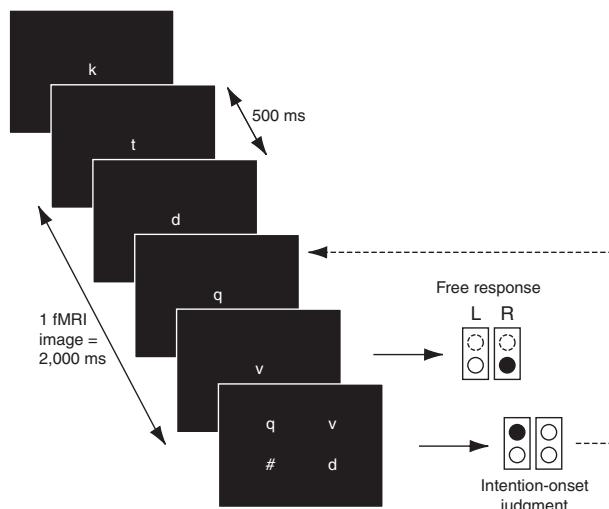
Chun Siong Soon<sup>1,2</sup>, Marcel Brass<sup>1,3</sup>, Hans-Jochen Heinze<sup>4</sup> & John-Dylan Haynes<sup>1,2</sup>

**There has been a long controversy as to whether subjectively 'free' decisions are determined by brain activity ahead of time. We found that the outcome of a decision can be encoded in brain activity of prefrontal and parietal cortex up to 10 s before it enters awareness. This delay presumably reflects the operation of a network of high-level control areas that begin to prepare an upcoming decision long before it enters awareness.**

The impression that we are able to freely choose between different possible courses of action is fundamental to our mental life. However, it has been suggested that this subjective experience of freedom is no more than an illusion and that our actions are initiated by unconscious mental processes long before we become aware of our intention to act<sup>1–3</sup>. In a previous experiment<sup>1</sup>, electrical brain activity was recorded while subjects were asked to press a button as soon as they felt the urge to do so. Notably, their conscious decision to press the button was preceded by a few hundred milliseconds by a negative brain potential, the so-called 'readiness potential' that originates from the supplementary motor area (SMA), a brain region involved in motor preparation. Because brain activity in the SMA consistently preceded the conscious decision, it has been argued that the brain had already unconsciously made a decision to move even before the subject became aware of it.

However, these intriguing experiments have left a number of controversial questions open<sup>4–6</sup>. First, the readiness potential is generated by the SMA, and hence only provides information about late stages of motor planning. Thus, it is unclear whether the SMA is indeed the cortical site where the decision for a movement originates<sup>7</sup> or whether high-level planning stages might be involved in unconsciously preparing the decision<sup>8</sup>, as was seen in studies on conscious action planning<sup>9–12</sup>. Second, the time delay between the onset of the readiness potential and the decision is only a few hundred milliseconds<sup>1</sup>. It has been repeatedly argued that potential inaccuracies in the behavioral measurement of the decision time at such short delays could lead one to misjudge the relative timing of brain activity and intention<sup>3–6</sup>. Third, does any leading brain activity indeed selectively predict the specific outcome of a choice ahead of time? To rule out the idea that any leading activity merely reflects unspecific preparatory activation<sup>13</sup>, it is necessary to study free decisions between more than one behavioral option<sup>11,14</sup>.

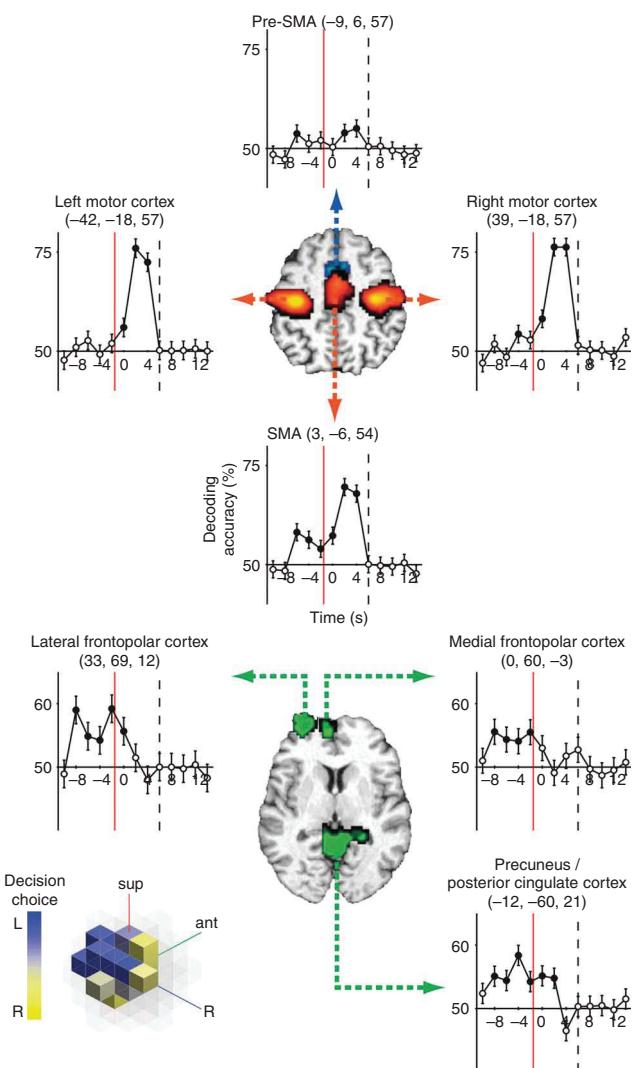
Here we directly investigated which regions of the brain predetermine conscious intentions and the time at which they start shaping a motor decision. Subjects who gave informed written consent carried out a freely paced motor-decision task while their brain activity was measured using functional magnetic resonance imaging (fMRI; see Fig. 1 and **Supplementary Methods** online). The subjects were asked to relax while fixating on the center of the screen where a stream of letters was presented. At some point, when they felt the urge to do so, they were to freely decide between one of two buttons, operated by the left and right index fingers, and press it immediately. In parallel, they should remember the letter presented when their motor decision was consciously made. After subjects pressed their freely chosen response button, a 'response mapping' screen with four choices appeared. The subjects indicated when they had made their motor decision by selecting the corresponding letter with a second button press. After a delay, the letter stream started again and a new trial began. The freely paced button presses occurred, on average, 21.6 s after trial onset, thus leaving sufficient time to estimate any potential buildup of a 'cortical decision' without contamination by previous trials. Both the left and right response buttons were pressed equally often and most of the



**Figure 1** Measuring the onset time of conscious motor intentions. Subjects viewed a letter stream that was updated every 500 ms (shown here only for a few frames). At some point they spontaneously made the decision to press either the left or right button using their corresponding index finger (free response). Subsequently, they were presented with a response-mapping screen that instructed subjects as to which second button to press to report the time at which they consciously made the motor decision (**Supplementary Methods**).

<sup>1</sup>Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1A, 04103 Leipzig, Germany. <sup>2</sup>Charité – Universitätsmedizin Berlin, Bernstein Center for Computational Neuroscience, Haus 6, Philippstrasse 13, 10115 Berlin, Germany. <sup>3</sup>Department of Experimental Psychology and Ghent Institute for Functional and Metabolic Imaging, Ghent University, Henri Dunantlaan 2, 9000 Ghent, Belgium. <sup>4</sup>Department of Neurology II, Otto-von-Guericke University, Leipziger Strasse 44, 39120 Magdeburg, Germany. Correspondence should be addressed to J.-D.H. (haynes@bccn-berlin.de).

Received 8 January; accepted 21 March; published online 13 April 2008; doi:10.1038/nn.2112



**Figure 2** Decoding the outcome of decisions before and after they reached awareness. Color-coded brain areas show regions where the specific outcome of a motor decision could be decoded before (bottom, green) and after (top, red) it had been made. The graphs separately depict for each time point the accuracy with which the subject's free choice to press the left or right button could be decoded from the spatial pattern of brain activity in that region (solid line, left axis; filled symbols, significant at  $P < 0.05$ ; open symbols, not significant; error bars, s.e.m.; chance level is 50%). As might be expected, the decoding accuracy was higher in cortical areas involved in the motor execution of the response than in areas shaping the upcoming decision before it reaches awareness (note the difference in scale). The vertical red line shows the earliest time at which the subjects became aware of their choices. The dashed (right) vertical line in each graph shows the onset of the next trial. The inset in the bottom left shows the representative spatial pattern of preference of the most discriminative searchlight position in frontopolar cortex for one subject (ant, anterior; sup, superior; see **Supplementary Fig. 9** online).

was executing the motor response. As expected, two brain regions encoded the outcome of the subject's motor decision during the execution phase: primary motor cortex and SMA (Fig. 2). Next, we addressed the key question of this study, whether any brain region encoded the subject's motor decision ahead of time. Indeed, we found that two brain regions encoded with high accuracy whether the subject was about to choose the left or right response prior to the conscious decision (threshold  $P = 0.05$ , family-wise error-corrected for multiple spatial and temporal comparisons; Fig. 2, see **Supplementary Figs. 5** and **6** online for full details). The first region was in frontopolar cortex, BA10. The predictive information in the fMRI signals from this brain region was already present 7 s before the subject's motor decision. Taking into account the sluggishness of BOLD responses, the predictive neural information will have preceded the conscious motor decision by up to 10 s. There was a second predictive region located in parietal cortex stretching from the precuneus into posterior cingulate cortex. Notably, there was no overall signal increase in the frontopolar and precuneus/posterior cingulate during the preparation period (**Supplementary Fig. 5**). Rather, the predictive information was encoded in the local spatial pattern of fMRI responses, which is presumably why it has not been noticed before. When the statistical threshold was relaxed, several other regions of frontal cortex showed predictive information, albeit less pronounced (**Supplementary Table 1** online). We also ensured that there was no carry-over of information between trials, so that the high decoding performance preceding the motor decision by up to 10 s cannot reflect decoding related to the previous trial (**Supplementary Methods** and **Discussion** online). We also ensured that decoding was not based on movement artifacts (**Supplementary Fig. 7** online).

