How the Brain Translates Money into Force: A Neuroimaging Study of Subliminal Motivation

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Materials and Methods
Figs. S1 to S10
References

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How the Brain Translates Money into Force: A Neuroimaging Study of Subliminal Motivation

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Unconscious motivation in humans is often inferred but rarely demonstrated empirically. We imaged motivational processes, implemented in a paradigm that varied the amount and reportability of monetary rewards for which subjects exerted physical effort. We show that, even when subjects cannot report how much money is at stake, they nevertheless deploy more force for higher amounts. Such a motivational effect is underpinned by engagement of a specific basal forebrain region. Our findings thus reveal this region as a key node in brain circuitry that enables expected rewards to energize behavior, without the need for the subjects' awareness.

Humans tend to adapt the degree of effort they expend according to the magnitude of reward they expect. Such a process has been proposed as an operant concept of motivation (*1*–*3*). Motivational processes may be obvious, as when a prospector spends days in extreme conditions seeking gold. The popular view is that motivation can also be unconscious, such that a person may be unable to report the goals or rewards that drive a particular behavior. However, empirical evidence on this issue is lacking, and the potential brain mechanisms involved in converting expected rewards into behavioral activation are poorly understood.

We developed an experimental paradigm to visualize unconscious motivational processes, using functional magnetic resonance imaging. A classical approach to trigger unconscious processing is subliminal stimulation, which can be implemented by means of masking procedures. The terminology we use in this report is based on a recent taxonomy (*4*), in which a process is considered subliminal if it is attended but not reportable. Successful brain imaging studies of subliminal processes have focused so far on processing words (*5*, *6*) as well as emotional stimuli (*7*, *8*). In our study, the object of masking was an incentive stimulus for a future action, represented by the amount of reward at stake. The question we asked is whether, and how, the human brain energizes behavior in proportion to subliminal incentives.

We developed an incentive force task, using money as a reward: a manipulation that is consistently shown to activate reward circuits in the human brain (*9*–*11*). The exact level of motivation was manipulated by randomly assigning the amount at stake as one pound or one penny. Pictures of the corresponding coins were displayed on a computer screen at the beginning of each trial, between two screenshots of "mask" images (Fig. 1). The reportability of the monetary stakes depended on their display duration, which could be 17, 50, or 100 ms. The perception of the first two durations was determined as subliminal in a preliminary behavioral test, where subjects reported not seeing anything other than the mask. The third duration was consistently associated with conscious perception of the stimuli and their associated amount.

To characterize the effects of the monetary stakes, we recorded not only brain activity but also skin conductance and hand-grip force. Skin conductance response (SCR) is linked to autonomic sympathetic arousal (*12*) and is thereafter interpreted as reflecting an affective evaluation of the monetary stake. Hand-grip force is understood to be a measure of behavioral activation. Online visual feedback of the force exerted was displayed as a fluid level moving up and down within a thermometer depicted on the screen (Fig. 1). Subjects were instructed that the higher the fluid level rose, the more of the monetary stake they would get to keep. At the end of the trial, subjects were given visual

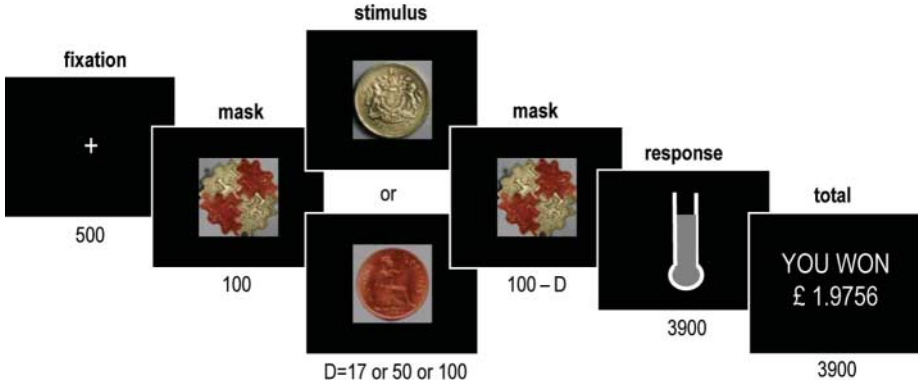

Fig. 1. The incentive force task. Successive screens displayed in one trial are shown from left to right, with durations in ms. Coin images, either one pound (£1) or one penny (1p), indicate the monetary value attributed to the top of the thermometer image. The fluid level in the thermometer represents the online force exerted on the hand grip. The last screen indicates cumulative total of the money won so far.

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feedback of the amount of money that they had accumulated. Thus, this cumulative total was increased after every trial, though negligibly so when one penny was at stake.

For the analysis of brain activity, we first examined the main contrast between monetary stakes, in the conscious condition, at the time of stimulus onset (Fig. 2, middle column). After correction for multiple comparisons over the whole brain (family-wise error, $P < 0.05$), the only significant activation was located bilaterally in the basal forebrain, bordering several structures encompassing the ventral striatum, ventral pallidum (VP), extended amygdala, and basal nucleus of Meynert. These structures have been conceptualized as forming output channels for the limbic system, which is devoted to emotional and motivational functions (*13*). According to fiber tracing studies, reward-related information may access these structures either by a subcortical route via the hippocampus and/or amygdala or by a cortical route via the orbitofrontal and/or anterior cingulate areas (*14*–*17*).

