Increased Motor Cortex Excitability for Concealed Visual Information

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Abstract

Deceptive behaviour involves complex neural processes involving the primary motor cortex. The dynamics of this motor cortex excitability prior to lying are still not well understood. We sought to examine whether corticospinal excitability can be used to suggest the presence of deliberately concealed information in a modified version of the Guilty Knowledge Test (GKT). Participants pressed keys to either truthfully or deceitfully indicate their familiarity with a series of faces. Motor-evoked-potentials (MEPs) were recorded during response preparation to measure muscle-specific neural excitability. We hypothesised that MEPs would increase during the deceptive condition not only in the lie-telling finger but also in the suppressed truth-telling finger. We report a group-level increase in overall corticospinal excitability 300 ms following stimulus onset during the deceptive condition, without specific activation of the neural representation of the truth-telling finger. We discuss cognitive processes, particularly response conflict and/or automated responses to familiar stimuli, which may drive the observed non-specific increase of motor excitability in deception.

Keywords: Deception; Motor cortex excitability; Lie detection; Guilty knowledge test (GKT); Motor evoked potential (MEP); Transcranial magnetic stimulation (TMS);

Introduction

Lying and deceit are integral parts of the human condition (Vrij, 2000). For generations the prime motivation for studying deception has been to improve the capacity of various organisations to detect lies (Verschuere, Spruyt, Meijer, & Otgaar, 2011). The increasing dependency of societies on legal and security systems has facilitated an even greater need for robust lie detecting techniques (Bond & Robinson, 1988; Buckholtz & Faigman, 2014; Vrij, Mann, Kristen, & Fisher, 2007). Indeed, the status quo of commercial polygraphy, which is based on peripheral and indirect measures of arousal and paradigms with questionable validity, fuels consistent demand for other scientifically grounded alternatives (Ben-Shakhar & Elaad, 2003; Meijer, Verschuere, Gamer, Merckelbach, & Ben-Shakhar, 2016). Still, as yet, only limited attempts at developing lie detectors that are based on diverse neural measurements (Farah, Hutchinson, Phelps, & Wagner, 2014) have been reported.

Cognitive models of deception suggest that the suppression of the truth and the neural correlates of this process are critical for novel lie detection technologies (Abe, Suzuki, Mori, Itoh, & Fujii, 2007; Spence, 2004; Vrij et al., 2008). Several studies have demonstrated that changes in neural activity in motor areas such as the primary and premotor cortex reliably reflect these cognitive processes (Farah et al., 2014; Langleben et al., 2005). An effective way to measure motor cortex activity is via motor-evoked potentials (MEPs). MEPs are muscular responses induced by transcranial magnetic stimulation (TMS) which are used to index the strength of an action tendency in M1 or adjacent premotor areas (cf. Bestmann et al., 2008; Gandevia & Rothwell, 1987; Kiers, Fernando, & Tomkins, 1997). By administering TMS prior to response execution and recording MEPs from different hand muscles, one can both assess overall corticospinal excitability and compare the strength of motor plans

associated with each specific muscle. Despite the widely accepted role of motor response suppression in deception, this method has been little used in polygraphic settings.

To date a handful of studies have used MEPs to demonstrate a significant role for motor cortex excitability in deception. Lo and colleagues (Lo, Fook-Chong, & Tan, 2003a) showed an increase in corticospinal excitability measured in motor-evoked potentials one second after lying regarding factual non-personal information. This change in neural activity was considered to result from either awareness of the conflict, anticipation of punishment or indeed the continued suppression of the truthful information. Similar findings were found (in the left but not right motor cortex) in a study of sports fans who were asked to lie in a blocked fashion (Kelly et al., 2009). In a previous study from our lab (Hadar, Makris, & Yarrow, 2012a) using facial stimuli, an increase in the MEPs of the muscle associated with the truthful response was observed in lie trials. Surprisingly, to date no further studies have attempted to address lie detection using single pulse TMS. It thus remains unclear whether overall corticospinal excitability can provide a cue regarding truthfulness when using common assessment procedures.

The assessment of one's physiological response to the presentation of concealed information is at the heart of many deception detection paradigms. In the 'guilty knowledge test' (GKT, also termed Concealed Knowledge Test or CKT) (Lykken, 1959; Seymour & Kerlin, 2007), widely used in interrogative polygraphy, both rare relevant stimuli (e.g. items implying crime-scene knowledge) and frequent irrelevant stimuli are shown. Subject must confirm/disconfirm previous encounters with the stimuli. This simple technique allows experimenters to measure both behavioural responses (such as reaction time (RT) and accuracy) and neural responses specific to the infrequent deviant stimuli.

In terms of neural activity, the GKT inserts automatic recognition of a relevant stimulus among other neutral stimuli thereby creating a distinct 'oddball' brain response. This neural response is reflected in a particular EEG signature, namely an increase in the P300 component. It is considered to be the result of increased processing allocated for the familiar stimuli as compared with other background stimuli (Fabiani et al., 1987). This concept has been successfully used by numerous groups to uncover concealed familiarity with crime-related information in both experimental studies and real-life investigations (Ben-Shakhar & Dolev, 1996; Ganis & Schendan, 2012; Verschuere, Rosenfeld, Winograd, Labkovsky, & Wiersema, 2009). For instance, Farwell and Donchin (Farwell & Donchin, 1991) modified the GKT to enable more reliable application of the task. Regardless of the controversy around the commercial use of this technique (Rosenfeld & Labkovsky, 2010) the modified GKT paradigm has been adopted by several researchers and has proved to be conducive to the study of deception (e.g. Ben-Shakhar & Elaad, 2003; Langleben et al., 2002; Rosenfeld, 1988). In short, instead of having only rare relevant stimuli (e.g. crime scene knowledge) and frequent irrelevant stimuli, their paradigm incorporates an additional, small set of irrelevant items that is learnt prior to testing. Items included in this additional list are defined as Targets and require positive identification as such during the test. This modified version of the GKT extends the range of neutral or otherwise 'truthful' responses.