Finally, we also assessed the degree to which the timing of the decision could be predicted ahead of time. We found that decoding of the time decision was possible as early as 5 s preceding the motor decision, but mainly from pre-SMA and SMA, whereas in the frontopolar and parietal cortex this was only possible just before the motor decision (**Supplementary Fig. 5**). Thus, there appears to be a double dissociation in the very early stages between brain regions shaping the specific outcome of the motor decision and brain regions determining the timing of a motor decision. At later stages, right before the conscious decision, both of these regions begin to encode timing and handedness information.

Finally, to further investigate the involvement of frontopolar cortex and precuneus in selecting intentions, we investigated voluntary decisions where subjects have to decide between left and right responses at an externally determined point in time. In this case, the time when a decision is selected is under experimental control. This revealed that frontopolar cortex was already predictive during the selection of the

intentions (88.6%) were reported to be consciously formed in 1,000 ms before the movement (**Supplementary Methods** and **Supplementary Figs. 1–3** online).

We directly assessed how much predictive information each brain region contained about the specific outcome of a motor decision at various time points before and after it reached awareness. For each time point, we measured how much information could be decoded from local patterns of fMRI signals in various brain regions using statistical pattern recognition techniques<sup>15</sup> (**Supplementary Fig. 4** online). These pattern-based decoders were trained to predict the specific outcome of a subject's motor decision by recognizing characteristic local brain patterns associated with each choice. This highly sensitive approach had several advantages over previous studies. First, it allowed us to investigate any potential long-term determinants of human intentions that preceded the conscious intention far beyond the few hundred milliseconds observed over the SMA<sup>1,14</sup>. Second, it allowed us to separately investigate each brain region and determine how much information each region had about the outcome of a motor decision. Finally, our approach allowed us to identify whether any leading brain activity indeed selectively predicted the outcome of the subject's choice, rather than reflecting potentially nonspecific preparatory processes.

To validate our method, we first investigated which brain regions this decision could be decoded from after it had been made and the subject

response, whereas the predictive information in precuneus began after the selection during the delay. This is consistent with a trend in the main experiment that showed that the information in lateral frontopolar cortex had already peaked at the earliest time point. One interpretation of this finding is that frontopolar cortex was the first cortical stage at which the actual decision was made, whereas precuneus was involved in storage of the decision until it reached awareness. Notably, the intention was selected consciously in this control experiment, suggesting that similar networks might be involved in conscious and unconscious preparation of decisions (see **Supplementary Methods** and **Supplementary Fig. 8** online for full details).

Taken together, two specific regions in the frontal and parietal cortex of the human brain had considerable information that predicted the outcome of a motor decision the subject had not yet consciously made. This suggests that when the subject's decision reached awareness it had been influenced by unconscious brain activity for up to 10 s, which also provides a potential cortical origin for unconscious changes in skin conductance preceding risky decisions<sup>8</sup>. Our results go substantially further than those of previous studies<sup>1–15</sup> by showing that the earliest predictive information is encoded in specific regions of frontopolar and parietal cortex, and not in SMA. This preparatory time period in high-level control regions is considerably longer than that reported previously for motor-related brain regions<sup>1,14</sup>, and is considerably longer than the predictive time shown by the SMA in the current study (**Supplementary Fig. 5**). Also, in contrast with most previous studies<sup>1,13</sup>, the preparatory time period reveals that this prior activity is not an unspecific preparation of a response. Instead, it specifically encodes how a subject is going to decide. Thus, the SMA is presumably not the ultimate cortical decision stage where the conscious intention is initiated, as has been previously suggested<sup>7</sup>. Notably, the lead times are too long to be explained by any timing inaccuracies in reporting the onset of awareness, which was a major criticism of previous studies<sup>4–6</sup>. The temporal ordering of information suggests a tentative causal model of information flow, where the earliest unconscious precursors of the motor decision originated in frontopolar cortex, from where they

influenced the buildup of decision-related information in the precuneus and later in SMA, where it remained unconscious for up to a few seconds. This substantially extends previous work that has shown that BA10 is involved in storage of conscious action plans<sup>9–11</sup> and shifts in strategy following negative feedback<sup>12</sup>. Thus, a network of high-level control areas can begin to shape an upcoming decision long before it enters awareness.

*Note: Supplementary information is available on the Nature Neuroscience website.*

#### ACKNOWLEDGMENTS

The authors would like to thank D. Passingham and H. Lau for valuable comments and T. Mildner and S. Zysset for help with scanning. This work was funded by the Max Planck Society and the German Federal Ministry of Education and Research.

#### AUTHOR CONTRIBUTIONS

J.-D.H., C.S.S., M.B. and H.-J.H. conceived the experiment. C.S.S. and J.-D.H. carried out the experiment. C.S.S. analyzed the data. J.-D.H. and C.S.S. wrote the paper.

Published online at <http://www.nature.com/natureneuroscience>  
Reprints and permissions information is available online at <http://npg.nature.com/reprintsandpermissions>

1. Libet, B. *et al.* *Behav. Brain Sci.* **8**, 529–566 (1985).
2. Wegner, D.M. *Trends Cogn. Sci.* **7**, 65–69 (2003).
3. Haggard, P. *Trends Cogn. Sci.* **9**, 290–295 (2005).
4. Van de Grind, W. *Conscious Cogn.* **11**, 241–264 (2002).
5. Glynn, I.M. *Nature* **348**, 477–479 (1990).
6. Joordens, S., van Duijn, M. & Spalek, T.M. *Conscious. Cogn.* **11**, 231–240 (2002).
7. Eccles, J.C. *Arch. Psychiatr. Nervenkr.* **231**, 423–441 (1982).
8. Bechara, A., Damasio, H., Tranel, D. & Damasio, A.R. *Science* **275**, 1293–1295 (1997).
9. Koehlein, E., Basso, G., Pietrini, P., Panzer, S. & Grafman, J. *Nature* **399**, 148–151 (1999).
10. Burgess, P.W., Quayle, A. & Frith, C.D. *Neuropsychologia* **39**, 545–555 (2001).
11. Haynes, J.D. *et al.* *Curr. Biol.* **17**, 323–328 (2007).
12. Hampton, A.N. & O'Doherty, J.P. *Proc. Natl. Acad. Sci. USA* **104**, 1377–1382 (2007).
13. Lau, H.C., Rogers, R.D., Haggard, P. & Passingham, R.E. *Science* **303**, 1208–1210 (2004).
14. Haggard, P. & Eimer, M. *Exp. Brain Res.* **126**, 128–133 (1999).
15. Haynes, J.D. & Rees, G. *Nat. Rev. Neurosci.* **7**, 523–534 (2006).

