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Planning of visually guided reach-to-grasp movements: Inference from reaction time and contingent negative variation (CNV)

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Abstract

We performed electroencephalogram (EEG) recording in a precuing task to investigate the planning processes of reach-to-grasp movements in human. In this reaction time (RT) task, subjects had to reach, grasp, and pull an object as fast as possible after a visual GO signal. We manipulated two parameters: the hand shape for grasping (precision grip or side grip) and the force required to pull the object (high or low). Three seconds before the GO onset, a cue provided advance information about force, grip, both parameters, or no information at all. EEG data show that reach-to-grasp movements generate differences in the topographic distribution of the late Contingent Negative Variation (lCNV) amplitude between the 4 precuing conditions. Along with RT data, it confirms that two distinct functional networks are involved with different time courses in the planning of grip and force. Finally, we outline the composite nature of the lCNV that might reflect both high- and low-level planning processes.

Descriptors: Contingent negative variation, Reaction time, Grasping, Precuing

Human and nonhuman primates naturally position their hand and fingers for stable object grasp. Reach-to-grasp movements require the transformation of target-related visual information into a well-defined pattern of muscular contraction for grasping (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). Many authors consider "planning" to be a major stage among the processes that link perception to action (Andersen & Cui, 2009; Churchland & Shenoy, 2007; Crammond & Kalaska, 2000; Herbort & Butz, 2010; Hoshi & Tanji, 2007; Leuthold, Sommer, & Ulrich, 2004; Requin, Brener, & Ring, 1991; Riehle, 2005; Rosenbaum, 1980; Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007; Summers & Anson, 2009; Wise, 1985). The term "planning" often refers, more or less explicitly, to the concept of motor program (Ghez et al., 1997; Lépine, Glencross, & Requin, 1989; Leuthold & Jentzsch, 2009; Prabhu et al., 2007; Requin et al., 1991; Riehle & Requin, 1989; Rosenbaum, 1980; Rosenbaum et al., 2007; Summers & Anson, 2009; Wise, 1985). According to this concept, kinematics (e.g., direction, extent, and velocity) and kinetics (e.g., muscle activity, forces, and joint torques) parameters are specified before movement execution to form a program (or plan). The program is then translated into a motor command that controls muscle activity (Keele, 1968; Rosenbaum, 1980).

The precuing paradigm (Rosenbaum 1980, 1983) has been commonly used to characterize the processes related to the planning of distinct movement parameters (Bock & Eversheim, 2000; Favilla & De Cecco, 1996; Lépine et al., 1989). In the precuing reaction time (RT) task, a preparatory signal (or precue) provides advanced information about one or several parameters of a movement (e.g., direction, amplitude, or force) that has to be executed as fast as possible after an imperative GO signal. It is assumed that the precued parameter(s) are planned during the preparatory period (PP; i.e., the delay between the precue and the GO) and not during RT. According to Rosenbaum (1980), variations of RT in the precuing paradigm inform about the times necessary to specify distinct parameters, whether they are specified serially or in parallel and in which order they are specified. However, RT is only the final product of a long chain of covert processes that link stimulus to response. The reliability of inferences based exclusively on RT has been severely criticized because this indirect measurement is inappropriate to disentangle the complex mechanisms involved in movement planning (Goodman & Kelso, 1980; Requin et al., 1991; Zelaznik, 1978). To compensate for this weakness, numerous studies enhanced the precuing paradigm with a psychophysiological approach based on electroencephalogram (EEG) event-related potentials (ERPs; Meyer, Osman, Irwin, & Yantis, 1988; for a review, see Leuthold et al., 2004).

Most of these ERP studies examined the Contingent Negative Variation (CNV; Walter, Cooper, Aldridge, McCallum, & Winter, 1964), a sustained EEG negativity recorded during the PP.

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PSYCHOPHYSIOLOGY

When the PP is long enough, the CNV can be subdivided into two components: the early CNV (eCNV) and the late CNV (lCNV; Rohrbaugh & Gaillard, 1983). The lCNV has a centro-parietal distribution with maximum amplitude on the vertex (electrode Cz) and starts 1–1.5 s before the GO for fixed PP. lCNV is considered to be an index of motor planning, as it is preferentially elicited in motor tasks and strongly influenced by motor variables (Bareš, Nestrašil, & Rektor, 2007; Prescott, 1986; Rohrbaugh & Gaillard, 1983). Typically, RT decreases and lCNV amplitude increases with the amount of advanced information. This classical precuing effect on lCNV amplitude is approximately the same on all electrodes where a lCNV is present. These observations were validated for a number of kinematics and kinetics parameters such as movement direction (Jentzsch, Leuthold, & Ridderinkhof, 2004; Leuthold, Sommer, & Ulrich, 1996; MacKay & Bonnet, 1990; Wild-Wall, Sangals, Sommer, & Leuthold, 2003), force at a single joint (MacKay & Bonnet, 1990; Ulrich, Leuthold, & Sommer, 1998), movement duration (Leuthold & Jentzsch, 2009; Vidal, Bonnet, & Macar, 1995), movement amplitude (Leuthold & Jentzsch, 2009), and effectors (Jentzsch et al., 2004; Leuthold et al., 1996; Ulrich et al., 1998; Wild-Wall et al., 2003). Leuthold et al. (2004) interpreted the inverse relationship between RT and CNV in the framework of a "dual-process model of motor preparation." According to this model, movement planning is achieved by successive stages of information processing.

The first stage is reflected in lCNV amplitude. It would specify each movement parameters independently because each parameter, when precued alone, increases lCNV amplitude. The movement parameters would also be specified in an abstract, "muscle-unspecific" manner. Indeed, lCNV amplitude increases even when the precued parameters are insufficient to plan which muscles will be required to perform the movement. For instance, a force precue increases lCNV amplitude even in the absence of a direction precue that specifies if the movement will involve activation of the flexor or extensor muscles (Ulrich et al., 1998). Finally, lCNV modulations suggest a parallel organization of the planning processes for the different movement parameters (Ulrich et al., 1998). The neural activity underlying these parallel processes would sum up during PP and result in a larger increase in lCNV amplitude when two parameters are precued compared to one. Leuthold et al. (2004) assumed that this first stage in movement planning corresponds to the shaping of a motor program by higher order motor areas (supplementary motor area [SMA] and cingulated motor area [CMA]) and might explain the precuing effect observed on RT.

The second stage corresponds to the implementation of the motor program into a muscle-specific motor command in premotor areas (PMAs) and the primary motor cortex (M1; Leuthold & Jentzsch, 2001). This assumption is based on the measurement of another ERP: the lateralized readiness potential (LRP). The LRP quantifies the asymmetrical distribution of EEG signals between the two hemispheres. LRP has its physiological origin located within M1 (DeSoto, Fabiani, Geary, & Gratton, 2001; Kristeva, Cheyne, & Deecke, 1991; Leuthold & Jentzsch, 2002), and its onset would reflect the time of hand motor activation within this area (Gratton et al., 1990; Kristeva et al., 1991). The LRP can be recorded during the PP when the subject knows in advance which hand to use (Kutas & Donchin, 1980). Thus, the LRP is used as a tool to detect the onset of hand motor planning (Masaki, Wild-Wall, Sangals, & Sommer, 2004). Ulrich et al. (1998) suggested that, in contrast to the lCNV, the motor processes revealed by the LRP are muscle specific. The LRP amplitude increases only if the pattern of muscle activation required for movement execution can be planned in advance, that is, when all the movement parameters are precued together.

So far, almost all ERP studies of movement planning have focused on single-joint movements or simple key press responses (for a review, see Leuthold et al., 2004). Some authors investigated planning processes of more complex reaching (Leuthold & Jentzsch, 2009) or grasping and transport movements (van Schie & Bekkering, 2007). However, to our knowledge, planning of visually guided reach to grasp in a precuing reaction-time task was never investigated with an EEG approach. This is, in our view, a gap that has to be filled for several reasons. First, findings about single-joint movements can hardly be used to make direct inferences about the mechanisms underlying the control of a grasping movement. Indeed, grasping implies the control of multiple degrees of freedom and the interaction between multiple limb segments that do not occur in single-joint movement tasks (Kalaska, 2009). Second, grasping movements are everyday life actions, with more ecological value than single-joint movements. They are of particular interest in the growing field of brain–machine interfaces (BMI), because the hand is an essential effector for direct interaction with the outside world. Recent reports suggest that EEG-based BMIs have the potential to enable brain control of a simple neuroprosthetic hand (Logar et al., 2008; Müller-Putz, Scherer, Pfurtscheller, & Rupp, 2005). Finally, whereas the neuronal correlates of grasping movement have been extensively studied in monkeys (Brochier & Umiltà, 2007; Rizzolatti & Luppino, 2001), they are less precisely described in humans (Castiello, 2005). Most of our knowledge comes from neuropsychological (Jeannerod, 1988) and functional magnetic resonance imaging studies (Culham, Cavina-Pratesi, & Singhal, 2006) and more recently from transcranial magnetic stimulation (TMS) studies (Koch & Rothwell, 2009). These approaches suggest that in humans, like in monkeys, reach-to-grasp movements involve a large network of interconnected structures in the parietal and frontal lobes (Brochier & Umiltà, 2007; Castiello & Begliomini, 2008; Rizzolatti & Luppino, 2001). Virtual lesions induced by TMS reveal that this cortical network is differentially involved for the control of distinct reach-to-grasp movement parameters. In particular, a temporal dissociation between planning processes for hand shaping and grip force scaling is observed when TMS is applied over the anterior intraparietal area (AIP), a parietal structure closely involved in reach-to-grasp movement (Davare, Andres, Clerget, Thonnard, & Olivier, 2007). Complementary to TMS and other approaches, EEG provides a quantitative measure of the whole brain's electrical activity and reveals the time course of brain activity modulations throughout movement planning and execution. It is only through the use of converging techniques with different characteristics that we might fully understand how the human brain controls the grasping function (Castiello & Begliomini, 2008).

This article has two main objectives: The first one is to investigate whether RT and CNV modulations in visually guided reach-to-grasp movements are consistent with the modulation reported by others in single-joint movements. The second objective is to provide deeper insights into the neuro-functional basis of grasping in human. We used a precuing paradigm in which subjects had to perform a natural grasping movement toward a visually perceived target object. We manipulated two different movement parameters that could be jointly or independently

precued: the hand shape for grasping and the overall force required to pull the object.

Following the dual-process model of movement planning (Leuthold et al., 2004), we predicted a classical precuing effect on lCNV amplitude: lCNV should be larger when either the grip or the force are precued alone when compared to the situation in which no information is given in the precue. Moreover, if the planning processes related to hand position and force scaling are organized in parallel, lCNV amplitude should be the largest when both parameters are simultaneously precued. We also hypothesized that EEG may reveal differential cortical activation for the control of grip and force, as these two parameters can be independently perturbed by TMS during movement preparation (Davare et al., 2007).

