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When the Brain Changes Its Mind: Flexibility of Action Selection in Instructed and Free Choices

Stephen M. Fleming[1], Rogier B. Mars[1,2], Thomas E. Gladwin[3,4] and Patrick Haggard[1]

[1]Institute of Cognitive Neuroscience and [2]Sobell Department of Motor Neuroscience and Movement Disorders, University College London, WC1N 3AR, UK, [3]Rudolf Magnus Institute of Neuroscience, Department of Psychiatry, University Medical Center Utrecht, 3584 CG Utrecht, the Netherlands and [4]Department of Psychiatry, Stuivenberg Hospital, 2060 Antwerpen, Belgium

The neural mechanisms underlying the selection and initiation of voluntary actions in the absence of external instructions are poorly understood. These mechanisms are usually investigated using a paradigm where different movement choices are self-generated by a participant on each trial. These "free choices" are compared with "instructed choices," in which a stimulus informs subjects which action to make on each trial. Here, we introduce a novel paradigm to investigate these modes of action selection, by measuring brain processes evoked by an instruction to either reverse or maintain free and instructed choices in the period before a "go" signal. An unpredictable instruction to change a response plan had different effects on free and instructed choices. In instructed trials, change cues evoked a larger P300 than no-change cues, leading to a significant interaction of choice and change condition. Free-choice trials displayed a trend toward the opposite pattern. These results suggest a difference between updating of free and instructed action choices. We propose a theoretical framework for internally generated action in which representations of alternative actions remain available until a late stage in motor preparation. This framework emphasizes the high modifiability of voluntary action.

Keywords: action selection, event-related potential, motor preparation, voluntary action

Introduction

Many human actions are determined by a combination of current external cues and internal representations within the brain, such as memories, goals, and motivations. "Free choices" can be defined as actions occurring when current external cues guiding behavior are largely absent. In particular, the choice of which of a number of possible alternative actions to make in a given situation is an important aspect of free choice because most situations afford a number of possible responses. In the laboratory, participants are often instructed to choose between different movements from trial to trial (for comprehensive reviews, see Passingham and Lau 2006; Hallett 2007). This is then compared with "instructed-choice" tasks, in which a stimulus informs the participant which action to select on each trial. Recent neuroimaging and transcranial magnetic stimulation studies have suggested that a distributed network of brain areas involving the presupplementary motor area (pre-SMA) and dorsolateral prefrontal cortex (dlPFC) is specifically active in free selection (Ammon and Gandevia 1990; Deiber et al. 1991; Jahanshahi et al. 1995; Jenkins et al. 2000; Hadland et al. 2001; Nachev et al. 2005; Lau et al. 2006; but see Elsinger et al. 2006). In contrast, the dorsal premotor cortex may play a key role in linking external stimuli to actions (Halsband and Passingham 1985; Simon et al. 2002; Hanakawa et al. 2006; Mars et al. 2008; for a review, see Wise et al. 1997).

Neuroimaging studies have generally focused on this dissociation between different neural networks involved in free and instructed choice. However, it is difficult to equate the 2 conditions on a number of possible confounding factors, such as response conflict, working memory, and effort (Botvinick et al. 2001; Hadland et al. 2001; Lau et al. 2006). Consequently, here we take a different approach, looking not at whether different neural networks are active during the initial selection of instructed or free choices but by looking at the "updating" of action representations that were freely selected or selected in response to an explicit instruction. A similar approach has recently become popular in neurophysiological studies of attention and action (see Rushworth and Taylor 2006). This approach allows us to make inferences about differences in the representation of action plans in the brain following free and instructed choices by looking at the neural processes involved in updating these representations.

This study accordingly used event-related brain potentials (ERPs) to identify neural correlates of the process of changing one selected action plan for another. Two recent neuroimaging studies have used similar methods. Nachev et al. (2005) asked subjects to choose between 2 saccadic targets under conditions of free selection or instruction by an external stimulus. On some trials, they were instructed to make the other saccade by a "change" cue occurring after the "go" cue. Using functional magnetic resonance imaging (fMRI), they found distinct subregions of the pre-SMA engaged in initial action selection and in changes to ongoing responses. However, their design emphasized conflict at a relatively late stage of motor preparation by requiring the response change "after" the go cue. By this time, the initial response has already been committed for execution. In contrast, Mars et al. (2007) presented instruction cues prior to action execution, finding selective activation of a right frontoparietal network when the cue instructed a switch of action plans during preparation. However, they did not include a free-choice condition. Thus, to our knowledge, no previous study has investigated the brain processes involved in free and instructed choice by requiring subjects to switch their choice between 2 alternative action plans in response to unpredictable cues. In particular, no previous ERP study has focused on the updating of endogenously selected action representations, prior to action execution.

In the present study, participants selected an action through free or instructed choice, according to condition. An instruction to change the action plan sometimes occurred in the interval before the appearance of a cue signaling action

execution. This design allows us to assess the status and flexibility of the initial action selection by investigating the processes involved in "changing your mind." We predict that the neural processes of the initial selection of action, measured by ERPs, will differ between free and instructed-choice trials. Given reports of activity in inferior parietal areas during the reprogramming of actions (Rushworth et al. 2001; Rushworth and Taylor 2006; Mars et al. 2007), we focus specifically on the P300, an ERP component recorded over central–parietal electrodes and suggested to be elicited in, among others, temporoparietal areas (Polich 2007; Corbetta et al. 2008).