# **□upplementar □nformation**

## **□nconscious □eterminants o□ ree □ecisions in the human brain**

Chun Siong Soon<sup>1,2</sup>, Marcel Brass<sup>1,3</sup>, Hans-Jochen Heinze<sup>4</sup> & John-Dylan Haynes\*<sup>1,2</sup>

<sup>1</sup>Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1A, 04103 Leipzig, Germany  
<sup>2</sup>Charité – Universitätsmedizin Berlin, Bernstein Center for Computational Neuroscience,  
Haus 6, Philippstrasse 13, 10115 Berlin, Germany

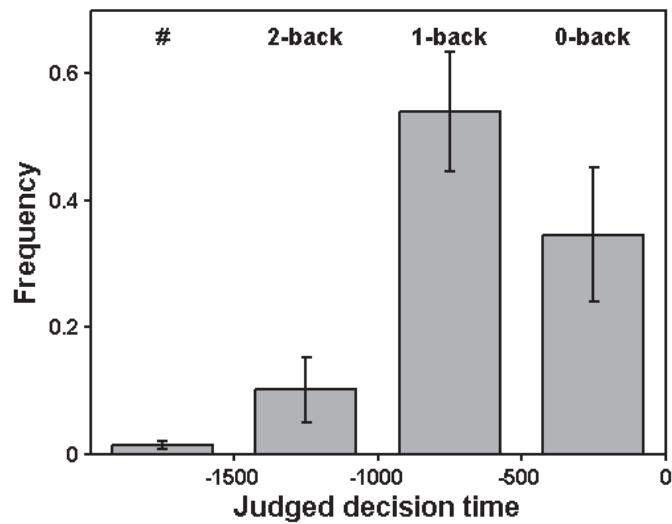
<sup>3</sup>Department of Experimental Psychology and Ghent Institute for  
Functional and Metabolic Imaging, Ghent University, Henri Dunantlaan 2, 9000 Ghent, Belgium

<sup>4</sup>Department of Neurology II, Otto-von-Guericke University, Leipziger Strasse 44, 39120 Magdeburg, Germany

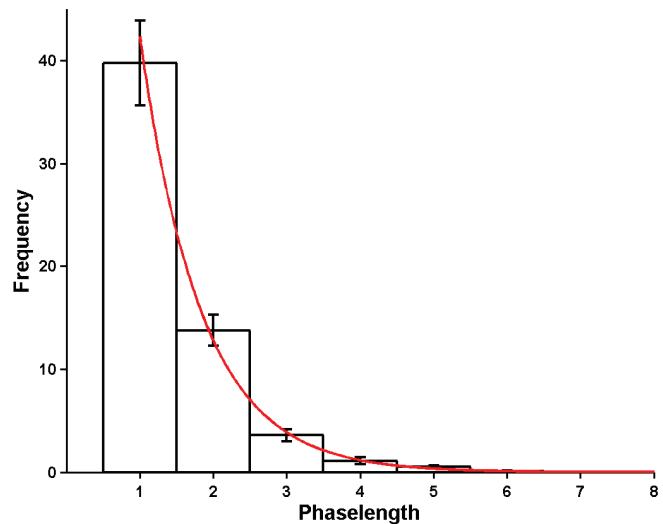
\*Please address correspondence to: John-Dylan Haynes, Charité – Universitätsmedizin Berlin, Bernstein Center for Computational Neuroscience; Haus 6, Philippstrasse 13, 10115 Berlin; Phone: +49 (0)30 341 6762  
Email: [haynes@bccn-berlin.de](mailto:haynes@bccn-berlin.de)

## SUPPLEMENTARY MATERIAL

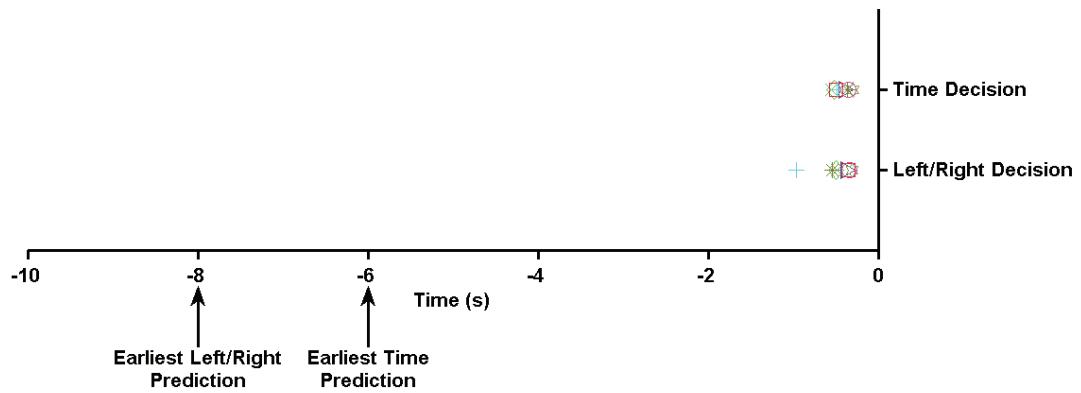
### **SUPPLEMENTARY FIGURES**



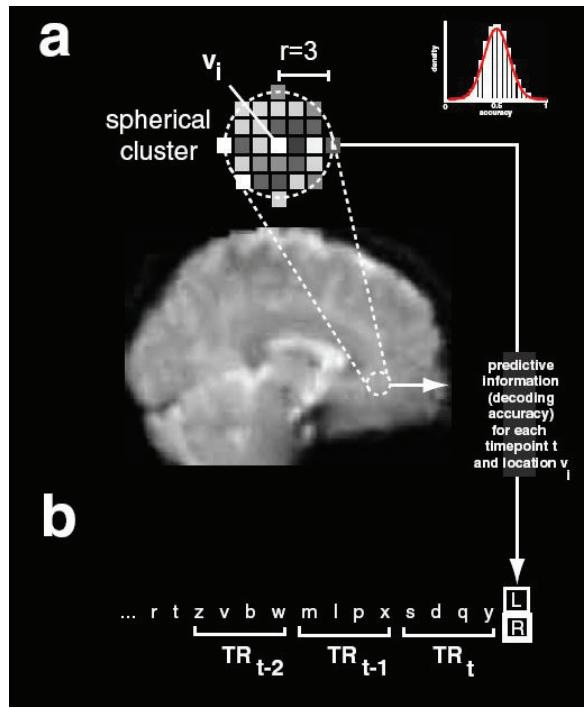
Supplementary Figure 1: The distribution of timing judgements in the main experiment.



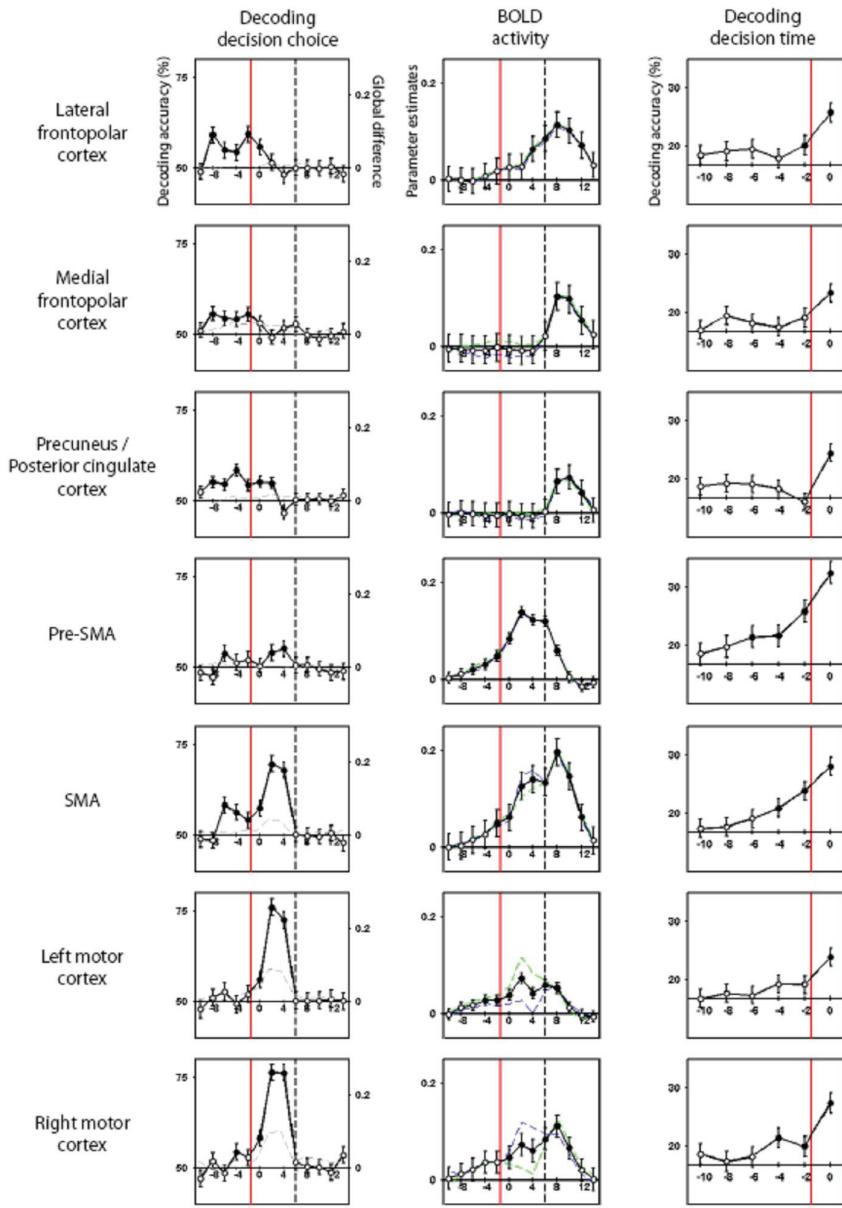
Supplementary Figure 2: Histogram of sequence lengths. The distribution of sequences of N trials where subjects chose the same button before switching reflects an exponential distribution (fitted here in red) suggesting that subjects responded randomly from trial to trial.



Supplementary Figure 3: Behavioural control experiment on decision timing. Subjects were required to judge either the timing of their Left/Right decision (“Left/Right Decision”) or the timing of their decision to press the button (“Time Decision”). The symbols show the average reported timing judgements separately for each subject. Reports for both of these decision times were within 1,000 ms preceding the motor response (0 ms in this figure) and long preceded the earliest prediction of the Left/Right decision from brain activity.