Critically, versions of the GKT have also been used to assess peripheral motor indices of response conflict in deception-like settings (Seymour & Schumacher, 2009). For instance, Seymour & Schumacher compared surface electromyography (EMG) from hand muscles during neutral and deceitful bimanual responding in a modified GKT. Instead of having only rare relevant stimuli (e.g. crime scene knowledge, Probe Items) and frequent irrelevant stimuli (Filler items) which, when lying about probes, dictate the same overt response, their paradigm incorporated a third, small set of additional items which was learnt prior to testing

(Targets) and required a different overt response. This modified version of the GKT extends and diversifies the range of motor responses and discourages automatic responding with a single motor response throughout the procedure (e.g. pressing 'no' with one digit repeatedly). Indeed, it enabled researchers to find greater EMG activity (i.e. partial errors) in the resting hand for lie (Probe) compared with true (Filler) motor responses, despite the same overt motor responses in the responding hand.

To date, motor cortex excitability measures have not been examined as potential lie detection indices in the GKT. Given the central role of the motor cortex and the GKT in deception research this is an important gap to bridge (although the variable nature of the MEP suggests that it may be of greater relevance for theoretical accounts of deception than in applied settings). Importantly, unlike other imaging techniques, MEPs provide neural information with high temporal resolution which is specifically localised in the motor cortex / corticospinal tract. Furthermore, the application if this technique, compared to fMRI, is relatively cheap and simple and the resulting single-channel outputs require little computational expertise. Nevertheless, the use of brain stimulation does carry some safety issues and thus both practical and ethical concerns may limit its commercial application.

The present study has therefore utilised the GKT in combination with single-pulse TMS MEPs with three aims. The first aim was to assess whether corticospinal excitability is increased prior to deceitful responses in the widely used research paradigm of the GKT. Facial stimuli were employed to more closely mimic real-life scenarios where suspects conceal recognition of a familiar person or hide knowledge of a victim. The second aim was to measure whether the neural activity specifically associated with the truthful motor response can be dissociated from generalised cortical excitability as previously reported in different deception paradigms. The final aim was to further elucidate the temporal dynamics

of the neural activity in (mainly) M1 during deception by measuring excitability at several time points adjacent to response execution.

Method

Participants

Overall 15 participants were recruited (6 males, mean=23.1, SD=1.8) using on-campus university advertisements, and 12 consented to participate in the study. This sample size was selected informally, based on the three experiments reported in Hadar et al., 2012. All participants were naive healthy right-handed volunteers with normal or corrected to-normal-vision. Participants provided informed consent and were screened for TMS contraindications. All participants completed a medical questionnaire, screening for neurological and other medical problems, as well as other contraindications to TMS as detailed elsewhere (Keel, Smith & Wassermann, 2001). They were compensated financially for their time (7.5 GBP/hr). The study was approved (2011) by the City, University of London Psychology Department Ethics Committee.

Stimuli

36 human faces (Hancock, 2004) served as stimuli. Half of the faces were female faces and all faces were matched on luminance, background colour, gaze direction and facial expression. Faces were presented as greyscale 100x130 pixels portraits (~4.94 x 5.81° visual angle). For each participant 6 faces (3 females) served as a Probe set, six faces served as a Target set and the remaining 24 constituted the Filler face set. Allocation of faces to sets was fully counterbalanced across participants so that across a sample of 6 participants all 36 faces serve once as a Probe, once as a Target and four times as Fillers.

Apparatus

E-Prime 2.0 was used on a lab PC for the presentation of all stimuli and control over TMS pulses. Subjects sat on a comfortable chair 50 cm in front of a 19-inch CRT monitor refreshing at 100 Hz. Their right hand was supported by a foam pad and positioned palm

down while their thumb and little finger each rested on suitably shaped response keys. These mapped onto 'Yes'/'No' responses consistently throughout the experiment. The response-digit mapping was reversed for half of the participants. Response keys were attached to a serial response box feeding back to E-prime. Participants were free to change positions during setup time in order to find the most comfortable position.

EMG recording

Two surface Ag/AgCl EMG electrodes (22 x 28 mm, part no.SX230FW, Biometrics Ltd.) were placed over the Abductor Digiti Minimi (ADM) of the right hand and a nearby reference site, approximately 2 cm apart. Two others were similarly placed to record 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 second dedicated PC. Participants were instructed to use continuous auditory feedback coming from a speaker placed one meter to their left to ensure that muscles were fully relaxed (the speaker received signals from both muscles). Digital data was exported and analysed offline using MatLab 6.51 (The Mathsworks Inc., 2003, U.S.A.).

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 sagittal and coronal planes. The coil was held manually at this position above the motor hot spot, with position guides marked on the subject's head using coloured face paint. Intensity of pulses was set around 110%-120%

(mean=114.1%, SD= 4.8) of resting motor threshold (RMT) in order to elicit MEPs of around 1 millivolt 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. Stimulation frequency never exceeded 0.3 Hz. In total, 216 pulses were administered during the experimental session. Pulses were administered either at the onset of the imperative stimulus, 300 ms, or 400 ms later. These intervals were selected on the basis of previous MEP and RT results in similar tasks (Hadar et al., 2012a). A post-report form was used to document any adverse effects of TMS (suspected seizures (see Hadar, Makris, & Yarrow, 2012b), headaches, muscular discomfort and anxiety).

