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Citation: 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), pp. 1721-1731. doi: 10.1111/psyp.12737

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Motor-evoked potentials reveal a motor-cortical readout of evidence accumulation for sensorimotor decisions

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Abbreviated title: MEPs reveal evidence accumulation in M1

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Abstract

Many everyday activities require time-pressured sensorimotor decision making. Traditionally, perception, decision and action processes were considered to occur in series, but this idea has been successfully challenged, particularly by neurophysiological work in animals. However, the generality of parallel processing requires further elucidation. Here, we investigate whether the accumulation of a decision can be observed *intrahemispherically* within human motor cortex. Participants categorised faces as male or female, with task difficulty manipulated using morphed stimuli. Transcranial magnetic stimulation, applied during the reaction-time interval, produced motor-evoked potentials (MEPs) in two hand muscles that were the major contributors when generating the required pinch/grip movements. Smoothing MEPs using a Gaussian kernel allowed us to recover a continuous time-varying MEP average, comparable to an EEG component, permitting precise localisation of the time at which the motor plan for the responding muscle became dominant. We demonstrate decision-related activity in the motor cortex during this perceptual discrimination task, suggesting ongoing evidence accumulation within the motor system even for two independent actions represented within one hemisphere.

Introduction

Many human activities require a near-instant decision about how to react to a visual cue. Although traditional models emphasised a serial progression from perception to decision and only subsequently to action, this idea has been regularly challenged within the human behavioural literature (e.g. Frith & Done, 1986; Hommel, 2004). Furthermore, neuroscientific investigations have revealed that time-varying neural activity in the primary motor cortex (M1) can actually reflect cognitive processes in a seemingly continuous manner (Georgopoulos et al., 1989). In the past decade considerable evidence from trained monkeys has suggested a role for neural computations of motor origin in the decision process (Gold and Shadlen, 2007).

One criticism of the robust findings in monkeys when generalised to humans relates to their extensive training, which is likely to produce a durable sensorimotor mapping of the two response alternatives. Such mappings may automate decision-related neural activity in the motor system, and this activity does not guarantee involvement of the motor system in the decision process in less constrained situations. Hence obtaining converging evidence from humans is important.

A handful of studies have now attempted to provide neurometric evidence in humans to support the role of the sensorimotor (and particularly the motor) cortex in the decision-making process (Donner et al., 2009; Kelly & O'Connell, 2013; Selen et al., 2012). Donner et al. (2009) used electroencephalography (EEG) to record lateralised Beta-band power over motor areas during a motion detection task. By requiring lateralised responses to indicate "present"/"absent" decisions, they showed a clear correlation between motoric beta and the process of evidence accumulation. Selen and colleagues (2012) used EMG to measure arm reflex gains during a task involving selection between flexion and extension of antagonist muscles. They tracked the development of two distinct motor plans by assessing the reflex

state at various time points prior to response execution, demonstrating a perceptual decision variable of motor origin.

Transcranial magnetic stimulation (TMS)-evoked MEPs provide another viable method to track decisions as they evolve in the motor system for specific actions (e.g. Klein, Olivier & Duque, 2012). This has been shown for both complex evaluative decisions (Klein-Flügge and Bestmann, 2012) and for situations of strong response conflict (Verleger et al., 2009; Hadar et al., 2012; Michelet et al, 2010). For instance, Klein et al. (2012) created a context where reward was often unequal for each of two possible responses, and demonstrated that interhemispheric (i.e. between-hand) decisions result in larger MEPs in the selected hand prior to response execution. Earlier, Michelet and colleagues (2010) had employed a modified flanker task in which participants responded with flexion or extension of the thumb and MEPs were recorded during the reaction-time period. Their study neatly demonstrated accumulation of neural evidence for a particular response during RT. However, considered collectively, it is not clear whether these findings extend to both simple perceptual decisions without conflict (e.g. targets without flankers) and to situations where there is no exogenous reward/value to be calculated as part of the decision process. Indeed, previous modelling work in humans has demonstrated marked differences in the neural processes underlying reward-based decisions as compared with state/stimulus-based decisions (Gläscher et al. 2010).

To provide a more complete picture of motor-cortical involvement in speeded decision making, it also seems worth considering various means for expressing a decision that may impose different anatomical and neural linkages between action alternatives. When considering the literature as a whole, such methodological variation should help determine what aspects of the brain's decision-related response generalise across different response configurations. For example, decisions between hands imply specifically long-range

interhemispheric neural linkages, while decisions between flexion/extension of the thumb imply an anatomically imposed mutual inhibition. In order to obtain concurrent *intra*hemispheric data concerning two largely independent response alternatives involving the same hand, one can stimulate a single point on the motor cortex and measure MEPs from two distinct hand muscles associated with different responses (Bestmann et al., 2008; Hadar et al., 2012; Makris et al., 2011, 2013).

Here we develop methods to help visualise such digit-specific MEP data as a continuous signal (similar to EEG but more tightly constrained to have a corticospinal locus) and subsequently compare both its response-locked and stimulus-locked properties. Such differential signal-locking comparisons have been previously used in EEG studies to isolate the relative contribution of perceptual-cognitive and motor mechanisms to response selection (Osman and Moore, 1993; Leuthold et al., 1996). This logic is illustrated in Figure 1 part A, which schematises the effect of making the decision more difficult when MEP timing has been expressed relative to the moment of either stimulus onset or response onset. Notice in particular how a brain signal which incorporates the decision process will emerge earlier for hard decisions when the data are time-locked to the response. Here, we applied this logic in an attempt to demonstrate a process of continuous evidence accumulation akin to a visually guided decision variable in the motor cortex. We did this by varying the difficultly of a (simple) visual discrimination task and measuring its effect on the temporal dynamics of *intrahemispheric* MEP signals.

Method

Participants

Eight healthy participants (six males; Mean age = 30.0, SD = 9.4; 7 right handed) completed the experiment. Six participants were naïve to the purpose of the experiment. The experimental procedures were approved by the City University London Psychology Department Ethical Committee. All participants gave their informed consent before beginning the study, having been informed of its unusually long duration compared to typical experimental/TMS research.

Stimuli

Sixteen faces served as testing material for the experiment. The stimuli were based on four different morphed continua of faces created in a previous study (Huart et al., 2005). They consisted of 4 ambiguous male faces, 4 ambiguous female faces, 4 non-ambiguous male faces and 4 non-ambiguous female faces. These faces formed two sets for hard and easy gender categorisations.