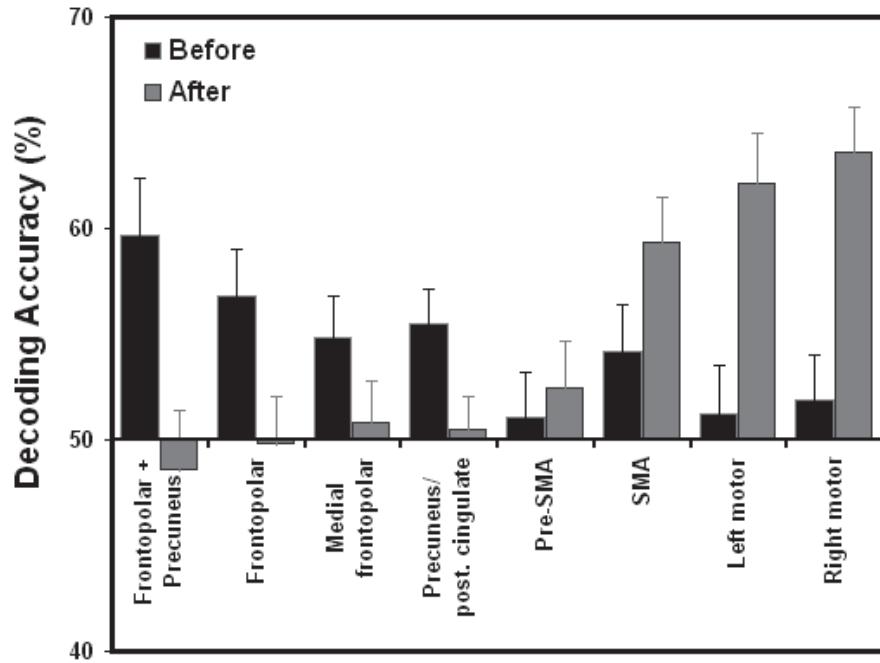


**Supplementary Figure 4:** Multivariate decoding from local spatial patterns using a moving “searchlight”<sup>29,36</sup>. (a) Surrounding each voxel  $v_i$  a spherical cluster with radius of 3 voxels is defined. A multivariate decoding algorithm based on support vector classifiers<sup>37</sup> is used to assess how well the subject’s decision can be decoded and hence predicted from this local pattern of brain activity. (b) The decoding accuracy is estimated separately in 13 time bins around the button press. Prior to classification the EPI images are spatially normalised to an MNI stereotactic template. Then the decoding results are combined across multiple subjects in a second-level analysis for each time point and position separately (see **Supplementary Methods** for details). The inset in the top right hand corner shows that the histogram of decoding accuracies follows a Gaussian normal distribution centered on chance level (50 %).

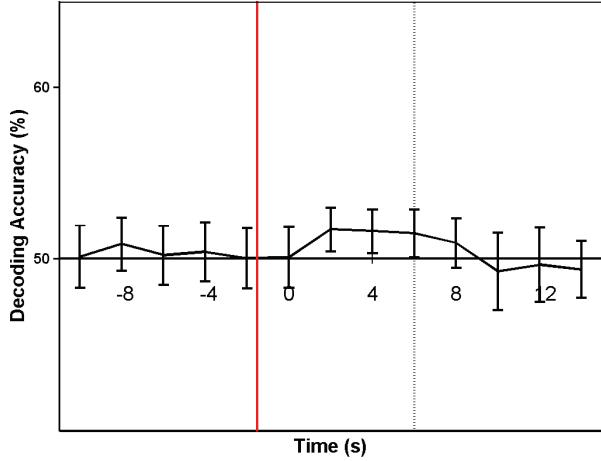


**Supplementary Figure 5:** Full decoding results of decision outcome and decision timing. The *left column* shows brain regions from which the *outcome* of a decision could be decoded either before or after it had reached awareness. The plot depicts separately for each timepoint the accuracy with which the subject's "free decision" to press the left or right button could be decoded from the spatial pattern of brain activity in that region (solid line, left axis; filled symbols: significant at  $p < 0.05$ ; open symbols: not significant; error bars = s.e.m.; chance level is 50 %). The vertical red line shows the *earliest* time when the subjects made their decision. In several regions, including left and right motor cortex and SMA, there was information related to the subject's choice *after* it had reached awareness and the motor response was being executed. In the SMA, there was also an earlier phase

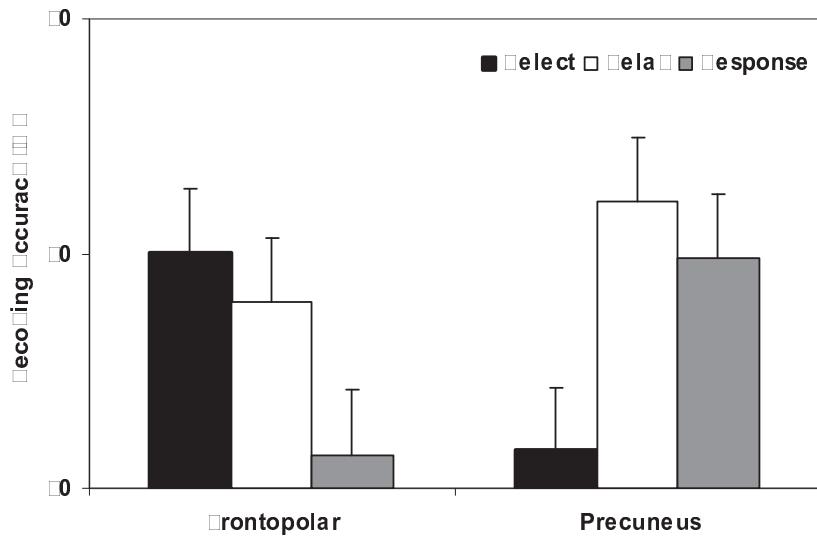
beginning around 5 s prior to the conscious decision during which the upcoming decision could be predicted before it entered awareness. However, the earliest predictive information was found in more high-level brain regions, the frontopolar cortex (both lateral and medial) as well as the precuneus. These areas already contained information predictive information 7 s before the decision entered awareness, or 10 s when taking into account the delay of the fMRI response with respect to neural activity. The dotted (right) vertical line in each graph shows the onset of the *next* trial. Note that decoding of the current intention was at chance level during the next trial suggesting there was no carry-over of information to the next trial. The *middle column* shows activity averaged across searchlight voxels for each region and each time point. This reveals that more motor-related brain regions show a gradual increase in activity across the pre-decision period, however this activity is unspecific for the choices and not related to the outcome of the decision. In order to assess whether any predictive information was caused by overall signal differences between the two conditions, rather than by the local micro-pattern of brain activity, the *overall signal* at each timepoint was also plotted separately for the left and right button presses (green and blue dashed lines). As expected, the overall signals in contralateral motor cortex increased *after* the subject had decided for the left or right button press. However, in all other brain regions the decoded information was not based on such global differences, but on differences in local micropatterns (see e.g., **Supplementary Fig. 9**). In all brain regions except primary motor cortex the overall activity for left and right response was virtually identical to the average response, and hence not visible on the graphs. This can also be seen by observing the gray dashed line in the left column, which directly plots the difference between these overall activity levels (right axis). As expected, only left and right motor cortex showed a difference in overall signal for the two conditions, with right motor cortex being more strongly activated by left button presses and vice versa. Please note that there are two differences between the main effects in this study and previous work on free decisions. In contrast to work on the readiness potential<sup>11-12</sup>, the main level of activity in motor-related brain regions began to increase as early as 5 sec prior to the decision. One potential explanation is that decision time in our study was unconstrained, so possibly also unspecific preparatory activity was able to build up over a longer period of time. Also, in contrast to previous studies<sup>13,17</sup>, we did not find significant activation of the dorsolateral prefrontal cortex, presumably reflecting a lower memory load because our subjects were not required to keep track of previous responses to balance left and right button presses across trials (see **Supplementary Methods**). Please also note the unspecific activation at the onset of the next trial in frontopolar cortex and in precuneus. The *right column* shows the results of an additional analysis where a classifier was trained to recognize at which of 6 *time windows* the decision would be made rather than which *outcome* it would have (thus, chance level is here 16.7 %). Note that there is a double dissociation between brain regions with early prediction of the timing (pre-SMA, SMA) and brain regions with late prediction of timing but early prediction of the outcome (frontopolar cortex, precuneus).