Signal processing

Data was aligned to the time of the TMS pulse and analysed offline. Each MEP was visually inspected for EMG activity in the 200 ms preceding the TMS pulse. Such trials were discarded. Peak-to-peak MEP amplitude was calculated for the remaining trials[1]. For each participant, amplitudes in each muscle 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.

Experimental procedure

Participants were presented with the trial events schematized in detail in Fig.1. The procedure consisted of 'Probe' and 'Target' learning phases separated by a distracter task. This learning procedure was then followed by a test phase in which TMS pulses were administered and MEPs were measured (Schumacher, Seymour, & Schwarb, 2010).

[1] The MEP is a highly stereotyped response, reliably occurring within a window of only a few milliseconds for a given participant.

Probe learning phase. Each learning phase required participants to study six faces and was repeated three times. On each trial a randomly selected face from the set was displayed centrally on the monitor until participants asked the experimenter to continue. In order to verify adequate encoding of the stimulus participants were presented with one of six randomly selected questions concerning the face shown (e.g. 'how thick were the person's eyebrows?') In addition, participants were randomly presented with either the same face again or with its mirror-reversed image. Participants used the two response keys while simultaneously saying "yes"/"no" to indicate whether the face at this orientation was presented before or not. Finally, participants were asked to rate the face's attractiveness and appearance of honesty on a 1-10 scale and to estimate the person's age (Travis, Seymour & Kerlin, 2007).

Distractor task. Following the Probe learning phase participants were presented for 10 minutes with simple mathematical equations. Participants used the response keys to answer whether the equations were correct or not.

Target Learning Phase. The second learning phase consisted of another set of six faces that served as Target faces in the subsequent test phase. The learning procedure employed for this set was identical to that of the first learning phase but without the additional rating task (Schumacher et al., 2010).

Test Phase. The test phase comprised two repetitions of one block consisting of 108 trials. The 36 faces (6 Probe, 6 Target and 24 Fillers) were presented in a random order, 3 times each within a block, i.e. once at every stimulation interval (see below). The test phase began with written instructions requiring participants to answer truthfully when asked about familiarity with faces from the Target set and deny familiarity (lie) to faces from the Probe set. They were also asked to genuinely deny familiarity with any new faces they saw (i.e.

Filler items). After a verbal recap, participants were presented with the sequence of events shown in Fig.1.

Each trial started with the presentation of a central fixation cross for a duration of one second followed by a randomised presentation of one of the 36 facial stimuli. A TMS pulse was then administered. The face remained on screen until a response was registered. Participants then returned to a relaxed position, with fingers on the response buttons for the duration of an inter-trial interval (ITI) of a uniform random duration (3.5-4.5s). In trials where a response was delayed for more than 2 s a text box appeared indicating 'too slow' and the trial was repeated. Accuracy feedback was presented every 10 trials.

Statistical analysis

A three factor (3X3X2) repeated-measure design was employed. The first factor was stimulation interval (TMS either 0, 300 or 400 ms after face onset). The second factor, honesty, compared Probe, Target and Filler sets. The third factor, digit, contrasted MEPs recorded from the little finger with the thumb. These were re-coded as 'responding' and 'non- responding' digit according to each participant's digit-response mapping (little finger/thumb presses mapped to "yes"/"no" responses), which was reversed for half of the sample (c.f. Tandonnet, Garry, & Summers, 2011). These data were submitted to a 3 way repeated measure ANOVA for MEP measurements (Target items requiring positive identification were not included in the MEP analysis as they contained a positive identification motor response). For behavioural data, the digit factor was collapsed and a 3x3 within-subjects ANOVA was conducted contrasting different sets of items within each stimulation interval. Alpha level was set at 0.05 for all tests with Greenhouse-Geisser corrections where appropriate and Fisher's LSD tests were used for post-hoc comparisons. Effects sizes and their confidence interval (95% CI) were reported for all ANOVAs.

Results

Behavioural data

Mean accuracy data are presented in Fig.2. Accurate responding implies correctly (and truthfully) identifying Targets, correctly (and truthfully) denying familiarity with Fillers, and correctly (but falsely) denying familiarity with Probes. Data were submitted to a within-subjects ANOVA comparing Probe, Target and Filler stimuli. A significant main effect of honesty condition on accuracy was found ($F(2,22)=6.4$, $P<0.01$, $\eta\rho^2=0.36$, $\eta\rho^2$ CI 0.075-0.5). Posthoc tests revealed higher accuracy in Filler items compared with Probes ($p< 0.001$). This accuracy advantage for Filler items was only marginally significant when compared against Target items ($p=0.09$) and no significant difference between Target and Probe stimuli was found.

Mean RT was separately calculated for each stimulation interval (0, 300, 400 ms) given the potential effect of stimulation timing on RT (see Fig.2). Data were submitted to a 3X3 repeated-measures ANOVA. As expected a significant main effect of Honesty was found ($F(2,22)=58.3$, $P<0.001$, $\eta\rho^2=0.84$, $\eta\rho^2$ CI 0.7-0.88). Post hoc tests confirmed longer responses to Probes ($p<0.001$) where responses represented a lie as compared with Fillers yielding a truthful response (but in both cases, denying knowledge of the face). Longer responses were also found to Targets ($p<0.01$) when compared with Filler responses (both truthful, but opposite regarding whether the face is known). No differences were found between Target and Probe responses. Interestingly, a significant main effect of stimulation time also emerged ($F(2,22)=6.3$, $P<0.01$, $\eta\rho^2=0.36$, $\eta\rho^2$ CI 0.075-0.52). Post hoc tests revealed a trend towards response slowing with later TMS pulse delivery. As shown in Fig.2c, responses were slower

in the middle and final stimulation interval compared with the first stimulation interval ($p<0.01$). No significant interaction was found ($F(4,44)<1$).