Materials and Methods

Participants

Seven females and 7 males (mean age: 26.2 years; range: 19–40 years) each participated in a single 2½-hour session. The study was approved by the local ethics review committee and was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. Participants gave informed consent before the start of the experiment and were compensated £20 for their time.

Stimuli and Response Apparatus

Participants sat in a dimly lit, quiet room and viewed stimuli presented on a computer monitor. Responses were made using a custom-built button box, with the index finger of each hand placed over buttons either side of the body midline. Cue stimuli were presented in yellow on a light gray background for 250 ms (see Fig. 1). Participants were instructed to prepare a left of right key press by an arrow pointing to the left or right or were given a free choice which was indicated by a bidirectional arrow and which required participants to freely prepare either a left or a right response. Following a 1450-ms delay in "change/stay" trials, a yellow square or diamond represented the instruction to either change response preparation to the opposite hand or maintain preparation to respond with the hand previously instructed or chosen. The assignment of change/stay cues was counterbalanced between participants.

A green circle (the go cue) signaled the initiation of the response 950 ms after the change/stay cue. Occasional "short" trials served to test whether subjects truly prepared following S1. On such trials, the go cue appeared after the first delay interval (1450 ms), without presentation of a change/stay cue. A further small proportion of trials ended with a red circle in place of the usual go cue. This required participants to withhold any prepared response ("no-go" trials). All stimuli subtended a visual angle of approximately 1.8° at a viewing distance of 65 cm.

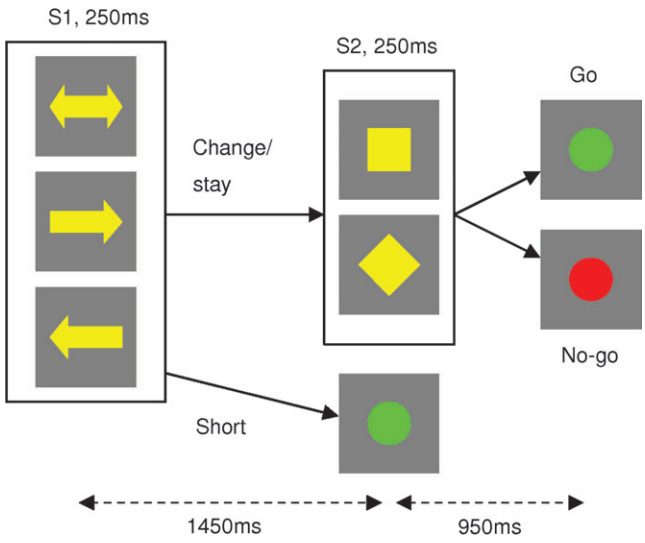

Figure 1. Action selection and reprogramming task. Participants were asked to prepare a left or right button press at S1 (instructed trials) or were given a free choice (free trials) over which of these actions to prepare. The S2 cue indicated whether the action plan should be changed (28%), maintained (28%), or executed (44%). Change and stay cues were counterbalanced across participants.

Procedure

Participants were first familiarized with the experimental stimuli. They then performed 2 behavioral pretest blocks to assess whether they used cues to prepare responses in advance, as they were instructed. The pretest blocks consisted of equal numbers of "baseline" and "short" trials. Baseline trials consisted of a question mark cue (250 ms), followed after a 1450-ms delay by a left, right, or bidirectional green arrow stimulus (250 ms) requiring an immediate response. The short trials were as described above. Thus, advance preparation was not possible on baseline trials but was possible on short trials. If subjects used cues to prepare responses in advance, reaction times (RTs) should be shorter on short trials than on baseline trials.

In the main experiment, stimuli appeared in the sequence displayed in Figure 1. The trial ended after the participant had responded to the go cue or withheld their response in accordance with a no-go cue. The intertrial interval was 2500 ms. Each participant performed a total of 432 trials divided into 8 equal blocks. In all, 44% of trials were "short," 28% "change," and 28% "stay." Equal numbers of "instructed" and "free" trials were present for each of these 3 conditions. In all, 20% of all change/stay trials were no-go, requiring the participant to withhold their planned response. The order of trial types was randomized within blocks.

This trial design aimed to encourage advance preparation and maintenance of preparation both between S1 and S2 and between S2 and the go/no-go cue in 2 key ways. First, a significant proportion of short trials were included, where the go cue appeared at S2. Second, an individual RT deadline was introduced based on performance in the behavioral pretest (calculated as mean RT in short trials + 2 standard deviations [SDs]). Error feedback was provided when responses were made in anticipation of the go cue or later than the individual RT deadline. Mixing free and instructed trials randomly within blocks ensured that free actions could not be selected and prepared in advance of the onset of each trial.

Electrophysiological Recordings

Electroencephalographic (EEG) activity was recorded from 27 Ag/AgCl electrodes evenly distributed over the scalp. All electrodes were referenced to AFz during recording and re-referenced offline to linked mastoids. Vertical and horizontal electrooculer activity was recorded from electrodes positioned above and below the left eye and from the left and right outer canthi, respectively. EEG signals were sampled at 500 Hz and resampled offline at 250 Hz.