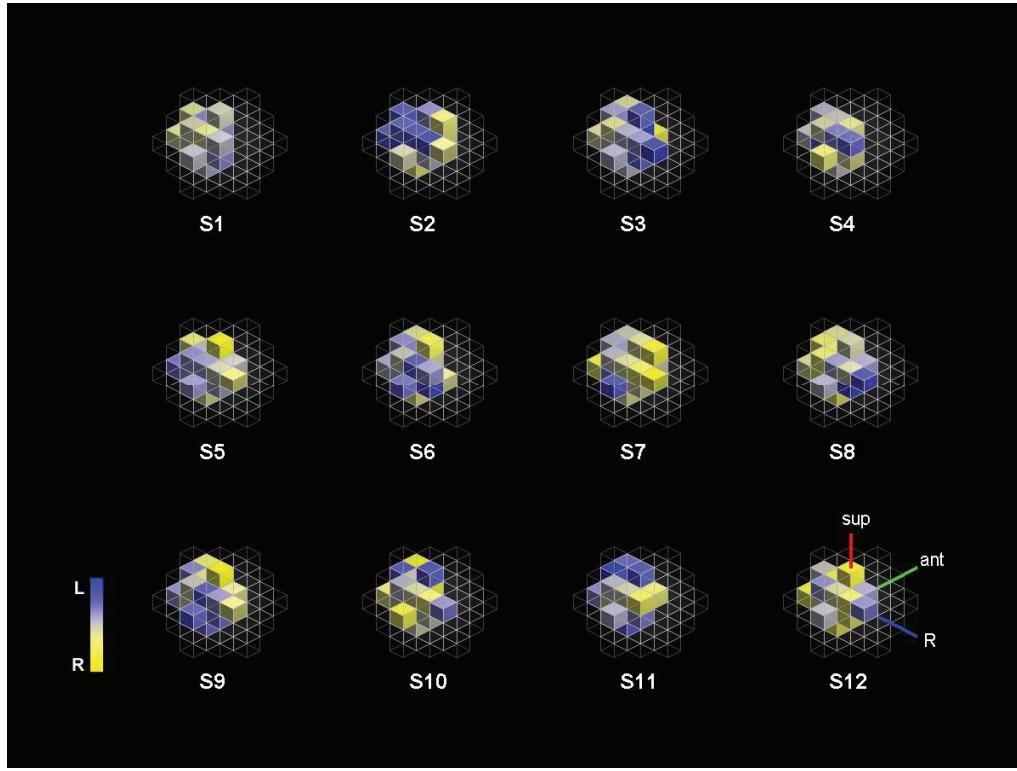
Supplementary Figure 6: Decoding across multiple brain regions. Average decoding accuracy across 4 time points before the decision (black) and 4 time points after the decision (grey). There is a clear dissociation between brain regions encoding information about future intentions prior to a decision and brain regions encoding information following the decision. Please note that due to the temporal delay of the hemodynamic response the small lead times in SMA/pre-SMA of up to several hundred milliseconds reported in previous studies<sup>11-12,38</sup> are below the temporal resolution of our method. Hence, we cannot exclude that other regions contain predictive information in the short period immediately preceding the conscious intention. The two leftmost bar plots show the *combined* decoding accuracy when pooling signals from the two most predictive brain regions frontopolar cortex and precuneus. There is a trend for the decoding accuracy to be slightly better than from the individual regions as would be expected by pooling informative pattern signals.



Supplementary Figure 7: Decoding the outcome of a decision from motion parameters. In order to exclude that decoding was influenced by potential head motion correlated with the subject's decision we investigated whether it was possible to decode the outcome of the decision from movement parameters obtained from motion correction. For this analysis the 6 motion correction parameters (x-translation, y-translation, z-translation, x-rotation, y-rotation and z-rotation) were extracted separately for left and right choice trials, and separately for 13 timepoints  $t$  from 10 s before until 16 s after the conscious decision. This covered the same temporal range as the main decoding analysis (see **Supplementary Methods**). For each timepoint  $t$ , this yielded 2 sets of 6-dimensional pattern vectors of each trial, representing the estimated motion related to subjects choosing left versus right button presses. For a given timepoint  $t$ , we used multivariate pattern recognition with a linear support vector machine to assess whether the subject's head motion provided any information about left versus right button choices. A model was trained using data from 9 runs, and tested on the independent 10th run. This training and testing cycle was repeated 10 times, with a different run as the test data set each time (10-fold cross-validation). For each timepoint  $t$ , the classification accuracies across subjects were then assessed using Student's t-test. Head motion did not significantly predict button choice at any timepoint ( $p>0.2$  for all timepoints).



Supplementary Figure 8: Decoding for cued decision timing. Decoding accuracy in frontopolar cortex and precuneus in a control experiment where subjects were cued when to freely select one of two hands for a response. Predictive information regarding the selected hand arose first in frontopolar cortex (MNI coordinates 39, 45, 12), already during the selection, and only later in precuneus (MNI -9, -57, 45). In contrast to frontopolar cortex, the precuneus continued to encode the chosen hand during the response period. SMA (MNI 12, -3, 51) also contained information about which hand was selected, especially during the delay period, presumably because subjects started preparing for the upcoming motor action (select: 59.3 %, delay: 67.3 %, response 60.0 %). As in the main experiment, pre-SMA (-9, 6, 57) had no predictive information during the selection period, but some information was present during the delay period (select: 51.8 %, delay 57.0 %, response 54.2 %).



**Supplementary Figure 9:** Example of voxel selectivity for a representative searchlight (position with peak decoding accuracy in frontopolar cortex). The spherical clusters at that position are shown for all 12 subjects. The selectivity for each voxel for either a left or right decision is colour coded in blue and yellow respectively. The selectivity profiles clearly indicate that some voxels are activated stronger preceding either left or right decisions, thus pointing towards a distributed encoding of long-term predictive information.

## SUPPLEMENTARY TABLES

Supplementary Table 1. Brain areas encoding intention prior to conscious decision

X	Y	Z	Z Score	
33	69	12	6.58	Frontopolar cortex
0	60	-3	5.12	Anterior medial prefrontal cortex
3	60	-15	4.90	Anterior medial prefrontal cortex
-21	45	9	5.26	Anterior cingulate cortex
3	18	51	4.97	Pre-SMA
-12	-60	21	6.98	Posterior cingulate cortex
3	-57	39	5.20	Precuneus

Brain areas from which subsequent intention could be predicted from neural activity prior to conscious decision at a relaxed threshold of  $p_{\text{uncorrected}} < 0.00001$  (no cluster threshold; MNI standard coordinates).

**Supplementary Table 1:** When the cluster threshold was removed, several other smaller regions became apparent that had significant predictive information. These regions were mainly aligned along the medial wall of prefrontal cortex and were especially in anterior medial prefrontal cortex, and to a lesser degree in the SMA.

## SUPPLEMENTARY DISCUSSION

An important question is which exact role the early predictive information plays in preparing the upcoming response. In our study, a highly specific network of brain regions predicted the outcome of the motor decision. These regions included frontopolar cortex (BA10), a parietal region stretching from precuneus to posterior cingulate, and to a lesser degree medial prefrontal cortex (see **Supplementary Table 1**). These regions have previously been shown to be involved in executive control, free selection and self-reflection about intentions<sup>1-4</sup>; however their relevance for unconscious preparation of intentions has not been demonstrated previously. Frontopolar cortex has often been implicated in tasks requiring high-level executive control, especially in tasks that involve storing conscious intentions across a delay<sup>1-3</sup>. Also, it has been shown that activity in this region can build up even prior to execution of simple movements<sup>5</sup>, as in our study. It has long been known that parietal cortex plays an important role in processing of motor intentions<sup>6-7</sup>. The more inferior medial regions found in our study stretch from precuneus to posterior cingulate cortex. These regions have been involved in several tasks closely related to intentions, including prospective processing<sup>2</sup>, self-

reflection<sup>4,8</sup>, awareness<sup>4</sup>, and even as here in free-choice tasks<sup>9</sup>. Finally, our findings also have important implications for the role of motor-related brain regions that have been previously assumed to play a key role in determining future decisions<sup>10-11</sup>. We indeed found that SMA contained predictive information as implicated previously in free-selection tasks<sup>9,11-19</sup>. However, the onset of this information was much later than in higher-level control regions. Importantly, in the earliest stages preceding the decision our study also revealed a double dissociation between cortical information predictive of the *outcome* of a decision (frontopolar cortex and precuneus) and information predictive of the *timing* of a decision (especially SMA and pre-SMA).

A second important question relates to the neural origin of the information contained in the predictive spatial patterns. One possible explanation could be that there is a fine-grained clustering of cells with similar preferences for one of the two decision outcomes and that this clustering is smaller than the size of conventional functional areas. In the visual cortex, information encoded in similar fine-grained patterns of visual cortex can be read out using pattern recognition. This is typically explained as a “biased sampling” or “aliasing” of fine-grained feature columns by the individual fMRI voxels<sup>20</sup> and is confirmed by simulations based on realistic neural topographies<sup>21-22</sup>. This raises the question whether the informative spatial patterns we found might point to the existence of a similar columnar architecture in prefrontal cortex, where cells might be clustered according to similar roles in selective cognitive control. Such a columnar architecture has been highly debated as a general principle of cortical organisation<sup>23-24</sup>. It remains unclear whether there is such a topographic organisation in prefrontal cortex<sup>25-27</sup>. Alternatively, our classification patterns might reflect the sampling of a distributed population code for different tasks, as has been proposed from the findings of similar studies on object recognition<sup>28</sup>. Future optical imaging studies will be able to extend our findings by studying the local spatial topography of executive signals in prefrontal cortex.