Electrophysiological results

Adverse effects of TMS

One participant self-reported mild anxiety, mild headache and mild muscle discomfort as a result of the stimulation at the end of the experiment. Two other participants reported mild headache. None of the participants self reported severe symptoms. One participant suffered a suspected seizure or syncope during the initial search for a stimulation spot and was replaced in initial recruitment (see Hadar et al., 2012b, for a full case report; this event was reported to and investigated by the City University Senate Research Ethics Committee).

Data preprocessing

On average 8.6% (SD=5.4%) of MEPs were discarded from the analysis for each participant due to pre-activation in one of the two recording channels. A 3x2 repeated-measures ANOVA, with Interval (0,300,400) and Honesty (Filler vs. Probe) as within-subjects factors compared the number of trials excluded across conditions and found no significant differences ($F(4,44)<1$).

Stimulus-Locked MEP Results

For the MEP analysis we focussed on just two stimulus sets (Fillers and Probes) as these conditions were matched in terms of their required response (denying familiarity) but varied in terms of the presence/absence of a lie. Normalised MEP data were submitted to a 3x2x2 repeated measures ANOVA crossing Interval (0,300,400), Honesty (Filler vs. Probe) and Digit (responding vs. non-responding) variables. Target ('truthful recognition') items were not included in the MEP analysis as they required a motor response with a different

digit which was used less often and thus could not be compared with the remaining two sets (as response frequency is known to modulate MEPs via motor preparation; Bestmann et al., 2008). No significant main effects were observed. A significant two-way interaction emerged between the Honesty and Interval factors ($F(2,22)=5.9$, $p<0.01$, $\eta\rho^2=0.35$, $\eta\rho^2$ CI 0.06-0.51). As shown in Fig.3 the overall MEP size, across both digits, was higher in Probe trials compared to Filler trials at the middle stimulation interval. To further break down this analysis, paired sample t- tests were carried out comparing total MEP size in Probe and Filler trials for each stimulation point. Results highlighted greater activation in the Probe condition than in the Filler condition only during the middle stimulation interval ($t(11)=-3.05$, $P<0.05$) but not in the first and final delivery times ($t(11)=1.05$, $p=0.6$, $t(11)=1.6$. $p=0.3$, respectively). No further significant interactions were found.

TMS: Response-Locked MEP Results

Filtered and normalised MEP data from each participant were locked to response onset (Hadar, Rowe, Di Costa, Jones, & Yarrow, 2016). MEP exclusion was conducted using the same procedure described in the previous section. To extract a valid measure of the temporal development of motor responses across participants the data were allocated into three equal time bins from 2000 ms to 200 ms prior to response onset (2000-1401; 1400-801; 800-201 ms). Since the last stimulation point was administered 400 ms following stimulus onset and RT was on average 1 second there were no MEPs within 200 ms of response onset (see Fig.2). The top-down allocation of time bins resulted in seven missing cells distributed across 4 participants where fewer than 10 MEPs were obtained within a particular time window. Five of these missing data points were at the earliest time bin and two were from the late time bin. These missing data points were treated with linear interpolation.

Data were subsequently submitted to a 3x2x2 repeated measures ANOVA with response locked Interval (early, middle, late), Honesty (Filler vs. Prob) and Digit (responding vs. non-responding) as within subjects variables. No significant main effects were found. No significant interactions with the Honesty variable were found. A significant 2x3 interaction was found between the digit and interval factors ($F(2,18)=9.4$, $p<0.01$, $\eta\rho^2= 0.51$), effectively demonstrating the selection of the responding finger over the non-responding finger over the course of the reaction time period.

Discussion

Behavioural data

In this experiment, participants made deceitful familiarity judgements about recently learnt faces and responded truthfully to previously unseen faces and to an additional group of recently learnt faces. They were required to provide speeded responses using their thumb and little finger immediately after the presentation of the face while corresponding MEPs were recorded. The present response-time results replicated previous findings with similar paradigms (Schumacher, Seymour, & Schwarb, 2010; Seymour & Kerlin, 2007; Seymour & Schumacher, 2009). Responses made to Filler items were significantly quicker and more accurate than responses to Target and Probe items.

This RT pattern is highly consistent with previous studies using the memory exclusion task (Rosburg & Mecklinger, 2017) - a task with a similar structure to the GKT utilised here. The most consistent effect is shorter RTs for filler items as compared with all other conditions. It has been suggested that the newness of a presented facial stimulus is sufficient for its rejection, while familiar facial stimuli necessitate retrieval of source-specifying information prior to final identification (Rosburg & Mecklinger, 2017; Seymour & Kerlin, 2008).

