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The Truth-telling Motor Cortex: Response Competition in M1 Discloses Deceptive Behaviour

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Running head: Response Competition Reveals Deception

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Abstract

Neural circuits associated with response conflict are active during deception. Here we use transcranial magnetic stimulation to examine for the first time whether competing responses in primary motor cortex can be used to detect lies. Participants used their little finger or thumb to respond either truthfully or deceitfully regarding facial familiarity. Motor-evoked-potentials (MEPs) from muscles associated with both digits tracked the development of each motor plan. When preparing to deceive, the MEP of the non-responding digit (i.e. the plan corresponding to the truth) exceeds the MEP of the responding digit (i.e. the lie), whereas a mirror-reversed pattern occurs when telling the truth. This give away response conflict interacts with the time of stimulation during a speeded reaction period. Lies can even activate digit-specific cortical representations when only *verbal* responses are made. Our findings support neurobiological models which blend cognitive decision-making with motor programming, and suggest a novel index for discriminating between honest and intentionally false facial recognition.

Highlights

► Single-pulse TMS can be used to study intra-hemispheric response preparation. ► Response competition dynamics can differentiate between truth-telling and deceit. ► Lying involuntarily activates motor plans associated with the truth in M1.

Keywords

- Response competition;
- Response selection;
- Deception;
- Lie detection;
- Motor evoked potential (MEP);
- Transcranial magnetic stimulation (TMS);
- Response inhibition

1. Introduction

Deception is commonplace in human communication, engaging multiple cognitive processes ([Ekman, 2009] and [Spence, 2004]). Social interactions often involve deceptive behaviours, used to maximize personal gain or avoid punishment ([Nardini, 1987] and [DePaulo et al., 2003]). At present the most widely used tool for lie-detection is the polygraph (Pollina et al., 2004) which is based on indirect peripheral physiological measures. Recent imaging studies have demonstrated that neural circuits associated with response conflict and response inhibition are strongly implicated in deception ([Abe et al., 2006], [Abe et al., 2007], [Bhatt et al., 2009], [Kozel et al., 2004], [Lee et al., 2010], [Langleben et al., 2005], [Nunez et al., 2005] and [Schumacher et al., 2010]). Indeed, cognitive models of deception posit the activation of the truth as one of the early processes underlying deception, which could lead to conflict. However, to date the involuntary activation of a population of neurons representing the truth in lying has not been demonstrated.

Several researchers have noted the consistent involvement of the anterior cingulate cortex (ACC) and dorsolateral prefrontal cortex (DLPFC), areas associated with cognitive control and conflict monitoring, in deceptive behaviour ([Abe et al., 2006], [Bhatt et al., 2009], [Lee et al., 2010], [Nunez et al., 2005] and [Schumacher et al., 2010]). Abe et al. (2006) used positron emission tomography (PET) to show that the activation of conflict monitoring areas such as the ACC is specific for denying knowledge of an event rather than confabulating knowledge of an event. In a study by Nunez et al. (2005), increased activation within the ACC and DLPFC was found particularly when participants falsified autobiographical facts. They also found parallel behavioural effects expressed in increased reaction time (RT) for deceptive responses, which they attributed to interference from a potent true response, similar to the effects found in traditional conflict paradigms such as the Stroop and the Flanker tasks ([Eriksen and Eriksen, 1974] and [Stroop, 1935]). More recently Bhatt and colleagues (2009) asked participants to deliberately misidentify familiar faces in a format similar to police 'line-ups' used with crime suspects. Triads of faces, with one face being shown prior to the task, were streamed, and participants were instructed to deny recognition of the familiar face and instead indicate familiarity of an alternative novel face. As in previous work with verbal questioning, imaging data showed that increased activation in a network of areas, including the ACC and DLPFC, was associated with deceptive behaviour.

To the extent that the act of deception entails suppression of a potent true response and the generation of an alternative, it is not surprising that the ACC and the DLPFC appear to be highly active. Both of these areas have been strongly implicated in error processing, response competition, and conflict monitoring (e.g.[Botvinick et al., 1999], [Braver et al., 2003] and [Carter et al., 1998]). However, despite the wealth of literature on response conflict, and the emerging literature on lie detection, to date, no empirical attempts have been made to utilise the cortical dynamics of response conflict for the detection of a lie. Seymour and Schumacher (2009) have perhaps come closest to

such an attempt, by using electromyography (EMG) to detect conflict at the motor output level. In their task, which is similar to intentional false responding in facial recognition, participants had to falsely indicate that some previously presented words were new, whilst responding truthfully to a second group of previously presented words. Additionally a third 'filler' group of unseen words was also shown, requiring a truthful ('new') response. In this experiment, responses were given with either the right or the left hand and EMG was recorded from two corresponding muscles. Analysis of correct trials revealed a greater number of partial errors (partial activation of the incorrect response) in the first condition, in which false responding was required. The authors interpreted this pattern as evidence for a conflict in the response preparation stage within a serial model incorporating competition between (1) automatic familiarity and (2) a slow level-headed recollection process. Thus, falsifying information reliably resulted in conflict between responding muscles.