Apparatus

E-Prime 2.0 (Schneider, Eschman, & Zuccolotto, 2002) running on a PC was used for the presentation of all stimuli and control over TMS pulses. Subjects sat ~50 cm in front of a 19-inch CRT monitor refreshing at 100 Hz. The response device (see Figure 1) was adapted from Makris et al. (2011). It consisted of a plastic cylinder, at the top of which a small pressure button was attached, so that each time the cylinder was squeezed with a power grip, activating the Abductor Digiti Minimi (ADM) muscle, the button would be pressed.[1] The

[1] Although one might not expect ADM activation to be maximal for this action, we have found that with appropriate positioning of our apparatus we can achieve a reliable response in most participants, alongside a fair degree of independence from the contrasting pinch action and a reasonable degree of comfort and inter-trial muscular relaxation. Other configurations have generally proved less successful in meeting these various constraints.

second component was a small plastic pressure-switch that was taped to the inside tip of the participant's thumb. Pressing involved a squeeze using the index finger and thumb, resulting in contraction of the first dorsal interosseous (FDI) muscle. Participants were instructed to hold the device with their dominant hand, holding the switch with their index finger and thumb, and grasping the cylinder with the third and little fingers against their palm, but relaxing completely between responses. The response mapping (e.g. pinch = male, squeeze = female) was counterbalanced across participants.

EMG recording

Two surface Ag/AgCl EMG electrodes (22 x 28 mm, part no.SX230FW, Biometrics Ltd.) were placed approximately 2-3 cm apart, over the ADM muscle of the dominant hand and a nearby reference site (just above the styloid process of the right ulnar). Two other electrodes were similarly placed to record from the FDI muscle 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 two speakers placed on the left and right (and receiving copies of EMG from the FDI and ADM respectively) to ensure that muscles were fully relaxed between responses. Digital data was exported and analysed offline using MatLab (The Mathworks, Natick, MA, 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 contralateral (typically left) hemisphere to elicit MEPs in both the ADM and FDI (the hand "motor hot spot") with the handle pointing backwards/laterally approximately midway between the sagittal and coronal planes. Intensity of pulses was set around 110-120% 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 around 3 out of 6 single pulses when the hand was fully relaxed. Stimulation frequency never exceeded 0.2 Hz. In total, 1,600 pulses were administered during the experimental sessions (which were conducted in separate blocks, typically of 400 TMS trials each, spread over a few days). A post-report form was used to document any adverse effects of TMS (suspected seizures, headaches, muscular discomfort and anxiety).

Procedure and design

Training. The experiment was preceded by a short training session of 80 trials. Each trial began with the centralised presentation of a fixation cross for 3250-4500 milliseconds (ms). The fixation cross was followed by a randomised presentation of one of the 16 faces. The stimulus remained on the screen until a response was given unless no response was given within two seconds, in which case the trial was stopped and a 'too slow' message appeared for one second. Stopped trials were re-entered into the randomised pool of remaining trials. Participants were required to respond as quickly as possible to the gender of the face. The average RT of the slowest 20 practice trials was calculated to the nearest 125 ms (pRT) and subsequently used in the experiment for the construction of five stimulation time bins (outlined next).

Experiment. The experimental procedure is schematised in Figure 1 part B. Each trial began with the centralised presentation of a fixation cross for 3250-4500 ms. The fixation cross was followed by one of the 16 faces at random. The stimulus remained on the screen for 2000 ms regardless of button presses. A TMS pulse was administered at a uniform random time point within one of five time bins based upon individualised RT during practice (pRT). This constraint on timing randomisation was added in order to ensure a sufficient number of MEPs across the entire response preparation time. The time bins used covered the regions 0-20% pRT, 20-40% pRT, 40-60% pRT, 60-80% pRT and 80-100% pRT; hence stimulation could occur at any time from 0-100% pRT. Participants were required to respond quickly and accurately regarding stimulus gender, and not to wait for the TMS pulse. Overall TMS was applied to each face 20 times within each time bin, yielding 1600 stimulation trials. In addition, in order to obtain RT estimates which were not contaminated by the magnetic pulse, each face was presented 20 times in a non-TMS condition. Thus, the experiment employed a randomised presentation of 1920 trials.[2]

Data pre-processing and analysis

MEPs for each trial were displayed aligned to the onset of the TMS pulse. An algorithm checked for EMG activity on either channel in the 300 ms immediately preceding the TMS pulse (and also the interval between pulse and MEP) and flagged its decision, which then had to be manually accepted or rejected (in order to catch rare trials where the algorithm failed). The criterion for EMG detection was set at any deflection > 50uV + mains noise, with

[2] One of the non-naive participants completed their first two blocks with a different response setup, which proved less effective for isolating the FDI and ADM muscles. These data were discarded, so the participant contributed only 960 trials to the analysed data set. For a second (non-naïve) participant, a technical problem led to a loss of 147 trials in the final recording session. Note that each participant spent around 8 hours in the lab, so we preferred to avoid rejecting/replacing participants.

the latter term reflecting the amplitude of any 50 Hz excursions detected during muscle quiescence. The 50 Hz term was generally very small, due to the use of active EMG. These pre-activation trials, as well as those where no response was detected, or technical failures occurred, were discarded. A second algorithm detected the onset of the EMG burst driving the participant's response (i.e. their EMG RT) based on integrated rectified EMG in a sliding window (length 100 ms, calculated sample by sample). As with pre-activation, the algorithm could be manually corrected during trial inspection (button RT was displayed to assist with this process). There was no information in the display indicating which kind of stimulus (easy or hard) had been presented, such that pre-processing was conducted blind to the main experimental manipulation.

Overall, ~48% of trials were discarded from the analysis during this step (ranging from 31-71% across participants), leaving 6233 MEPs (3029 from easy trials and 3204 from hard trials) for further analysis. This high exclusion rate stems partly from the need to maintain both muscles relaxed between the execution of rapid button presses (in the majority of MEP studies, the hand is at constant rest during the experimental session). More importantly, in order not to interfere with participants' natural RT distribution but still record MEPs immediately adjacent to response execution, the randomised timing of pulses included many trials in which the response actually preceded the stimulation. Put simply, the design aimed to acquire data right up until the final stages of the stimulus-response process and hence a substantial portion of the (later stimulation) data is theoretically and physiologically irrelevant (due to the onset of a voluntary response beating the TMS pulse). Given the natural variability in RTs, some loss of data is unavoidable if a signal that covers the full RT period is to be recovered.

A further subset of trials (~3% and ~8% of the remaining trials in easy and hard conditions respectively) was removed because the response indicated an incorrect gender

categorisation. Thus, overall, a substantial number of TMS trials were removed from the analysis, but the multiple recording sessions for each participant ensured that many (2933 easy and 2952 hard) trials remained. MEP amplitude for these trials was calculated as the maximal peak-to-peak difference in an individualised window that consistently captured this event, typically around 20-30 ms after pulse administration. For each participant, amplitudes in each muscle were z-transformed separately for the FDI and ADM within each session (combining data across easy and hard conditions) in order to give an equivalent measure for the two responses. This is a valuable noise-reduction measure when comparing MEPs from two different muscles, given that the magnitudes of evoked responses vary between muscles. Channels were then reclassified as either responding or non-responding, depending upon the correct response for that trial and the assignment of gender to key for that participant. The data processing pipeline is illustrated in Figure 2.

