Introduction

Perception of effort, the conscious sensation of how heavy and strenuous a physical task is (Borg, 1998), is an important aspect of our subjective experience of volition. It provides information about task difficulty, is involved in the adaptive expenditure of energy, and contributes to the feeling of conscious will (Preston & Wegner, 2009). Nonetheless, little is known about the neurophysiology of perception of effort. It is thought that the signal underlying perception of effort arises in the brain from corollary discharges of the central motor command. This corollary discharge theory suggests that perception of effort should be significantly correlated with the magnitude of central motor command. However, very little direct evidence exists that perception of effort indeed correlates with movement-related brain activity (Barry & Enoka, 2007; Enoka & Stuart, 1992).

Our study published in Psychophysiology was designed to provide the first neurophysiological evidence in support of the corollary discharge theory of perception of effort (de Morree, Klein, & Marcora, 2012). We used two experimental manipulations to vary central motor command and perception of effort during a simple motor task: unilateral weight lifting with the elbow flexors. We asked our participants to lift a light and a heavier weight with a fatigued and a nonfatigued arm. The elbow flexor muscles of the fatigued arm were weakened using an eccentric fatiguing protocol. Lifting the heavier weight would require a higher central motor command to the muscles than lifting the light weight and lifting the weights with the fatigued arm would require a higher central motor command than lifting the weights with non-fatigued muscles. Perception of effort was expected to increase in parallel with central motor command.

To measure perception of effort, we used the Rating of Perceived Exertion (RPE) scale (Borg, 1998). To measure central motor command, we used the EEG-derived Movement-Related Cortical Potential (MRCP). The amplitude of this potential reflects the magnitude of activity in motor areas of the brain. It can be measured by averaging EEG activity time-locked to the onset of voluntary muscle contractions (Shibasaki & Hallett, 2006). There is consensus that the main generator sources of the MRCP are the presupplementary motor area, the supplementary motor area, the premotor cortex, and the primary motor cortex (Deecke & Kornhuber, 2003; Ikeda & Shibasaki, 2003; Shibasaki & Hallett, 2006). The amplitude of the MRCP can therefore be considered a direct neurophysiological measure of central motor command.

Methods

We present data of 16 healthy male participants (aged 27 ± 7 years; mean, SD) who volunteered to visit our laboratories on two occasions. The first visit was for familiarisation and the second was the experimental session. Participants were randomly assigned to have either their right or their left arm fatigued. The fatiguing protocol was completed on an isokinetic dynamometer. Participants were required to maximally resist elbow extensions generated by the dynamometer. Contractions were repeated until a 35% strength loss was reached. After the fatiguing protocol, participants performed a weight lifting protocol while EEG and biceps brachii EMG were recorded. This part of the experiment took place in a Faraday cage to minimise electrical noise and distraction. Participants sat on a chair with their arms on supports that were positioned next to their waist with cushions under their elbows. They repeatedly lifted a handheld dumbbell in a set rhythm, each time touching a flexible ruler placed 2 cm above the dumbbell (Figure 1).

Fig. 1: Experimental set-up of the weight lifting protocol.

The weight of the dumbbell was either 20% or 35% of the individual’s maximum. Participants fixed their gaze on a fixation cross presented at eye level on a 17” monitor connected to a PC. E-Prime 1.2 was used to present the rhythm for lifting the weights. Beeps were presented at a rate of 1 s^-1. Rest periods were indicated by 6 low tone beeps and the cues to raise and lower the weight were two high tone beeps, resulting in lifts that lasted ± 2 s in total. Participants were required to lift the same two absolute weights with the fatigued arm and the nonfatigued arm, giving a total of four blocks: light fatigued, heavy fatigued, light nonfatigued, and heavy nonfatigued. The blocks were presented in a random order. Each block consisted of 50 trials. After every set of 10 lifts, the RPE scale appeared on the screen and participants rated the average effort experienced during those 10 lifts.
Electrophysiological recording

