An ERP study of cognitive architecture and the insertion of mental processes: Donders revisited

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Abstract

In his seminal paper, Donders proposed that Choice reaction time (RT) tasks differ from Go/No-go RT tasks only by the insertion of a response decision operation. We evaluated this possibility by comparing the time course of Laplacian-transformed ERPs, recorded over the primary (M1s) and supplementary motor areas (SMAs) in a Choice and in a Go/No-go task. Laplacian-transformed ERPs showed that a component that develops over the SMAs during the RT of Choice tasks vanishes in our Go/No-go task. This indicates that a process, absent in the Go/No-go task, was "inserted" in the Choice task. The Choice versus Go/No-go manipulation also modified the motor command: the activity recorded over M1s and the delay separating EMG onset from response completion depended on the nature of the task. This indicates that, although a process was inserted in the Choice task, it was not "purely" inserted, contrary to Donders' initial assumption.

Descriptors: Insertion, Reaction time, ERPs, Laplacian, SMA, M1

Donders (1868/1969) laid the foundations for studying cognitive architecture through the analysis of reaction time (RT). A premise of his proposal was that this architecture depended on the task to be performed. Donders developed three tasks that are still at the core of experimental psychology nowadays: In a typical version of his task A (Simple RT task), subjects had to respond as fast as possible with a right-hand response to the stimulation of the right foot. Since the stimulation and the response were known in advance, Donders reasoned that, to perform the task, subjects simply had to detect the stimulation (sensory processes) and execute the response (motor processes). In his task B (Choice RT task), subjects had to respond with a right-hand response to a right-foot stimulation, and with a left-hand response to a left-foot stimulation. In this task, in addition to detecting the stimulus and executing the response, the subject had to discriminate the stimulus and to select the appropriate response. Finally, in his task C (Go/No-go task), both feet were stimulated but the subjects had to respond with the right hand when the right foot was stimulated, but not to respond to left-foot stimulation. In this case, although there was no uncertainty about the response, the subject still had to discriminate the stimuli. Based on these tasks, he

developed the subtractive method with the aim of measuring the duration of mental operations. Sensory and motor processes were assumed to be identical for Donders' A (simple RT), Donders' C (Go/No-go), and Donders' B (choice RT) tasks. Donders' C performance required the insertion of a stimulus discrimination module in between the sensory and motor processes, while Donders' B performance further required the insertion of a "response decision"[1] module. By subtracting the RT obtained for the different tasks, he sought to measure the durations of the added modules. Importantly, the method assumes a strong version of operation insertion, often termed "pure insertion," which amounts to considering that stimulus discrimination and response decision can be added or suppressed without altering the completion of sensory and motor processes. Pure insertion was early criticized on the basis of introspective reports (Külpe, 1893). Rigorous analyses suggest, however, that pure insertion may hold in certain tasks such as memory scanning tasks. Evidence in favor of pure insertion, relying on fine distributional analysis, has been reported (Ashby, 1982; Ashby & Townsend, 1980); however, although interesting, these did not address the pure insertion issue in the frame of Donders' A, B, and C tasks. In this frame, though, Gottsdanker and Shragg (1985) directly addressed the question of pure insertion. They studied a between-hand "choice" RT, in which a fully informative precue was used. The temporal relationship between the precue and an imperative signal was varied across trials. For brief intervals between precue and imperative signal (including 0 ms intervals), the RT

[1]We consider here that Donders' response decision process (in Donders' terms, this process reflects the voluntary orientation of will towards the required response) is to be understood as selection and/or programming processes.

measured from precue to response onset remained invariant. For longer intervals, the RT to the imperative stimulus was equal to simple RT. These results are predicted if stimulus identification and response selection are supplementary operations that would be purely inserted in a choice RT task as compared to a simple RT one. However, it seems that these results can also be predicted by alternative continuous models (e.g., McClelland, 1979).

Leocani, Cohen, Wassermann, Ikoma, and Hallett (2000), using transcranial magnetic stimulation, reported that the excitability of the corticospinal pathway involved in the response increases in the latest part of the RT period in Donders' A, B, and C tasks. In a chronometric perspective, they noticed that, although RTs increased notably from A to B tasks (the C one yielding intermediate RTs), the time course of the increase of corticospinal excitability remained fairly unchanged, relative to the occurrence of the motor response. Although the aim of the authors was not to address the pure insertion issue, their results led them to conclude that "... the increased efferent activity to the limb that must be moved occurs, at least partially, in series with discriminative-decisional processes which require more or less time according to the paradigm" (p. 1170), suggesting that the between-tasks differences in "upstream" discriminative-decisional processes left virtually unchanged the time course of the motor processes, at least in their (latest) corticospinal component. However, the experimental constraints inherent to transcranial magnetic stimulation (TMS) only allow a limited number of stimulation time windows. As a consequence, the temporal resolution of the method could be too coarse to reveal small "upstream" influences on motor processes.