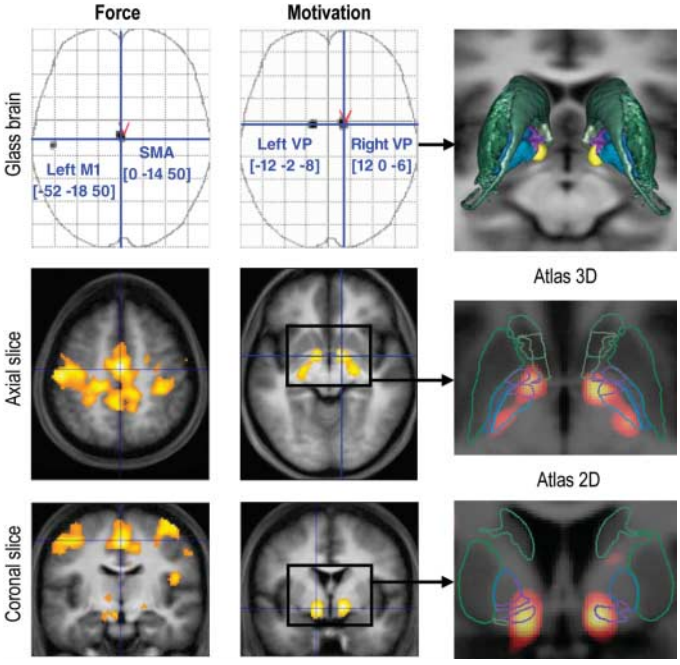

Fig. 2. SPMs of brain activity. Voxels displayed in gray on glass brains showed a significant effect at $P < 0.05$ after correction for multiple comparisons over the entire brain. The [*x*, *y*, *z*] coordinates of the different maxima refer to the Montreal Neurological Institute (MNI) space. Axial and coronal slices were taken at global maxima of interest indicated by red symbols on the glass brains. SPMs are shown at a lower threshold ($P < 0.001$, uncorrected) and were superimposed on the average structural scan to localize significant activations. The images in the left column show regression with the amount of force produced, whatever the condition. The images in the middle column show contrast between conscious pounds and pennies trials (£1 to 1p, 100 ms). For this contrast, SPMs were coregistered with an atlas of the basal ganglia (right column). Caudate, putamen, and accumbens are shown in green; external and internal pallidum are shown in blue, with limbic sectors in violet.

To improve anatomical localization, we coregistered the statistical parametric map (SPM) with a recent histology-based atlas of the basal ganglia, which was designed to distinguish between functional territories (*18*, *19*). Activation foci overlapped with limbic territories of both external and internal pallidal segments (Fig. 2, right column), which together form the VP. The main inputs to the VP come from the ventral striatum, where reward-related activations have been consistently found (*9*–*11*). VP activation might denote engagement of the same ventral striato-pallidal pathway, with a shift in its expression being related to the nature of the upcoming task. More specifically, ventral striatal activity has been linked to reward prediction and reward prediction error during learning (*20*, *21*). Rather than concentrating on learning, our design focused on motivation during effort, which elicited specific processing in the VP. Our finding accords well with evidence in rodents, showing that VP neurons encode rewarding properties of environmental stimuli (*22*), and suggests a role for the VP in incentive motivation. Furthermore, lowering the threshold ($P < 0.001$, uncorrected) revealed that activation extended posteriorly, within nonlimbic territories of the pallidum, pointing out a plausible route by which the VP may influence cortical motor areas (*14*, *15*).