The transformation of an abstract cognitive conflict (induced by deceptive behaviour) into a tangible motor conflict opens new avenues for the development of lie detection techniques, and can also shed light on the mechanisms underlying motor decision making. Verbal yes/no responses, which serve as the basis for most lie detection research, can be easily substituted with manual responses, requiring consistent activation of two distinct muscles. [Cisek, 2006] and [Cisek, 2007] constructed a model, based upon single-cell recording experiments in the macaque brain, simulating how plans for moving a digit in two opposing directions compete in pre-motor areas. According to the model the selection of a single motor output is achieved via mutual inhibitory competition between neural populations representing different directions for movement. He speculated that motor decision-making processes are constantly biased by projections from other brain areas. Importantly Cisek's computational simulations and the confirmatory neural data suggest that response selection entails parallel response preparation for multiple candidate responses. Therefore, the process of selecting a response does not necessary entail a discrete selection mechanism. Indeed, in the past decade evidence has accumulated in favour of such parallel activation views of response conflict which cast doubt on the traditional idea (Pashler, 1991) of a serial selection process with discrete stages of selection and motor preparation (e.g. [Desoto et al., 2001], [Fleming et al., 2009], [Taylor et al., 2007] and [Verleger et al., 2009]).

Here, we examine whether the dynamics of response competition, as expressed in primary motor cortex (M1), can be used to reveal deceptive behaviour, by making use of single-pulse transcranial magnetic stimulation (TMS). In this approach, muscular responses induced by TMS, known as motor evoked potentials (MEPs), are used to index the strength of an action tendency in M1 or adjacent premotor areas (cf.[Bestmann et al., 2008], [Gandevia and Rothwell, 1987] and [Kiers et al., 1997]). Single pulses, given at different moments prior to response execution but after stimulus presentation, can provide information about the dynamics of the interaction between two responses. For instance, Verleger et al. (2009) used a bimanual flanker task to compare the strength of incorrect premature response representations (activated by the flankers) with that of correct representations. Participants moved their left or right index fingers, as directed by a central arrow, whilst ignoring compatible or incompatible peripheral stimuli. Ipsilateral and contralateral M1 were stimulated at various moments prior to response execution. MEPs were found to be larger for the responding hand

compared with the non-responding hand. However, this effect was modulated by the irrelevant flankers, e.g. MEPs in the responding hand were larger in compatible conditions compared with incompatible or neutral conditions. Crucially, MEPs of the non-responding hand decreased closer to response execution and the reverse pattern was evident for MEPs of the responding hand. Thus, the relationship between the MEP amplitude of two responses can in principal be used to reveal how premature or even concealed response tendencies evolve during motor preparation.

In the current series of studies, binary choices concerning the facial recognition of famous and non-famous people were used to frame the cognitive act of deception within a response-conflict paradigm. Participants used their right little finger or thumb (or an associated verbal response in Experiment 3) to deceptively or truthfully indicate facial familiarity. By administering TMS prior to response execution in both truthful and deceitful conditions, we could compare the MEPs linked to the two competing responses. We predicted that the MEP of the non-responding digit should be larger when lying, particularly in the period immediately after stimulus onset, because of automatic activation of this objectively correct motor response. Such a finding would demonstrate the potential of highly localised motor activity to reveal deceitful behaviour. It would also help elucidate how stimulus presentation triggers the preparation of multiple responses within a single effector, casting further doubt on the notion of an isolated serial selection stage during motor decision making.

2. Experiment 1

2.1. Method

2.1.1. Participants

Eight right-handed participants (5 male; mean age = 26, SD = 3.4) were tested. Participants were screened for contraindications for TMS, and also their ability to relax their muscles fully between manual responses. They were compensated financially for their time. The study was approved by the City University Psychology Department Ethics Committee.

2.1.2. Stimuli

Sixteen faces served as stimuli. Four were of famous politicians and four were of famous film actors/actresses (in both cases half male, half female; pictures found online). For each famous person, the face of a non-famous person from the Karolinskaor NimStimstimulus sets ([Lundqvist et al., 1998] and [Tottenham et al., 2009]) was matched on sex, skin colour, gaze direction and facial expression. All faces were presented as greyscale 100 × 130 pixels portraits (~4.94 × 5.81° visual angle).

2.1.3. Apparatus

E-Prime 2.0 (Schneider et al., 2002) ran on a lab PC to present stimuli and control TMS pulses. Subjects sat 50 cm in front of a 19-inch CRT monitor refreshing at 100 Hz. The right hand rested on a foam pad, positioned palm down with thumb and little finger each touching digital response keys (Fig. 1). Electromyography and TMS were combined to measure MEPs from two intrinsic muscles of the right hand (the Abductor DigitiMinimi, or ADM, and first dorsal interosseous, or FDI) using standard methods (cf. Makris et al., 2011).