This example, however, shows that the insertion issue can be addressed by analyzing brain activities thought to be involved in response decision and execution, so as to decipher whether these activities are affected by the type of task performed by the participants. Obviously, timing is essential for these issues, and it is important to use a method allowing a fine temporal resolution. As to the temporal resolution, event-related potential (ERP) recordings are particularly fit, but the spatial resolution of conventional EEG data is known for being fairly poor. This is critical in reaction time paradigms where post-stimulus and pre-response ERPs tend to overlap, owing to the joint effects of their (1) temporal proximity and (2) volume conduction (Kutas & Donchin, 1980). However, the Laplacian transformation has proven efficient to separate these different components. Acting as a high-pass spatial filter, the Laplacian eliminates (or, at least, strongly attenuates) volume conduction effects (Babiloni, Cincotti, Carducci, Rossini, & Babiloni, 2001), yielding a good approximation of the corticogram (Gevins et al., 1987). Importantly for the purpose of the present study, response-locked Laplacian transformed data revealed a—so far unnoticed—phasic negative wave (N-40) focused over the fronto-central electrodes and likely originating from the medial-frontal cortex, including the supplementary motor areas (SMAs) (Vidal, Grapperon, Bonnet, & Hasbroucq, 2003). This wave develops prior to the activation of the primary motor areas in choice RT (Donders' B) tasks (Carbonnell, Hasbroucq, Grapperon & Vidal, 2004; Vidal et al., 2003), and its amplitude is reduced when information about the response to be produced is available to the subject (Carbonnell et al., 2004). These two facts make the N-40 a good candidate for reflecting the response decision process. If such were the case, according to the insertion view, the N-40 should disappear in a Go/No-go (Donders' C) task.

One assumption of pure insertion is that the response execution processes are the same in the Donders' B and C tasks. Motor

processes implemented after the response has been selected are often considered to be reflected by the lateralized readiness potential (LRP: Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). In the context of between-hand choice RT (Donders' B) tasks, this widely acknowledged measure is obtained by subtracting the activities recorded by the electrodes located over the primary motor cortex (M1) ipsilateral to the response from the activities recorded over M1 contralateral to the response (Coles, 1989; Mordkoff & Grosjean, 2001). However, as stressed by Gratton and his colleagues, the LRP cannot "... distinguish cases in which one response is activated from cases in which the other response is inhibited. ... For these reasons, it would be useful to obtain a *separate* measure of the activation of each response channel." To achieve this goal, "... we need to remove the influence of other potentials" (Gratton et al., 1988, p. 339), due to volume conduction effects. It is now possible to analyze separately the (ipsilateral and contralateral) subcomponents of the LRP by applying the Laplacian transformation to conventional ERP data. This transformation has proven efficient to separate two subcomponents of the LRP issuing from M1s contralateral and ipsilateral to the response: In between-hand choice RT tasks, just before the response, a negative wave develops over the involved (contralateral) sensorimotor cortex and, symmetrically, a positive wave develops over the non-involved (ipsilateral) sensorimotor cortex (Praamstra & Seiss, 2005; Vidal et al., 2003). The status of contralateral activation is straightforward: its temporal relationships with EMG onset indicates that it corresponds to the initial slope (isMP; Tarkka & Hallett, 1991) of the motor potential (Deecke, Scheid, & Kornhuber, 1969). From intracerebral recordings in monkeys (Arezzo & Vaughan, 1975, 1980) and in humans (Ikeda, Lüders, Burgess, & Shibasaki, 1992; Ikeda et al., 1995; Neshige, Lüders, & Shibasaki, 1988), there is good evidence that this component represents the activation of the motor cortex contralateral to the responding hand and, more specifically, that it arises from layer V of area 4. This layer corresponds to that of the pyramidal neurons from which the efferent volley is sent to subcortical structures.