#### *Neural encoding of conscious intentions*

An interesting question is which brain regions encode the intention when it

enters into conscious awareness a few hundred milliseconds prior to the movement. Previous studies have demonstrated that conscious intentions *following* a free decision<sup>29</sup> and following strategy shifts after negative feedback<sup>-30</sup> are also encoded in BA10. Here we show that this region also encodes unconscious determinants of human decisions, which means that selective activation of this region is not sufficient for awareness of an intention. The precuneus has been assumed to play a role in the neural correlates of self-consciousness<sup>8</sup>. Our data, however, suggest that the precuneus also contains unconscious mental representations regarding future motor decisions that have not yet reached awareness. Hence, predictive information on its own, in frontopolar cortex or precuneus, is not sufficient for explaining the awareness of the future intention. It has been previously argued that SMA might encode the perceived intention because it is more activated when subjects attend to the intention as opposed to the motor response<sup>19</sup>. However, the presence of unconscious information in SMA in our study (albeit later than in frontopolar cortex and precuneus) implies that it does not encode the conscious experience of having a free intention, unless the additional assumption is made that SMA can encode both conscious and unconscious information at different times.

#### *No carry-over of information between trials*

For several reasons the early prediction presumably does not reflect a carry-over of information between trials. First, the distribution of response sequences clearly resembles an exponential distribution without sequential order, as would be expected if subjects decide randomly from trial to trial which button to press (**Supplementary Fig. 2**). This is presumably because in contrast to previous studies<sup>13,17</sup> we did not ask subjects to balance left and right button presses across trials, thus encouraging decisions that were independent of previous trials. Second, our chosen analysis method (the finite impulse response model, see **Supplementary Methods**) is designed to separate the effects of the current trial from the previous and the following trial. It is highly efficient as long as both types of responses are equally frequent, with variable inter-trial intervals, as here. Third, the early onset of predictive information in prefrontal and parietal regions occurred long after the end of the previous trial (approximately 12 s), which is far beyond the relaxation time of the hemodynamic response. Fourth, the predictive

information first increases with temporal distance from the previous trial, which is not compatible with the information being an overlap from the previous trial. Fifth, time points that overlap into the next trial revealed no carry-over of information (see **Supplementary Fig. 5**, left column). Taken together, the high predictive accuracy preceding the decision reflects prospective information encoded in prefrontal and parietal cortex related to the decision in the *current* trial.

## SUPPLEMENTARY METHODS

### *Subjects*

36 right-handed subjects (18 female, age range 21 – 30 years) were tested in a behavioural selection test, from which 14 subjects (seven female, age range 21 – 30 years) were selected to participate in the fMRI experiment (see *Behavioural Paradigm*).

### *Behavioural Paradigm*

Subjects performed a freely paced motor task while their brain activity was measured using functional magnetic resonance imaging. At the beginning of each trial period, consonants were presented in the middle of the screen, one at a time for 500 ms without gap, and subjects were asked to passively observe this letter stream (see **Fig. 1**). This modification to Libet's clock measurements was made to render the sequence unpredictable, and also to avoid inaccuracies in time judgement that can occur with rotating stimuli<sup>31</sup>. The order of presentation was randomized under the constraint that there were no repetitions within a sequence of 8 consonants. Subjects were told to relax and to press either the left or right button with the index finger of the corresponding hand immediately when they became aware of the urge to do so. They were to remember the consonant that was on the screen when they made the conscious decision which button to press (and not when the button was actually pressed). After the button was pressed, the screen went blank for 2,000 ms. Then, a response mapping screen was presented for 2,000 ms. This showed three consonants and a hash symbol ('#') arranged in a square configuration. The three consonants were the last three consonants that were presented ('0-back', '1-back' and '2-back' relative to the button press). The configuration of choices was

randomized so that subjects could not plan and prepare which action to execute before the response mapping screen appeared. Subjects were asked to indicate which consonant was on the screen when they made the decision which button to press. This gave an indication of the time when subjects became conscious of the intention which button to press, covering a possible range of 0-1,500 ms prior to the actual button press, which was chosen based on the pilot experiments. For example, selecting the ‘1-back’ consonant would indicate that the subject was conscious of the intention about 500-1,000 ms prior to the button press. If the consonant presented at the onset of the conscious intention was not available, subjects were to select the hash (#) symbol. Choice of this symbol indicates a delay of longer than 1,500 ms and suggests that the movement was not executed immediately when the conscious intention was felt, or that the subject was not paying attention to the consonants. This option was rarely chosen (1.4 %) and mainly ensured that the subject was performing the task as instructed (see **Supplementary Fig. 1**). The screen then went blank for 2,000 ms again before the next trial period began with the presentation of a new stream of consonants. Importantly, in order to facilitate spontaneous behaviour, we did not ask subjects to balance the left and right button selections. This would require keeping track of the distribution of button selections<sup>32</sup> in memory and would also encourage preplanning of choices. Instead, we selected subjects that *spontaneously* chose a balanced number of left and right button presses without prior instruction based on a behavioural selection test before scanning (see also **Supplementary Figs. 1-2**). This was performed on a previous day and was carried out to select subjects who were able to perform the task according to the above instructions. Each subject went through 10 runs, each lasting 5 minutes. A lateralization index was calculated to measure the ratio between total left button presses (L) and total right button presses (R) using the formula:  $(L-R)/(L+R)$ . To increase the chances of getting approximately balanced distributions of left and right button choices during the fMRI session, only subjects who had lateralization indices below 0.30 were selected for the fMRI experiment. Subjects were not told of this criterion. In addition, subjects were given only minor instructions to encourage the spontaneity of movement choice and execution. As in previous studies<sup>12</sup> we explicitly asked subjects not to make button selections based on any kind of pattern. They were specifically asked not to be too eager to initiate a

button press when the consonants first appeared, or to maintain a constant state of readiness for the movement. Instead, they should stay as relaxed as possible while looking at the consonants for some time. This served two purposes. The first was to let their mental activity settle down to a stable state, so that any build-up of neural activity prior to the movement could be clearly observed. The second reason was to avoid the overlapping of hemodynamic responses from different trials, so as to facilitate unambiguous interpretation of the blood oxygen level dependent (BOLD) signal prior to the button press. It was stressed to subjects that the time and choice of movement was completely up to them, but that it should be executed without hesitation once they made the decision which button to press. They were also asked to avoid any form of preplanning for choice of movement or time of execution.

On most trials (90.1 %) subjects reported that the intention occurred within 1,000ms prior to the motor response (**Supplementary Fig. 1**). On a small number of trials (8.5 %) subjects reported that the intention had preceded the response by between 1,000 and 1,500 ms (**Supplementary Fig. 1**). Hence, in most trials the conscious intention occurred within the fMRI volume preceding the button press. Please note that the temporal resolution with which the judgement was measured was four times higher than the resolution of our fMRI measurements and thus fully sufficient for the present purposes of investigating long-term determinants of conscious intentions.

We also conducted a behavioural control experiment with 8 of the 12 subjects who were still available, to further corroborate the timing measurements. First, we addressed the question whether the brief delay between intention and motor response reported by the subjects might be due to the limited number of response alternatives for reporting the letter that was on the screen when the decision was made. Subjects were allowed to respond with any consonant on the keyboard in order to report the time of their motor decision (i.e., yielding 21 possible alternative times or up to 10.5 seconds). It was confirmed using this unconstrained report that the delay between decision and button press was below one second. Second, using the same procedure we also let subjects rate the *time* when they decided *when* to press a button rather than *which* button to press. Both the decisions for the button and for the timing were made approximately at the same time just preceding the

button press. There was no significant difference between the “Left/Right” decision ( $-962$  ms, s.e.m. =  $149$  ms) and the “time” decision ( $-866$  ms, s.e.m. =  $65$  ms),  $t_7 < 1$  (see **Supplementary Fig. 3**), and both decisions were made within one second before the freely selected button press. This confirms that subjects were making the motor decisions at a much later stage than the long-leading brain activity that was predictive of their response. Finally, it is unlikely that subjects decided for one of the two response hands long in advance of their button press. If an early conscious decision for one of the two motor outputs had been made, one would expect to find covert motor preparation for the chosen movement, so the response should be decodable from motor (or premotor) cortex long before a button is pressed (as is the case in studies where the response is cued well in advance of the cue for when to respond). However, in our experiment we find that motor cortex only contains information at the time around the response (taking into account the delay in the hemodynamic response), whereas frontopolar cortex and precuneus have information long before the perceived timing of the decision. We believe this points strongly towards a late decision for one of the two responses, as also indicated by the psychophysical findings.