We determined both stimulus and response-locked stimulation times for each MEP, where response-locked times were relative to the EMG RT. In order to allow the pooling of trials across participants, stimulation times were normalised for each participant as a percentage of their overall median EMG RT in non-TMS trials. MEPs were then collated into smooth time-varying signals by applying a Gaussian smoothing kernel:

$$\hat{Y}(t) = \frac{\sum_{i=1}^{N} e^{(-\frac{(t-t_i)^2}{2\sigma^2})} Y_i}{\sum_{i=1}^{N} e^{(-\frac{(t-t_i)^2}{2\sigma^2})}} \quad (1)$$

Where the N contributing MEPs each have magnitude Y_i and occur at normalised time t_i. We calculated smoothed signals in 1% median EMG RT time steps (i.e. every ~5 ms) and used a smoothing kernel with a full-width half-maximum of 5% median EMG RT.[3] We

[3] Although more commonly applied in the spatial domain, this Gaussian smoothing approach has several features which seem appropriate when applied to MEPs which have been delivered at random times.

generated these smoothed signals for the responding muscle, the non-responding muscle, and the difference between them, in both easy and hard conditions, and for both stimulus-locked and response-locked data. We then applied non-parametric bootstrapping with 2000 iterations to generate bootstrap confidence intervals via the basic (pivotal) method. For data like these, consisting of matched pairs, a significant effect equates to a one-sample contrast between their difference scores and zero. Significant increases in activation for the responding over the non-responding muscle were therefore flagged whenever the (one-tailed) 95% confidence interval around the difference signal did not overlap zero.

Because our smoothed MEP signals contained multiple data points, significant differences for a few time steps were not indicative of an overall significant divergence between the responding and non-responding muscles. In order to control the familywise error rate, significant divergence was tested using a *difference counter*, which incremented for every significant difference and decremented for each non-significant difference, with the constraint that it could never fall below zero. A threshold value was set for this counter which maintained the type one error rate at 5%.[4] Our main interest was the initial time at which MEPs from the responding muscle began to dominate those of the non-responding muscle. Once the counter reached threshold, the point at which it had most recently begun incrementing from zero was taken as the divergence point. Conceptually, this approach is somewhat similar to the application of a cluster test, requiring a prolonged and near-

In particular, a Gaussian kernel can be straightforwardly applied to a signal that has non-uniform temporal sampling, without requiring any prior signal interpolation. Like a simpler moving average, it has good time-domain properties for removing white noise. However, it also shows smooth frequency-domain stop-band attenuation, with a gradual roll off that seems appropriate when the exact frequency content of the signal is unknown.

[4] The counter's threshold for divergence was selected based on Monte-Carlo simulations of the null hypothesis. Experimental data were simulated repeatedly (499 iterations of 3000 data pairs per iteration, consisting of uniform random stimulation times in the range 0-100% EMG RT and their associated Gaussian-distributed MEP difference scores). On each iteration, smoothing, bootstrapping and difference counting was applied as described previously. False positive divergences were summed across iterations and then normalised to yield an expected proportion for type I errors. Repeated simulations using different counter threshold values indicated that a counter threshold of eight equated to a familywise alpha < 0.05.

continuous section of point-by-point significant divergence to generate an overall significant effect.

The main purpose of the divergence point calculation was to determine whether the easy and hard categorisation conditions diverged at different times (see Figure 1 part A). Importantly, divergence points were calculated in an identical manner in each condition. To assess any differences between them, a permutation test was constructed using 999 random resamples. On each resample, the association between each MEP pair and its condition (easy or hard) was broken, then randomly reassigned, to construct two new scrambled data sets (of the same sizes as the original easy/hard sets). Divergence points were determined for each scrambled "condition" as described above for the real data. The *difference* between these divergence points was then retained to form a resampled null distribution, against which the difference obtained in the actual data could be compared for statistical significance, using a two-tailed alpha of 0.05.

Modelling

In a final step, we implemented a popular model of speeded choice, the drift-diffusion model (Ratcliff and McKoon, 2008), to assess whether our smoothed MEP signal had characteristics broadly compatible with a neural process of evidence accumulation.

The six-parameter drift-diffusion model that we implemented assumes that evidence accumulates from a mean starting position z situated between two boundaries, with the lower decision boundary at position 0 and an upper boundary at position a. We fixed z to the midpoint of the two boundaries, but allowed a to vary as a free parameter. The start position was randomised from trial to trial using a uniform distribution centred on z. This distribution's width s_z was a second free parameter. A third parameter controlled the degree

to which the mean accumulation rate v was greater in the easy compared to the hard condition. Within a trial, the change in accumulated evidence at each time step was drawn from a Gaussian distribution with mean v_i (for the ith condition) and standard deviation s (as a fourth free parameter). Accumulation rates also varied from trial to trial, with this Gaussian noise controlled by the standard deviation parameter s_v. The final free parameter, t_{er}, reflected the mean non-decision component of reaction time, which we modelled as a Gaussian random variable with standard deviation fixed at 2% median RT.

We opted to use the non-TMS RT data to fix model parameters, and then predict the neurometric accumulation profile without allowing any further parametric flexibility. Normalised RT data from easy and hard conditions were converted to deciles of the RT distributions for both correct and erroneous responses. The diffusion model was maximum-likelihood fitted to these transformed data using the quantile method proposed by Heathcote et al. (2002), with model predictions generated via simulation. Each parameter combination was assessed based on 100,000 simulated responses, with best-fitting parameters sought using the Nelder-Mead simplex algorithm (Nelder and Mead, 1965; O'Neill, 1971) which was seeded iteratively from multiple start values.

The most suitable neurometric signal to model is the difference in MEP responses between the responding and non-responding digits, which will cancel out non-specific spinal influences contributing to both MEP measures equally. This signal has an intuitive correspondence with the process of evidence accumulation in the drift diffusion model. We predicted this neurometric signal via simulation (using the parameters estimated in non-TMS trials). On each of 1,000,000 iterations, a diffusion profile was simulated (under the assumption that the entire non-decision time, t_{er}, preceded the onset of accumulation) along with the uniform-random timing of a TMS pulse. Just as in our actual experiment, the simulated MEP difference value at this time was retained, but only if the TMS pulse had

arrived before a decision was reached. Simulated difference MEPs were then collated and smoothed via the same data analytic methods described previously, in order to generate model predictions.

Results

Behavioural data

Median RT on correct non-TMS trials in the easy condition ranged from 412 to 665 ms across participants. As intended, all participants responded slightly more slowly in the hard condition (with medians ranging from 425 to 690 ms). Following normalisation to each individual's overall median correct RT, data were pooled across participants. Correct responses were significantly faster in the easy-categorisation condition (median = 98.7%) compared to the hard-categorisation condition (median = 101.9%, $t_{[2061]} = 3.78$, $p < 0.001$)[5]. Participants also made significantly more response errors for hard gender categorisations compared with easy ones (mean easy accuracy = 97.6%, mean hard accuracy = 95.0%, $\chi^2_{[1]} = 8.75$, $p = 0.003$). However, our stimuli were not all equally effective in this regard. The four male/female face pairings we used differed considerably in the degree to which speed and accuracy had been affected by the partial morphing manipulation (see Figure 3).[6]

[5] For consistency with the analysis of MEPs (presented next) RT inferential statistics were applied by collating trials from different participants and considering whether these samples of trials (from the population of all trials that these particular participants might have recorded) implied a significant difference at *that* population level. We will consider the issue of the level of inference we have adopted in the discussion. Note, however, that in the case of RT, where it was possible to determine median scores on a per participant basis, a difference could also be found when the target of inference was the (more standard) wider population of potential participants ($t_{[7]} = 3.44$, $p = 0.011$).