One might expect that the conflict state, which is *unique* to Probe trials, will further slow responses as compared with Target trials, where recollection is required but there is no conflict (because recollection reinforces familiarity in dictating a positive response). However, our data suggest no significant RT differences between Probe and Target trials. Such similar RTs for targets and probes can be expected (Rosburg & Mecklinger) when the source information of both targets and nontargets is recollected (the so-called “recall and

reject" strategy; Clark, 1992). In contrast, when subjects focus on the target category and reject old items that do not match the target category ("target prioritization"; Herron & Rugg, 2003) Rosburg & Mecklinger (2017) showed that probes correctly rejected as nontargets are associated with slower responses than correctly identified targets (regardless of conflict in the task). Given this theoretical background, we revisited our non-significant probe-target contrast (which had a Cohen's d of around 0.4, slightly above the ~0.25 average effect size that has been estimated via meta-analysis for memory exclusion studies showing EEG evidence of the episodic recollection of probe items). However, we had only 12% power to detect this particular effect, and would have required 128 participants to achieve even 80% power, so no strong conclusion can be drawn regarding the strategy employed by our participants. All in all, the present RT findings simply replicate the most consistent behavioural report from previous studies using similar paradigms, showing that responses in Filler trials were quicker than responses in Probe trials.

One additional behavioural finding was faster RTs in trials where the TMS pulse was delivered simultaneously with the onset of the face compared with trials where the pulse was delivered 300 or 400 ms into the presentation. This is plausibly the direct influence of the TMS pulse on the response preparation process. Specifically, first interval (0 ms) pulses are unlikely to interrupt response preparation as the response motor program has not yet been generated at this point in time. By contrast in the two later interval conditions it can be assumed that at the time of delivery the manual response is already partly prepared. Thus, the sudden magnetic interruption and the consequent firing of numerous motor cortex neurons may have delayed the execution of these motor programs (Day et al., 1989; Pascual-Leone et al., 1992; Ziemann, Tergau, Netz, & Hömberg, 1997).

MEP Data

In line with previous studies, MEP data revealed a transient increase in the overall cortico-spinal excitability (CSE) in false facial recognition when compared to truthful recognition (Kelly et al., 2009; Lo, Fook-Chong, & Tan, 2003b). Specifically, 300 ms after face onset the overall excitability of motor cortex areas controlling both the ADM and the FDI was greater in lying than in truth telling. This difference dissipated in measurements taken 100 ms later where CSE was similar in both Probe and Filler conditions (see Fig.3).

Increases in CSE prior to the generation of a lie have been reported in two other papers using very different paradigms, as discussed in the introduction. Lo and colleagues (2003) measured MEPs after asking participants to lie or tell the truth in two sets of either complex (e.g. 'how old are you?') or simple (e.g. 'Are you a man?') questions. This previous study differs from the current paradigm in several crucial features. First, responses were verbal rather than motor. Second, the task consisted of whole blocks of lying and truth-telling, a design which is remote from real-life scenarios. Third, the time of stimulation was temporally removed from early stages of response planning. Thus, although the study appears to report a similar finding of a deception-related increase in CSE, it may reflect different underlying brain processes.

In another MEP study subjects were required to lie or tell the truth in a blocked fashion regarding their affiliation to sports teams (Kelly et al., 2009). Results again confirmed a deception-related increase in CSE, but this time the pattern was significant only for left hemisphere stimulation. Again, the paradigm, response mode and time of stimulation relative to lie onset were substantially different from the present research approach. Nonetheless, taken together with the present results, it appears that at various points along the trajectory of generating false information and/or hiding concealed knowledge there is an increase in motor cortex excitability.

The origins of this generalised increase in terms of cognitive and motor processes cannot be unambiguously identified (Mameli & Mrakic-Sposta, 2010; Priori et al., 2008; Spence et al., 2004). Previous findings in our lab demonstrated the role of response conflict in deception within this exact time window (Hadar et al., 2012a). Specifically, we found that MEPs from just the non-responding digit where enhanced during lying, consistent with the preparation of a motor plan for a truthful response. Hence, the current increase in excitability may reflect co-occurrence of motor plans associated with the suppressed truthful response and with the executed lie response. Here, the trend in the data was towards relatively greater activation of the non-responding digit at 400 ms when a lie was being told. Furthermore, the decrease in overall excitability at the 400 ms interval is consistent with the notion of a momentary activation of the truth response 300 ms after presentation (Hadar et al., 2012) and subsequent suppression of this automated but unwanted activity at the 400 ms interval. However, since the three-way interaction term was non-significant, no direct evidence was found to support this idea in the current data.

Important limitations and caveats to the study should be mentioned at this juncture. First, as discussed above the MEP pattern observed here is limited in its capacity to illuminate the intricacies of intra-hemispheric response selection. It was anticipated that the dynamics of competition between responses associated with the ADM and the FDI would be made clearer due to the use of temporally proximate second and third stimulation intervals, but this was not the case. Second, the digit to response allocation enabled a meaningful comparison of only Probe and Filler stimuli in terms of MEPs (by dint of comparing MEP only from the non-responding digit). This implies that in the absence of a digit-specific effect we cannot rule out the possibility that the greater MEPs to Probe vs. Filler items could have resulted from differences in brain activity to familiar vs unfamiliar stimuli rather than from deception-related factors. Nevertheless, in the context of the GKT, lying always involves

response to a familiar item (denying familiarity) and thus the question of whether the elevated excitability is familiarity or conflict induced may be less critical in terms of application. Third, the development of a motor plan over time in the motor cortex is reflected, among other things, in the magnitude of the MEP and thus MEPs are highly sensitive to RT. Hence, we do not claim that the MEP effects found here are independent from potential confounding RT effects.[2] Fourth, it was expected that such differences would become more apparent as a result of the additional response-locked analysis, but they did not. However, the relatively wide temporal distribution of the data (compared with high-density MEP data where response-locked analysis has been previously used, cf. Hadar et al., 2016; Spieser et., 2018) and the top-down allocation of time bins (used to aggregate a statistically meaningful amount of MEPs) resulted in a relatively noisy data set and perhaps reduced the likelihood of observing a significant group effect. Finally, in light of the small group effect size the present MEP results are not promising in terms of individual diagnostic accuracy, and thus have only theoretical rather than applied implications at this stage.