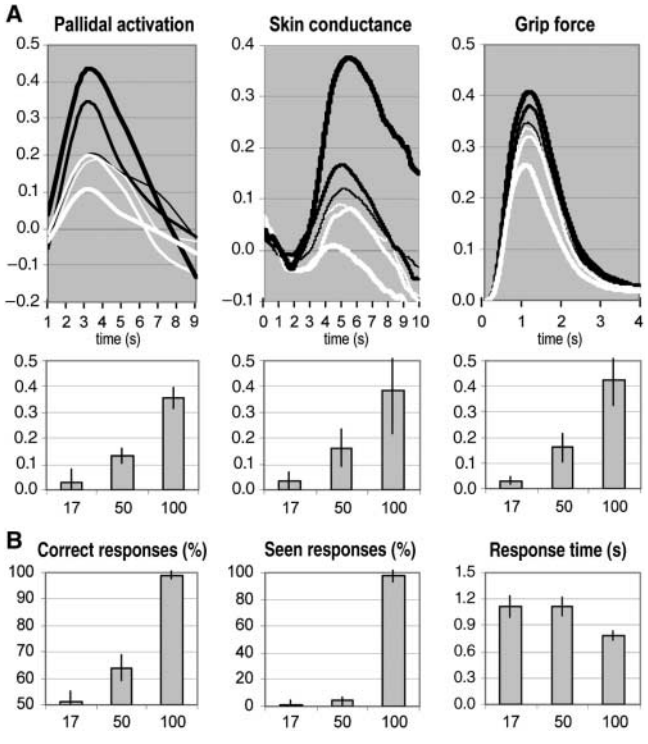

Fig. 3. Main effects of stimulus duration. (**A**) Incentive force task. Time courses were averaged across trials for the different stimuli (black lines indicate £1 and white lines indicate 1p) and durations (thin, intermediate, and thick lines indicate 17, 50, and 100 ms, respectively). Time 0 corresponds to the moment of stimulus display. The histograms indicate the effect of motivation (£1 to 1p), and the error bars indicate SEM. Pallidal activation is expressed as percentage of blood oxygen level–dependent signal change. Force and skin conductance are expressed in proportion of the highest measure. (**B**) Perception task. Stimuli were the same as in (A). Possible responses were "seen £1," "seen 1p," "guess £1," and "guess 1p." A "correct" response means that the subject chose the stimulus that had been displayed. A "seen" response means that the subject perceived all or part of the stimulus. Error bars indicate SEM.

To dissociate motivation per se from force production, we next examined brain activity that was linearly related to the amount of force produced, whatever the condition (Fig. 2, left column). After correction for multiple comparisons over the whole brain (family-wise error, $P < 0.05$), significant activations were found in the supplementary motor area (SMA) and in the primary motor area (M1). Unlike the pallidum, these structures have previously been shown to activate in relation with the amount of force produced (*23*–*25*). Moreover, M1 activation was observed on the left side, which was consistent with the use of the right hand for the task, whereas pallidal activation was bilateral. Thus, in our analysis, the dissociation was clear-cut, probably reflecting the fact that monetary stakes were constant throughout the task, while grip force decreased trial after trial, probably as a result of fatigue (fig. S1). Such dissociation suggests that

motivational processes mediated by the VP include modulation of SMA activity, which in turn drives muscular contractions via M1.

We next asked whether such a circuit was engaged by subliminal incentives. We averaged parameter estimates (Fig. 3A, left panels) over the pallidal voxels that showed significant activation in the previous SPM. The contrast between monetary stakes was significant for 100 and 50 ms (paired *t* tests, both *P* values < 0.001) but not for 17 ms. No significant activation was found elsewhere in an SPM estimated for this contrast at 50 ms, even with our liberal threshold (*P* < 0.001, uncorrected). Thus, only the VP appeared in position to modulate behavioral activation according to subliminal incentives and hence to underpin a low-level motivational process, as opposed to a conscious cost-benefit calculation. Again, such a role accords well with experiments on rodents, which show that VP manipulations influence goal-directed behavior, as seen with self-stimulation after electrode implantation in the VP (*26*) or impaired acquisition of conditioned-place preference after the generation of VP lesions (*27*).

We next sought to link our imaging results to simultaneously measured autonomic and behavioral responses. The dynamics of responses recorded from skin conductance electrodes indicated that they were triggered at the time of stimulus display, with a typical SCR profile starting at 2 s post-stimulus and peaking around 5 s (*12*). Comparison between monetary stakes showed significant effects at 100 and 50 ms (paired *t* tests, both *P* values < 0.05) but not at 17 ms (Fig. 3A, middle panels). Thus, like fear-relevant stimuli (*28*), subliminal incentives could be evaluated affectively, with subjects being more responsive to images of pounds than to those of pennies. Autonomic responding was not a mere side effect of force production, because it evolved with a different temporal profile throughout the task. Indeed, grip force decreased for consciously perceived pennies, while skin conductance increased for consciously perceived pounds (fig. S1). Regarding grip force, we found similar dynamics, whatever the condition: subjects giving a short squeeze, with peak latency at around 1 s, and relaxing before the next trial (Fig. 3A, right panels). Hence, similar results were found when considering either the height of the peak or the area under the curve. Comparing between monetary stakes, significant effects were found at 100 ms, 50 ms, and even at 17 ms (paired *t* tests, all *P* values < 0.01). Thus, the brain could energize behavior in proportion to the reward at stake, even when subjects could not see it.

Finally, we controlled for subjective perception with a forced choice task (Fig. 3B). While still in the scanner, subjects were shown the same masked stimuli and had to report whether they saw a coin, and which coin they thought it was, either from seeing it or from guessing. Based on the percentage of correct responses, the analysis could then be restricted to all situations where subjects guess at chance level about stimulus identity (fig. S2). Even in these situations, pallidal activation and hand-grip force were significantly higher for pounds as compared to pennies (paired *t* tests, both *P* values < 0.01). As with the preliminary test, subjects reported seeing almost no stimuli at 17 and 50 ms and almost all stimuli at 100 ms. Compared to the 100-ms condition, subjects also had similarly long response times at 17 and 50 ms, indicating that they were experiencing the same degree of uncertainty about stimulus identity. Thus, subjective perception changed as a function of category, from subliminal to conscious, between 50 and 100 ms. In contrast, objective markers of motivation (pallidal activation, SCR, and hand-grip force) gradually increased with stimulus duration.