Methods

Participants

Fourteen subjects (5 men, age mean = 24 years, age range = 21 to 41 years) verbally attested to be right-handed, to have normal or corrected-to-normal vision, and to have no medical history that might interfere with the task. Subjects gave their informed consent according to the declaration of Helsinki. The experiment was performed under a license obtained from the ethics committee of the Aix-Marseille University.

Apparatus

Subjects sat in an adjustable chair in front of the experimental apparatus at a comfortable distance and height (Figure 1A). Two switches were located at the front and were used to initiate each trial. The target object was a parallelepiped (60 × 38 × 30 mm) located 13 cm away from the switches at 14 cm high and rotated 45° from the vertical axis. The object was attached to the anterior end of a low-friction horizontal shuttle. A Hall-effect sensor was used to measure object displacement over a maximal distance of 15 mm. Force sensitive resistance (FSR) sensors were used to measure contact forces on the four object sides. To optimize the quality of force measurements, the FSR were inserted between the object surface and thin stainless steel plates (1 mm thickness) on which subjects positioned their fingers for grasping. Inside the apparatus, a 200-g weight was attached to the posterior end of the shuttle by way of a string–pulley system. An electromagnet was used to add or remove an additional 500 g to the object weight (total weight = 700 g). The turning on or off of the magnet was undetectable by the subject. A purpose-built force gauge fitted with one FSR sensor was used to measure load force during object pull.

A CRT computer monitor (17-in.) stood behind the apparatus at 1 m viewing distance. Arbitrary cues were made up of five large LED-like signals and were displayed in the bottom center part of the screen to minimize the visual distance between the cues and the object. In this situation, subjects could grasp the object while keeping their gaze on the cue, that is, without the necessity of a vertical ocular saccade. Four red LEDs (13 mm diameter) were positioned in a virtual square (4° visual angle). In the middle of this square a yellow LED (8 mm diameter) was used as a fixation point (FP).

Task

We manipulated two movement parameters during the experiment: the hand shape to grasp the object and the overall force required to pull it. The illumination of the two left or right LEDs instructed the subject to use one of two different grips: a precision grip (PG), between the tips of the index finger and thumb, or a side grip (SG), between the tip of the thumb and the lateral surface of the index finger (Figure 1B). Illumination of the two bottom or top LEDs instructed the subject that pulling the object required a low (LF) or high (HF) force, respectively (Figure 1C). The grip and force cues could be combined to instruct the subject to perform one of the four different response types (Figure 1D).

Every trial followed the same sequence of events (Figure 2A). Subjects self-initiated the trial at their own pace by positioning their hands on the two front switches. Switches' closure triggered FP illumination. Five hundred milliseconds after FP onset the precue was illuminated for 200 ms. The preparatory period (PP) between the precue onset and the imperative GO signal lasted 3 s. The GO signal instructed the subjects to reach, grasp, and pull the object using the right hand. The subject had to hold the object for 1 s to complete the trial. A successful trial ended at the extinction of all LEDs and the appearance of a positive feedback

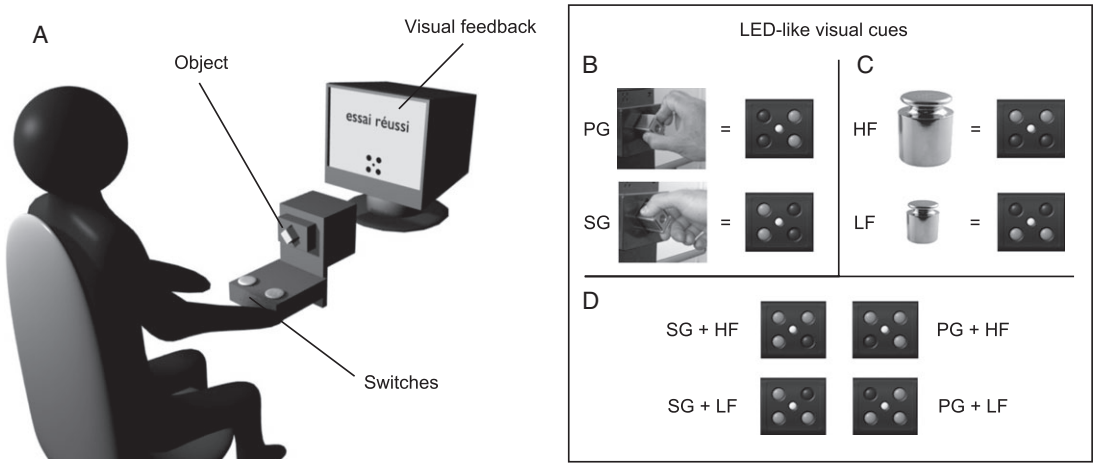

Figure 1. Experimental apparatus and visual cues. A: Schematic illustration of the experimental apparatus. B: The precision grip (PG) and the side grip (SG) and their corresponding visual cues. C: The two different force levels and their corresponding visual cues (HF: high force, LF: low force). D: The four combined cues associated with the four response types required in the task (PG+HF: precision grip and high force, PG+LF: precision grip and low force, SG+HF: side grip and high force, SG+LF: side grip and low force).

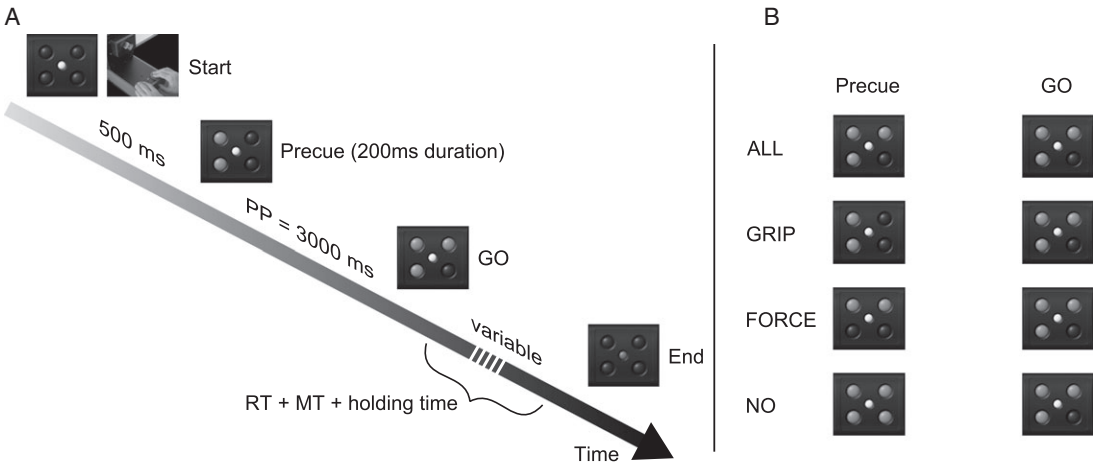

Figure 2. Trial sequence and precuing conditions. A: The different steps of a typical trial sequence. B: Example of visual cues when a side grip and a high force were required (SG+HF response type) in the four different precuing conditions.

message above the LEDs ("essai réussi," i.e., correct trial). The subject could then release the object and relax. Because CNV amplitude and RT are known to vary with PP duration (van der Lubbe, Los, Jaskowœki, & Verleger, 2004), we opted for a fixed PP duration (3 s). To prevent subjects anticipating the GO onset, trials in which the RT was below 150 ms were aborted. In addition, no-go trials were randomly presented. No-go trials were similar to other trials except that the GO did not appear. The subjects had to keep their hands on the switches and wait until a positive feedback appeared on the screen ("NOGO réussi," i.e., successful no-go), which indicated the end of the trial.

Subjects were instructed to react as fast as possible to the GO signal. Trials in which they reacted too slowly (RT > 700 ms) were aborted. They had to use both the grip and force cues to properly execute the movement. In particular, they were constrained to anticipate the object weight in order to keep the object displacement velocity within a narrow range (90 mm/s < velocity peak < 160 mm/s) for both the high and low weights. The trial was aborted when the subject's performance failed to match these task requirements. Flickering of the 4 red LEDs indicated trial failure and an error message specified the error type to the subject (Table 1). Subjects were instructed to avoid impeding movements such as eyeblinks, left hand movements, leg movements, or ocular saccades throughout the trial.

We used four experimental precuing conditions in which the precue provided full, partial, or no information about the movement parameters (Figure 2B). In the four conditions, the GO always provided all the information about grip and force.

Table 1. *The Different Error Types and Their Total Number across All Subjects (n = 14)*

Error type	No. (%)
Switch inappropriately released	33 (3.4%)
Too short RT (< 150 ms)	4 (0.4%)
Too long RT (> 700 ms)	31 (3.1%)
Too long MT (> 400 ms)	289 (29.4%)
Object grasped with the wrong grip	68 (7%)
Object prematurely released (holding time < 1 s)	0 (0%)
Object pulled too slowly	324 (33%)
Object pulled too fast	233 (23.7%)
Right switch released to reach the object in a no-go trial	0 (%)

- In the "ALL" condition, the precue provided information about grip and force (four different precues, PG+HF, PG+LF, SG+HF, SG+LF).
- In the "GRIP" condition, the precue provided only partial information about the grip (two different precues, SG or PG).
- In the "FORCE" condition, the precue provided only partial information about the force (two different precues, HF or LF).
- In the "NO" condition, the precue provided no information (all four red LEDs illuminated).

The subject had to wait for the GO to know which movement to perform.

Procedure

The experiment was divided into two sessions: a training session and an experimental session the following day. During the training session, task instructions were given to the subjects. The experimenter made a short demonstration and explained the different errors types. The subjects first performed several practice trials with no constraint on the RT and movement time (MT). Once the subjects felt comfortable in the task, they did 4 blocks of 16 trials (one per precuing condition) with all experimental constraints applied.

The following day, the subjects first performed another training set (4 blocks of 10 trials) before being prepared for EEG recordings. The experimental session per se was divided into two successive subsessions (S1 and S2). Each subsession was composed of four blocks of trials (one per precuing condition) presented in a pseudorandom order (e.g., GRIP, NO, ALL, and then FORCE). Within each block, the subjects had to perform 44 correct trials presented in a random order, 10 for each response type (PG+HF, PG+LF, SG+HF, or PG+LF) and four no-go trials (10%). All failed trials were reintegrated and presented randomly later in the block. Each subject performed a total of 352 correct trials (88 per precuing conditions) during the experimental session.