Data Analysis

Only correct go trials with RTs shorter than the individual deadline were included in the analysis. One participant was excluded due to a failure to follow task instructions in change trials. EEG data were imported into EEGLAB v 5.03 (Delorme and Makeig 2004) for analysis. Data were filtered between 0.05 and 35 Hz. Grand-averaged ERPs low-pass filtered at 11 Hz are displayed in the figures. Independent component analysis was used to remove eyeblink and electrocardiogram artifacts (Jung et al. 2000), and algorithms within EEGLAB identifying abnormal kurtosis and extreme data points were used to suggest additional artifacts for further manual rejection. One participant's data were excluded at this stage due to an abnormally large proportion of EEG artifacts. For the remaining 12 participants, a mean 4.4% of trials were excluded in this manner, with no more than 9% of trials rejected for any individual. EEG data were then sorted by trial type and averaged in separate epochs time locked to S1 or S2.

We additionally computed a time-frequency measure of lateralized action preparation, the motor-related amplitude asymmetry (MRAA),

based on the methods of Gladwin et al. (2006). Instantaneous amplitudes at C3 and C4 in the mu (9- to 13-Hz motor-related rhythm) frequency band were calculated over broad time windows by Morlet wavelet convolution The motor-related mu-band wavelet was defined as having a center frequency of 11 Hz and SD of 1.5 Hz, as used previously (De Jong et al. 2006).

The MRAA measure of lateralized action preparation was calculated by subtracting out activity common to C3 and C4 electrodes in the conventional way (Coles 1989):

$$\mathrm{MRAA}(t)=[(A_{C3}(t)_{\text{right hand}}-A_{C4}(t)_{\text{right hand}})+(A_{C4}(t)_{\text{left hand}}-A_{C3}(t)_{\text{left hand}})]/2.$$

The mu-MRAA was then normalized separately for each participant and experimental condition by dividing it by the average mu-band amplitude across both C3 and C4 electrodes at each time point. The output of this computation produces a percentage lateralized shift relative to the overall amplitude in the mu band for each condition (de Jong et al. 2006).

Statistical Tests

A preliminary analysis revealed no effect of response hand on either RTs or ERPs, so this variable was collapsed in subsequent analyses. ERPs at electrode Pz were selected for statistical analysis of stimulus-locked P300s (Waszak et al. 2005; Polich 2007). Based on an inspection of the scalp distribution of the difference wave, electrode FCz was selected for statistical analysis of the contingent negative variation (CNV) prior to S2. Both behavioral, ERP and MRAA data were analyzed using repeated-measures analysis of variance (ANOVA); Greenhouse–Geisser corrections were used when appropriate. Planned comparisons using paired-samples *t*-tests were performed to analyze simple main effects when interactions were observed.

Results

Behavior

Participants made very few errors in instructed selection of the 2 alternative actions, averaging 98.8% correct responses. Due to the individual response time deadline designed to encourage action preparation, some late response errors were expected, but these were still made relatively infrequently (mean over all trial types, 7.4%; SD 4.0%). In free-choice trials, there was a small but significant bias toward initial preparation of the right button press (mean 59.0%; SD 6.9%).

RTs were entered into a repeated-measures ANOVA with factors of trial type (change/stay, short) and choice (free, instructed). Mean RTs in experimental trials are displayed in Figure 2(*a*). RTs were 47 ms faster in change/stay trials than in short trials, giving a main effect of trial type ($F_{1,11}$ = 7.57, P < 0.05). No effects of choice or the interaction of choice and trial type were found, indicating similar preparation levels in instructed and free trials.

Compared with baseline trials in the behavioral pretest, the RT difference with both short (t_{11} = 15.76, P < 0.001) and change/stay trials (t_{11} = 17.60, P < 0.001) was highly significant, as shown in Figure 2(*b*). As baseline trials were designed to preclude advance response preparation before the onset of the go cue, this result confirms that motor preparation is evident across the whole trial, whether measured at S2 (short trials) or following a further delay period (change/stay trials). RTs were lower in change/stay trials than in short trials (t_{11} = 2.56, P < 0.05), reflecting the continued preparation throughout the S2–go interval.

Event-Related Potentials

ERP analysis primarily focused on the reprogramming of the selected action following the change cue (ERPs to change and stay cues). Additionally, we examined differences between conditions in the initial choice process itself and in the level of motor preparation that each type of choice afforded (ERPs during the S1–S2 interval).

ERPs to Change and Stay Cues

In all, 44% of all trials were short trials, on which a go cue was presented at S2. On the remaining 56%, the S2 cue instead required either covert change or maintenance of the selected action plan. Following the change/stay cue, 4 types of trials are available for comparison due to our 2 × 2 factorial combination of the instructed/free choice at S1 and the change/stay cue at S2. Average voltages in 6 50-ms time windows between 300 and 600 ms at electrode Pz were selected for further analysis (Fig. 3). The baseline for comparison was an interval of 200 ms prior to S2 onset. A 2 × 2 × 6 ANOVA with factors choice (free, instructed), change (change, stay), and time was carried out.