[6] The differential effectiveness of our stimuli was apparent in a repeated-measures factorial ANOVA on median RTs in each of 4 (stimuli) x 2 (difficulty of discrimination) cells, which revealed an interaction between these factors ($F_{[3,21]} = 3.58$, Huynh-Feldt-corrected $p = 0.031$).

Stimulus-locked MEP data

Figure 4 panel A shows the smoothed aggregated MEP data from all participants and the estimated point of divergence between MEPs recorded from responding and non-responding muscles. We applied this analysis by collating trials from all participants, because stable estimates of divergence could not be obtained on a per participant basis. Significant divergence occurred around 52% of the median response time after stimulus onset for the easy categorisation condition, compared with 51% after stimulus onset for the hard task. Data were subjected to a permutation test to explore whether the point of divergence differed reliably between the hard and easy categorisation conditions. The difference between the two conditions was not found to be significant when compared to the distribution of such differences in the randomly resampled data ($p = 0.819$). For a signal originating at the hand motor hot spot, very similar divergence points in easy and hard conditions are not consistent with a serial neurocognitive architecture (in which meaningful motor activation should arise only following a decision, and thus later in hard conditions; see Figure 1). However, a null finding is at best suggestive, so we sought positive evidence.

Response-locked MEP data

The same procedure was repeated for the response-locked data (see Figure 3 panel B). This revealed divergence 33% / 39% of median RT before the time of EMG onset for easy and hard categorisation conditions respectively. This difference was in the predicted direction if corticospinal excitability provides a continuous readout of the decision process, rather than simply varying after a decision is reached (see Figure 1). However, the permutation test on this difference was not significant ($p = 0.207$).

Focussed (post-hoc) analysis

In light of the promising trend found in the response-locked MEP data, and the clear differences observed in the efficacy of our four stimulus pairs to induce changes in decision difficulty (see Figure 3) we conducted a second more focussed analysis by removing the potentially diluting influence of the two ineffective face pairs (Figure 3, bottom two panels). Hence we analysed data from only the 3132 trials involving the two face pairs where easy/hard differences in the decision process were clearly predicted by RT measures (Figure 3, top two panels). Note that this post-hoc division of the data is based exclusively on the RT results from the *non-TMS* trials, not the trials that generated the MEP data used for this analysis.

For the focussed stimulus-locked analysis, we once again obtained no significant difference in divergence times for the easy and hard conditions (although by chance the divergence now appeared quite large: Hard – easy = 9%, $p = 0.693$; see Figure 4 panel C). However, for the response-locked analysis the divergence we observed in the complete data set now became more pronounced and reliable (see Figure 4 panel D) and reached conventional levels of significance (Hard – Easy = -9%, $p = 0.034$).

Modelling

Having established that MEPs in our task showed characteristics highly suggestive of the continuous transmission of decision information to the motor hot spot, we wished to demonstrate a qualitative correspondence between our smoothed collated MEP signals and the process of continuous evidence accumulation that is believed to support speeded sensorimotor decision making (Ratcliff et al., 1999; Gold and Shadlen, 2007). To this end, we

used RT data from all non-TMS trials to estimate appropriate parameters for a drift-diffusion model of the decision process. RT data and the best-fitting model predictions are shown in Figure 5 panel A, which demonstrates that the model predicted our RT data adequately.[7]

In a second step, we predicted our MEP data (specifically the difference between MEPs from responding and non-responding muscles, ΔMEP) from this same model fit, with no further parametric flexibility introduced (i.e. in a manner conceptually similar to a cross-validation procedure, but with the validation set comprising an entirely different form of data from the training set, being neurometric rather than chronometric in nature). Our only modification of the predicted ΔMEP signal was to vertically rescale it from the arbitrary units of the accumulator model to reach a maximum defined by the observed ΔMEP data. Model predictions and data are illustrated in Figure 5 panel B for both stimulus-locked and response-locked data.

The profiles predicted by the model, which assume that the TMS-evoked difference between responding and non-responding muscles is a direct reflection of the evidence accumulation process, show some striking qualitative similarities with observed ΔMEP data (although the timing of predicted accumulation does appear delayed, especially in the stimulus-locked analysis format). These panels also illustrate key predictions for a parallel neurocognitive architecture (cf. Figure 1), i.e. accumulation begins at similar times for easy and hard judgements in the stimulus-locked analyses, but begins earlier for hard judgements in the response-locked analyses. An additional prediction (slower accumulation in easy conditions) is also illustrated and qualitatively matched in the data, at least for the stimulus-locked analysis.

[7] The fit is not perfect, and it seems possible that our RT distributions exhibited some slightly unusual features, probably arising from the combination of data from multiple participants (even though normalised).

Discussion

Using TMS and concurrent EMG recording, we introduced a novel method to extract high-resolution neurometric data corresponding to two separate response representations residing within one hemisphere. To our knowledge this is the first attempt to generate a continuous readout of corticospinal activity using motor-evoked potentials (MEPs). Stimulus and response-locked analyses of this continuous signal together demonstrated decision-related activity in the motor cortex during a perceptual discrimination task: The temporal cost generated by harder gender categorisations was clearly observable in motor processes. Hence, a *perceptually* more taxing decision resulted in longer *motoric* activity relating specifically to the selected action, despite equal motor requirements.

Behavioural data confirmed that the easy condition resulted in faster and more accurate decisions than the hard condition for a subset of our stimuli. Focussing on these stimuli, we observed that when MEP signals were locked to stimulus onset, gender discrimination difficulty had no significant effect on the time of MEP divergence (which provides a sensitive measure of when one response starts to be selected, e.g. Tandonnet et al., 2011). This finding challenges serial models of decision making, as under these accounts harder gender categorisations would be expected to delay the accumulation of evidence towards one of the two response alternatives and thus delay action selection. Instead the response-locked analysis showed that response-specific processing in motor regions successfully predicted the increased RT produced by adjusting the difficulty of the perceptual discrimination.

While we found no effect of stimulus difficulty on stimulus-locked divergence times, in some previous EEG/lateralised readiness potential (LRP) studies the point of

interhemispheric signal divergence in stimulus-locked analyses did reflect perceptual decision variables (e.g. Experiment 3 in Rinkenauer et al., 2004) . However, they used a flanker task, where the perceptual conflict is more dominant and both stimulus-locked and response-locked signals may show competition between response alternatives. We discuss this issue further below.

EEG measures are also somewhat ambiguous with regard to the generating neural loci, whereas we can be more confident that our MEP signal originates from the corticospinal tract.[8] However, the exact anatomical locus of the functionally defined hand motor hot spot is a matter of debate. Although it is often assumed to be M1, and specifically the "hand knob" that lies in the middle bend of the central sulcus, several studies have suggested that the motor hot spot may show anatomical variation across participants. For example, Ahdab, Ayache, Brugières, Farhat, and Lefaucheur (2016) use MRI-guided TMS to conclude that the position of the hot spot is (largely) bimodal across participants, with a typical locus at either the central sulcus (M1/hand knob) or towards the precentral sulcus (pre-motor cortex).