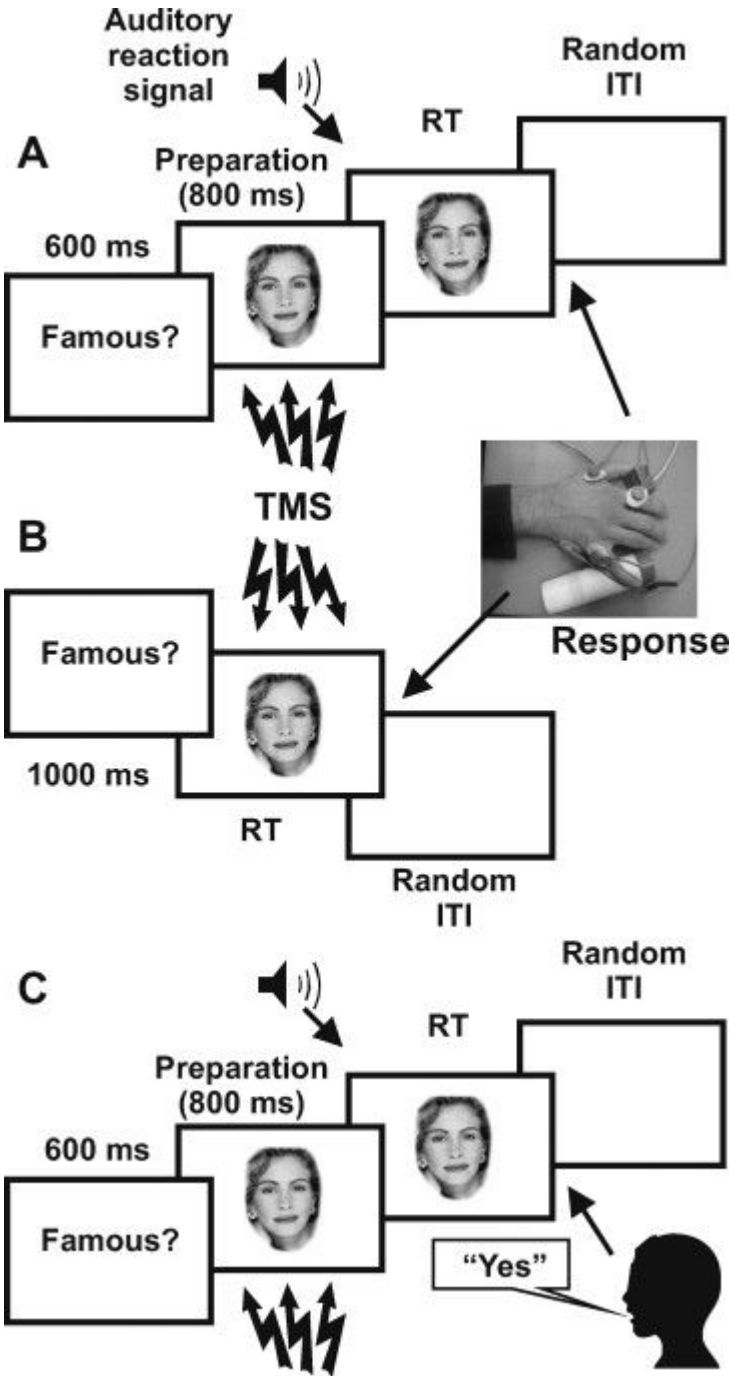

Fig. 1. Schematic of experimental procedures. (A) Experiment 1. Participants were prompted to continuously fixate at the centre of the monitor and to use their thumb and little finger to indicate whether the face shown was that of a famous person or not once they heard an auditory imperative stimulus. During this preparation interval a single pulse of TMS was administered on 25% of trials, either 200, 500 or 800 ms after face onset. Depending on participant counter-balancing, the example stimulus shown here could require either a lie or the truth. (B) Experiment 2. Here, face onset served as the reaction signal (i.e. there was no preparation interval). Stimulation was administered either 0, 300, or 600 ms after stimulus onset on the majority (90%) of trials. Each participant lied and told the truth about all stimuli, counterbalanced across the different blocks. (C) Experiment 3. Here, a verbal response ("yes" or "no") was used whilst the hand remained completely relaxed. Participants again lied about different stimuli in different blocks. However, the preparatory interval was reinstated, with TMS delivered 20, 220 or 520 ms after stimulus onset (50% of trials) prior to an auditory go

signal. Note that the verbal responses had previously been associated with manual responses during a training phase.

EMG recording. Two 22 mm × 28 mm surface Ag/AgCl EMG electrodes recorded from the Abductor DigitiMinimi (ADM) of the right hand. Two others recorded from the first dorsal interosseous (FDI) of the same hand. EMG (bandpass filtered 20–450 Hz) was collected at 1000 Hz via a 13 bit A/D Biometrics Datalink system (version 7.5, Biometrics Ltd., Ladysmith, VA, U.S.A., 2008) and stored on a dedicated PC. EMG was also passed to a speaker to provide a warning when muscles were not fully relaxed. Participants were prompted to monitor their motor activity by relaxing their muscle whenever loud muscle noise persisted between responses.

TMS protocol. Pulses were applied using a 70 mm figure-of-eight coil (external casing diameter ~90 mm for each loop) connected to a MagstimRapid^2 biphasic stimulator (The Magstim Co. Ltd., Whitland, Carmarthenshire, U.K.). The coil was held tangentially to the skull, over the optimal spot at the left M1 to elicit MEPs in both the ADM and FDI, with the handle pointing backwards/laterally approximately midway between the saggital and coronal planes. Intensity of pulses was set around 110–117% of resting motor threshold (RMT) in order to elicit MEPs of around 1 mV amplitude in both the ADM and the FDI. Individual RMTs were determined prior to the experiment as the minimal intensity required to elicit an MEP ~50 μV in amplitude (peak to peak) in at least 3 out of 6 single pulses when the hand was fully relaxed. A post-report form was used to document any adverse effects of TMS (suspected seizures, syncope, headaches, muscular discomfort and anxiety) which are reported elsewhere (Hadar et al., in press).