A main effect of choice ($F_{1,11}$ = 6.68, P < 0.05) was found due to the P300 being larger overall in instructed-choice trials. There was no main effect of the change cue, but there was a significant interaction between the change cue and time ($F_{5,55}$ = 3.37, P < 0.05). As expected for a time-varying waveform, there was a main effect of time ($F_{1,11}$ = 5.19, P < 0.05). Most importantly, there was a significant interaction of choice and change ($F_{1,11}$ = 6.08, P < 0.05). The interaction reflects the fact that the effect of covert change was more marked following instructed choices than free choices, with the opposite pattern seen for covert maintenance (see Fig. 3, right-hand panel). This pattern was consistent over time: interaction with time ($F_{5,55}$ = 1.37, P > 0.2). Modulation of

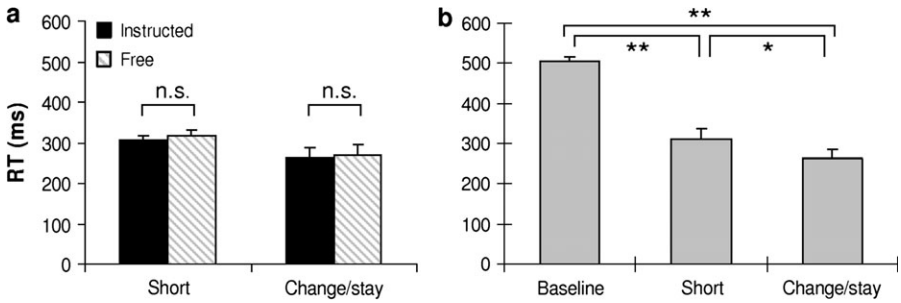

Figure 2. Mean RT data (+standard error of the mean) averaged over all participants. (*a*) Behavioral data from the main experiment showing that average motor preparation did not differ between choice conditions. (*b*) Comparison of RT data in experimental trials to a pretest baseline condition, demonstrating that participants significantly engaged in motor preparation for both short trials (response at S2) and change/stay trials (response at the end of the trial). One asterisk (*), P < 0.05; two asterisks (**), P < 0.001.

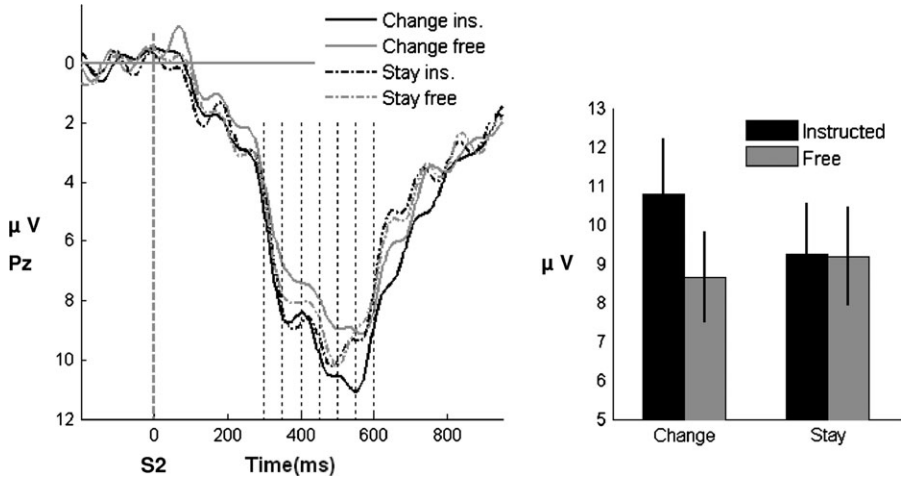

Figure 3. Grand average ERPs at Pz locked to S2 and sorted by trial type. The choice × change factorial design gives 4 conditions. Time is relative to the onset of S2; the time windows entered into the ANOVA are indicated with broken lines. The right panel displays the mean amplitudes (±standard error of the mean) for each trial type extracted from a time window between 520 and 540 ms (the maximum of the instructed-change − free-change difference wave). The interaction between choice and change conditions is reflected in a greater P300 in instructed-change trials than instructed-stay trials, with a trend toward the opposite pattern in free-choice trials.

the P300 at central–parietal electrodes was confirmed by examining the scalp distribution of the difference wave driving the interaction effect (instructed change – free change; Fig. 4).

The interaction shown in Figure 3 was further examined by paired *t*-tests between each of the free and instructed choice × change cue combinations. The time window for these tests (520–540 ms following S2) was chosen based on the maximum of a difference-of-differences wave which tracks the strength of the interaction effect. Larger average P300 activation in instructed-change than free-change trials was confirmed (t_{11} = 2.57, P < 0.05). No significant difference was evident between instructed-stay and free-stay conditions. Specifically, the S2 ERP results reveal that instructed-choice trials lead to greater P300 amplitudes than free-choice trials when participants are required to change their action plans.