Regardless of whether our MEPs mainly reflect activation in M1, premotor cortex, or some mixture of these, the (lateral) corticospinal tract projects directly onto the final common pathway for motor commands to the upper limbs, and we believe that few would consider its structure-function mapping to be anything other than motoric. While our null finding in the stimulus-locked analysis is inconclusive, the pattern observed in the response-locked analysis therefore rules out a single perceptual-motor update prior to response execution as a full account of our data. This study therefore provides neurophysiological evidence of a continuous flow of information regarding the decision to the motor system, and that this evidence accumulation occurs at the intra-hemispheric level. It suggests that motor activity is

[8] Of course this corticospinal activation will itself be a reflection of the inputs that regions such as M1 are receiving from a wider brain network, which we cannot measure independently here.

not instigated only after the preceding cognitive processes have terminated. Rather, the motor hot spot continuously reflects, and possibly even helps determine, the dynamics of the decision process.

Both behavioural and continuous MEP data showed some correspondence to predictions made by the drift diffusion model. Most importantly, the model, when fitted only to our RT data, also gave a surprisingly good qualitative fit to the MEP data. Early MEP activity did not discriminate between response alternatives, but once ΔMEP started to deviate from zero, suggesting the start of accumulation, growth occurred more rapidly for easily discriminated stimuli than for the difficult to discriminate stimuli in stimulus-locked data (Figure 5b). Given that no parametric manipulation was used to match neural data to model predictions, the model's success is compelling, reinforcing the notion that corticospinal excitability reflects the process of decision accumulation.

It is of some interest to point here to differences between these findings and those of Michelet et al. (2010) as, to our knowledge, theirs is the only other published TMS study of intrahemispheric response competition within the RT period. Using the flanker task they showed a delay in *stimulus-locked* MEP separation with increased conflict. However, they note that the flanker task may be a special case. This is because it actually instructs the wrong response, a fairly extreme way to prolong the decision process that might yield a large number of completed but then countermanded decisions. Indeed, their MEP data looks less like a delayed decision than like an incorrect decision countermanded by a correct one. By contrast in our hard gender face task there is greater perceptual uncertainty but no mixed message. Our study also employed both a response-locked analysis and smoothed MEP data (obtained at a great many time points). These techniques permitted a firmer conclusion regarding motor involvement in the decision process which could not be drawn from the methodology used by Michelet et al. (2010), because without the use of response locking it

did not permit a positive statistical inference regarding the key prediction of a parallel architecture (see Figure 1 part A).

Another important difference is our use of partly dissociated muscle groups (FDI and ADM) versus Michelet et al.'s use of a single muscle (FDI) with two opposing movements, flexion and extension, implying an inherently antagonistic relationship. In our study, two isolated muscles within one hemisphere showed parallel activity during the decision process. Michelet et al.'s choice yielded a clear indication of inhibition in the selection process while ours showed some indication of suppression of non-responding MEPs, but only in easy categorisations (Figure 4b; note the slight reduction in non-responding MEP magnitude during the ~50 ms following signal divergence). Given that the link between flexion and extension is inhibitory in nature, demonstrating inhibition in the present design might have provided stronger evidence for the role of inhibitory processes in selection. However, MEPs ride atop general (e.g. spinal-level) modulations in excitability, so a drop in amplitude does not necessarily imply selective inhibition of a motor plan. Future studies using a control measure of spinal excitability (Hasbroucq et al., 2000) could shed more light on the degree of inhibition between competing populations.

Complementary evidence in support of our findings comes from Selen et al. (2012) using a random dot motion task. They measured reflex gains (using EMG) directly from proximal hand flexor and extensor muscles without any neural intervention during response preparation. Their findings are consistent with ours, showing a continuous update projected downstream to the muscles as the evidence for a particular response gradually accumulates. Thus converging data from different levels in the motor system suggest that the perceptual brain continuously conveys decision information to motor cortex.

The current findings are also consistent with evidence against serial/sequential models in the interhemispheric domain in man (cf. Soto et al. 2009; Klein-Flügge and Bestmann

2012; Verleger et al. 2009; Praamsta & Seiss, 2005). Klein-Flügge and Bestmann (2012) also used both stimulus and response-locked analyses to demonstrate that corticospinal excitability can reliably predict the outcome of a decision prior to completion of the decision process. They found that the point of separation between the response-locked MEP signals of the chosen and unchosen responses occurs earlier in hard decisions as compared with easy decisions. In their study MEP signals for each response alternative were taken from different sets of trials as they did not use concurrent intrahemispheric recording of two competing MEPs. Nevertheless, their data in the cognitive (value-laden) decision domain closely match our findings in the perceptual decision domain. Similarly, a widely cited event-related optical signals (EROS) study also showed parallel activation of motor plans in relative proximity to response execution (DeSoto et al., 2001). Similar conclusions have been drawn based upon numerous LRP studies using between-hand decisions (e.g. Jentzsch & Leuthold, 2004). Thus it can tentatively be concluded that both intra and inter-hemispheric response selection is represented continuously in motor cortex.

Our analysis method has implications for the population to which we are effectively generalising when reporting statistical significance. When a summary statistic (e.g. the difference between divergence points for easy/hard trials) is constructed on a per participant basis, and then assessed via a standard single-level statistical technique (e.g. a paired t-test), inferences can be made about the existence of the effect in the wider population of human experimental participants. The large number of TMS trials required to reliably construct a continuous signal from isolated MEPs makes this approach challenging, particularly given the general reluctance of participants to take part in non-clinical TMS experimentation. However, more careful design may potentially mitigate such difficulty, for instance by applying less pulses proximate to movement initiation and by more extensive pilot work with visual stimuli. Here we are making inferences that apply only to the wider population of

potential TMS/MEP trials from which we sampled, i.e. to all potential trials that might be collated from our particular set of participants. Hence our inferences cannot be said to apply to people in general except to the extent that the processes which we are studying are common between our particular sample and the more general population. Note, however, that this limitation has often been accepted in neuroscientific research, for example in low-N visual psychophysics studies or monkey neurophysiology.

Our study had some further limitations. First, to obtain statistical significance we resorted to a post-hoc analysis in which we isolated the most effective stimuli (based on RT) and then analysed only the corresponding MEP data. Note that these two sets of data were independent, so there was no "double dipping" or similar statistical sleight of hand. However, this deviation from the planned analysis implies that our findings should be considered exploratory rather than confirmatory. Second, we employed a response-locked analysis, typical in EEG research. However, unlike EEG, TMS can perturb (as well as measure) action tendencies, which means that the moment of action may have been affected (either speeded or slowed) by the TMS pulse. This can distort the response-locked timeline in complex ways. However, such perturbations should be equivalent between the easy and hard conditions of our design and are hence unlikely to have affected our key result, i.e. the earlier divergence between responding and non-responding MEP signals in trials with a more challenging perceptual discrimination. Third, because participants in our experiment had to relax their muscles between responses, we provided continuous auditory feedback on EMG. This could be considered as a kind of dual-task load accompanying the primary task of face discrimination. However, this load was constant across our experimental conditions so should not have affected our comparisons in any systematic manner.