2.2. Statistical analysis

Data was aligned to the time of TMS and analysed offline. Each MEP was visually inspected for EMG activity in the 300 ms preceding TMS. The decision to reject trials was based on the detection of EMG activity greater than 50 μV peak to peak within this time window. Such trials were discarded. In all experiments reported here this filtering procedure included the exclusion of trials in which a response was given prior to pulse delivery. The EMG screening was conducted using a display that showed digital signals aligned to TMS pulses, but provided no indication of experimental condition. Peak-to-peak MEP amplitude was then calculated for correct trials. For each participant, amplitudes were z-transformed (by separately combining all data for the FDI and ADM) in order to give an equivalent measure for the two responses. Medians were then taken for the different conditions. Inferential statistics were two-tailed, with Greenhouse–Geisser corrections where appropriate.

2.3. Design and procedure

A four factor (3 × 2 × 2 × 2) repeated-measures design was employed. The first factor was stimulation interval (TMS 200,500 or 800 ms after face onset). The second factor, honesty, compared truth to deceit. The third factor, face type, contrasted famous and non-famous faces, yielding lies that were either denials or confabulations. The fourth factor, digit, contrasted MEPs recorded from the little finger and thumb. These were re-coded as ‘responding’ and ‘non- responding’ digit according to

participant's digit-response mapping (little finger/thumb presses mapped to “yes”/“no” responses), which was reversed for half of the sample.

The allocation of faces to lie and truth conditions was counterbalanced across subjects in the following manner. The sixteen faces were divided into four sets, each containing two famous and two matched non-famous faces. Each participant was required to lie about just one set and tell the truth about the remaining three sets of faces. However, just one of the three truth sets was selected for TMS. Four distinct combinations of one lie and one truth set were therefore prepared for TMS trials, with a quarter of participants receiving each combination. The 16 faces were each presented six times during an experimental block. Single-pulse TMS was administered in one half (i.e. three) of the presentations of (1) the lie set and (2) the selected truth set (so once at each stimulation interval). The remaining two sets of truth faces served only as fillers, in order to dilute the TMS trials. Hence, each block consisted of 96 trials in pseudo-randomised order except that TMS could not occur on two consecutive trials. Seven such blocks generated 672 trials, containing 14 TMS trials at each combination of interval, honesty, and face-type.

Before starting the experiment, participants answered 30 simple ‘Yes’/‘No’ questions (e.g. ‘do you speak English?’) to practice the response mapping and ensure that they could relax hand muscles between responses. They were then shown two famous and two non-famous faces and told to lie when asked by the computer about these specific people. On each experimental trial, participants fixated the word “famous?” for 600 ms before a face appeared. They then prepared but withheld their response until the presentation of an auditory imperative stimulus (a pure tone) after another 800 ms (see Fig. 1a). Following their response, a blank inter-trial interval (ITI) of 500–1500 ms preceded the next trial.

3. Results and discussion

Accuracy data was averaged across the sample revealing an overall error rate of 6.8% (SD = 5.7%). No significant differences in accuracy were found between the lie and truth conditions. Incorrect trials were excluded when deriving MEP measures.

The complex design balanced competing demands regarding the duration of the experiment, and the desirable frequencies of lies, TMS pulses, and responses with each digit. To reflect reality, lying was made less likely than telling the truth. TMS was therefore more likely in trials where participants lied (to keep the overall stimulation rate down). These facts suggest caution when interpreting the main effect of honesty, which may have been influenced by learnt expectancies. Interactions with digit are therefore critical, as the a priori likelihood of reacting with the responding and non-responding digits was equal and independent of all other factors. With this in mind, MEP data were submitted to a 3 × 2 × 2 × 2 repeated-measures ANOVA. Crucially, the ANOVA revealed that honesty (truth versus lie) affected MEP size *differently* in responding compared with non-responding digits, thereby confirming the existence of suppressed motor tendencies in M1 during deception ($F(1,7) = 13.59$, $p < 0.01$, $\eta_p^2 = 0.66$; Fig. 2b). Paired sample *t*-tests on this averaged data (Fig. 2b) highlighted that in deceitful responses, the MEPs of the non-responding digit were significantly larger than those of the responding digit ($t(7) = 2.89$, $p < 0.05$) whilst the reverse pattern was confirmed for truth telling ($t(7) = 2.92$, $p < 0.05$). Hence, in deception, as in other situations of response conflict, a motor plan is generated automatically for the "incorrect" response (Fig. 2c). Of course in deception, this incorrect response represents the truth. In this experiment, the three-way interaction between honesty, digit and interval was not significant ($F(1,7) = 0.23$, $p = 0.97$), signifying a relatively consistent two-way interaction across the three stimulation intervals (Fig. 2a). This may seem odd, because at some point the motor plan for the executed response must come to dominate over the non-responding digit. We hypothesised that competition between the two populations of neurons is resolved later, within RT itself, rather than within the motor preparation interval.