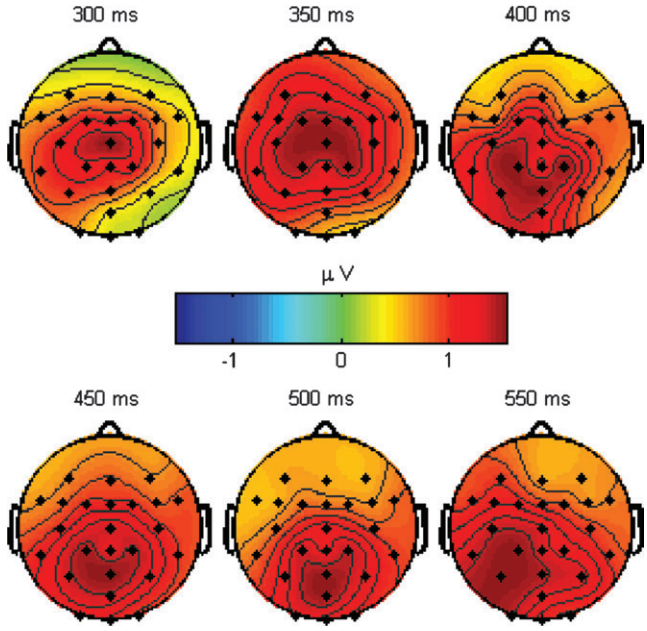

Figure 4. Scalp distribution of the difference wave of interest following S2 (instructed change − free change). Maxima over central–parietal electrodes are consistent with the interaction effect shown in Figure 3 being driven by a modulation of the P300.

ERPs during the S1–S2 Interval

To further investigate differences in brain potentials elicited under conditions of free and instructed action selection, we investigated both ERPs elicited by the original instruction cue (S1) and preparatory components during the S1–S2 interval.

The stimulus-locked epochs to the instruction cue (S1) were averaged over short, change, and stay trials and referenced to a baseline of 200 ms prior to stimulus onset. The scalp topography of the difference wave (instructed – free) revealed maxima located over parietal cortex, suggesting modulation of the P300 (Fig. 5). The grand averages at Pz for free and instructed trials are displayed in the right-hand panel of Figure 5. Average voltages in 6 50-ms time windows from 300 to 600 ms were entered into a 2 × 6 ANOVA with factors choice (instructed, free) and time. A significant main effect of choice was found, reflecting the fact that free choices led to smaller P300 amplitudes than instructed choices ($F_{1,11}$ = 9.32, P < 0.05). As expected for a time-varying waveform, there was a main effect of time ($F_{5,55}$ = 4.33, P < 0.01). The choice × time interaction was also significant due to the 2 waveforms converging toward the end of the analyzed epoch ($F_{5,55}$ = 4.49, P < 0.05).

The CNV was defined as the slowly rising negativity in the 800 ms prior to S2 and is assumed to reflect nonspecific motor preparation. The maximal difference in the CNV was located at FCz, leading to the choice of this electrode for subsequent analysis (Fig. 6, left panel). To analyze the development of the CNV, average voltages in 8 equal time windows of 100 ms prior to S2 were entered into a 2-way ANOVA with factors of choice (instructed, free) and time (8 levels from –800 to 0 ms). CNV amplitudes were greater following instructed than free choices, yielding a main effect of choice ($F_{1,11}$ = 10.89, P < 0.01). There was a main effect of time ($F_{7,77}$ = 4.52, P < 0.05), and the interaction between choice and time was also significant ($F_{7,77}$ = 4.89, P < 0.01). This interaction arose because instructed choices produced a greater early CNV than

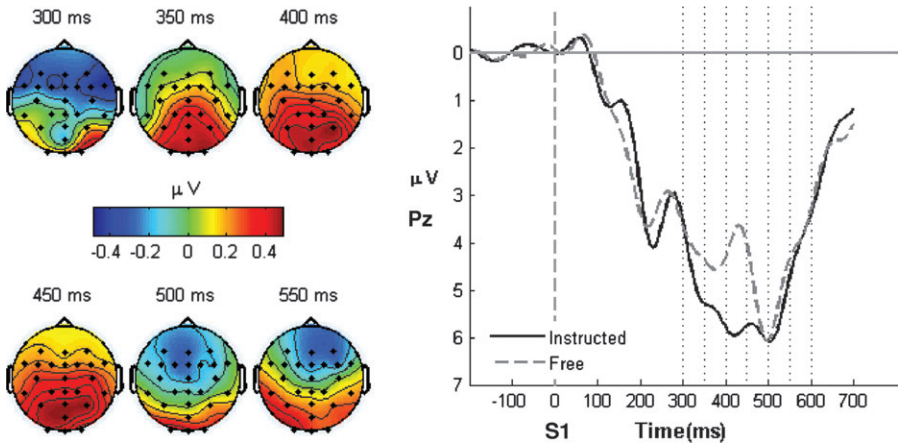

Figure 5. S1-locked ERPs and scalp maps. The left panel shows the scalp distribution of the grand average difference wave (instructed − free), revealing a maximum over parietal electrodes. The right panel shows the grand average ERPs sorted by choice condition (instructed, free) at electrode Pz, plotted against time relative to the onset of S1. The time windows used for entry into the choice × time ANOVA are indicated by broken lines.