In summary, this study showed that within-hand grasp-specific measures of corticospinal excitability can reveal a process of continuous evidence accumulation entirely

within a single hemisphere of the motor system. This has been demonstrated here using a simple perceptual decision task with a stimulus that did not evoke any overt response competition. The use of a fine-grained response-locked analysis showing the development of a bias between two competing responses demonstrates clearly that when decisions are associated with an immediate action, they are reflected, moment by moment, in the motor cortex.

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Figure Legends

Legend to Figure 1

Schematic of the experimental predictions and procedure. **A.** Logic of stimulus-locked and response-locked analyses. An experimental manipulation is introduced which prolongs the decision stage of a sensorimotor task. Under a stimulus-locked analysis, a neural signature which represents the commands sent to the motor effector should manifest later when the decision is hard. By contrast, a neural signature which represents both decision and action should begin at the same time for easy and hard decisions. However, under a response-locked analysis, this pattern reverses: A neural signature associated with decision making will manifest earlier for a difficult decision, whereas a neural signature associated with the motor command will occur at the same time regardless of decision difficulty. **B.** Experimental procedure. Participants made speeded responses (by either pinching or squeezing) to indicate the gender of face stimuli. TMS was delivered at random times during the reaction-time period. **C.** Illustration of our typical response / EMG electrode configuration.

Legend to Figure 2

Schematic of data-processing pipeline. MEPs were collected across the RT period from both the FDI and ADM muscles and z transformed within each muscle. The top row of graphs shows individual MEPs for one example participant for correct responses in the easy stimulus condition. Data are separated by response and muscle. Running averages, calculated with a Gaussian smoothing kernel, are shown to assist visualisation, but the smoother was only actually applied following further collation of data, described next. In the second row of graphs, data from all participants have been collated following time normalisation to each

participant's median RT. In the third row, data are combined from both muscles based on whether they represent the responding or non-responding muscle on that trial. Finally, in the slightly sunken central graph, data points represent the difference between responding and non-responding muscles on each trial. Smoothed data from this step were used to calculate the point where the responding muscle came to dominate the non-responding muscle (see Figure 4).

Legend to Figure 3

Reaction time distributions from non-TMS trials in easy (black) and hard/morphed (white) face-discrimination conditions, plotted separately for each face pair. Stimulus pairs are ordered (top to bottom) according to how well the morphing manipulation induced the intended decrement in speed and accuracy. RTs have been normalised for each participant (based on their easy/hard combined median) prior to pooling.

Legend to Figure 4

Z-transformed MEP signals generated by smoothing MEPs with a Gaussian kernel. Signals are shown separately for MEPs recorded from the responding (blue) and non-responding (red) muscles during the reaction-time period of correct responses. Lighter background coloured regions show 95% bootstrap confidence intervals. The dashed grey lines (associated with the right-hand greyed ordinates) plot the number of MEPs falling within the full-width half-maximum of the Gaussian smoothing kernel. This measure indicates how sampling varied across the RT period, reflecting for example the rejection of more trials later on as a result of the response increasing tending to precede the TMS pulse. Green ticks denote individual points of significant divergence between the responding and non-responding muscle signals. Black arrows illustrate where significant aggregations of

such points (which control the familywise error rate) first emerge. **A.** Stimulus-locked analysis incorporating the entire data set. **B.** Response-locked analysis incorporating the entire data set. **C.** Stimulus-locked analysis focussing on those stimuli for which the morphing manipulation had the intended effect on both RT and error rates (see Figure 2). **D.** Response-locked analysis focussing on those stimuli for which the morphing manipulation had the intended effect on both RT and error rates (see Figure 2). The asterisk (*) denotes a significant difference in the time of divergence between responding and non-responding muscles (permutation $p = 0.034$).

Legend to Figure 5

A. Comparison between RT data and the predictions of the best fitting drift-diffusion model for non-TMS trials in easy and hard conditions. The model was maximum-likelihood fitted using deciles of the cumulative distribution function (CDF), but probability distribution functions (PDFs) are also shown to assist visualisation of RT distributions. Note that incorrect trials (blue, right-hand ordinate) are shown on a magnified scale relative to the much more frequent correct trials (red, left-hand ordinate). **B.** Comparison between Z-transformed smoothed MEP difference signals from easy (black) and hard (white) conditions and the corresponding predictions of a drift diffusion model (shown in red and blue respectively). Both stimulus-locked (top) and response-locked (bottom) analyses are shown. Note that model predictions are obtained based only on fits to the (independent) RT data shown in part A. The only further modification was a vertical rescale to the arbitrary evidence accumulation values (applied identically to stimulus and response-locked data in easy and hard conditions) based on the maximum observed MEP-difference magnitude in stimulus-locked conditions.

Figure 1

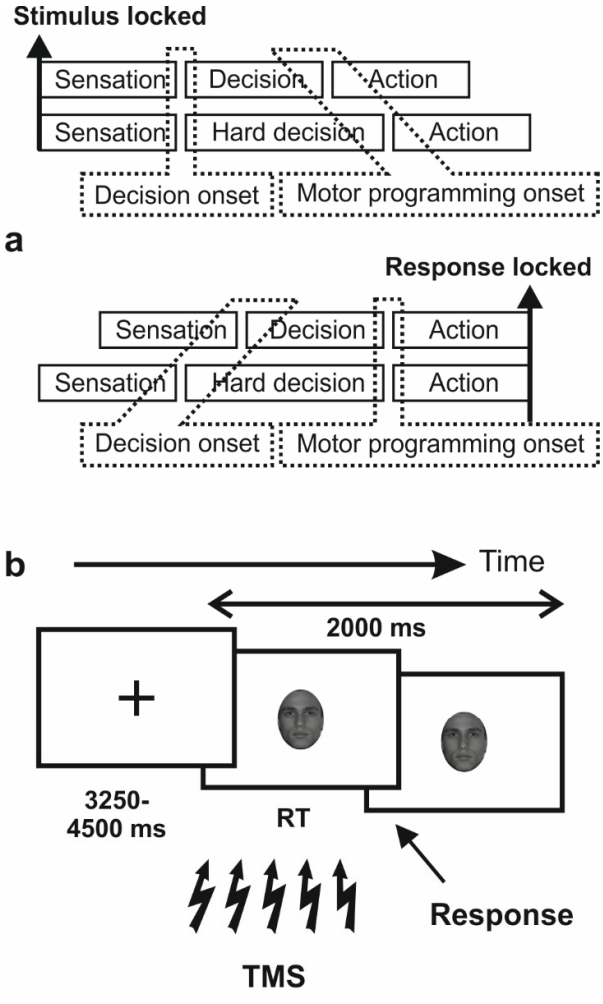

Stimulus locked
Sensation
Decision
Action
Sensation
Hard decision
Action
Decision onset
Motor programming onset
a
Response locked
Sensation
Decision
Action
Sensation
Hard decision
Action
Decision onset
Motor programming onset
b
Time
2000 ms
3250-
4500 ms
RT
Response
TMS
c