Data Recordings

EEGs were recorded from 62 Ag/AgCl electrodes mounted on an elastic cap (Waveguard Active Shield, Advanced Neuro

Technology [ANT], Enschede, the Netherlands) positioned according to the 10–20 method. The ground electrode was positioned over the frontal cortex. The EEG signals were recorded using a common average reference. Skin–electrode impedances were kept below 10 kΩ and checked after each block of trials. EEGs were amplified using a Refa8 high-density amplifier (ANT). No filtering was applied during acquisition. Bipolar electrodes were used to record electrooculogram (EOG) along with task-related analog signals (grip and load forces, object displacement). All signals were sampled at 1024 Hz with ASA 4.0 (ANT Software). A custom-written software in Labview 8.5 (National Instruments) was used to control the task and to measure RT, MT, and errors.

Data Analysis

All trials with a behavioral error (cf. Table 1) were excluded from the analyses. Because eye movements are known to provoke potential variation diffusing from corneo-retinal dipole to scalp (Hillyard & Galambos, 1970), correct trials with visually identified EOG artifacts (blink or saccade) were also excluded. Similarly, we excluded correct trials showing slow drifts in the signal (>100 μV) between the beginning of the trial and the GO onset because slow drifts might alter slow ERP potentials.

Behavioral data. The RT was defined as the time between the GO onset and the right switch release. The MT was defined as the time between the switch release and object contact (i.e., the reaching time). For each subject, RT and MT were averaged for precuing conditions (ALL, GRIP, FORCE, NO) and response types (PG+HF, PG+LF, SG+HF, SG+LF). We also computed the number of errors for each precuing conditions and response types. Force signals were filtered off-line with a 40-Hz low-pass Butterworth filter. They were averaged for response types time-locked to object contact in a 2400-ms analysis window (150 ms before to 2250 ms after object contact). The peak grip force was used as an index to statistically compare the amount of grip force applied by the subjects on the object. To assess how rapidly the subjects applied forces on the object, the rates of change of the grip and load forces as well as the object horizontal velocity were computed from the first derivative of the filtered data (Johansson & Westling, 1988). The peak grip force rate and load force rate as well as the peak velocity were used for statistical analyses.

Electrophysiological data. EEG signals were analyzed in a 3400-ms time window encompassing the whole PP (400 ms before cue onset to 200 ms after GO onset). For each trial and electrode, a baseline voltage was computed over a 400-ms time window preceding cue onset. This baseline was subtracted from the raw EEG signals trial by trial. EEGs were then averaged time-locked to GO onset for precuing conditions and response types. This averaging procedure was repeated for all electrodes and subjects. Our statistical analysis focused on the late part of the CNV. As in previous studies (Jentzsch et al., 2004; Leuthold & Jentzsch, 2009; Ulrich et al., 1998; Wild-Wall et al., 2003), we computed the average CNV amplitude in the last 200-ms window preceding GO onset when the lCNV amplitude is the largest. Difference voltage maps (see below, Figure 5A, bottom row) were calculated by subtracting the topographic map for the noninformative condition (NO, Figure 5A, top row) to the three informative conditions (ALL, GRIP, and FORCE, Figure 5A, top row). Visual inspection of the difference voltage maps and all individual electrodes revealed that groups of adjacent electrodes localized in a distinct region of the scalp were characterized by a similar precuing effect on lCNV amplitude. On the basis of these observations, we compared the precuing effects by pooling 14 electrodes in four regions of interest with approximately the same number of electrodes in each of them (Figure 5B, bottom right). We selected a mid-fronto-central cluster (MFC, electrodes Cz and FCz); a controlateral fronto-central cluster (CFC, electrodes C1, C3, FC1, and FC3), and a parietal cluster (P, electrodes CPz, Pz, P1, and P2). Although difference voltage maps only revealed a marginal precuing effect over the ipsilateral side of the scalp, we still included an ipsilateral fronto-central cluster in the analyses (IFC, electrodes C2, C4, FC2, and FC4) to statistically assess differences in precuing effects between the two hemispheres. The four clusters covered approximately the entire zone of the scalp where the lCNV was present.

Statistical Analysis

For RT, MT, errors, and forces, we used a three-way repeated measures analysis of variance (ANOVA) with precuing conditions (ALL, GRIP, FORCE, NO), grip (PG, SG), and force (HF, LF) as within-subject factors. Prerequisite assumptions for repeated measures ANOVAs, normality and sphericity, were systematically checked using Shapiro–Wilk's test and Mauchly's test, respectively. When the normality assumption was not met, we used a nonparametric test, if possible, or data transformation, if not. When the sphericity assumption was not met, we used a corrected p value (Greenhouse & Geisser, 1959) and reported the corresponding ε value. Post hoc procedures were performed with Tukey's test.

A four-way repeated measures ANOVA was used to analyze lCNV amplitude with clusters (MFC, CFC, IFC and P), precuing conditions (ALL, GRIP, FORCE, NO), grip (PG, SG), and force (HF, LF) as within-subject factors.

The Clusters × Precuing Conditions interaction was significant (see Results), revealing a difference in the spatial distribution of potentials between the experimental conditions. These topographic variations may indicate qualitative differences in the generators (i.e., generator orientation, location, number, and/or relative strength) responsible for the signal recorded on the scalp. To test this hypothesis, we statistically compared the topographic distribution of lCNV amplitudes between the four precuing conditions following data normalization using the vector length method (McCarthy & Wood, 1985). This method ensures that interaction effects are not due to overall amplitude differences between subjects and conditions. It is a well-recognized approach to compare topographic distributions (Tunney, Fernie, & Astle, 2010) and is suitable for EEG signals recorded with a common average reference (Jing, Pivik, & Dykman, 2006).

In addition, we investigated the topographic differences in more detail by performing, on each cluster individually, a three-way repeated measures ANOVA with precuing conditions (ALL, GRIP, FORCE, NO), grip (PG, SG), and force (HF, LF) as within-subject factors. This approach is subject to a Type I error rate inflation with the number of tests performed (i.e., multiplying the number of tests increases the risk of observing significant effects by chance). To avoid this risk, we corrected the .05 α threshold using the Bonferroni–Holm adjustment. This adjustment is less conservative than the typical Bonferroni adjustment and suitable for EEG/MEG data (Vecchiato et al., 2010).

Finally, we analyzed in more detail the precuing effect within the parietal cluster to assess if the planning of grip and force involves two spatially segregated networks within the parietal region, as proposed by Davare et al. (2007). We statistically compared precuing effects for each electrode within this cluster using a four-way repeated measures ANOVA with electrodes (CPz, Pz, P1 and P2), precuing conditions (ALL, GRIP, FORCE, NO), grip (PG, SG), and force (HF, LF) as within-subject factors.

Results

Subsessions

The relatively high number of error trials (an average of 20% errors per subject) indicates that the task was difficult to perform. Therefore, we first compared mean RTs, MTs, and number of errors between the two experimental subsessions (S1 vs. S2) to detect a possible learning effect during the course of the experiment. A four-way repeated measures ANOVA was used on RT and MT with sessions (S1, S2), precuing conditions (ALL, GRIP, FORCE, NO), grip (PG, SG), and force (HF, LF) as within-subject factors. There was no significant difference between the two subsessions, RT: $F(1,13) = 0.636$, $p = .44$; MT: $F(1,13) = 4.147$, $p = .06$. For each error type the Wilcoxon signed-rank test for matched pairs yielded no significant differences in error number between S1 and S2 (all $ps > .05$). Therefore, because behavioral performances did not differ significantly between the two subsessions, the behavioral and electrophysiological data from S1 and S2 were pooled together for all subsequent analysis.

Behavioral Data

RT. Results obtained on RT are illustrated in Figure 3A. The three-way repeated measures ANOVA revealed a significant main effect of precuing conditions, $F(3,39) = 67.582$, $p < .01$, $\varepsilon = .49$. A post hoc procedure revealed the following order: ALL (318 ms) < GRIP (352 ms) < FORCE (400 ms) < NO (431 ms), all $ps < .01$. This order is observed for all subjects. We also observed a significant main effect of grip, $F(1,13) = 17.101$, $p < .01$ and a Grip × Force interaction, $F(1,13) = 16.884$, $p < .01$. This result reveals that subjects reacted faster to execute a precision grip than a side grip (369 ms for PG vs. 381 ms for SG) and that the difference between PG and SG (12 ms) was larger for the high force (15 ms) than the low force (9 ms). There was no main effect of force, $F(1,13) = 0.625$, $p = .44$, and no other significant interaction (all $ps > .05$).

MT. Results obtained on MT are illustrated in Figure 3B. There was no significant main effect of precuing conditions, $F(1,13) = 0.651$, $p > .59$. Therefore, the MT was not influenced by the number and the nature of advanced information provided by the cue. The main effect of force, $F(1,13) = 41.093$, $p < .01$, reveals that movement was executed significantly faster when the object was heavy rather than light (284 ms for HF vs. 315 ms for LF). The main effect of grip was also significant, $F(1,13) = 24.500$, $p < .01$. The precision grip was executed faster than the side grip (288 ms for PG vs. 311 ms for SG). None of the interactions were significant (all $ps > .05$).

Errors. Results obtained on errors are illustrated in Figure 3C. Error data did not reach the normality assumption criteria. In order to apply the same statistical procedure as for RT and MT, we first performed a square-root transformation on the raw error data to reduce right skew and kurtosis. Square-root transformation is commonly used to reach normality assumption criteria when the variable is a count (Sokal & Rohlf, 1995). The main effect of precuing conditions was the only significant effect, $F(3,39) = 4.488$, $p < .01$. This result reveals that the NO condition in which the error number is maximal (315 for the NO condition) contained significantly more errors than, at least, the GRIP condition, in which the error number is minimal (177 for GRIP, 227 for ALL, and 263 for FORCE). Thus, subjects were both less accurate and slower to react in the NO condition than in the other precuing conditions. This latter observation suggests that the precuing effect observed on RT did not result from a speed–accuracy trade-off.

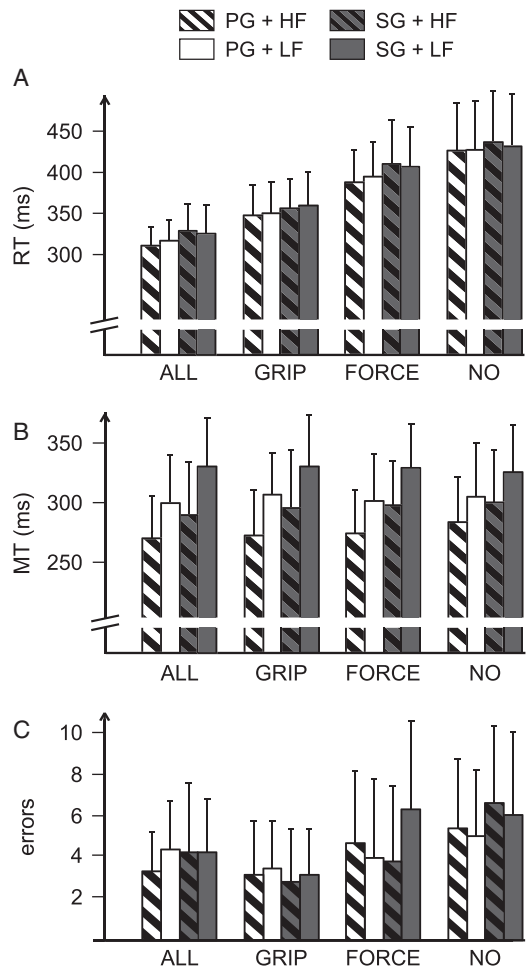

Figure 3. Behavioral results. Mean reaction times (A), mean movement times (B), and mean error number (C) as a function of precuing condition (ALL: full informative precue, GRIP: partial hand shape precue, FORCE: partial force precue, NO: noninformative precue) and response type (PG+HF: precision grip and high force, PG+LF: precision grip and low force, SG+HF: side grip and high force, SG+LF: side grip and low force). Error bars indicate standard deviation.