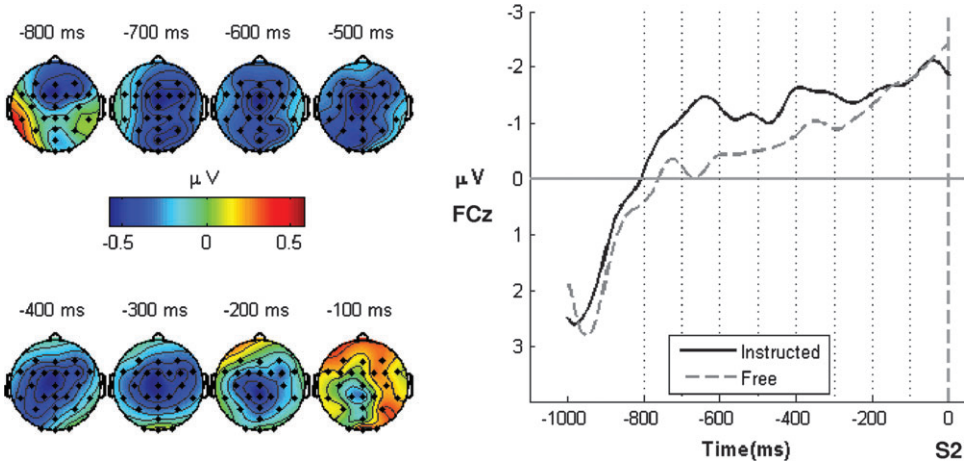

Figure 6. Preparatory potentials (CNV) prior to S2. The left panel shows the scalp distribution of the grand average difference wave (instructed − free), revealing a maximum over frontocentral electrodes. The right panel shows the grand average CNV sorted by choice condition (instructed, free) for electrode FCz. Time is relative to the onset of S2. Broken lines indicate the time bins used for entry into the time × choice ANOVA.

free choices. From Figure 6, it can be seen that the CNVs for the 2 conditions converge and there was no significant difference in the last 100 ms prior to S2 onset (t_{11} = 0.50, $P > 0.5$).

Motor-Related Amplitude Asymmetry Analysis

We considered the possibility that participants ignored the change/stay cue in free-choice conditions. The free-choice condition allows either button press to be made at the time of the go cue. Subjects might thus ignore the change/stay cue, make the response they had prepared at S1, and nevertheless perform the task successfully. This strategy would make the S2 change stimulus irrelevant in free trials and thus might be expected to lead to lower P300 amplitudes. However, if the change cue were ignored in free-choice trials, we would not expect any change in the lateralization of preparatory potentials indicating that movement preparation had switched from one hand to the other. We therefore computed motor-related amplitude asymmetry (MRAA, Gladwin et al. 2006), which is a sensitive measure of lateralized action preparation (De Jong et al. 2006).

The average mu-MRAA waveform for change trials is shown in the left-hand panel of Figure 7, with response hand defined by the final response made at the time of the go cue. (Note that negative values indicate greater cortical desynchronization, corresponding to greater motor preparation, contralateral to the response hand.) In both instructed and free trials, the mu-MRAA is positive at the start of the trial, indicating preparation of the opposite hand to that used to make the final response. At the time of the change cue, the desynchronization reverses lateralization, consistent with a switch from preparing to respond with one hand to preparing to respond with the other hand. This switch was analyzed by extracting the peak value in 100-ms time windows around the maximum asymmetries before and after the change cue and analyzing the data using a 2 × 2 ANOVA with factors of time period (pre-cue vs. post-cue) and choice type (free vs. instructed). The analysis showed a significant difference in MRAA between pre-cue and post-cue ($F_{1,11}$ = 29.2, $P < 0.001$), no main effect of choice type ($F_{1,11}$ = 0.037, P = 0.85), and no

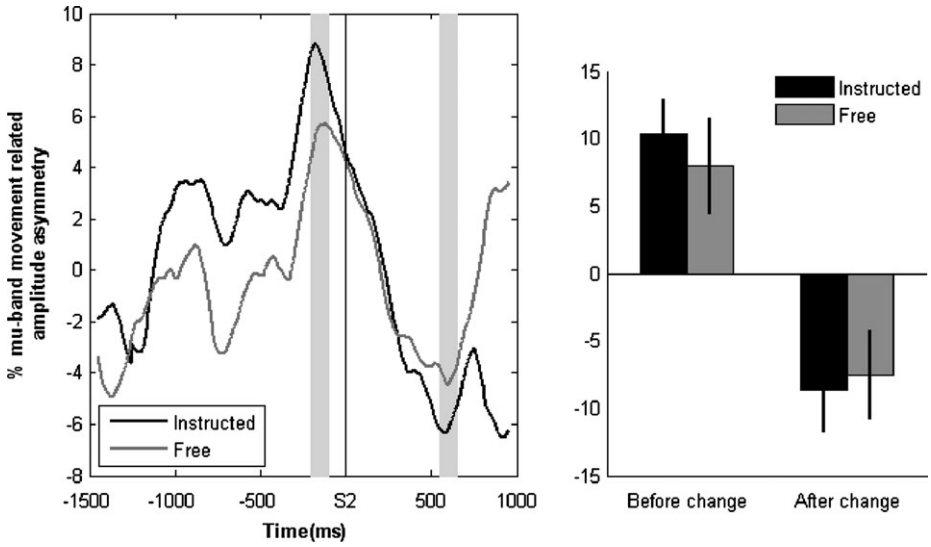

Figure 7. MRAA in change trials. The left panel shows the time course of the normalized MRAA in both instructed and free trials in the mu band (9–13 Hz). Time is relative to the onset of the change cue. The gray panels indicate the time bins used for statistical analysis of the reversal. The right panel displays the mean peak amplitudes (±standard error of the mean) extracted from these time windows.

interaction ($F_{1,11} = 0.249$, $P = 0.63$). Planned comparisons using 2-tailed 1-sample *t*-tests against 0 confirmed significant lateralization of the mu-MRAA in the predicted directions both before (instructed, $t_{11} = 4.21$, $P < 0.01$; free, $t_{11} = 2.29$, $P < 0.05$) and after (instructed, $t_{11} = 2.77$, $P < 0.05$; free, $t_{11} = 2.34$, $P < 0.05$) the change cue (Fig. 7, right panel).