These results indicate that motivational processes involved in boosting behavior are qualitatively similar, despite whether subjects are conscious or not of the reward at stake. Consistently, the same basal forebrain region underpinned subliminal and conscious motivation. Such subcortical localization might relate to the simple and repetitive nature of the task, rendering strategic control unnecessary. However, differential sympathetic arousal denoted by SCRs argues against an interpretation in terms of mere stimulus-response habit formation, which is known to involve the basal ganglia (*29*). More generally, our paradigm offers a potential tool to discriminate between motor and affective components of motivation for financial reward in humans, analogous to the dissociation between wanting and liking food reward described in rodents (*30*). Such a tool may be particularly useful in exploring negative symptoms, like those manifested in depression or schizophrenia, involving acute dysfunction within the motivational process.

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SUPPORTING ONLINE MATERIAL

Material and methods

Subjects

The study was approved by the National Hospital for Neurology and Neurosurgery and the Institute of Neurology joint Ethics Committee. Subjects were recruited via Gumtree website and screened for exclusion criteria: left handedness, age below 18 or above 39, regular taking of drug or medication, history of psychiatric or neurological illnesses and contra-indications to MRI scanning (pregnancy, claustrophobia, metallic implants). All included subjects gave informed consent prior to taking part. A total of 18 subjects were scanned: 9 males (mean age 24.3 ± 5.4 years) and 9 females (mean age 25.9 ± 3.7 years).

Behavioral task and analysis

Subjects had first to read the instructions (see below) about the different tasks, which were later explained again step by step. Before scanning, subjects were familiarised with the masks and stimuli in a practice task. They were shown the basic sequence of computer screenshots (Fig. 1) used in all tasks designed for this study: cross / mask / stimulus / mask. The stimulus could be a penny (1p) or a pound (£1) coin. Subjects were asked to report whether or not they saw the coin, by pressing the left or right key. Different durations were used, all multiples of 17 ms, due to the refreshment rate of the computer screen (60 Hz). In the first trials the stimulus was displayed during 100 ms, and then its duration was decreased by 17 ms, following a stair-case procedure, until the subjects consistently (in 3 consecutive trials) reported not being able to see anything except the mask. With this method we found that 50 ms was sufficiently short to ensure all subjects could not perceive the stimuli.

Subsequently subjects were brought inside the scanner. They were invited to find an optimal body position, lying down with a power grip in the right hand, the arm folded up over the belly. The hand grip was made of two moulded plastic cylinders compressing an air tube. The tube led to the control room, where it was connected to a transducer able to convert air pressure into voltage. Thus compression of the two cylinders by an isometric handgrip resulted in the generation of a differential voltage signal, linearly proportional to the force exerted. The signal was fed into the stimuli presentation PC via a signal conditioner. Stimuli presentation was programmed with Cogent

2000 (Wellcome Department of Imaging Neuroscience, London, UK). The visual stimuli were displayed behind the scanner on a projector screen, which subjects could see via mirrors positioned over their eyes. The dynamic changes of recorded signal were used to provide subjects with a real time visual feedback about the force being exerted on the grip, as a fluid level moving up and down within a thermometer (see Fig. 1).

We calibrated the baseline ("just do nothing") and measured the maximal force ("squeeze the grip as hard as you can"). The thermometer was displayed on the screen, to let the subject practice moving up and down the fluid level. The scale was adjusted so that each subject would reach half of the total height of the thermometer when producing his/her maximal force. This was implemented to avoid ceiling effects in case the maximal force had been underestimated. In parallel to the force, we also continuously monitored galvanic skin conductance levels, from electrodes placed on the middle and index fingers of the left hand. However, due to technical problems, we could only record skin conductance data in 12 subjects out of 18.

Subjects then performed the incentive force task, divided into 3 sessions of 13 minutes. Each session contained 15 repetitions of 6 trial types, for a total of 90 trials. The 6 trial types correspond to 6 different stimulations, according to a 2*3 factorial design: 2 monetary stakes (1p and £1) and 3 different durations (17, 50 and 100 ms). In every trial the subject had to fixate the central cross and pay attention to the subsequent flickering image, composed of 3 successive screens: mask / stimulus / mask. When the thermometer appeared on the screen, subjects had to squeeze the power grip. They were told that the height they reached within the thermometer determined the fraction of the monetary stake they would keep. At the end of every trial a cumulative total was displayed, indicating the amount of money a subject had won so far. Subjects believed they were playing for real money, but at the end their payoff was rounded up to a fixed amount (£30). Before leaving they were debriefed about their feelings and intentions in the different situations (seeing £1, seeing 1p, seeing nothing).