#### *FMRI Acquisition*

A Bruker 3T Medspec 30/100 scanner (Ettlingen, Germany) was used to acquire functional MR EPI volumes with 30 slices at an isotropic resolution of  $3 \times 3 \times 3$  mm resolution covering prefrontal, parietal and most of temporal cortex (TR = 2,000 ms; TE = 30 ms; tilt 10 degrees axial to coronal; FOV 192x192x90). Ten runs of 150 functional MRI volumes were acquired for each subject. A 46-slice whole brain EPI image was also acquired to facilitate spatial normalization. Two subjects were subsequently excluded from further analysis due to their behavioural performance during the fMRI session. One subject showed disproportionately more frequent selection of right button presses (lateralization index of  $-0.37$ ), which might lead to unbalanced estimation accuracy of the BOLD response. The other subject selected the ‘hash’ symbol for 24.5 % of button presses, suggesting that many of her button presses were not spontaneous. The remaining subjects had an average lateralisation index of 0.01.

### *Data Preprocessing*

Data were preprocessed using SPM2 (<http://www.fil.ion.ucl.ac.uk/spm>). After discarding the first two images to allow for magnetic saturation effects, the remaining functional images were then realigned. The functional images were then transformed into standard MNI space by first coregistering with a full-brain EPI image, followed by spatial normalization to the MNI EPI template. Then the functional images were subjected to two different analyses.

### *Analysis 1: Conventional GLM*

The first analysis was designed to identify brain regions where *overall* increases in neural activity occurred prior to the onset of a conscious decision. The preprocessed functional images were smoothed with a 6 mm FWHM Gaussian filter. Then a general linear model (GLM) was estimated for each subject with images concatenated across all runs. Since in our case there was no specific prediction regarding the temporal profile of the shape of the fMRI response timecourse, we used a finite impulse response (FIR) predictor to model fMRI responses<sup>33</sup>. The freely chosen button selections were modelled using 26 FIR regressors, 13 for left and 13 for right button presses, covering a time range from 10 s before until 16 s after the button press. The second button presses with which subjects indicated the onset time of their conscious intention were modelled as covariates consisting of single events convolved with a standard hemodynamic response function (HRF). The parameter estimates from the 26 FIR regressors of each subject were then entered into a second-level random-effects one-way ANOVA. The localisation of SMA and pre-SMA was based on standard criteria<sup>34</sup>.

### *Analysis 2: Decoding of intentions using pattern classification*

In a second analysis we used established techniques for multivariate pattern classification<sup>29,35</sup> to identify cortical regions that predicted whether the subject was about to press the left or right button even prior to their conscious decision to do so (see **Supplementary Fig. 4**). First, we estimated a modified general linear model for each run with regressors as described above but now based on unsmoothed data. This change was made to maximize sensitivity and allow extraction of the full

information present in the spatial patterns, which would have been reduced by smoothing. Then in order to search in an unbiased fashion for predictive voxels we used a “searchlight” approach<sup>29,36</sup> which examines the information in local spatial patterns of brain activity surrounding each voxel  $v_i$ . Thus, for each  $v_i$  we investigated whether its local environment contained spatial information that would allow decoding of the subject’s decision. For a given voxel  $v_i$  we first defined a small spherical cluster of  $N$  voxels  $c_{1..N}$  with radius of three voxels centred on  $v_i$ . For each gray matter voxel  $c_{1..N}$  in the fixed local cluster we extracted the unsmoothed parameter estimates separately for left and right choice trials, and *separately for 13 time points t* between 10 seconds before and 16 seconds after the conscious intention arose. This yielded two  $N$ -dimensional pattern vectors  $\mathbf{x}^{“L”,t,r,1..N}$  and  $\mathbf{x}^{“R”,t,r,1..N}$  for each run  $r$  and time point  $t$ , representing the spatial response patterns in the local cluster in trials where the subject chose a left versus a right button press. For a given time point  $t$  and spatial position  $v_i$  we used multivariate pattern recognition to assess how much intention-related information was encoded in the local pattern. To achieve this we assigned the pattern vectors  $\mathbf{x}^{“L”,t,r,1..N}$  and  $\mathbf{x}^{“R”,t,r,1..N}$  for nine of the ten imaging runs  $r$  to a “training” data set that was used to train a linear support vector pattern classifier<sup>37</sup> (with fixed regularisation parameter  $C=1$ ) to correctly identify response patterns related to the two different intentions the subject was currently holding. The classification was performed using the LIBSVM implementation (<http://www.csie.ntu.edu.tw/~cjlin/libsvm>).

The amount of intention-related information present within this local cluster could then be assessed by examining how well the intentions during the remaining independent tenth or “test” data set were classified. Good classification implies that the local cluster of voxels spatially encodes information about the specific current intention of the subject (see **Supplementary Fig. 9** for examples of spatial response patterns). In total, the training and test procedure was repeated ten times, each with a different run assigned as test data set yielding an average decoding accuracy in the local environment of the central voxel  $v_i$  (10-fold cross-validation). Then the procedure was repeated for the next time point  $t$  and then for the next spatial position at voxel  $v_j$ . The average decoding accuracy for each time point and each voxel was then used to create 3-dimensional spatial maps of decoding accuracy for

each position  $v_i$  and each time point  $t$  in prefrontal cortex. This yielded 13 images of predictive accuracy for each subject, one for each time point relative to the onset of the conscious intention.

Because the subjects' images had previously been normalised to a common stereotactic template it was possible to perform a second-level analysis where we computed on a voxel-by-voxel basis how well decoding could be performed on average across all subjects from each time point and each position in the brain. For this purpose the decoding images were smoothed with a 6 mm FWHM Gaussian filter. These spatial images of local decoding accuracy were entered into a one-way ANOVA with 13 levels, one for each timepoint. Regions that predicted the subsequently chosen button were identified using a t-contrast based on all timepoints prior to the decision onset (using a familywise error correction for multiple comparisons, 50-voxel cluster threshold). We also conducted a second analysis where we removed the cluster threshold (see **Supplementary Table 1**). A similar ANOVA based on unsmoothed decoding images yielded very similar results (not shown).

We also conducted a further decoding analysis where we assessed to which degree the timing of the decision, rather than its outcome can be decoded. A multi-class pattern classification analysis was performed to identify cortical areas which contained early predictive information about when participants would decide to make a button press. As in the main decoding analysis described above, a spherical “searchlight” (radius of 3 voxels) approach was used. For each spherical cluster, a multi-class support vector machine was trained to classify the time bin which a particular data point came from. Correct identification of the time bin prior to the time of conscious intention indicates that it is possible to predict how much later the conscious intention will occur. Six time bins (six possible classes) were interrogated, covering 10 s to 0 s before the button press. Again, 10-fold cross-validation was performed, each cycle involving 9 training runs and one independent test run. The “searchlight” went through the whole brain, yielding 6 images of classification accuracy for each subject, one for each timepoint before the conscious intention. To assess statistical significance across participants, a one-way ANOVA with 6 levels, one for each timepoint, was performed on smoothed decoding

accuracy images (6 mm FWHM Gaussian filter). The time of conscious intention could be significantly predicted from pre-SMA and SMA (t-contrast based on all timepoints, familywise error correction for multiple comparisons, 50-voxel cluster threshold). There was a linear increase in classification accuracy as the conscious intention approached. These results are reported in **Supplementary Fig. 5** (right column). Because the time bins chosen for the analysis and the time relative to the decision are not independent we performed an additional analysis to test whether decoding was indeed possible when only focusing on two early time points. We conducted a new time decoding analysis using only two of the earlier timepoints: 1) the earliest timepoint showing above chance classification (6 seconds prior to decision), and 2) the earliest timepoint interrogated (10 seconds prior to decision). As in the earlier analyses, a spherical “searchlight” (radius of 3 voxels) approach was used. For each spherical cluster, a support vector machine was trained to classify which of the two time bins a particular data point came from. Again, 10-fold cross-validation was performed, each cycle involving 9 training runs and one independent test run. This yielded 2 images of classification accuracy for each subject, one for each time bin tested. These images were smoothed (6 mm FWHM Gaussian filter) before a second level random effects group analysis was performed. As in the earlier time-decoding analysis, decoding accuracy in the pre-SMA was above chance (56.7 %,  $p < 0.00001$ , uncorrected).

In order to exclude that our decoding results were influenced by motion we also attempted to decode the outcome of a decision directly from the estimated movement of the subject. However, the motion parameters contained no information related to the decision, hence precluding that our results were driven by head motion (**Supplementary Fig. 7**).