Forces. Figure 4 shows the average force and object position traces for one typical subject. The same three-way ANOVA procedure as for RT, MT, and errors was used to analyze, separately, grip force peaks, grip force rate peaks, load force rate

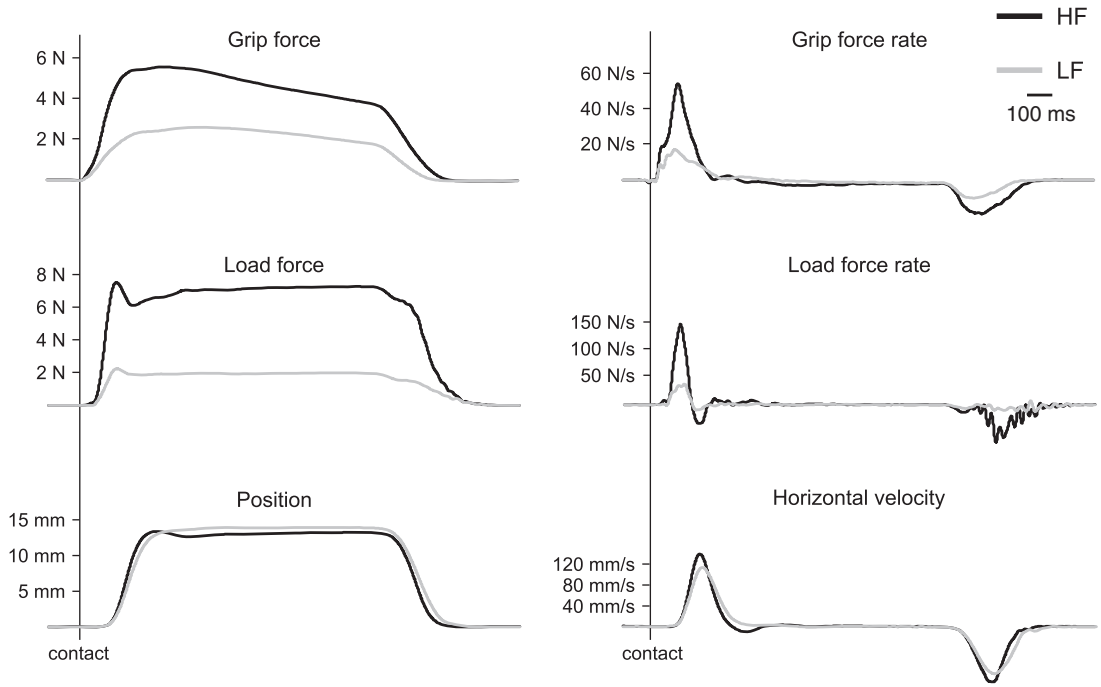

Figure 4. Force, object position, and velocity traces. Mean grip force, mean load force, and mean object position traces (left) and grip force rate, load force rate, and object horizontal velocity traces (right) for one typical subject as a function of the two different force levels (HF: high force, LF: low force). Traces are time-locked to object contact (vertical lines).

peaks, and object velocity peaks. Analysis revealed significant main effects of force, significant main effects of grip and Force × Grip interactions for grip force peaks, grip force rate peaks, and load force rate peaks (all $ps < .01$). Thus, grip force and load force were greater and applied faster when the object was heavy rather than light. This effect was more pronounced for SG than for PG. Grip force peak analysis yielded also a main effect of precuing conditions, $F(3,39) = 6.264$, $p < .01$. A post hoc procedure revealed that the NO condition was significantly different from ALL and GRIP ($ps < .01$). More force was applied on the object when no information was provided in advance. This was specific to HF as revealed by the significant Precuing Condition × Force interaction, $F(3,39) = 3.370$, $p = .03$. Analysis on object velocity peak revealed a significant main effect of force, $F(1,13) = 10.413$, $p < .01$, and grip factor, $F(1,13) = 8.369$, $p = .01$. Object velocity was greater when the object was heavy and when a SG was used for grasping.

In sum, RT decreased with the amount of advance information. In partial conditions in which information about a single variable was provided in advance, subjects reacted faster with advance information about grip rather than force. Moreover, subjects reacted faster when a PG was required, and this effect was even larger for HF movements. Force rates, object velocity, and MT varied neither with the type of advance information nor with their number. MT varied with response types: PG+HF < SG+HF < PG+LF < SG+LF. This was also the case for the peak grip force, peak grip force rate, peak load force rate, and peak velocity: SG+HF > PG+HF > SG+LF > PG+LF. In every precuing condition, subjects applied the grip and load forces faster to grasp the heavy object. Similarly, subjects applied more force and at a faster rate when using a SG. Finally, subjects used, on average, more grip force to grasp the object when no information was provided in advance.

Electrophysiological Data

Figure 5A (top row) shows topographic voltage maps of lCNV amplitude (average signal on a 200-ms window before GO onset). For all precuing conditions the lCNV was centro-parietally and bilaterally distributed and maximal at the vertex. The ANOVA showed a main effect of clusters, $F(3,39) = 5.717$, $p < .01$, which indicated that the lCNV amplitude was different across regions of the scalp. It is maximal on the MFC cluster as shown in Figure 5B (maximum at Cz, mean amplitude: -9.3 μV). The significant main effect of precuing conditions, $F(3,39) = 8.860$, $p < .01$, and the significant Cluster × Precuing Condition interaction, $F(9,117) = 2.001$, $p = .04$, indicated that the lCNV amplitude was modulated by the precuing conditions and that this modulation varied across the clusters (Figure 5B). Moreover, the clusters × precuing conditions interaction survived the vector length normalization, $F(9,117) = 2.331$, $p = .04$. The analysis performed on each cluster individually revealed that three main significant effects of precuing conditions survived the Bonferroni–Holm adjustment, MFC cluster: $F(3,39) = 8.042$, $p < .01$ ($\alpha_{adjusted} = .012$); CFC cluster: $F(3,39) = 5.108$, $p < .01$ ($\alpha_{adjusted} = .016$); P cluster: $F(3,39) = 3.906$, $p = .02$ ($\alpha_{adjusted} = .025$). The main effect of precuing conditions for the IFC cluster was not significant, $F(3,39) = 1.842$, $p = .19$ ($\alpha_{adjusted} = .05$), $\varepsilon = .55$. Post hoc procedures revealed the following orders:

- MFC: ALL (-8.9 μV) = FORCE (-8.6 μV) < GRIP (-6.9 μV) = NO (-6.4 μV).
- CFC: ALL (-4.1 μV) < FORCE (-2.1 μV) = GRIP (-1.9 μV) = NO (-1.4 μV).
- P: ALL (-3.9 μV) = FORCE (-3.8 μV) = GRIP (-4.0 μV) < NO (-1.6 μV).
- IFC: ALL (-4.4 μV) = FORCE (-3.9 μV) = GRIP (-3.7 μV) = NO (-3.1 μV).