Discussion

The scientific study of free choice has largely eluded neuroscience because the methodological requirement for experimental control seems incompatible with the concept of unconstrained choice that is under study. In the experiment presented here, we studied the status of endogenous action selection by examining neural activity associated with modifying choices in response to a cue requiring a switch between 2 alternative action plans. Participants were either instructed which hand to prepare to respond with or were given a free choice. Following a short delay, a second cue (S2) indicated whether to execute, change, or maintain the selected action plan. In the latter 2 trial types, a third cue was presented after a second short delay, indicating that the response should then be executed. The delay periods between cues enabled separation in time of the processes of action selection, reprogramming or updating, maintenance, and execution, allowing independent analysis of event-related brain potentials (ERPs). We found that P300 amplitudes in response to a change cue were greater following reprogramming of an instructed choice than a free choice. One of the most influential interpretations of the P300 relates it to "context updating" (Donchin and Coles 1988). Within this framework, the P300 differences we observe suggest that freely chosen actions may be more flexible and modifiable than instructed plans. Previous comparisons of internally generated and externally triggered actions have emphasized activity in qualitatively different neural networks that converge onto a single action execution system, although this claim has been controversial in part due to a number of possible confounding explanations (Botvinick et al. 2001; Hadland et al. 2001). In contrast, our results suggest a quantitative difference in the underlying representations of free and instructed action plans, as revealed by the extent of covert updating required in response to unpredictable cues.

Our behavioral data showed that our task encouraged similar covert action preparation for both free and instructed choices. Short trials, in which a go cue unpredictably occurred at the time of S2, had lower RTs than an unprepared baseline condition, as did change/stay trials where participants reacted to the go signal. These results suggest that participants did indeed select an action following S1, prepared the appropriate response, and maintained it during the delay period. Importantly, RTs did not differ between free and instructed trials. This suggests that participants were equally prepared for free and instructed choices and moreover that the 2 types of choice did not differ in unspecific ways such as arousal, attention, or effort. However, despite similar levels of preparation on instructed and free-choice trials, neural responses to a cue requiring change or maintenance of ongoing movement plans were quite different in the 2 cases. The change/stay cue acted as a probe to examine how action plans are represented in free and instructed choices. To our knowledge, this is the first time the question of free versus instructed action selection has been studied in this manner, focusing on the reprogramming of an action rather than the initial selection process.

The greatest P300 amplitudes were found following instructed-change trials. In a recent fMRI study, Mars et al. (2007) reported that additional frontoparietal areas are recruited during covert response reprogramming compared with normal action selection, in agreement with this result. We found low P300 amplitudes when participants changed a freely selected response plan, producing a significant interaction between free/instructed choices and the change/stay cue. Indeed, there was a trend for greater engagement of P300-related processes when freely chosen action plans were maintained than when they were changed. An analysis of changes in lateralized action preparation around the time of the change cues suggested that these differences were not

simply due to subjects ignoring the change/stay cues in free-choice conditions. Rather, we found a significant reversal in lateralized movement preparation induced by the change cue in both free and instructed trials and no reliable difference between reversals in these 2 conditions. Our results are consistent with an intrinsic difference between the brain processes that maintain instructed and endogenous action plans. Previous work has found that activity related to action reprogramming is localized to the inferior parietal areas (Rushworth et al. 2001; Rushworth and Taylor 2006; Mars et al. 2007), thought to be one source of the P300 (Polich 2007; Corbetta et al. 2008). Thus, if the P300 is taken as an index of context updating (Donchin and Coles 1988), our results suggest that endogenous action plans have a higher flexibility than instructed plans. This is particularly interesting in regard to suggestions that the P300 has a role in linking perception to action (Verleger et al. 2005).

Our design additionally allowed us to look at brain potentials associated with the initial action selection and subsequent preparation of the action. These provide important information about the mechanisms of action preparation for different choice types. Following the initial cue specifying the response type (S1), larger S1-P300 amplitudes were seen in response to an instructed-choice cue than to a cue indicating a free choice. We cannot rule out a contribution of stimulus frequency to this P300 difference: The bidirectional, free-choice arrow was seen twice as frequently as either the unidirectional left arrow or the unidirectional right arrow. However, a study by Waszak et al. (2005), which balanced the stimulus exposure for free- and instructed-choice cues, obtained results comparable to ours. Moreover, both free and instructed-choice conditions were balanced for the meaning of the choice cues, if not for surface form, because free and instructed choice were equally likely. Therefore, we can assume that our P300 effect reflects a difference between free- and instructed-choice processes rather than a difference in the visual surface forms used to cue these choices. We additionally examined the effect of choice on the CNV, taken to be functionally equivalent to the readiness potential (Kornhuber and Deecke 1965) and reflecting motor preparation (Rektor 2000; Cunnington et al. 2003; Leuthold et al. 2004). Free choices produced smaller CNVs than instructed choices during the earlier part of the preparation interval (see Fig. 6).