Figure 2

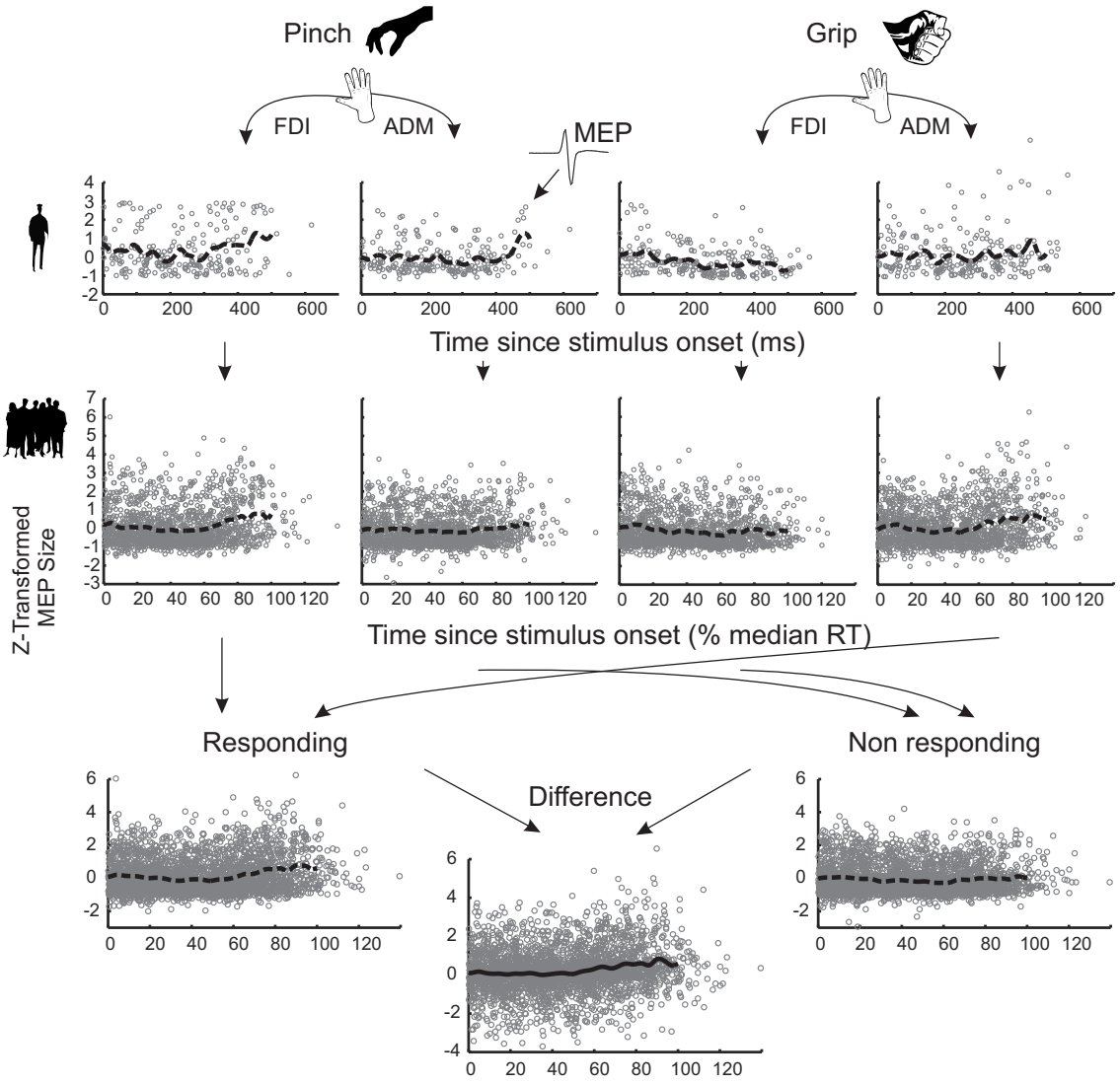

Pinch
Grip
FDI
ADM
MEP
FDI
ADM
Time since stimulus onset (ms)
Z-Transformed MEP Size
Time since stimulus onset (% median RT)
Responding
Non responding
Difference

Figure 3

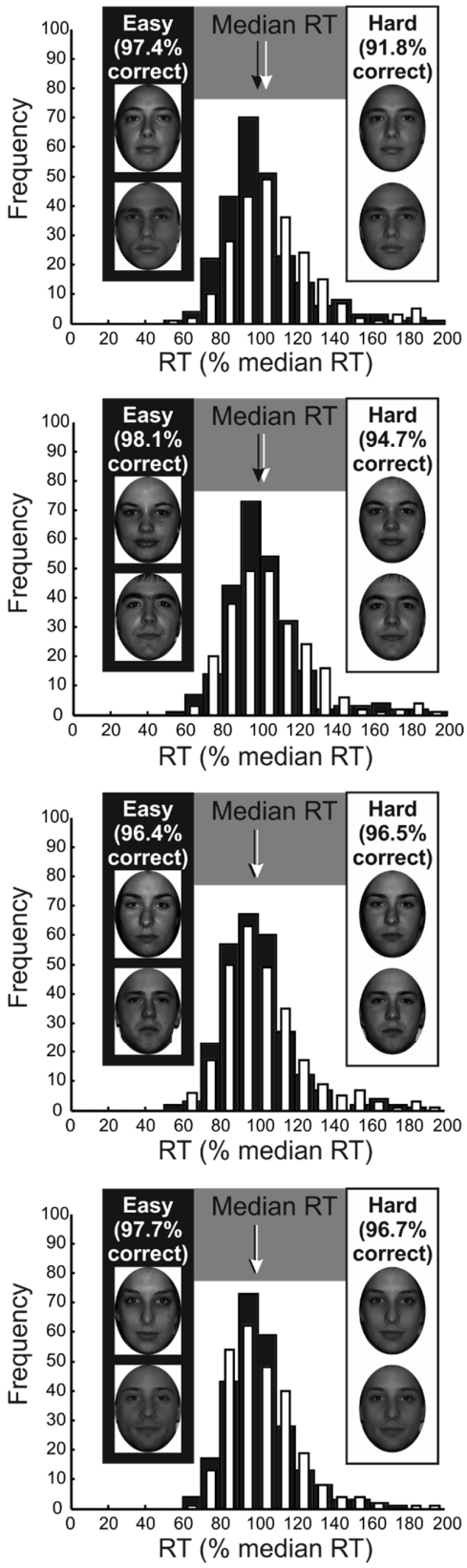

Easy
(97.4%
correct)
Median RT
Hard
(91.8%
correct)
Frequency
RT (% median RT)
Easy
(98.1%
correct)
Median RT
Hard
(94.7%
correct)
Frequency
RT (% median RT)
Easy
(96.4%
correct)
Median RT
Hard
(96.5%
correct)
Frequency
RT (% median RT)
Easy
(97.7%
correct)
Median RT
Hard
(96.7%
correct)
Frequency
RT (% median RT)