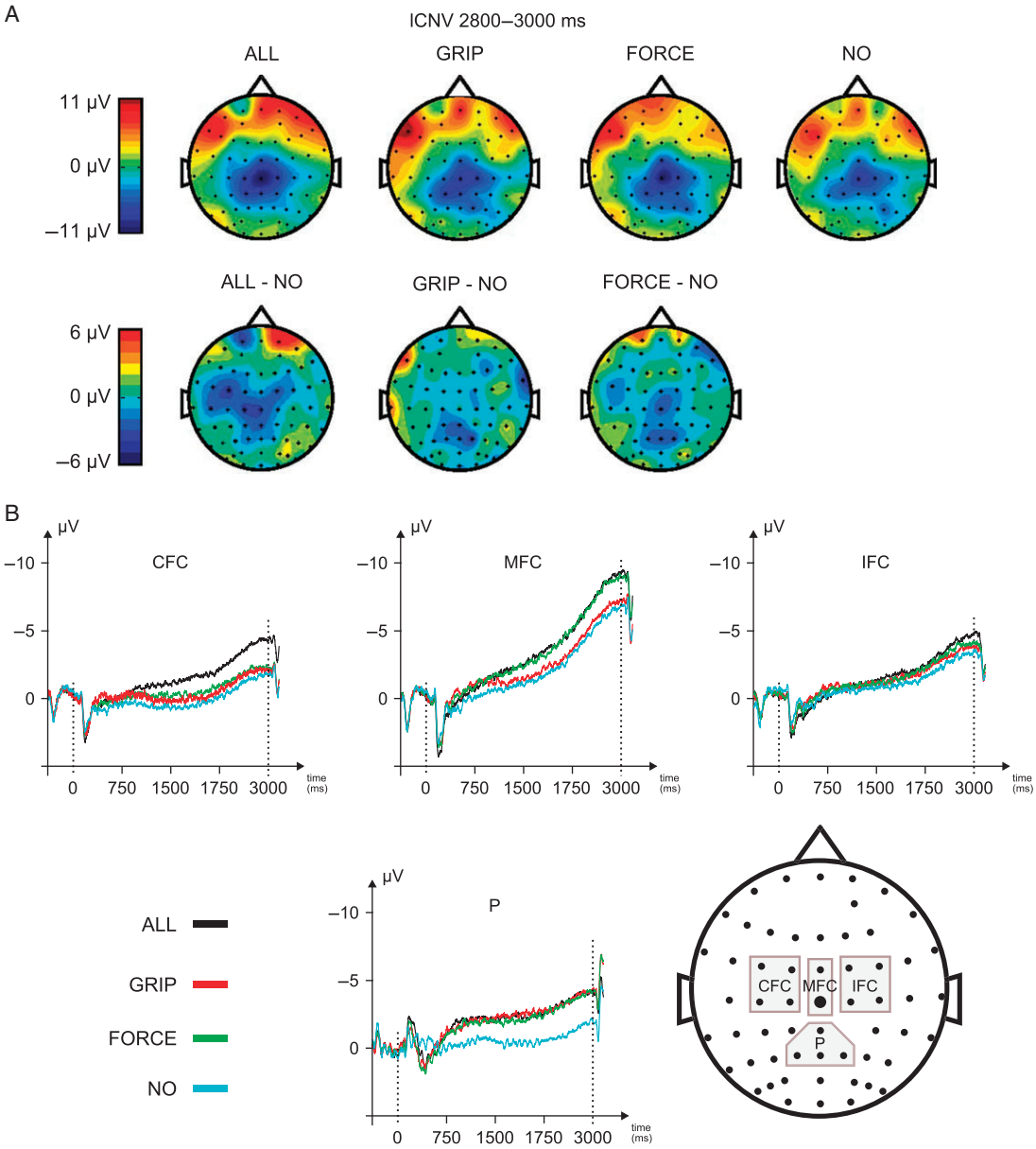

Figure 5. EEG results. A: The top row illustrates topographic voltage maps of the mean lCNV amplitude in the 200 ms preceding GO onset. The maps are averaged across all trials and subjects for each precuing condition. The bottom row illustrates difference voltage maps. The map for the noninformative condition (NO) was subtracted from the maps for each informative condition (ALL, GRIP, FORCE). Color transitions in the color scales represent 1 µV steps. B: Averaged CNV traces as a function of precuing conditions for the four regions of interest. The left and right vertical dotted lines represent precue and GO onsets, respectively. The head-shaped diagram at the bottom right shows the location of the four clusters and the electrodes (black dots) within each of them. The large dot represents Cz. MFC: mid-fronto-central cluster (electrodes Cz and FCz). CFC: controlateral fronto-central cluster (electrodes C1, C3, FC1, and FC3). IFC: ipsilateral fronto-central cluster (electrodes C2, C4, FC2, and FC4). P: parietal cluster (electrodes CPz, Pz, P1, and P2).

For all significant effects, $ps < .05$, and for all nonsignificant effects, $ps > .05$. These results confirmed that the precuing effects on lCNV amplitude illustrated in Figure 5B were different in the four clusters.

The between-electrode comparison within the parietal cluster revealed a main effect of electrodes $F(3,39) = 3.369$, $p = .03$. The lCNV amplitude was greater for CPz, which is closer to the vertex. The main effect of precuing conditions was also significant, $F(3,39) = 3.725$, $p = .02$, but the Electrode × Precuing Condition interaction did not reach significance, $F(9,117) = 0.512$, $p = .68$, $\varepsilon = .34$. These results indicate that all electrodes within the parietal cluster present a similar precuing effect.

Discussion

We used EEG recordings in a precuing reaction time task to study the brain mechanisms involved in the planning of natural grasping movements toward a visually presented object. Two parameters were precued jointly or independently: the grip to grasp the object and the overall force required for object pulling. We assessed how RT and CNV amplitude were modulated by the amount and type of advance information provided by the precue.

In term of behavioral performance, our results are in keeping with previous precuing studies (Goodman & Kelso, 1980; Lépine et al., 1989; Leuthold & Jentzsch, 2009; Leuthold et al., 1996;

MacKay & Bonnet, 1990; Riehle, MacKay, & Requin, 1994; Riehle & Requin, 1995; Rosenbaum, 1980; Ulrich et al., 1998; Wild-Wall et al., 2003). RT decreased with the amount of advance information. This result indicates that the subjects followed the task requirements and used the precue appropriately to react as fast as possible after the GO signal. MT was influenced by the type of response but not by the precuing conditions. Together, RT and MT reveal that the precued parameter(s) influenced selectively the processes preceding movement execution. Moreover, the MT variations demonstrate that the force was planned before movement onset. In particular, the fact that MT was significantly shorter in the high force than in the low force condition shows that the force was anticipated and not adjusted online using the sensory feedback at the skin–object interface. The force profiles during object pulling were also typical of anticipatory adjustments of contact forces (Johansson & Westling, 1988). As soon as the fingers touched the object, the grip and load forces were applied faster in HF than LF trials. As a result, the peaks grip force rate and load force rate were significantly greater for HF than LF trials. Also, the pulling time was, on average, shorter in HF than in LF trials. Altogether, behavioral performances strongly support the assumption that the subjects used the force cue to anticipate the object weight and to adjust its behavior to the task constraints.

EEG recordings revealed a typical lCNV with a centro-parietal distribution and maximal amplitude at the vertex (Cz). The main effect of precuing conditions shows that lCNV amplitude was dependent on the type of precue provided to the subject. Also, the Cluster $\times$ Precuing Condition interaction indicates that the precuing effect varied between clusters. The interaction was maintained after normalizing the data. Although this latter result should be interpreted with caution (Urbach & Kutas, 2002), it suggests that the topographic variations of the lCNV amplitude between precuing conditions are due to differential activations between neuronal generators and not to concomitant changes in the overall strength of the entire set of generators. In other words, at least two generators with distinct strength, orientation, and/or location would be required to produce the observed signal recorded at the scalp level. These topographic differences were analyzed in more detail for each cluster separately. Three of the four regions (MFC, CFC, P) showed a significant main effect of precuing conditions on lCNV amplitude. However, none of them presented the typical gradual increase of lCNV amplitude with the amount of advanced information as originally described for single-joint movements (Leuthold et al., 2004). Our results are now discussed in the framework of the "dual-process model of movement preparation" outlined by Leuthold et al. (2004).

Dual-Step Planning of Reach-to-Grasp Movements

The separate analysis of the precuing effect on each of the four clusters reveals some important features about the planning mechanisms involved in reach-to-grasp movements.

The lCNV amplitude recorded on the parietal region (P cluster) was significantly larger in all three informative precuing conditions (GRIP, FORCE, and ALL) than in the noninformative precuing condition (NO). No significant difference was found between the three informative precuing conditions. Several studies have already pointed out that the modulation of lCNV amplitude by specific motor variables is likely to reflect the activation of planning processes preceding movement onset (Bareš et al., 2007; Prescott, 1986; Rohrbaugh & Gaillard, 1983). In agreement with this hypothesis, the precuing effect on the parietal region suggests that the planning processes for the grip and force parameters have two main properties similar to those characterizing the first step of the dual-process model of movement preparation. First, these planning processes are independent, meaning that the planning of one parameter could occur without any information about the other. Indeed, each parameter when precued on its own evoked an increase in lCNV amplitude. This result agrees with nonhuman primate studies using intracortical recording and demonstrating the independent planning of kinematics and kinetics parameters (Alexander & Crutcher, 1990; Riehle & Requin, 1995). Second, the planning processes present muscle-unspecific properties as proposed by Ulrich et al. (1998). An increase in lCNV amplitude was observed before the subject actually knew which pattern of muscle activation was required to perform the task. This was the case in the FORCE condition in which the subject knew in advance the overall force required in the forthcoming movement but not if the force would be applied using a side grip or a precision grip. These interpretations raise two issues. First, it could be argued that the planning processes for force are not strictly muscle unspecific, as the set of muscles used to achieve the two hand positions broadly overlaps. In this context, the force cue could be used to plan the global level of muscle activation required for both precision and side grips. However, this hypothesis is unlikely, because these two hand positions are characterized by highly distinctive patterns of EMG activation in a large set of extrinsic and intrinsic hand muscles (Brochier, Spinks, Umiltà, & Lemon, 2004). Second, despite the increase in lCNV amplitude in the two partial precuing conditions (GRIP and FORCE) we did not observe a further increase in late CNV amplitude when both parameters were precued together (in the ALL condition). Ulrich et al. (1998) argued that the additive effect on lCNV amplitude with the amount of advance information reflects a parallel organization of movement planning processes. In our study, the lack of additive effect might be explained by a temporal shift in the planning processes for hand position and force. This view is supported by the study of Davare et al. (2007) showing a temporal dissociation for the processing of hand shape and force during the RT period. It is possible that a similar dissociation occurs for long PP (>2 s), during which the planning of a given parameter could occur earlier than the other. In consequence, the activity of these two processes would not sum up during the fully informative condition. This hypothesis would imply that the CNV shows temporally segregated precuing effects for the GRIP and FORCE conditions. Figure 5B shows that it was not the case. So, on the basis of our data, it is not possible to conclude whether motor planning processes follow a parallel or a serial organization.

On the central region (MFC cluster), the force precue increased the lCNV amplitude at the same level as the full-informative precue. Advance information about grip had no effect on the lCNV amplitude. This result suggests that the generator underlying the signal recorded on Cz and FCz is implicated in the advance processing of the force but not the grip parameter. This modulation of the lCNV differs from the typical precuing effect reported by others, that is, the gradual increase in lCNV amplitude with the amount of advance information (Leuthold & Jentzsch, 2009; for a review, see Leuthold et al., 2004). Despite the discrepancy with previous studies and in line with the results on the parietal region, the precuing effect on the central region

fits with the principles defining the first planning step of the dual-process model. Indeed, in this region too, the force precue when presented alone generated an increase in the lCNV amplitude. As argued previously for the parietal region, it indicates that lCNV might reflect abstract, muscle-unspecific processes. Moreover, because the grip precue does not influence lCNV amplitude on its own (GRIP) or in combination with the force precue (ALL), it further argues for the independence of the processes related to force and hand position. Together, results on the central region and the parietal region suggest that the planning processes are more distributed for force than for grip. Whereas a grip precue increased late CNV amplitude only in the parietal region, the force precue increased the lCNV amplitude in both parietal and central regions. This observation is consistent with findings showing that force-related planning processes are widely distributed across several motor regions (Riehle et al., 1994), including the left part of the AIP (Davare et al., 2007) and the anterior basal ganglia nuclei (Wasson, Prodoehl, Coombes, Corcos, & Vaillancourt, 2010). In contrast, grip-related processes seem predominantly restricted to the parietal-premotor network (Castiello & Begliomini, 2008; Davare, Andres, Cosnard, Thonnard, & Olivier, 2006; Davare et al., 2007; Jeannerod et al., 1995; Rizzolatti & Luppino, 2001). Davare et al. (2007) showed that the planning of grip and force involves two spatially segregated networks located within the parietal region: bilateral AIP for hand shape and left AIP for force scaling. This finding predicts that, over the parietal cortex, lCNV amplitude should show a bilateral increase in the GRIP condition and a stronger increase above the left compared to the right hemisphere in the FORCE condition. However, in our study, topographical differences for the GRIP and FORCE conditions were found between the parietal and mid-central clusters, whereas no difference was found within the parietal cluster. First, this discrepancy may be related to the fact that our work focused on the preparatory processes before the GO signal, whereas Davare et al. (2007) investigated the processes occurring during RT. Second, several areas of the posterior parietal cortex, including AIP, are known to be involved in grasping movements (Brochier & Umiltà, 2007; Fogassi & Luppino, 2005). These areas are likely to contribute in a different way than AIP to the modulation of the lCNV amplitude recorded over the parietal region. Despite the differences in the experimental protocol and the results, our study and the study of Davare et al. (2007) jointly argue for the involvement of partially separated cortical network for the planning of hand position and force.