Summary

This study demonstrates an increase in motor cortex excitability during the process of generating deceitful responses in the GKT. The total CSE, as measured in averaged MEPs from two muscles on the responding hand, is transiently greater in deception compared with truth-telling during the preparation of a response. This finding could be employed in principle to distinguish between genuine and false recognition of facial stimuli in the context of GKT, but our group-level effect is more likely to inform the development of theory and subsequent polygraphic procedures that to be directly applicable. The finding of increased excitability in

[2] In a supplementary analysis utilising RT as a covariate the effect remained significant. However, we have not reported this analysis in detail because data loss meant that it was limited to only a subset of participants.

deception is consistent with previous reports using other, highly variable, lab-based deception tasks (Kelly et al., 2009; Lo et al., 2003b). This consistency of findings despite the variability of paradigms leads to the conclusion that measures of general CSE may also serve as a useful vicarious index of response conflict in deception detection.

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References

Abe, N., Suzuki, M., Mori, E., Itoh, M., & Fujii, T. (2007). Deceiving others: distinct neural responses of the prefrontal cortex and amygdala in simple fabrication and deception with social interactions. *Journal of Cognitive Neuroscience*, *19*(2), 287–295.

Ben-Shakhar, G., & Dolev, K. (1996). Psychophysiological Detection Through the Guilty Knowledge Technique: Effects of Mental Countermeasures. *Journal of Applied Psychology*, *81*(3), 273–281.

Ben-Shakhar, G., & Elaad, E. (2003). The validity of psychophysiological detection of information with the Guilty Knowledge Test: A meta-analytic review. *Journal of Applied Psychology*, *88*(1), 131–151.

Bestmann, S., Harrison, L. M., Blankenburg, F., Mars, R. B., Haggard, P., Friston, K. J., & Rothwell, J. C. (2008). Excitability during Preparation for Action. *Current Biology*, *18*(10), 775–780.

Bond, C. F., & Robinson, M. (1988). The evolution of deception. *Jounrnal of Nonverbal Behaviour*, *12*(4), 295–307.

Buckholtz, J. W., & Faigman, D. L. (2014). Promises, promises for neuroscience and law. *Current Biology*. 24(18), R861-R867.

Clark, S. E. (1992). Word frequency effects in associative and item recognition. *Memory & Cognition*, *20*(3), 231–243.

Day, B. L., Rothwell, J. C., Thompson, P. D., Maertens De Noordhout, A., Nakashima, K., Shannon, K., & Marsden, C. D. (1989). Delay in the execution of voluntary movement by electrical or magnetic brain stimulation in intact man. Evidence for the storage of motor programs in the brain. *Brain: A Journal of Neurology*, *112 (Pt 3*, 649–663.

Fabiani, M., Gratton, G., Karis, D., & Donchin, E. (1987). Definition, identification, and reliability of measurement of the P300 component of the event-related brain potential. Advances in psychophysiology, 2(S 1), 78.

Farah, M. J., Hutchinson, J. B., Phelps, E. A., & Wagner, A. D. (2014). Functional MRI-based lie detection: scientific and societal challenges. *Nature Reviews Neuroscience*, *15*(2), 123–131.

Farwell, L., & Donchin, E. (1991). The Truth Will Out: Interrogative Polygraphy ("Lie Detection") With Event-Related Brain Potentials. *Psychophysiology*, *28*, 531–547.

Gandevia, S. C., & Rothwell, J. C. (1987). Knowledge of motor commands and the recruitment of human motoneurons. *Brain*, *110*(5), 1117.

Ganis, G., & Schendan, H. E. (2012). Concealed semantic and episodic autobiographical memory electrified. *Frontiers in Human Neuroscience*, *6*, 354.

Hadar, A. A., Makris, S., & Yarrow, K. (2012a). The truth-telling motor cortex: Response competition in M1 discloses deceptive behaviour. *Biological Psychology*, *89(2)*, 495-502.

Hadar, A. A., Makris, S., & Yarrow, K. (2012b). Single-pulse TMS related syncopal spell in a healthy subject. *Brain Stimulation, 5,* 652–653.

Hadar, A. A., Rowe, P., Di Costa, S., Jones, A., & Yarrow, K. (2016). Motor-evoked potentials reveal a motor-cortical readout of evidence accumulation for sensorimotor decisions. *Psychophysiology, 53(11)*, 1721-1731.

Hancock, P. (2004). Hancock, P., . Psychological Image Collection at Stirling,. *University of Stirling Psychology Department., 2000*.

Herron, J. E., & Rugg, M. D. (2003). Retrieval Orientation and the Control of Recollection.

Journal of Cognitive Neuroscience, *15*(6), 843–854.

Keel, J. C., Smith, M. J., & Wassermann, E. M. (2001). A safety screening questionnaire for transcranial magnetic stimulation. Clinical neurophysiology, 112(4), 720.

Kelly, K. J., Murray, E., Barrios, V., Gorman, J., Ganis, G., & Keenan, J. P. (2009). The effect of deception on motor cortex excitability. *Social Neuroscience*, *4*(6), 570–4.

Kiers, L., Fernando, B., & Tomkins, D. (1997). Facilitatory effect of thinking about movement on magnetic motor-evoked potentials1. *Electroencephalography and Clinical Neurophysiology/Electromyography and Motor Control*, *105*(4), 262–268.