These data suggest that free-choice cues did not produce the same level of rapid "automatic" visuomotor processing associated with an instruction to perform a specific response. The smaller P300 and later CNV for free-choice trials are both consistent with endogenous selection between alternative actions taking longer than stimulus-based selection. Toward the end of the delay period, however, the CNV converges for both instructed and free trials, indicating that final levels of motor preparation are the same in free and instructed trials as the second visual cue becomes imminent. This is in agreement with the similar short-trial RTs for the 2 conditions, indicating similar levels of final motor preparation. Overall, the pattern of RTs, CNV, and MRAA suggests that participants prepared equally for free and instructed choices. Although the 2 conditions did not seem to differ in level of preparation, they do result in differential neural representations, as shown by the differential P300 responses to the S2 cue.

A recent computational model of action selection (Cisek 2006) proposes that multiple potential actions are represented in premotor cortex. Biases from visual stimuli and internal goal states are represented by posterior parietal cortex and prefrontal cortex neural populations, respectively. The model was supported by finding neurons in premotor cortex tuned to an action that was not selected and indeed not eventually executed (Cisek and Kalaska 2005). In the context of our experiment, instructed choices might correspond to the parietal biasing signal, whereas endogenous choices might correspond to the prefrontal biasing signal. The endogenous bias during free choices would presumably be weak relative to the stimulus-based biasing signal for instructed choice. If endogenous biasing signals are weak, both alternative actions might be prepared and produce preparatory depolarization of motor cortical areas. Strong mutually inhibitory links within and between the motor cortices ultimately force the system to a decision in favor of one action or the other. If one cortical representation becomes slightly more active than the other, perhaps simply because of randomness in neural firing, mutual inhibition ensures a winner-takes-all effect.

The dlPFC is one possible source of the biasing signal in free choice. This area is activated in random sequence generation (Jahanshahi et al. 2000) and voluntary action (Frith et al. 1991; Passingham 1993; Jahanshahi et al. 1995; Lau et al. 2004). This model is, however, likely to be a significant oversimplification and greater interaction between areas would be expected—for instance, feedback signals reflecting changes in visuomotor transformations have been found in the activity of parietal neurons (Zhang and Barash 2000), consistent with the role of the parietal cortex in coding intentions (Snyder et al. 1997; Anderson and Buneo 2002).

Our data have interesting parallels with that reported by Dorris and Glimcher (2004). They recorded from lateral intraparietal area (LIP) while monkeys made eye movements to obtain water rewards. In instructed-choice trials, LIP neurons were found to reflect the relative value of 2 response options. In contrast, during freely made choices in a mixed-strategy game, the firing of LIP neurons encoding each response was more finely balanced. Despite our study not including an explicit reward component, our instructed trials presumably involve motivation to avoid incorrect responding in a way that free-choice trials do not. This motivational influence might boost biasing signals, resulting in stronger specificity of instructed choices, seen as greater S1-P300 and early CNV in our data. Conversely, in free-choice trials, multiple action representations are maintained in balance until a much later stage in the motor hierarchy because no one action is more desirable than any other. Free choices would thus be weakly held or at least weakly discriminative in the sense that the difference between activation levels for alternative actions is small relative to instructed choice. This balance has the advantage of allowing greater flexibility: A weakly held selection is easily changed.

In summary, we used an external change cue to force a switch between a prepared action plan and alternative. We used this method to investigate the neural basis of free selection and, in particular, to compare the difference in updating action representations following free and instructed action selection. We found that the neural processes related to the updating of the action plan differ. Free choices led to a lower amplitude P300 in response to change cues, in comparison to instructed choices. This did not merely reflect reduced preparation, lower arousal, or decreased attention to

the cue in free-choice conditions: Overt behavior measured with RTs was equivalent for the 2 choice conditions, as was the CNV prior to the change cue, and the reversal of motor lateralization triggered by the change cue. Rather, our results are consistent with the idea that when people freely choose between action alternatives, they do not in fact strongly commit to one action over another. In free selection, multiple possible action choices may be developed in parallel and may remain available until a late stage in the preparation process. These results are perhaps surprising given the traditional view that endogenous choices are both epistemologically and phenomenologically strong and incontrovertible (Horgan et al. 2003). This apparent weakness of endogenous choices has the important advantage that internally generated action is highly flexible. There is an obvious survival value to changing one's action plans rapidly and easily, avoiding the difficulty and time cost associated with countermanding an instructed choice (Nachev et al. 2005). Indeed, the ability to flexibly adjust voluntary action decisions in complex contexts is suggested to be a major component of intelligence (Thorndike 1911).

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Address correspondence to Stephen M. Fleming, Wellcome Trust Centre for Neuroimaging, 12 Queen Square, London WC1N 3BG, UK. Email: s.fleming@fil.ion.ucl.ac.uk.

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