In the controlateral region (CFC cluster), the lCNV amplitude was significantly larger for the full-informative condition only. It corresponds to the precuing effect usually observed in the LRP (Ulrich et al., 1998) and might reflect integration processes that take place within PMA (Beurze, Lange, Toni, & Medendorp, 2007; Hoshi & Tanji, 2000, 2006) and M1, which receives many cortico-cortical inputs from nonprimary motor areas, including the ventral premotor cortex (PMv; Dum & Strick, 2005; Prabhu et al., 2007), the dorsal premotor cortex (Dum & Strick, 2005; Koch et al., 2006), SMA (Dum & Strick, 2005), and the posterior parietal cortex (Koch et al., 2007). These integration processes would be activated only when all movement parameters are specified for the completion of the motor command. This situation occurs exclusively in the ALL precuing condition but not in the partial GRIP and FORCE precuing conditions. In this respect, the controlateral modulation of the lCNV amplitude seems to reflect the activity of the second, low-level planning system described in the dual process model of movement preparation. This system has a muscle-specific organization and would be controlled by the M1/PMA couple rather than by the SMA/CMA couple, which is responsible for the typical precuing effect on lCNV (Leuthold & Jentzsch, 2001; Leuthold et al., 2004). This is consistent with a recent TMS study showing that PMv-M1 interactions are muscle specific during grasp preparation (Davare, Montague, Olivier, Rothwell, & Lemon, 2009).

No precuing effect was observed on the ipsilateral region (IFC cluster). This is consistent with the fact that the task was performed only with the right hand. It differs from what was typically shown in most of the previous studies. For instance, Leuthold and Jentzsch (2009) observed that the precuing effect on lCNV amplitude was similar for both hemispheres. As discussed in the next section, this discrepancy may be related to the fact that our task involved complex reach-to-grasp movements.

In summary, our results support the main assumptions of the dual process model of movement preparation and extend them to multijoint reach-to-grasp movements. The topographic variations of lCNV amplitude modulations suggest that two mechanisms coexist and represent two stages in movement planning. First, movement parameters are processed separately in the mid-central and parietal regions. Following this first step of processing, movement parameters are integrated in low-level controlateral motor areas for the overt release of the motor command. Moreover, the planning of force seems to be widely distributed within the cortical motor system, whereas the planning of grip seems to be more localized. This interpretation implies that the modulations of lCNV amplitude represent the combination of high- and low-level motor planning processes. This assumption does not match earlier studies of simple single-joint movements in which lCNV reflects a single high-level planning process distributed over a large centro-parietal zone (for a review, see Leuthold et al., 2004). We now question if this discrepancy could relate to the fact that our study is focused on more complex and ecological reach-to-grasp movements.

Precuing Effects Are More Complex for Reach-to-Grasp than Single-Joint Movements

Our task required performing complex multijoint reach-to-grasp movements. These movements are known to activate a more widely distributed cortical network than simple single-joint movements. Indeed, numerous studies showed that reach-to-grasp movements involve a large fronto-parietal network (Brochier & Umiltà, 2007; Castiello & Begliomini, 2008; Rizzolatti & Luppino, 2001) among which a reach-related pathway and a grasp-related pathway can be distinguished (Binkofski et al., 1998; Cavina-Pratesi et al., 2010). Other studies showed that dexterous movements evoke greater activity and activate a larger network than simple ones (Ehrsson, Kuhtz-Buschbeck, & Forssberg, 2002; Kranczioch, Mathews, Dean, & Sterr, 2010; Kuhtz-Buschbeck et al., 2003). Moreover, using a paired-pulse TMS protocol, Cattaneo et al. (2005) demonstrated that reach-to-gasp movements activate highly specific networks that are not activated in non-object-driven movements. The specificity of the cerebral processes involved in reach-to-grasp movements has been indirectly confirmed by a recent study by Leuthold and Jentzsch (2009). They investigated ERP modulations in a precuing task for multiarticular reaching movements. In agreement

with their previous studies on single-joint movements (for a review, see Leuthold et al., 2004) but unlike in our study, they observed a typical precuing effect on lCNV amplitude with a homogeneous topographic distribution. No precuing effect was observed on the LRP, in keeping with the assumption that LRP modulations reflect hand-related processes (Wild-Wall et al., 2003). A key aspect of their experiment is that it involved only proximal movements and probably did not activate the cortical networks for visually driven reach-to-grasp movements. In contrast, our experiment required the complex coordination between the reaching and grasping components of reach-to-grasp movements. It has been demonstrated that the activation pattern of proximal muscles varied depending on the grip posture used to grasp an object (Martelloni, Carpaneto, & Micera, 2009). This observation implies that in our experiment, the coordinated activation of the reaching and grasping components had to be planned in advance to achieve a given grip.

Intracerebral recordings in epileptic patients indicate that during motor tasks, CNV originates from multiple cortical generators, including distinct motor areas such as M1, SMA, PMA, and the parietal cortex (Bareš et al., 2007; Hamano et al., 1997, Lamarche, Louvel, Buser, & Rektor, 1995). These motor areas are known to be major components of the reach-to-grasp networks (Jeannerod et al., 1995) and are activated in relation to movement planning (Baumann, Fluet, & Scherberger, 2009; Deiber, Ibanez, Sadato, & Hallett, 1996; Hoshi & Tanji, 2006; Riehle & Requin, 1995; Shima, Mushiake, Saito, & Tanji, 1996). In the present study, we suspect that the CNV generators are differentially activated during the planning of hand shape and force, as suggested by the topographic difference that subsisted after the normalization. We do not exclude that the CNV generators can be differentially activated during planning of distinct single-joint movement parameters. However, we strongly believe that, in contrast to reach-to-grasp movements, the planning of single-joint movements generates insufficient and/or inappropriate neuronal activity to evoke differential precuing effects at the scalp level. The pronounced asymmetry of lCNV precuing effects observed in our task but not in single-joint movements (e.g., Leuthold & Jentzsch, 2009) can be interpreted in a similar way. Reach to grasp movements require the combined activation of the proximal and distal body segments and therefore an extended activation of the cortical motor networks that predominates in the hemisphere controlateral to the working hand. Such asymmetry is likely to be weaker in simple single-joint movements and may be revealed using a method such as the LRP to measure it more directly (Wild-Wall et al., 2003).

Relation between lCNV Amplitude and RT

One claim of the dual-process model is that the processes responsible for the precuing effect on lCNV amplitude are also responsible for the precuing effect observed on RT. Indeed, these two measurements tend to be inversely correlated: The lCNV amplitude increases and RTs decreases with the amount of advance information (Leuthold & Jentzsch, 2009; Leuthold et al., 2004; Ulrich et al., 1998). In the present study, we obtained distinct precuing effects on lCNV amplitude in three different regions of the scalp. None of them showed a positive or negative correlation between changes in RT and lCNV amplitude for the four precuing conditions. Although a relation between lCNV amplitude and RT cannot be completely excluded, our results and others (Prescott, 1986; Rebert & Tecce, 1973) do not support a direct link between the two. MacKay and Bonnet (1990) observed that the correlation between CNV and RT is abolished following the Laplacian derivation of the EEG signals. The Laplacian derivation enhances the spatial resolution by reducing the contribution of remote sources to the local recordings (Gevins, 1989). This method is used in order to distinguish the different sources generating the signal recorded on the scalp. MacKay and Bonnet (1990) suggest that RT correlates with CNV amplitude when the latter represents the global activity of the motor network but not local activity in subcomponents of this network. In agreement with this hypothesis, we observed that the global EEG activity obtained by averaging MFC, CFC, P, and IFC signals show an inverse correlation between lCNV amplitude and RT: Global lCNV is the smallest in the NO condition (-3.1 μV), intermediate in the GRIP and FORCE conditions (-4.1 μV and -4.6 μV, respectively), and the largest in the ALL condition (-5.3 μV). This effect contrasts with the absence of correlation between RT and lCNV amplitude on each cluster independently. As argued in the previous section, the activity of each cluster is likely to reflect the activation of different functional components of the grasping network. In contrast, it is likely that in the case of single-joint movements the activity of the motor network subcomponents is poorly differentiated at the scalp level and that Laplacian derivation is required to reveal them. In conclusion, we suggest that in the context of complex grasping movements, the lack of correlation between RT and lCNV amplitude does not contradict the dual-process model of motor preparation.

Differential Time Course for the Planning of the Force and Grip Parameters

Mean RTs for the four precuing conditions revealed an additive effect. In the GRIP and FORCE conditions, respectively, mean RTs were 34 ms and 82 ms greater than in the ALL condition. The sum of these time differences ($34+82=116$ ms) is almost equal to the time difference between the ALL and the NO conditions (113 ms). According to Rosenbaum (1980), this additive effect indicates that the grip and force parameters are planned serially. However, Zelaznik (1978) pointed out that precues affect the number of stimulus–response (S-R) alternatives and influence the duration of response selection processes rather than planning processes per se. In this respect, the additive pattern of RT for the grip and force parameters cannot be strictly taken as evidence for a serial organization of movement planning. It is still noticeable that with the same number of S-R alternatives, the RT difference between the GRIP condition and the FORCE condition (48 ms) was significant. This result can be taken as an indication that the force-related planning processes occurring during RT are less time-consuming than the grip-related planning processes. An alternative explanation for the difference in RT between the GRIP and FORCE conditions is that the perceptual encoding of the cue is more difficult for the grip than the force parameter, as discussed by Leuthold and Jentzsch (2009). This hypothesis is very unlikely because we used very similar arbitrary LED-like signals to precue both parameters. Moreover, to our knowledge, all precuing studies that include a force parameter found that this parameter took a shorter time to process than any other parameter, even for the studies using different types of GO signals (MacKay & Bonnet, 1990; Riehle & Requin, 1995; Riehle et al., 1994; Ulrich et al., 1998).

Limitations of the Present Study

Some methodological factors might contribute to the discrepancies between our study and the previous ones focused on single-joint movements. Most of the previous works used a random design for the presentation of the different precuing conditions. In our study, we used a block design in which the subject knew the type of precue provided throughout a block of trials. This paradigm might lead to differences in the subject cognitive state (arousal, expectancy, attention, etc.) between the fully informative (ALL), partially informative (GRIP and FORCE), and noninformative (NO) precuing conditions. However, it is very unlikely that the difference between our results and others is explained by the experimental design (block vs. random). First, it has been shown that the precuing effect on lCNV is unaffected by the experimental design (Sangals, Sommer, & Leuthold, 2002). Second, in line with our results, most studies using a random design demonstrate a robust precuing effect in which lCNV amplitude is largest in the fully informative condition, intermediate in the partial conditions, and lowest in noninformative condition.