After the functional scan, while performing the incentive force task, subjects had a structural scan, while performing a perception task. This task was designed to apply two criterions for subliminal perception: percentage of subjective seeing and percentage of correct guessing. Subjects observed the same first 4 screens (cross / mask / stimulus / mask). Then they were asked to figure out which coin was displayed, and to have a guess if they could not see anything. Thus they were forced to choose one of the 4 responses written on the screen: seen £1 / seen 1p / guess £1 / guess 1p. The response was chosen by pressing the corresponding button on the keypad. Stimuli and durations

were the same as in the incentive force task, but there was no pressure on the response time. Each of the 6 trial types was repeated 30 times, for a total of 180 trials, lasting about 10 minutes on average.

For the incentive force task, two parameters were considered: skin conductance and hand grip force. Skin conductance was down-sampled at 100Hz and mean filtered. The response to stimuli was taken as the difference between the maximum reached within 2-8 s interval and the mean over 0-2 s interval. Hand grip force was down-sampled at 50Hz and we extracted both the maximum reached and the area under the curve over 0-4s post-stimulus interval. The two parameters were expressed in percentage of the highest measure and then compared between monetary stakes using one-tailed paired t-tests. Mean group results are also illustrated either as a time course for the different trial conditions (Fig. 3) or as peaks reached trial after trial throughout the 3 task sessions (Fig. S1).

For the perception task, three parameters were considered: percentage of correct responses (£1 or 1p), percentage of seen responses (as opposed to guess responses) and response times (whatever the response). These parameters were compared between conditions using one-tailed paired t-tests (see illustration in Fig. 3). Percentage of correct responses was used to define subliminal situations in the sense that subjects were guessing at chance level. Using chi-2 test at individual level, guessing was found not to be different from chance level (50%) in 24 situations: at 17 ms for all 18 subjects and at 50 ms for 6 subjects. Using paired t-test at group level, guessing was also found not to be different from chance, with an average of 51 ± 4 %. We also checked that the discriminability index (d') was not different from 0 in these situations, with an average of 0.19 ± 0.54. Percentage of seen responses was used to define subliminal situations in the sense that subjects had the subjective feeling to guess and not to see. These situations (n=36) correspond to the 17 and 50 ms in all subjects, with an average subjective seeing of 5 ± 16 %. The partitions operated by the two criterions for subliminal perception are illustrated in Fig. S2.

Images acquisition and analysis

T2*-weighted echo planar images (EPI) were acquired with blood oxygen dependant level (BOLD) contrast on a 3.0 Tesla magnetic resonance scanner. We employed a tilted plane acquisition sequence designed to optimize functional sensitivity in the orbitofrontal cortex and medial temporal lobes. To cover the whole brain with a short TR (1.95s), we used the following parameters: 30 slices; 2mm slice thickness; 2mm inter-slice gap. T1-weighted structural images were also acquired, co-registered with the mean EPI, normalised to a standard T1 template, and averaged across subjects to allow group level anatomical localization. An atlas of the basal ganglia (INSERM,

Hôpital de la Salpêtrière, Paris, France) was also deformed on average structural images to further ensure anatomical localisation. EPI images were analysed in an event-related manner, within a general linear model, using the statistical parametric mapping software SPM5 (Wellcome Department of Imaging Neuroscience, London, UK). The first 5 volumes of each session were discarded, to allow for T1 equilibration effects. Pre-processing consisted of spatial realignment, normalisation using the same transformation as structural images, and spatial smoothing using a Gaussian kernel with a full-width at half-maximum of 6mm.

We used a single statistical linear regression model for all our analyses, as follows. Each trial was modelled as having only 1 time point, corresponding to stimulus onset. Separate regressors were created for the 6 stimuli conditions (2 stimuli * 3 durations). For each condition the force produced by the subject was also included as parametric modulation. Thus the design matrix contained 12 regressors of interest, all convolved with a canonical haemodynamic response function (HRF). To correct for motion artefact, subject-specific realignment parameters were modelled as covariates of no interest. Linear contrasts of regression coefficients were computed at the individual subject level and then taken to a group level random effects analysis (one-sample t-test). A threshold of $P < 0.05$ after family-wise error (FWE) correction for multiple comparisons was applied to avoid any a priori on brain localisation. A more liberal threshold ($P < 0.001$, uncorrected) was also used to observe the extension of significant activations.

Our original question was whether brain circuits underlying subliminal and conscious motivation can be dissociated. We calculated a two-way analysis of variance, the two factors being motivation (amount of money at stake) and reportability (duration of stimulus display). We found no significant main effect of reportability, but significant main effect of motivation, as well as significant interaction between motivation and reportability, in the basal forebrain only (see Fig. S3). Moreover, positive effect of motivation (£1-1p) was activation of the same basal forebrain region, but with increased amplitude and significance, from short to long display durations. These data suggest that the brain circuits underlying subliminal motivation are not different from those underlying conscious motivation. We then explicitly addressed the question of whether the brain region responsible for conscious motivation also works at subliminal level. This region of interest (shown in Fig. 2) was defined as the set of voxels significantly activated, after FWE correction over the entire brain, by the contrast between pounds and pennies in the conscious condition (£1-1p, 100 ms). Within each subject, parameter estimates were averaged over these voxels, separately for all modalities of motivation and reportability. Significance of activation, for each of the 3 stimulus durations, was assessed at group level with paired t-tests between monetary incentives (£1-1p).