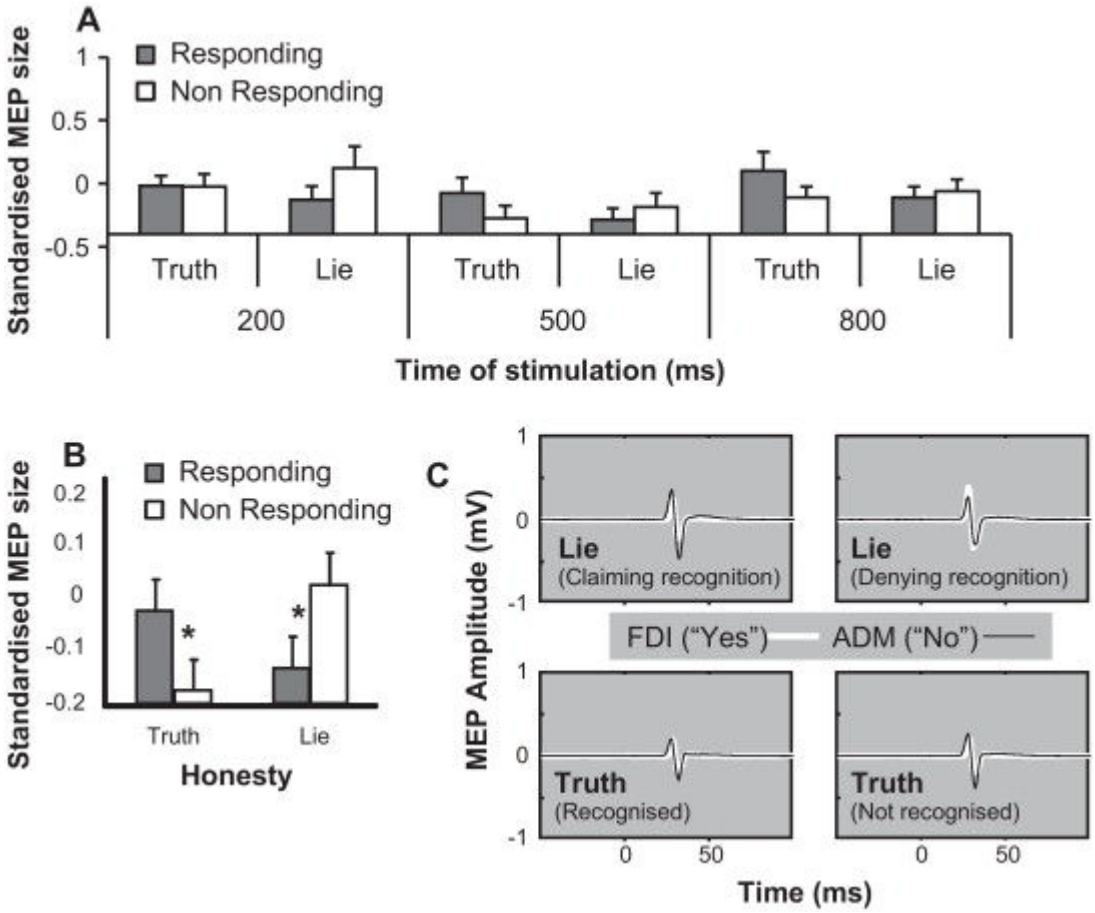

Fig. 2. Results from Experiment 1, showing activity of the neural population associated with the non-responding digit in lying but not in truth telling. Error bars denote standard errors. Asterisks (*) denote statistical significance for the key pairwise comparisons reported in the main text. (A) Mean of all participants' median peak-to-peak MEP *z*-scores in Experiment 1, presenting the full set of conditions. (B) The same data are shown for responding and non-responding digits in lie and truth trials, having been collapsed across stimulation intervals in line with the results of the ANOVA (see main text). (C) Average MEPs for the Abductor DigitiMinimi (ADM) and First Dorsal Interosseous (FDI) of a single subject from Experiment 1 at stimulation interval 200 ms. This participant used the thumb (FDI) to indicate 'yes' and the little finger (ADM) for 'no'. In both 'lie' conditions (i.e. lies made in response to either famous or non-famous faces) but not in the corresponding 'true' conditions, the MEP of the non-responding digit (ADM when falsely claiming recognition, FDI when falsely denying recognition) appears more active than that of the responding digit.

To verify such temporal modulation, in Experiment 2 we asked subjects to respond immediately following face onset, and measured MEPs within the RT (Fig. 1b). We also addressed a potential shortcoming in terms of the ecological validity of our deception paradigm, by introducing some free choice into the decision to lie. Participants were again presented with a stream of familiar and unfamiliar faces, but were required to intentionally misidentify a different group of faces *of their choice* in each block. To manage the extra demands this change placed on memory, groups of faces were now defined by straightforward features (non-famous men, non famous women, actors and politicians). The only constraint was that by the end of the session participant should have lied about each of the four face groups comprising the full stimulus set.

4. Experiment 2

4.1. Method

Experiment 2 used the same practice session, stimuli, apparatus and statistical analyses as Experiment 1. Thirteen right-handed participants were tested. One participant was rejected following data analysis, because they had < 5 MEPs per condition after screening for muscular pre-activation leaving a final sample of 12 (7 females, mean age = 25.6, SD = 6.1).

4.2. Design and procedure

Unlike Experiment 1, there was no requirement to withhold a response: the preparatory cue ("famous?"; 1000 ms) preceded the onset of a face, and participants then responded as quickly as possible, initiating a blank ITI of 3000–4000 ms. TMS was delivered within the reaction period, after 0, 300 or 600 ms.In each of four experimental blocks, participants lied about a *different* group of four faces (film stars, politicians, non-famous men, non-famous women) with the order reflecting the participant's own choice, noted down privately (e.g. 'block 1-politicians'). Hence each participant lied and told the truth equally often about each group of stimuli across the experiment. This arrangement meant that, unlike Experiment 1, one digit was used more often (75% of the time) in any given block, with little finger and thumb each being favoured in two out of four blocks. In each block, each of the four groups of faces was sampled repeatedly at random (with replacement) 27 times, to yield 9 presentations for each of the three stimulation intervals. Hence each block contained 108 stimulation trials (36 trials per TMS interval). The addition of 12 no-stimulation trials, comprising 3 random samples from each face group, yielded 120 trials per block. In this design, lies always used the favoured (75% likely) digit, whereas 1/3rd of truth trials (those from the same higher-order category as the lie set; famous or non-famous) used the non-favoured (25% likely) digit. For this reason, MEPs were not analysed from this non-favoured subset of truth trials, guaranteeing that the overall bias towards advanced preparation of the responding digit would be identical between truthful and deceitful conditions.