Figure 4

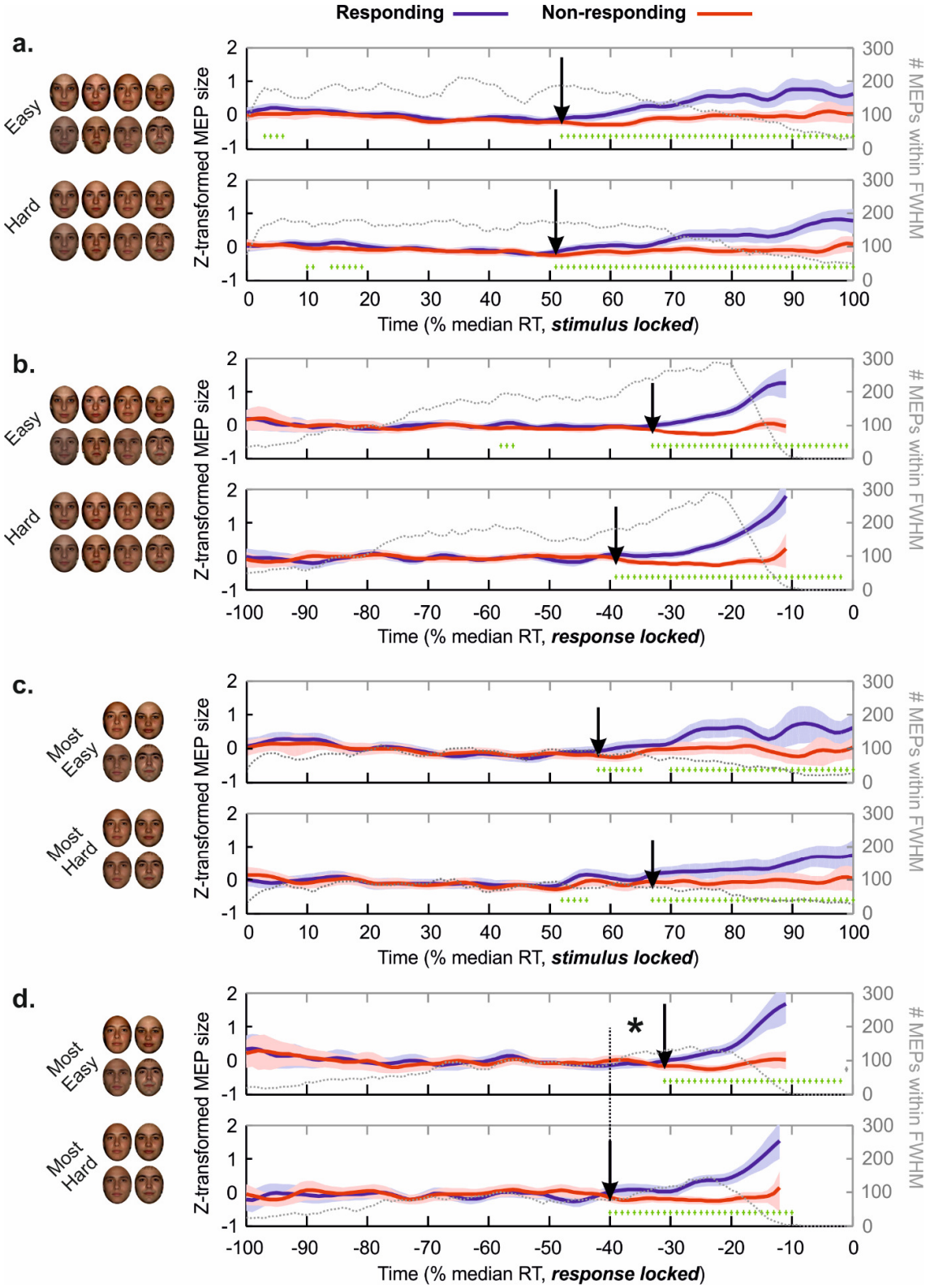
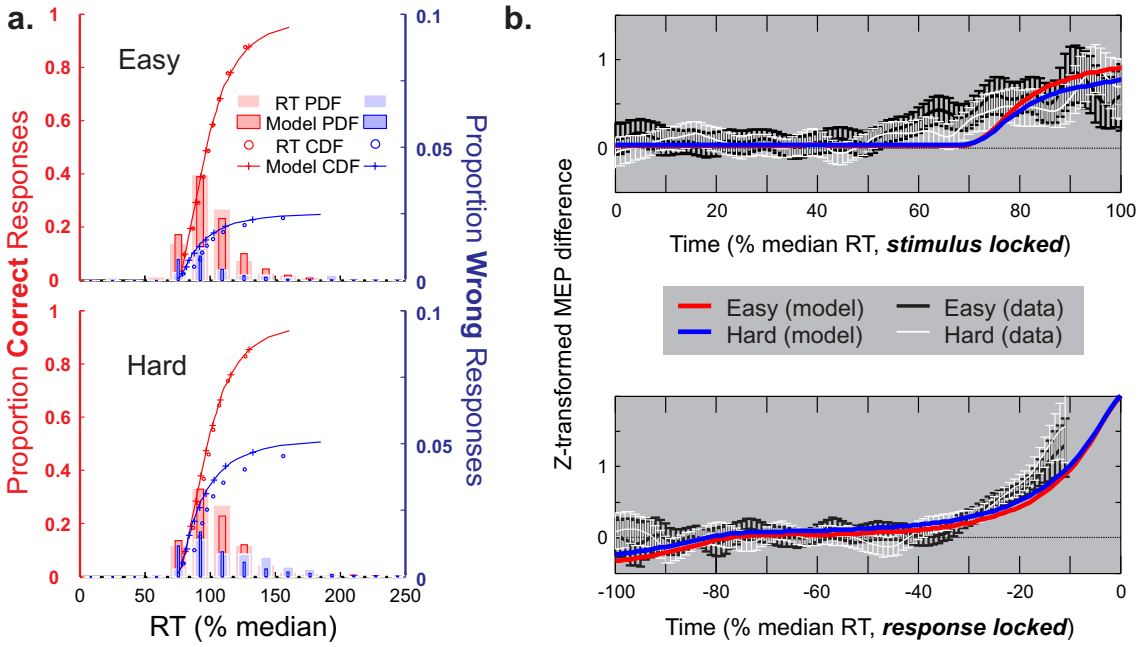

Responding
Non-responding
a.
Easy
Hard
Z-transformed MEP size
MEPs within FWHM
Time (% median RT, stimulus locked)
b.
Easy
Hard
Time (% median RT, response locked)
c.
Most Easy
Most Hard
Time (% median RT, stimulus locked)
d.
Most Easy
Most Hard
*
Time (% median RT, response locked)

Figure 5


a.
Easy
Hard
RT PDF
Model PDF
RT CDF
Model CDF
Proportion Correct Responses
Proportion Wrong Responses
RT (% median)
b.
Z-transformed MEP difference
Easy (model)
Hard (model)
Easy (data)
Hard (data)
Time (% median RT, stimulus locked)
Time (% median RT, response locked)