Langleben, D. D., Loughead, J. W., Bilker, W. B., Ruparel, K., Childress, A. R., Busch, S. I., & Gur, R. C. (2005). Telling truth from lie in individual subjects with fast event-related fMRI. *Human Brain Mapping*, *26*(4), 262–272.

Langleben, D. D., Schroeder, L., Maldjian, J. A., Gur, R. C., McDonald, S., Ragland, J. D., … Childress, A. R. (2002). Brain activity during simulated deception: an event-related functional magnetic resonance study. *NeuroImage*, *15*(3), 727–732.

Lo, Y. L., Fook-Chong, S., & Tan, E. K. (2003a). Increased cortical excitability in human deception. *Neuroreport*, *14*(7), 1021.

Lo, Y. L., Fook-Chong, S., & Tan, E. K. (2003b). Increased cortical excitability in human deception. *Neuroreport*, *14*(7), 1021–4.

Lykken, D. T. (1959). The GSR in the detection of guilt. *Journal of Applied Psychology*, *43*(6), 385–388.

Mameli, F., Mrakic-Sposta, S., Vergari, M., Fumagalli, M., Macis, M., Ferrucci, R., ... & Priori, A. (2010). Dorsolateral prefrontal cortex specifically processes general–but not personal–knowledge deception: multiple brain networks for lying. Behavioural brain

research, 211(2), 164-168.

Meijer, E. H., Verschuere, B., Gamer, M., Merckelbach, H., & Ben-Shakhar, G. (2016). Deception detection with behavioral, autonomic, and neural measures: Conceptual and methodological considerations that warrant modesty. *Psychophysiology*, *53*(5), 593–604.

Pascual-Leone, A., Valls-Solé, J., Wassermann, E. M., Brasil-Neto, J., Cohen, L. G., & Hallett, M. (1992). Effects of focal transcranial magnetic stimulation on simple reaction time to acoustic, visual and somatosensory stimuli. *Brain: A Journal of Neurology*, *115 (Pt 4*(Pt 4), 1045–1059.

Priori, A., Mameli, F., Cogiamanian, F., Marceglia, S., Tiriticco, M., Mrakic-Sposta, S., … Sartori, G. (2008). Lie-specific involvement of dorsolateral prefrontal cortex in deception. *Cerebral Cortex*, *18*(2), 451.

Rosburg, T., & Mecklinger, A. (2017). The costs of target prioritization and the external requirements for using a recall-to-reject strategy in memory exclusion tasks: a meta-analysis. *Psychonomic Bulletin & Review*, *24*(6), 1844–1855.

Rosenfeld, J. P., Cantwell, B., Nasman, V. T., Wojdac, V., Ivanov, S., & Mazzeri, L. (1988). A modified, event-related potential-based guilty knowledge test. International Journal of Neuroscience, 42(1-2), 157-161.

Rosenfeld, J. P., & Labkovsky, E. (2010). New P300-based protocol to detect concealed information: resistance to mental countermeasures against only half the irrelevant stimuli and a possible ERP indicator of countermeasures. *Psychophysiology*, *47*(6), 1002–1010.

Schumacher, E. H., Seymour, T. L., & Schwarb, H. (2010). Brain activation evidence for response conflict in the exclude recognition task. *Brain Research*, *1329*, 113–123.

Schumacher, E. H., Seymour, T. L., & Schwarb, H. (2010). Brain activation evidence for response conflict in the exclude recognition task. *Brain Research, 1329*, 113–23.

Seymour, T. L., & Kerlin, J. R. (2008). Successful detection of verbal and visual concealed knowledge using an RT-based paradigm. *Applied Cognitive Psychology, 22(4)*, 475-490.

Seymour, T. L., & Kerlin, J. R. (2008). Successful detection of verbal and visual concealed knowledge using an RT-based paradigm. *Applied Cognitive Psychology*, *22*(4), 475–490.

Seymour, T. L., & Schumacher, E. H. (2009). Electromyographic evidence for response conflict in the exclude recognition task. *Cognitive, Affective & Behavioral Neuroscience*, *9*(1), 71–82.

Spieser, L., Kohl, C., Forster, B., Bestmann, S., & Yarrow, K. (2018). Neurodynamic Evidence Supports a Forced-Excursion Model of Decision-Making under Speed/Accuracy Instructions.*eNeuro*, 4 June 2018, Eneuro .0159-18.2018.

Spence, S. A. (2004). The deceptive brain. *Journal of the Royal Society of Medicine*, *97*(1), 6.

Spence, S. a, Hunter, M. D., Farrow, T. F. D., Green, R. D., Leung, D. H., Hughes, C. J., & Ganesan, V. (2004). A cognitive neurobiological account of deception: evidence from functional neuroimaging. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *359*(1451), 1755–62.

Tandonnet, C., Garry, M. I., & Summers, J. J. (2011). Selective suppression of the incorrect response implementation in choice behavior assessed by transcranial magnetic stimulation. *Psychophysiology*, *48*(4), 462–9.

Verschuere, B., Rosenfeld, J. P., Winograd, M. R., Labkovsky, E., & Wiersema, R. (2009). The role of deception in P300 memory detection. *Legal and Criminological Psychology*,

14(2), 253–262.

Verschuere, B., Spruyt, A., Meijer, E. H., & Otgaar, H. (2011). The ease of lying. *Consciousness and Cognition*, *20*(3), 908–911.

Vrij, A., Mann, S. A., Fisher, R. P., Leal, S., Milne, R., & Bull, R. (2008). Increasing cognitive load to facilitate lie detection: The benefit of recalling an event in reverse order. *Law and Human Behavior*, *32*(3), 253–265.