Corresponding time courses (Fig. 3) were estimated by fitting a flexible basis set of finite impulse responses (FIRs), separated from the next by one scan (1.95s). Finally, brain areas underlying force production were isolated in a contrast including all parametric regressors whatever the condition (see Fig. 2).

INSTRUCTIONS

Part one is designed to determine at which threshold you can see masked coins.
Part two is designed to measure your maximal force.
Part three will allow you to use your force to win some of the coins.
Part four is designed to check out that you actually see the coins when you say so.

Part one

The masked coins that will be displayed on the screen can be either 1p (one penny) or £1 (one pound).
Whatever it is, you will be asked to say whether you have seen it or not.
Use your index finger for a “seen” response and the middle finger for an ‘’unseen’’ response.
Only choose “seen” when you are sure to have distinctly perceived all or part of the coin.
We will start with long durations and go to shorter ones until you consistently say that you see nothing.

Part two

The different steps will be announced on the screen.
During baseline calibration just do nothing.
During maximal force measurement squeeze the power grip as hard as you can.
During practice see how high you can move up the fluid in the thermometer displayed on the screen.

Part three

Every time a masked coin is displayed on the screen you will have to squeeze the power grip.
Squeezing the grip makes the fluid level move up in the thermometer as before.
The height you reach determines the fraction of the coin you will be allowed to keep.
The total amount of money that you have won so far will be written on the screen after every trial.
In short: the more you squeeze the more money you win!

Part four

Now you will have to say which coin was displayed on the screen.
Just have a guess when you have not seen anything.
Four choices will be available: seen £1 / seen 1p / guess £1 / guess 1p.
The 4 responses respectively correspond to your 4 fingers put of the keypad, from left to right.
Again choose the “seen” options when you are sure to have distinctly perceived all or part of the coin.