An elastic cap with a chin strap (EasyCap GmbH, Herrsching, Germany) was used to record EEG from 62 Ag/AgCl sintered ring electrodes using Abralyt high-chloride (10%) abrasive electrolyte gel (EasyCap GmbH) as a conducting agent. The same gel was used to abrade the skin under the electrodes. Two infraorbital electrodes were located about 2 cm vertically below each eye. All channels were referenced to a reference electrode positioned at Cz, while an electrode positioned at FPz served as ground. Electrode impedances were kept below 5 kΩ. The EEG was recorded at 1000 Hz with two DC amplifiers (BrainAmp DC, Brain Products GmbH, Gilching, Germany; bandwidth DC-1000 Hz, 16 bit A/D converter) and data were recorded using BrainVision Recorder 1.03.0003 (Brain Products GmbH). The sampling frequency of 1000 Hz was selected based on the requirements for EMG recording and analysis (Hermens et al., 1999), because we used the same amplifiers to record two unipolar surface EMG signals from the biceps brachii muscles.

Data analysis

Measuring EEG during strenuous exercise means that extra care needs to be taken during artefact removal, and a relatively high percentage of rejections should be expected. The specific artefacts related to exercise that might contaminate EEG data are mainly those related to facial and jaw muscle activity (de Morree & Marcora, 2010) and transpiration. In our study, we tested 21 participants in total. We had to exclude data of 5 participants due to excessive artefacts caused by facial and jaw muscle activity, transpiration, and eye blinking.

Data were analyzed using BrainVision Analyzer 2.0.1 (Brain Products GmbH). EEG data were filtered with a 0.05-40 Hz, 24 dB per octave bandpass filter and EMG data were filtered with a 20-400 Hz, 24 dB per octave bandpass filter. Correction of eye blink, eye movement, ECG, EMG, and single electrode artefacts was accomplished separately for each participant by subjecting the EEG data to an independent component analysis (Jung et al., 2000), identifying components related to these artefacts by their topography and shape, and removing them from the data. EEG data were re-referenced offline to the average reference and EMG signals were converted into bipolar, single-differential signals. EMG onset and offset were determined for each trial by visual inspection.

Subsequently, data were segmented from 2 s before until 4 s after EMG onset. Following this, a further lowpass filter was applied to the EEG data with a cut-off frequency of 5 Hz (which did not affect the shape and components of the MRCP). All trials were visually inspected, and trials containing any residual artefacts were excluded from further analyses. On average, 77 ± 9% (range: 60-94%) of the trials were retained after artifact rejection. Trials were then baseline corrected (baseline −2 · −1.5 s). Subsequently, average amplitudes were calculated for four periods (readiness potential: −1.5 · −0.5 s, weight raising: 0 · 1 s, weight lowering: 1 · 2 s, and recovery: 2 · 4 s) for each individual for each block. These average MRCP amplitudes were used for statistical analysis. Grand averages were obtained by averaging the waveforms of all participants within the blocks.

Results

As expected, RPE increased significantly with weight and with muscle fatigue (Figure 2). Moreover, we found significant effects of both the weight and the muscle fatigue manipulations on MRCP amplitudes (Figure 3). The only MRCP component that showed an increase in amplitude with both manipulations was MRCP amplitude during the weight raising period at electrode Cz. Correlational analysis confirmed statistically that MRCP amplitude during weight raising at electrode Cz correlated significantly with RPE across both our experimental manipulations (Figure 4).

Conclusion

The results suggest that MRCP amplitude during movement execution is a neural correlate of perception of effort. This study was the first to provide direct neurophysiological evidence that MRCP amplitude during movement execution correlates with perception of effort. This finding supports the corollary discharge theory, which proposes that perception of effort is the conscious awareness of the central motor command to the muscles. Further studies using brain imaging and neuropharmacological techniques, are necessary to identify more precisely the brain networks and neurotransmitters underlying perception of effort.
References