Vrij, A., Mann, S., Kristen, S., & Fisher, R. P. (2007). Cues to deception and ability to detect lies as a function of police interview styles. *Law and Human Behavior*, *31*(5), 499–518.

Vrij, & A. (2000). Detecting lies and deceit: The psychology of lying and the implications for professional practice. *Clinical Neuropsychologist*, *21*(5), 855–857.

Ziemann, U., Tergau, F., Netz, J., & Hömberg, V. (1997). Delay in simple reaction time after focal transcranial magnetic stimulation of the human brain occurs at the final motor output stage. *Brain Research*, *744*(1), 32–40.

Figure Legends

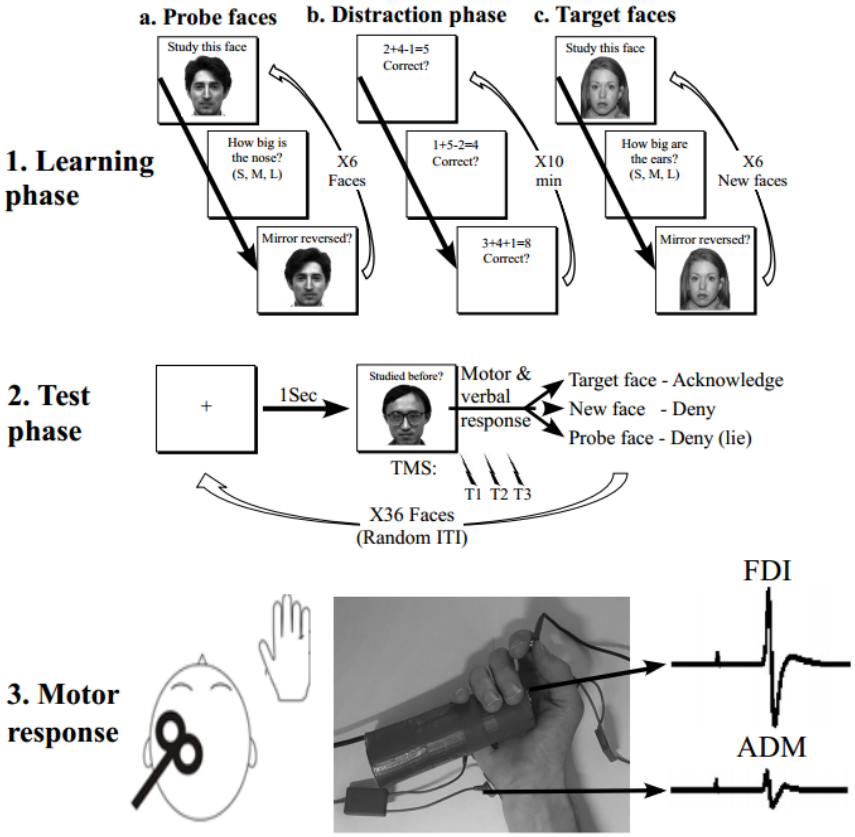


Figure 1

Overview of the experimental procedure, adapted from Schumacher et al., 2010. During the first study phase (a) each of the 6 faces was presented 3 times, each time with a different question to ensure sufficient encoding. After a ten minutes distracter task (b) participants memorised a second set of six faces, following an almost identical procedure to the first study phase (c). Finally, the recognition task (d) included faces from both phases as Probes and Targets and 24 additional faces serving as Filler items. Participants answered using specialised response keys to indicate recognition, lying only when shown faces from the first learning phase.

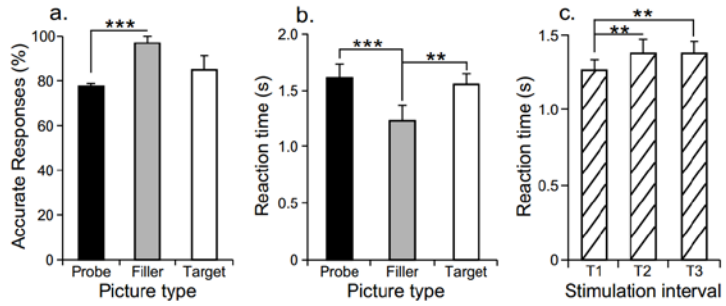
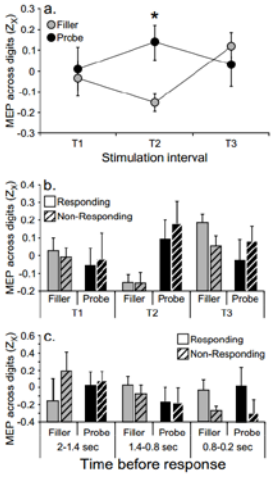


Figure 2

Bar charts presenting a summary of behavioural results. Mean acuracy for each honesty condition is shown in panel a. Panel b shows mean reaction times for Probe, Filler and Target trials averaged across the three stimulation intervals. Panel c presents mean reaction times in each stimulation interval averaged across the Probe, Filler and Target trials. Error bars represent standard error. **** p<0.005, *** p<0.0005**

Figure 3



Fluctuation of Cortico-spinal excitability across response preparation window for Filler and Probe trials. Panel a shows the means of all participants' median peak-to-peak MEP z-scores, averaged across the FDI and the ADM muscles, but separated into stimulation intervals and by Filler and Probe sets. Means of all participants' peak-to-peak MEP z-scores presenting the

full set of conditions are presented in panel b. Response-locked means of all participants' median peak-to-peak MEP z-scores (again presenting the full set of conditions) are shown in panel c. Error bars show standard errors.