#### *Control fMRI experiment: delayed motor intention*

Finally, in order to further investigate the functional roles of frontopolar cortex and precuneus, we conducted a control fMRI experiment. We investigated whether information about the chosen hand was already present during the conscious selection of an intention in a paradigm where the time point of selection was cued and thus under experimental control. This allows one to identify informative brain

regions at the precise time of selection of the intention, and to dissociate these from brain regions where information arises during the storage or response period. Seven subjects performed 10 runs of a delayed motor intention task. On each trial subjects freely decided whether to make a left or right button press when shown the cue “select”. The chosen response was not executed immediately, but the choice had to be maintained over a variable delay period (randomly distributed between 4 to 10 s), and was executed when a second cue, “respond”, was presented. Each subject was cued to perform 16 such trials per run, resulting in 160 trials in total. In each run 120 volumes were scanned. Otherwise scanning parameters were the same as in the main experiment (30 slices with an isotropic resolution of 3x3x3 mm resolution covering prefrontal, parietal and most of temporal cortex; TR = 2,000 ms; TE = 30 ms; tilt 10 degrees axial to coronal; FOV 192x192x90). In a small percentage of trials (3.30%) subjects failed to make a response within 2 s after the “respond” cue was presented. These trials were discarded from the analyses because subjects may not have been paying sufficient attention to the task during these trials. Overall, subjects chose roughly the same number of left and right responses (individual lateralization indices  $< 0.20$ ; average lateralization index =  $-0.04$ ). After preprocessing as in the main experiment, a general linear model was estimated for each run. The three phases selection, delay and response were modelled separately for left and right decision trials. The variable delay allowed for effective deconvolution of the three phases in each trial. We then investigated which cortical regions contained information about the intention (left or right button press) during the three phases (selection, delay, response) using the searchlight approach, as described before (see **Supplementary Fig. 8**). Frontopolar cortex, but not precuneus, contained information about the decision already during the selection phase ( $p<0.001$ , uncorrected). During the delay period both frontopolar cortex and precuneus contained predictive information about the intention ( $p<0.001$ , uncorrected). During the response phase only precuneus contained information about the decision. This suggests a dissociation between these two regions. Whereas frontopolar cortex was predictive already during the free selection period when the intention was formed, the precuneus was mainly predictive during the delay and execution period. This suggests that frontopolar cortex might be involved in generating the decision whereas precuneus might be involved in storing the

intention across a delay until the decision reaches awareness. This is consistent with previous work suggesting that the precuneus is involved in memory, self-referential processing and awareness<sup>39</sup>.

## SUPPLEMENTARY REFERENCES

1. Koechlin, E., Basso, G., Pietrini, P., Panzer, S. & Grafman, J. The role of the anterior prefrontal cortex in human cognition. *Nature* **399**, 148-151 (1999).
2. Burgess, P.W., Quayle, A. & Frith, C.D. Brain regions involved in prospective memory as determined by positron emission tomography. *Neuropsychologia* **39**, 545-555 (2001).
3. Sakai, K. & Passingham, R.E. Prefrontal interactions reflect future task operations. *Nat. Neurosci.* **6**, 75-81 (2003).
4. Vogt, B.A. & Laureys, S. Posterior cingulate, precuneal and retrosplenial cortices: cytology and components of the neural network correlates of consciousness. *Prog. Brain Res.* **150**, 205-217 (2005).
5. Groll-Knapp, E., Ganglberger, J.A. & Haider, M. Voluntary movement-related slow potentials in cortex and thalamus in man. *Progr. Clin. Neurophysiol.* **1**, 164-173 (1977).
6. Quian-Quiroga, R., Cui, H. & Andersen, R.A. J. Movement intention is better predicted than attention in the posterior parietal cortex. *Neurosci.* **26**, 3615-3620 (2006).
7. Sirigu, A., Daprati, E., Ciancia, S., Giraux, P., Nighoghossian, N. & Posada, A. Altered awareness of voluntary action after damage to the parietal cortex. *Nat. Neurosci.* **7**, 80-84 (2004).
8. Cavanna, A.E. & Trimble, M.R. The precuneus: a review of its functional anatomy and behavioural correlates. *Brain* **129**, 564-583 (2006).
9. Larsson, J., Gulyas, B. & Roland P. E. Cortical representation of self-paced finger movement. *Neuroreport* **7**, 463-468 (1996).
10. Eccles, J.C. The initiation of voluntary movements by the supplementary motor area. *Arch. Psychiatr. Nervenkr.* **231**, 423-441 (1982).
11. Libet, B. et al. Unconscious cerebral initiative and the role of conscious will in voluntary action. *Behav. Brain Sci.* **8**, 529-566 (1985).
12. Haggard, P. & Eimer, M. On the relation between brain potentials and the awareness of voluntary movements. *Exp. Brain Res.* **126**, 128-133 (1999).
13. Deiber, M.P., Passingham, R.E., Colebatch, J.G., Friston, K.J., Nixon, P.D. & Frackowiak, R.S. Cortical areas and the selection of movement: a study with positron emission tomography. *Exp. Brain Res.* **84**, 393-402 (1991).
14. Cunnington, R., Windischberger, C. & Moser, E. Premovement activity of the pre-supplementary motor area and the readiness for action: studies of time-resolved event-related functional MRI. *Hum. Mov. Sci.* **24**, 644-656 (2005).
15. Pedersen, J.R., Johannsen, P., Bak, C.K., Kofoed, B., Saermark, K. & Gjedde, A. Origin of human motor readiness field linked to left middle frontal gyrus by MEG and PET. *Neuroimage* **8**, 214-220 (1998).
16. Tanji, J. Sequential organization of multiple movements: involvement of cortical motor areas. *Ann. Rev. Neurosci.* **24**, 631-651 (2001).
17. Frith, C.D., Friston, K., Liddle, P.F. & Frackowiak, R.S. Willed action and the prefrontal cortex in man: a study with PET. *Proc. Biol. Sci.* **244**, 241-246 (1991).
18. Forstmann, B.U., Brass, M., Koch, I. & von Cramon, D.Y. Voluntary selection of task sets revealed by functional magnetic resonance imaging. *J. Cogn. Neurosci.* **18**, 388-398 (2006).
19. Lau, H.C., Rogers, R.D., Haggard, P. & Passingham, R.E. Attention to intention. *Science* **303**, 1208-1210 (2004).

20. Haynes, J.D. & Rees, G. Decoding mental states from brain activity in humans. *Nat. Rev. Neurosci.* **7**, 523-534 (2006).
21. Haynes, J.D. & Rees, G. Predicting the orientation of invisible stimuli from activity in human primary visual cortex. *Nat. Neurosci.* **8**, 686-691 (2005).
22. Kamitani, Y. & Tong, F. Decoding the visual and subjective contents of the human brain. *Nat. Neurosci.* **8**, 679-685 (2005).
23. Mountcastle, V.B. The columnar organization of the neocortex. *Brain* **120**, 701-722 (1997).
24. Horton, J.C. & Adams, D.L. The cortical column: a structure without a function. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **360**, 837-862 (2005).
25. Constantinidis, C., Franowicz, M.N. & Goldman-Rakic, P.S. Coding specificity in cortical microcircuits: a multiple-electrode analysis of primate prefrontal cortex. *J. Neurosci.* **21**, 3646-3655 (2001).
26. Averbeck, B.B., Sohn, J.W. & Lee, D. Prefrontal neural correlates of memory for sequences. *Nat. Neurosci.* **9**, 276-282 (2006).
27. Wallis, J.D. & Miller, E.K. From rule to response: neuronal processes in the premotor and prefrontal cortex. *J Neurophysiol.* **90**, 1790-1806 (2003).
28. Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P. Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* **293**, 2425-2430 (2001).
29. Haynes, J.D., Sakai, K., Rees, G., Gilbert, S., Frith, C. & Passingham, R.E. Reading hidden intentions in the human brain. *Curr. Biol.* **17**, 323-328 (2007).
30. Hampton, A.N. & O'Doherty, J.P. Decoding the neural substrates of reward-related decision making with functional MRI. *Proc. Natl. Acad. Sci.* **104**, 1377-1382 (2007).
31. Van de Grind, W. Physical, neural and mental timing. *Consc. Cogn.* **11**, 241-264 (2002).
32. Spence, S. & Frith, C.D. Towards a functional anatomy of volition. *J. Consc. Stud.* **6**, 11-29 (1999).
33. Henson, R. Analysis of fMRI time series. in *Human Brain Function, Second Edition*, (eds. Frackowiak, R.S.J. et al.) 793-822 (London: Academic, 2004).
34. Picard, N. & Strick, P.L. Motor areas of the medial wall: a review of their location and functional activation. *Cereb. Cort.* **6**, 342-353 (1996).
35. Norman, K.A., Polyn, S.M., Detre, G.J. & Haxby, J.V. Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends Cogn. Sci.* **10**, 424-430 (2006).
36. Kriegeskorte, N., Goebel, R. & Bandettini, P. Information-based functional brain mapping. *Proc. Natl. Acad. Sci. USA* **103**, 3863-3868 (2006).
37. Müller, K.R., Mika, S., Rätsch, G., Tsuda, K. & Schölkopf, B. An introduction to kernel-based learning algorithms. *IEEE Trans. Neur. Netw.* **12**, 181-201 (2001).
38. Kornhuber, H.H. & Deecke, L. Hirnpotentialänderungen bei Willkürbewegungen und passiven Bewegungen des Menschen: Bereitschaftspotential und reafferente Potentiale. *Pflügers Archiv* **284**, 1-17 (1965).
39. Cavanna, A.E. & Trimble, M.R. The precuneus: a review of its functional anatomy and behavioural correlates. *Brain* **129**, 564-583 (2006).