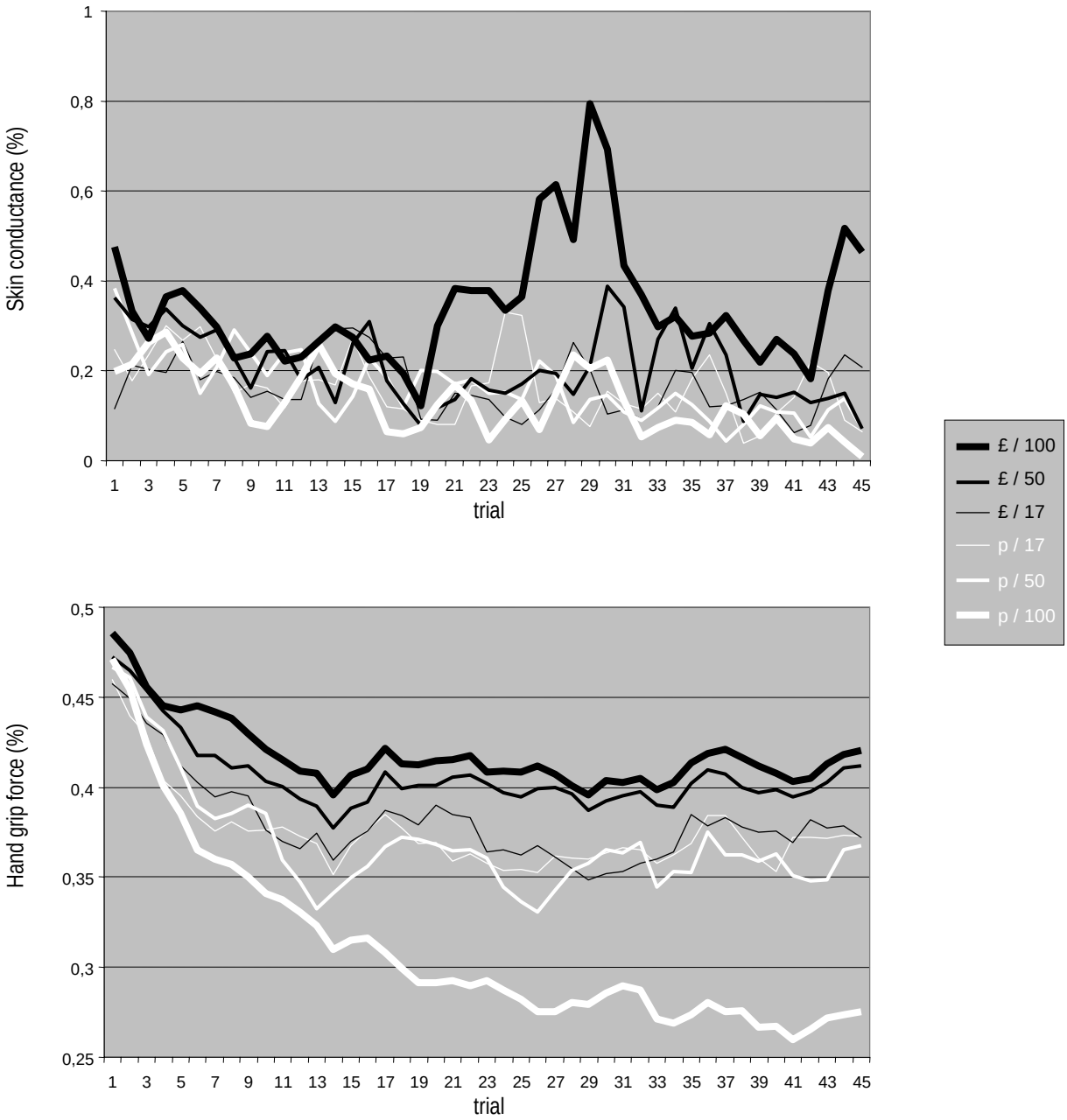

Fig. S1 Evolution of autonomic and behavioral responses with successive trials. Response peaks were extracted for each trial and expressed as percentages of the highest measure. The 3 sessions were concatenated to show all 45 trials for different stimuli (black is £1 and white is 1p) and durations (growing thicknesses are 17, 50 and 100 ms).

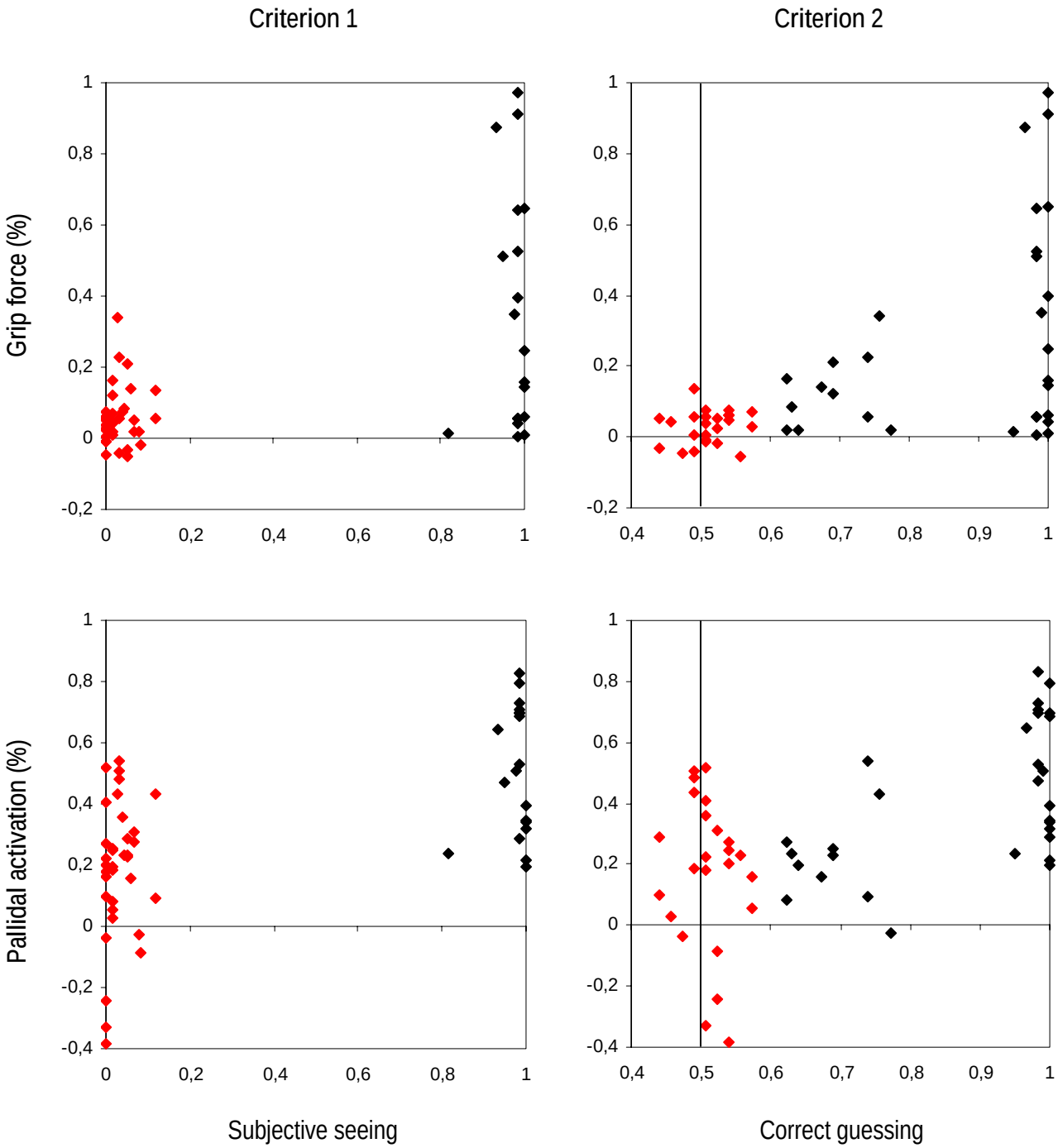

Fig. S2 Correlation between motivational effects and perceptive awareness. Y-axis indicates the difference between pounds and pennies on hand grip force (top) and activation of ventral pallidum (bottom). X-axis represents perception of monetary incentives according to two criterions: subjective feeling of seeing (left) and proportion of correct guessing (right). Each point is one subject tested with one duration of stimuli display. Red points are considered subliminal from being within the 95% confidence interval of perception assessed at the shortest duration (17 ms). According to criterion 1, subliminal perception means that percentage of seen responses is not different from 0. According to criterion 2, subliminal perception means that percentage of correct responses is not different from chance level (0,5)