5. Results and discussion

Mean incorrect responses for this sample remained relatively low (mean = 12.3%, SD = 7.1) and no significant differences in accuracy were found between levels of the honesty factor. A repeated-measures ANOVA comparing MEP size of the responding and non-responding digit for truthful and deceptive responses across the three stimulation intervals showed main effects of interval ($F(2,22) = 6.81$, $p < 0.05$, $\eta_p^2 = 0.38$) and digit ($F(1,11) = 6.88$, $p < 0.05$, $\eta_p^2 = 0.39$). The former showed how total corticospinal excitability increased towards the execution of the motor plan. The latter confirmed the overall greater excitation of the neural population controlling the responding digit compared with that representing the non-responding digit (Fig. 3a). In itself, this latter finding is trivial, because for this particular experiment there was a greater a priori expectancy of response for the responding digit: one digit was used on 75% of trials, and all the reported data comes from trials where the responding digit corresponds to this favoured digit. However, digit and interval interacted significantly ($F(2,22) = 6.08$, $p < 0.05$, $\eta_p^2 = 0.36$) demonstrating that across the three stimulation intervals there was a progressive selection of just one response (Fig. 3a) over and above any learnt expectations. Critically, as predicted, this two-way interaction was further modulated by honesty ($F(2,22) = 3.79$, $p < 0.05$, $\eta_p^2 = 0.26$). This three-way interaction (Fig. 3b) was investigated with three 2 × 2 ANOVAs crossing the digit and honesty factors for each time of stimulation. A significant interaction was found only at the 300 ms stimulation interval ($F(1,11) = 6.35$, $p < 0.05$, $\eta_p^2 = 0.39$). Follow-up paired *t*-tests highlighted that this interaction stemmed from the significantly larger MEP of the responding finger when telling the truth relative to when lying ($t(11) = 2.50$, $p < 0.05$) and the marginally significant increase in the non-responding finger when lying relative to telling the truth ($t = 2.17$, $p = 0.053$). Hence, this interaction corroborates our results from Experiment 1: lying appears to generate a response conflict, but under time pressure the “wrong” response (the truth) develops only briefly (around 300 ms after stimulus onset) with a correction having occurred by 600 ms.