The duration of the preparation period may be another factor contributing to the discrepancies between the present study and the previous ones. Many studies that used single-joint movements or simple button press also used short PP ($\leq$1500 ms). Movement preparation is a complex phenomenon comprising many physiological processes with different time courses (Jennings & van der Molen, 2005). For short PP, the different preparatory processes reflected in the CNV can overlap in time, and some may be diluted in others (Birbaumer, Elbert, Canavan, & Rockstroh, 1990; Gaillard, 1976; Rohrbaugh & Gaillard, 1983; Rohrbaugh, Syndulko, & Lindsley, 1976). In particular, CNV is viewed as the combination of the eCNV and the lCNV. It has been demonstrated that the eCNV is mainly modulated by the nature of the warning signal (Gaillard, 1976; Loveless & Sanford, 1974, 1975). For long PP, lCNV occurs approximately 1.5 s before the GO signal and follows the eCNV. Leuthold and Jentzsch (2009) showed that with a short PP duration of 1.5 s, similar precuing effects are observed for the eCNV (400 ms to 600 ms after precue) and the lCNV preceding GO onset. The authors assumed that the eCNV may also reflect motor processes and not only sensory processes. However, because they used a short PP, it is difficult to disentangle the influence of the sensory and motor processes on the EEG signals. Although the use of a long PP does not facilitate the comparison with previous studies, we assume that it is more suitable to separate in time sensory and motor processes and consequently to make reliable inferences about motor control mechanisms.

Conclusion

In the present study, RT and CNV measurements reveal that similar mechanisms are involved in the planning of reach-to-grasp and simple single-joint movements. However, we suggest that the planning of reach-to-grasp movements activates a larger motor network and generates topographic variation in lCNV precuing effects. Together, RT and EEG data confirm that two distinct functional networks are involved, with different time courses in the planning of grip and force. These two parameters are integrated in low-level motor areas to complete the motor command that control muscle contraction. We also outlined the composite nature of the lCNV that might reflect high- and low-level processes. Altogether, this work highlights the relevance of using EEG to study natural reach-to-grasp movement. These movements reveal some unique properties of cortical motor processes and refine our understanding of the functional properties of ERP signals.

References

Alexander, G. E., & Crutcher, M. D. (1990). Preparation for movement: Neural representations of intended direction in three motor areas of the monkey. *Journal of Neurophysiology*, *64*, 133–150.

Andersen, R. A., & Cui, H. (2009). Intention, action planning, and decision making in parietal-frontal circuits. *Neuron*, *63*, 568–583.

Bareš, M., Nestrašil, I., & Rektor, I. (2007). The effect of response type (motor output versus mental counting) on the intracerebral distribution of the slow cortical potentials in an externally cued (CNV) paradigm. *Brain Research Bulletin*, *71*, 428–435.

Baumann, M. A., Fluet, M. C., & Scherberger, H. (2009). Context-specific grasp movement representation in the macaque anterior intraparietal area. *Journal of Neuroscience*, *29*, 6436–6448.

Beurze, S. M., Lange, F. P., Toni, I., & Medendorp, W. P. (2007). Integration of target and effector information in the human brain during reach planning. *Journal of Neurophysiology*, *97*, 188–199.

Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., & Freund, H. J. (1998). Human anterior intraparietal area subserves prehension: A combined lesion and functional MRI activation study. *Neurology*, *50*, 1253–1259.

Birbaumer, N., Elbert, T., Canavan, A., & Rockstroh, B. (1990). Slow potentials of the cerebral cortex and behaviour. *Physiological Review*, *70*, 1–41.

Bock, O., & Eversheim, U. (2000). The mechanisms of movement preparation: A precuing study. *Behavioral Brain Research*, *108*, 85–90.

Brochier, T., Spinks, R. L., Umiltà, M. A., & Lemon, R. N. (2004). Patterns of muscle activity underlying object-specific grasp by the macaque monkey. *Journal of Neurophysiology*, *92*, 1770–1782.

Brochier, T., & Umiltà, M. A. (2007). Cortical control of grasp in non-human primates. *Current Opinion in Neurobiology*, *17*, 637–643.

Castiello, U. (2005). The neuroscience of grasping. *Nature Review Neuroscience*, *6*, 726–736.

Castiello, U., & Begliomini, C. (2008). The cortical control of visually guided grasping. *Neuroscientist*, *14*, 157–170.

Cattaneo, L., Voss, M., Brochier, T., Prabhu, G., Wolpert, D. M., & Lemon, R. N. (2005). A cortico-cortical mechanism mediating object-driven grasp in humans. *Proceedings of the National Academy of Sciences, U.S.A.*, *102*, 898–903.

Cavina-Pratesi, C., Monaco, S., Fattori, P., Galletti, C., McAdam, T. D., Quinlan, D. J., . . . Culham, J. C. (2010). Functional magnetic resonance imaging reveals the neural substrates of arm transport and grip formation in reach-to-grasp actions in humans. *Journal of Neuroscience*, *30*, 10306–10323.

Churchland, M. M., & Shenoy, K. V. (2007). Delay of movement caused by disruption of cortical preparatory activity. *Journal of Neurophysiology*, *97*, 348–359.

Crammond, D. J., & Kalaska, J. F. (2000). Prior information in motor and premotor cortex: Activity during the delay period and effect on pre-movement activity. *Journal of Neurophysiology*, *84*, 986–1005.

Culham, J. C., Cavina-Pratesi, C., & Singhal, A. (2006). The role of parietal cortex in visuomotor control: What have we learned from neuroimaging? *Neuropsychologia*, *44*, 2668–2684.

Davare, M., Andres, M., Clerget, E., Thonnard, J. L., & Olivier, E. (2007). Temporal dissociation between hand shaping and grip force scaling in the anterior intraparietal area. *Journal of Neuroscience*, *27*, 3974–3980.

Davare, M., Andres, M., Cosnard, G., Thonnard, J. L., & Olivier, E. (2006). Dissociating the role of ventral and dorsal premotor cortex in precision grasping. *Journal of Neuroscience*, *22*, 2260–2268.

Davare, M., Montague, K., Olivier, E., Rothwell, J. C., & Lemon, R. N. (2009). Ventral premotor to primary motor cortical interactions during object-driven grasp in humans. *Cortex*, *45*, 1050–10057.

Deiber, M. P., Ibanez, V., Sadato, N., & Hallett, M. (1996). Cerebral structure participating in motor preparation in humans: A positron tomography study. *Journal of Neurophysiology*, *75*, 233–247.

DeSoto, M. C., Fabiani, M., Geary, D. C., & Gratton, G. (2001). When in doubt, do it both ways: Brain evidence of the simultaneous activation of conflicting motor responses in a spatial Stroop task. *Journal of Cognitive Neuroscience*, *13*, 523–536.

Dum, R. P., & Strick, P. L. (2005). Frontal lobe inputs to the digit representations of the motor areas on the lateral surface of the hemisphere. *Journal of Neuroscience*, *25*, 1375–1386.

Ehrsson, H. H., Kuhtz-Buschbeck, J. P., & Forssberg, H. (2002). Brain regions controlling nonsynergistic versus synergistic movement of the digits: A functional magnetic resonance imaging study. *Journal of Neuroscience*, *22*, 5074–5080.

Favilla, M., & De Cecco, E. (1996). Parallel direction and extent specification of planar reaching arm movements in humans. *Neuropsychologia*, *34*, 609–613.

Fogassi, L., & Luppino, G. (2005). Motor functions of the parietal lobe. *Current Opinion in Neurobiology*, *15*, 626–631.

Gaillard, A. W. (1976). Effects of warning-signal modality on the contingent negative variation (CNV). *Biological Psychology*, *4*, 139–154.

Gevins, A. (1989). Dynamic functional topography of cognitive tasks. *Brain Topography*, *2*, 37–56.

Ghez, C., Favilla, M., Ghilardi, M. F., Gordon, J., Bermejo, R., & Pullman, S. (1997). Discrete and continuous planning of hand movements and isometric force trajectories. *Experimental Brain Research*, *115*, 217–233.

Goodman, D., & Kelso, J. A. S. (1980). Are movements prepared in parts? Not under compatible (naturalized) conditions. *Journal of Experimental Psychology: General*, *109*, 475–495.

Gratton, G., Bosco, C. M., Kramer, A. F., Coles, M. G., Wickens, C. D., & Donchin, E. (1990). Event-related brain potentials as indices of information extraction and response priming. *Electroencephalography and Clinical Neurophysiology*, *75*, 419–432.

Greenhouse, W. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, *24*, 95–112.

Hamano, T., Lüders, H. O., Ikeda, A., Collura, T. F., Comair, Y. G., & Shibasaki, H. (1997). The cortical generators of the contingent negative variation in humans: A study with subdural electrodes. *Electroencephalography and Clinical Neurophysiology*, *104*, 257–268.

Herbort, O., & Butz, M. (2010). Planning and control of hand orientation in grasping movments. *Experimental Brain Research*, *202*, 867–878.

Hillyard, S. A., & Galambos, R. (1970). Eye movement artefact in the CNV. *Electroencephalography and Clinical Neurophysiology*, *28*, 173–182.

Hoshi, E., & Tanji, J. (2000). Integration of target and body-part information in the premotor cortex when planning action. *Nature*, *408*, 466–470.

Hoshi, E., & Tanji, J. (2006). Differential involvement of neurons in the dorsal and ventral premotor cortex during processing of visual signals for action planning. *Journal of Neurophysiology*, *95*, 3596–3616.

Hoshi, E., & Tanji, J. (2007). Distinctions between dorsal and ventral premotor areas: Anatomical connectivity and functional properties. *Current Opinion in Neurobiology*, *17*, 234–242.

Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed movements*. Oxford: Oxford University Press.

Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends in Neuroscience*, *18*, 314–320.

Jennings, J. R., & van der Molen, M. W. (2005). Preparation for speeded action as a psychophysiological concept. *Psychological Bulletin*, *131*, 434–459.

Jentzsch, I., Leuthold, H., & Ridderinkhof, K. R. (2004). Beneficial effects of ambiguous precues: Parallel motor preparation or reduced premotoric processing time? *Psychophysiology*, *41*, 231–244.

Jing, H., Pivik, R. T., & Dykman, R. A. (2006). A new scaling method for topographical comparisons of event-related potentials. *Journal of Neuroscience Methods*, *151*, 239–249.

Johansson, R. S., & Westling, G. (1988). Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Experimental Brain Research*, *71*, 59–71.

Kalaska, J. (2009). From intention to action: Motor cortex and the control of reaching movements. *Advances in Experimental Medicine and Biology*, *629*, 139–178.

Keele, S. W. (1968). Movement control in skilled motor performance. *Psychological Bulletin*, *70*, 387–403.