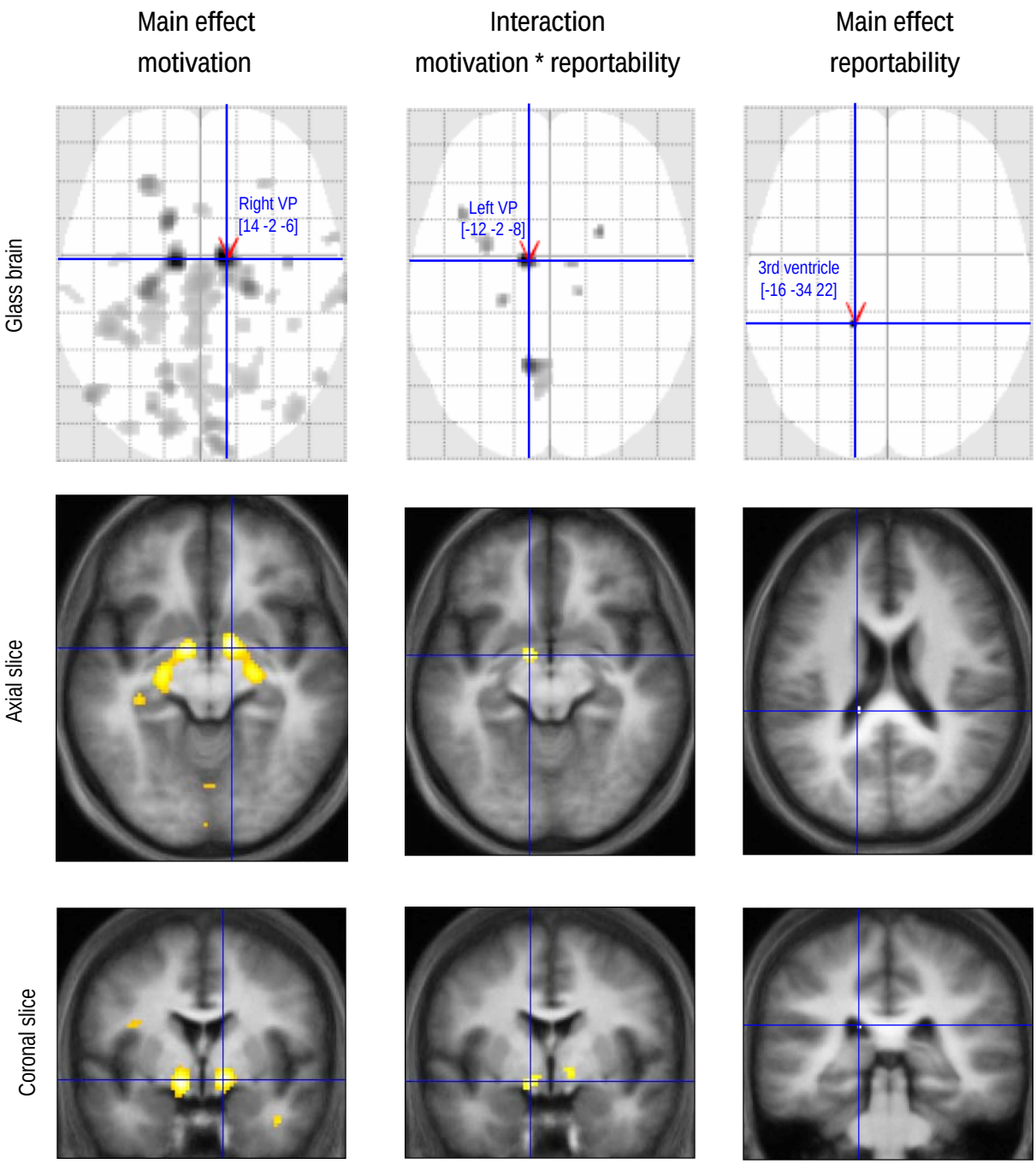

Fig. S3 Statistical parametric maps from 2-by-3 analysis of variance. The 2 factors were amount of money (motivation) and duration of display (reportability). To show the extent of activations a liberal threshold ($P < 0.001$, uncorrected) has been used, resulting in some obvious false positives. The [x y z] coordinates of the different maxima refer to the MNI space. Axial and coronal slices were taken at global maxima of interest indicated by red arrows on the glass brains.