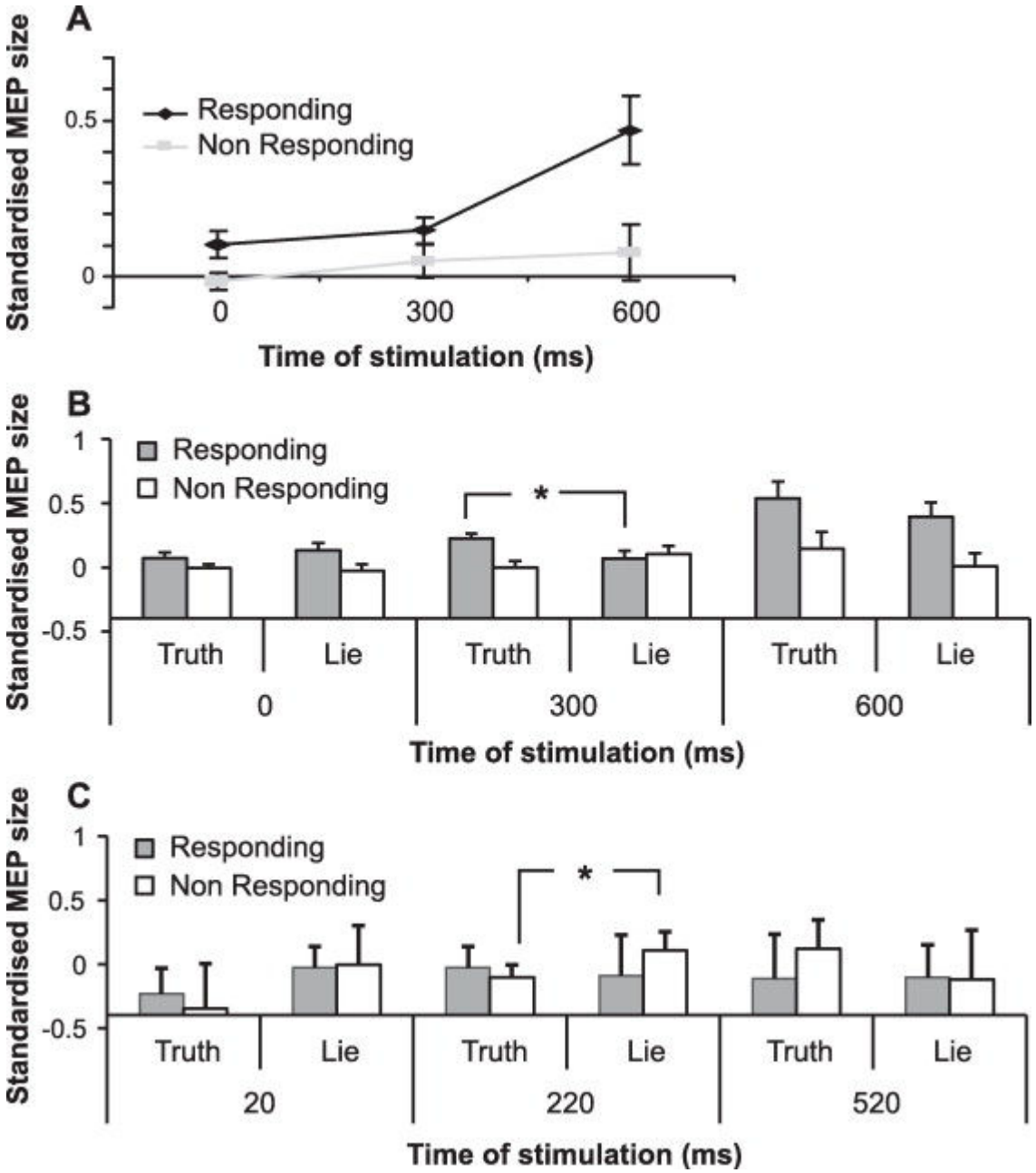

Fig. 3. (A) Digit by interval interaction in Experiment 2, illustrating the progressive selection of one response over the other in M1 during the decision-making process. (B) Further modulation of this interaction depending upon honesty of response, emphasising a significant digit by honesty interaction, but only in the middle stimulation interval. (C) Significant three-way (interval by digit by honesty) interaction in Experiment 3, where verbal responses were given without the need for hand motor planning. The digit by honesty interaction was significant only in the middle stimulation interval, showing a transient increase in the MEP of the non-responding digit in lying but not in truth telling.

In our first two experiments, MEP data was often contaminated by both failures to relax hand muscles fully between key presses and early onset of voluntary muscle contraction, resulting in the mean exclusion of 29% (SD = 14%) of trials in Experiment 1 and 24.8% (SD = 12%) of trials in Experiment 2 (but in equal numbers regardless of the honesty of the response). We conducted a third experiment in an attempt to enhance the potential practical utility of this technique by using verbal rather than motor

responses. In Experiment 3, prior to and interleaved with the deception task, participants answered a set of questions by pressing the two response keys whilst simultaneously producing a corresponding loud verbal response (“yes”/”no”). following this motor-verbal association stage (lasting ~ 2.5 h) participants completed a deception task whilst providing only verbal responses. We hypothesised that verbal responses that were strongly associated with a manual response would trigger a similar manual response conflict to that observed in our first experiments.

6. Experiment 3

6.1. Method

We employed identical stimuli, apparatus and statistical analyses to those used in Experiment 1. Four right-handed participants (4 females, mean age = 25.3, SD = 2.9) were tested.

6.2. Procedure

One hundred simple yes/no type questions served as training material, establishing the association between verbal and motor responses. This set of questions was randomised and presented 17.5 times during the experiment. Within these phases, on each trial one question was presented for 2500 ms followed by a tone, after which participants depressed one of the two response keys indicating yes/no whilst simultaneously saying “yes”/“no”. There were 1600 such trials at the start of the experiment. A shorter top-up phase (50 trials) followed each of the first three deception blocks.

The deception task consisted of four blocks each proceeded by instructions to lie about one of the four groups of faces identified in Experiment 2. Block order was randomised for each participant. Each trial consisted of preparatory (“Famous?”), then instructive (face) then imperative (tone) stimuli, with timing as per Experiment 1 (Fig. 1c). Participants relaxed their hands entirely, and two response pedals were used by an experimenter to register verbal responses. We opted to keep a priori expectations regarding the two digits equal (as in Experiment 1) but also use an easy-to-remember rule to categorise the faces that participants needed to lie about (as in Experiment 2). In each block, the four faces from the selected lie group (e.g. politicians), along with two other randomly selected famous faces (e.g. two actors) and their two matching non-famous faces (so overall four lie-faces and four true-faces) were presented six times each accompanied by TMS (with two presentations at each stimulation interval, here 20,220 and 520 ms). Note that each stimulus was used once as a TMS lie stimulus and once as a TMS true stimulus across the whole experiment. In any given block, the remaining eight ‘filler’ faces were presented without TMS. Six of these, which required the same response as that of the lie group, were presented twice each, and the two remaining faces, which required the opposite response, were presented 18 times each. This yielded an equal number of yes and no responses in each block. Hence, each block consisted of 96 pseudo-randomly ordered trials (except that TMS could not occur on two consecutive trials).

7. Results and discussion

Although the whole procedure was a lengthy one (~5 h), trial exclusions as a result of involuntary muscle activation were greatly reduced (overall mean exclusion rate 1.3%, SD = 0.1). This study also generated a relatively low percentage of incorrect responses (mean = 2.4%, SD = 1.9). This may be explained by the use of a preparatory period as in Experiment 1, combined with the easily identified lie and truth sets used in Experiment 2. MEP data again suggested activation of motor plans and response conflict in hand motor areas, this time generated by *verbal* responding. This was expressed in a significant three-way interaction ($F(2,6) = 8.5$, $p < 0.05$, $\eta_p^2 = 0.73$) between honesty (verbal lie/truth), associated digit, and interval (Fig. 3c). When broken down, the two-way interaction between honesty and digit was significant only for the middle stimulation interval ($F(1,3) = 19.4$, $p < 0.05$, $\eta_p^2 = 0.86$). Paired-sample *t*-tests found the MEP of the non-responding digit in truth trials to be significantly smaller than that of the non-responding digit in deception trials ($t(3) = 4.43$, $p < 0.05$) but this was not the case in the responding finger ($t(3) = -0.7$, $p = 0.4$). Like Experiment 1, this experiment used a preparatory period. Whereas in Experiment 1, TMS was first delivered 200 ms after stimulus onset, which was evidently sufficient time for a motor plan to develop in the non-responding digit during deception, in Experiment 3 a shorter TMS interval (20 ms) revealed baseline expectations (i.e. no preference for either response) and helped to drive an interaction with TMS interval. Intriguingly, the interaction also showed the dissipation of the erroneous motor plan by 520 ms, something which never occurred (even after 800 ms) in Experiment 1. This is most likely explained by the associative nature of the motor plan that was being assessed in Experiment 3: the fact that it emerged at all is impressive; for it to have been maintained throughout preparation for a *different* response would have been astonishing.