Koch, G., Franca, M., Olmo, M. F. D., Cheeran, B., Milton, R., Sauco, M. A., & Rothwell, J. C. (2006). Time course of functional connectivity between dorsal premotor and contralateral motor cortex during movement selection. *Journal of Neuroscience*, *26*, 7452–7459.

Koch, G., Olmo, M. F. D., Cheeran, B., Ruge, D., Schippling, S., Caltagirone, C., & Rothwell, J. C. (2007). Focal stimulation of the posterior parietal cortex increases the excitability of the ipsilateral motor cortex. *Journal of Neuroscience*, *27*, 6815–6822.

Koch, G., & Rothwell, J. C. (2009). TMS investigations into the task-dependent functional interplay between human posterior parietal and motor cortex. *Behavioral Brain Research*, *202*, 147–152.

Kranczioch, C., Mathews, S., Dean, P., & Sterr, A. (2010). Task complexity differentially affects executed and imagined movement preparation: Evidence from movement-related potentials. *PLoS One*, *5*, e9284.

Kristeva, R., Cheyne, D., & Deecke, L. (1991). Neuromagnetic fields accompanying unilateral and bilateral voluntary movements: Topography and analysis of cortical sources. *Electroencephalography and Clinical Neurophysiology*, *81*, 284–298.

Kuhtz-Buschbeck, J. P., Mahnkopf, C., Holzknecht, C., Siebner, H., Ulmer, S., & Jansen, O. (2003). Effector-independent representations of simple and complex imagined finger movements: A combined fMRI and TMS study. *European Journal of Neuroscience*, *18*, 3375–3387.

Kutas, M., & Donchin, E. (1980). Preparation to respond as manifested by movement-related brain potentials. *Brain Research*, *202*, 95–115.

Lamarche, M., Louvel, J., Buser, P., & Rektor, I. (1995). Intracerebral recordings of slow potentials in a contingent negative variation paradigm: An exploration in epileptic patients. *Electroencephalography and Clinical Neurophysiology*, *95*, 268–276.

Lépine, D., Glencross, D., & Requin, J. (1989). Some experimental evidence for and against a parametric conception of movement programming. *Journal of Experimental Psychology: Human Perception and Performance*, *15*, 347–362.

Leuthold, H., & Jentzsch, I. (2001). Neural correlates of advance movement preparation: A dipole source analysis approach. *Cognitive Brain Research*, *12*, 207–224.

Leuthold, H., & Jentzsch, I. (2002). Distinguishing neural sources of movement preparation and execution: An electrophysiological analysis. *Biological Psychology*, *60*, 173–198.

Leuthold, H., & Jentzsch, I. (2009). Planning of rapid aiming movements and the contingent negative variation: Are movement duration and extent specified independently? *Psychophysiology*, *46*, 539–550.

Leuthold, H., Sommer, W., & Ulrich, R. (1996). Partial advance information and response preparation: Inferences from the lateralized readiness potential. *Journal of Experimental Psychology: General*, *125*, 307–323.

Leuthold, H., Sommer, W., & Ulrich, R. (2004). Preparing for action: Inferences from CNV and LRP. *Journal of Psychophysiology*, *18*, 77–88.

Logar, V., Škrjanc, I., Belič, A., Brežan, S., Koritnik, B., & Zidar, J. (2008). Identification of the phase code in an EEG during gripping-force tasks: A possible alternative approach to the development of the brain–computer interfaces. *Artificial Intelligence in Medicine*, *44*, 41–49.

Loveless, N. E., & Sanford, A. J. (1974). Slow potential correlates of preparatory set. *Biological Psychology*, *1*, 303–314.

Loveless, N. E., & Sanford, A. J. (1975). The impact of warning signal intensity on reaction time and components of the contingent negative variation. *Biological Psychology*, *2*, 217–226.

MacKay, W. A., & Bonnet, M. (1990). Stretch reflex and reaction time correlates of preparation for movement direction and force. *Electroencephalography and Clinical Neurophysiology*, *76*, 47–62.

Martelloni, C., Carpaneto, J., & Micera, S. (2009). Characterization of EMG patterns from proximal arm muscles during object- and orientation-specific grasps. *IEEE Transactions on Biomedical Engineering*, *56*, 2529–2536.

Masaki, H., Wild-Wall, N., Sangals, J., & Sommer, W. (2004). The functional locus of the lateralized readiness potential. *Psychophysiology*, *41*, 220–230.

McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology*, *62*, 203–208.

Meyer, D. E., Osman, A. M., Irwin, D. E., & Yantis, S. (1988). Modern mental chronometry. *Biological Psychology*, *26*, 3–67.

Müller-Putz, G. R., Scherer, R., Pfurtscheller, G., & Rupp, R. (2005). EEG-based neuroprosthesis control: A step towards clinical practice. *Neuroscience Letters*, *382*, 169–174.

Prabhu, G., Voss, M., Brochier, T., Cattaneo, L., Haggard, P., & Lemon, R. N. (2007). Excitability of human motor cortex inputs prior to grasp. *Journal of Physiology*, *581*, 189–201.

Prescott, J. (1986). The effects of response parameters on CNV amplitude. *Biological Psychology*, *22*, 107–135.

Rebert, C. S., & Tecce, J. J. (1973). A summary of CNV and reaction time. In W. C. McCallum & J. R. Knott (Eds.), *Event-related slow potentials of the brain: Their relations to behavior* (pp. 173–178). Amsterdam: Elsevier.

Requin, J., Brener, J., & Ring, C. (1991). Preparation for action. In J. R. Jennings & M. G. H. Coles (Eds.), *Handbook of cognitive psychophysiology: Central and autonomic nervous system approaches* (pp. 357–448). New York: Wiley.

Riehle, A. (2005). Preparation for action: One of the key functions of motor cortex. In A. Riehle & E. Vaadia (Eds.), *Motor cortex in voluntary movements: A distributed system for distributed functions* (pp. 213–240). Boca Raton, FL: CRC Press.

Riehle, A., MacKay, W. A., & Requin, J. (1994). Are extent and force independent movement parameters? Preparation- and movement-related neuronal activity in the monkey cortex. *Experimental Brain Research*, *99*, 56–74.

Riehle, A., & Requin, J. (1989). Monkey primary motor and premotor Cortex: single-cell activiy related to prior information about direction and extent of an intended movement. *Journal of Neurophysiology*, *61*, 534–549.

Riehle, A., & Requin, J. (1995). Neuronal correlates of the specification of movement direction and force in four cortical areas of the monkey. *Behavioral Brain Research*, *70*, 1–13.

Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron*, *31*, 889–901.

Rohrbaugh, J., & Gaillard, A. W. K. (1983). Sensory and motor aspects of the contingent negative variation. In A. W. K. Gaillard & W. Ritter (Eds.), *Tutorials in event-related potential research: Endogenous components* (pp. 269–310). Amsterdam: Elsevier.

Rohrbaugh, J., Syndulko, K., & Lindsley, D. B. (1976). Brain wave components of the contingent negative variation in humans. *Science*, *191*, 1055–1057.

Rosenbaum, D. A. (1980). Human movement initiation: Specification of arm, direction, and extent. *Journal of Experimental Psychology: General*, *109*, 444–474.

Rosenbaum, D. A. (1983). The movement precuing technique: Assumptions, applications and extensions. In R. A. Magill (Ed.), *Memory and control of action* (pp. 231–274). Amsterdam: North-Holland.

Rosenbaum, D. A., Cohen, R. G., Jax, S. A., Weiss, D. J., & van der Wel, R. (2007). The problem of serial order in behavior: Lashley's legacy. *Human Movement Science*, *26*, 525–554.

Sangals, J., Sommer, W., & Leuthold, H. (2002). Influences of presentation mode and time pressure on the utilisation of advance information in response preparation. *Acta Psychologica*, *109*, 1–24.

Shima, K., Mushiake, H., Saito, N., & Tanji, J. (1996). Role for cells in the presupplementary motor area in updating motor plans. *Proceedings of the National Academy of Sciences, U.S.A.*, *93*, 8694–8698.

Sokal, R. R., & Rohlf, F. J. (1995). *Biometry: The principles and practice of statistics in biological research*. New York: Freeman & Co.

Summers, J. J., & Anson, J. G. (2009). Current status of the motor program: Revisited. *Human Movement Science*, *28*, 566–577.

Tunney, R. J., Fernie, G., & Astle, D. E. (2010). An ERP analysis of recognition and categorization decisions in a prototype-distortion task. *PLoS One*, *5*, e10116.

Ulrich, R., Leuthold, H., & Sommer, W. (1998). Motor programming of response force and movement direction. *Psychophysiology*, *35*, 721–728.

Urbach, T. P., & Kutas, M. (2002). The intractability of scaling scalp distributions to infer neuroelectric sources. *Psychophysiology*, *39*, 791–808.

van der Lubbe, R. H. J., Los, S. A., Jaskowœki, P., & Verleger, R. (2004). Being prepared on time: On the importance of the previous foreperiod to current preparation, as reflected in speed, force and preparation-related brain potentials. *Acta Psychologica*, *116*, 245–262.

van Schie, H. T., & Bekkering, H. (2007). Neural mechanisms underlying intermediate and final action goals in object use reflected by slow wave brain potentials. *Brain Research*, *1148*, 183–197.

Vecchiato, G., De Vico Fallani, F., Astolfi, L., Toppi, J., Cincotti, F., Mattia, D., . . . Babiloni, F. (2010). The issue of multiple univariate comparisons in the context of neuroelectric brain mapping: An application in a neuromarketing experiment. *Journal of Neuroscience Methods*, *191*, 283–289.

Vidal, F., Bonnet, M., & Macar, F. (1995). Programming the duration of a motor sequence: Role of the primary and supplementary motor areas in man. *Experimental Brain Research*, *106*, 339–350.

Walter, W. G., Cooper, D., Aldridge, V. J., McCallum, W. C., & Winter, A. (1964). Contingent negative variation: An electric sign of sensorimotor association and expectancy in the human brain. *Nature*, *203*, 380–384.

Wasson, P., Prodoehl, J., Coombes, S. A., Corcos, D. M., & Vaillancourt, D. E. (2010). Predicting grip force amplitude involves circuits in the anterior basal ganglia. *NeuroImage*, *49*, 3230–3238.

Wild-Wall, N., Sangals, J., Sommer, W., & Leuthold, H. (2003). Are fingers special? Evidence about movement preparation from event-related brain potentials. *Psychophysiology*, *40*, 7–16.

Wise, S. P. (1985). The primate premotor cortex: Past, present, and preparatory. *Annual Review of Neuroscience*, *8*, 1–19.

Zelaznik, H. (1978). Precueing response factors in choice reaction time: A word of caution. *Journal of Motor Behavior*, *10*, 77–79.

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