8. General discussion

Using single-pulse TMS, we examined whether conflict between competing responses in M1 can discriminate between intentionally false and true facial recognition. In Experiments 1 and 2 naïve participants used their little finger or thumb to indicate familiarity with famous and unknown faces. In Experiment 3 participants provided verbal responses which had been associated in advance with the same manual responses. By stimulating M1 prior to response execution, we could compare the MEPs linked to the two competing responses. We compared MEPs in correct trials from the digit that was used (the "responding digit") and the passive digit (the "non-responding digit"). In all three experiments we identified critical times when the MEPs of the non-responding digit were greater than the MEPs of the responding digit in trials where the former coded the truth, i.e. when subjects lied. By contrast, MEPs of the non-responding digit were smaller than the MEPs of the responding digit when the former response coded a lie, i.e. when subjects told the truth.

Our data are suggestive of intra-hemispheric mutual inhibition during response preparation. In the second experiment, as RT unfolded the population of neurons representing the to-be-executed response became increasingly active whilst the alternative response appeared inhibited. Notably, this progressive process was biased or delayed in deception trials: the truth was initially prepared, then some neural signal prompted the alternative response (i.e. the lie) to become preeminent. Biasing influences could originate from prefrontal and cingulate areas ([Frith, 2000], [Passingham, 1993] and [Lau et al., 2006]). Both areas have been implicated previously in the resolution of response conflicts and the act of deception ([Abe et al., 2006], [Abe et al., 2007], [Bhatt et al., 2009], [Kozel et al., 2004], [Lee et al., 2010], [Langleben et al., 2005], [Nunez et al., 2005] and [Schumacher et al., 2010]). Excitability of specific populations in M1 might for example be biased via cortico-cortical pathways to supplementary motor area (SMA), or striatal projections to M1 and the SMA.

Our results cannot be explained by early visual priming effects on M1 induced by the familiar faces, as we assessed two kinds of lying (denial for famous faces and confabulation for unknown faces) and no meaningful interactions were found with this factor. We do not claim that the neural signature we have observed here is unique to lying. In fact, we are quite certain that what it fundamentally reflects is response competition. Hence we are comfortable with various levels of explanation for our effect. For example, in our experiments lies were less frequent relative to truthful responses, so our results could reflect a higher-order task-switching effect (i.e. lying more often represented a shift from one response set to a reversed response set than did truthful responding). This account is not problematic for our interpretation, because our response frequencies were ecologically valid: lying really is, by and large, a reversal from a standard task set to an infrequent deceptive one. The key point is that lying will usually represent a response conflict, and can be detected on this basis. We do, however, note that in this paradigm lying was for low stakes. Future studies could incorporate a tangible punishment

and reward system, like that which accompanies real-life deception. Such studies should also investigate the degree to which the partial activation of the truth is determined by the frequency of lying within the task (e.g. Verschuere et al., 2011).

Neurobiological principles of response selection can also be tested against our data. The parallel process of excitation of one response and the suppression of the alternative one argues against diffusion models of decision making that stipulate independent activation in *both* of two response alternatives in a race, particularly in regard to intra-hemispheric competition (Smith and Ratcliff, 2004). Put differently, our data support the notion of reciprocal inhibition between two motor response alternatives (although this inhibition may not be direct). Inhibitory links which still allow activation of multiple response alternatives are central to the leaky competing accumulator model of simple perceptual choices (Usher and McClelland, 2001) and the affordance competition model of motor decision making (Cisek, 2007).

The results of Experiment 3 suggest that verbal responses can be associated with digit-specific motor plans strongly enough to trigger them involuntarily. A *verbal* lie will then briefly activate a *manual* motor plan associated with the truth, presumably via the activation of the verbal truth plan. This is consistent with the theory of event coding (Hommel et al., 2001). The finding may remove one barrier to developing a lie detector based on TMS. However, in many techniques, lie-detection accuracy has been shown to be weakened by participants' countermeasures (e.g. when using the ERP P300; [Mertens and Allen, 2008] and [Rosenfeld et al., 2001]). These would also hamper MEP-based detection, which requires voluntary muscle relaxation.

In summary, we have demonstrated how evolving motor activity in M1 can unmask intentionally hidden information. In our experiments, deception resulted in competition between the true and deceitful responses, detectable in average MEP sizes prior to execution. We conclude, based on the simultaneous and dynamic modulation of two motor plans, that decision-making operations do not serially precede the generation of motor plans *even when the goal is deception*. By demonstrating the presence of an M1 response conflict in deception, we offer an original platform for developing lie-detection techniques whilst also shedding light on the dynamics of response competition.

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