The ipsilateral positivity has been less studied, but converging evidence from different physiological methods suggests that it reflects motor inhibition. At the spinal level, Hoffman reflex technique has been applied in a between-hand choice RT (Donders' B) task. About 35 ms prior to EMG onset, the excitability of the motoneurons controlling the required response increased, while the excitability of the motoneurons controlling the non-required one decreased, revealing an inhibition of the motoneurons controlling the non-required response (Hasbroucq, Akamatsu, Burle, Bonnet, & Possamaï, 2000). Transcranial magnetic stimulation has been applied in a between-hand choice RT (Donder's B) task. In the latest period of the RT, the intracortical excitability (as evidenced by the duration of the silent period) of M1 involved in the response emission (contralateral) increased while the excitability of M1 involved in the non-required response (ipsilateral) decreased, revealing an inhibition of ipsilateral M1 (Burle, Bonnet, Vidal, Possamaï, & Hasbroucq, 2002). Analogous patterns of results have been reported regarding the excitability of the corticospinal pathway (as evidenced by the amplitude of the motor evoked potential): During the latest period of the RT, the excitability of the corticospinal pathway involved in the response increased while the excitability of the corticospinal pathway involved in the non-required response decreased (Leocani et al., 2000; Tandonnet, Garry, & Summers, in press; Verleger, Kuniecki, Möller, Fritzmannova, & Siebner, 2009). Thanks to these physiological observations, it seems safe

to consider that the negativity/positivity EEG pattern observed over M1 in the latest part of the RT period corresponds to an activation/inhibition pattern of contralateral/ipsilateral M1, respectively (see Burle, Vidal, Tandonnet, & Hasbroucq, 2004, for a more detailed discussion). A goal of the present study was hence to verify whether the activation/inhibition pattern would be the same in Donders' B and C tasks.

In summary, the ERPs recorded over medial frontal structures and the primary motor cortices offer the opportunity to directly test the (pure) insertion hypothesis by comparing Donders' B and C tasks. Assuming that the activation/inhibition pattern recorded over M1s and the N-40 can be taken as indices of motor processes and response decision, respectively, Donders' pure insertion assumption leads one to expect the N-40 (present in Donders' B) to disappear in a Donders' C task, while the activation/inhibition pattern over M1s should remain unchanged in a Donders' C as compared to a Donders' B task.

In the present study, the Donders' B task slightly deviates from the original Donders' B task. Indeed, in our variant of the Donders' B task, contrary to the canonical Donders' B task (where the Go vs No-go option is suppressed), we did not remove anything from the Donders' C task but, rather, we left the Donders' C task as it is and we added ("inserted") a choice on Go trials. We considered that this *modus operandi* allowed us to stick better to Donders' logic and to examine more accurately the insertion issue. In other words, we considered that this deviation from the Donders *procedure* allowed us to better realize his *rationale*.[2]

Method

Participants

Twelve participants (10 men, 2 women, from 20 to 51 years old; mean: 32.5) volunteered for this experiment. All subjects but one (one of the authors) were naïve regarding the task. They were all right-handed and had normal or corrected-to-normal vision. During the experiment, they were comfortably seated in an armchair placed in a Faraday cage, situated in a sound attenuated room. Written informed consent was obtained before the experiment.

Stimuli

The stimuli (response signals) consisted of four digits (3, 4, 7, or 8). Each digit written in white was presented in the centre of a faradized video monitor (Stim system of Neuroscan, Compumedics, Charlotte, NC, USA); total of visual angle: 1.5°).

Experimental Design

Responses consisted of right or left button presses on a response pad (Stim), given with the right or the left thumb, respectively. Responses had to be given as soon as possible after a response signal. Depending on the digit (the response signal) presented on the screen on a given trial, participants had either to respond (Go trials) with their right or left thumb, or not to respond (No-go trials). Go and No-go trials were equiprobable. The stimuli-to-response mapping was counterbalanced across participants. Half of the participants had to respond after the presentation of digits 3 or 4 ("Go digits"), whereas they did not have to respond after the presentation of digits 7 or 8 ("No-go digits"). The other half

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[2] We thank Prof. Verleger for suggesting this phrasing of our rationale.

had the reverse mapping. The presentation of the 4 possible digits was equiprobable.

There were two experimental conditions (Donders' B and Donders' C) delivered in separate blocks of trials. In the present study, the Donders' B task was not strictly identical to the original Donders' B as, in order to make the Donders' B and Donders' C tasks more readily comparable, No-go trials were also mixed with Go trials in the Donders' B condition:

Donders' B condition. On Go trials, participants had to respond either with the right or the left thumb. Half of the participants had to produce a right key press in response to the even "Go digits" and a left one for the odd "Go digit"; the other half had to produce a left key press in response to the even "Go digits" and a right one for the odd "Go digit." For example, for a given stimulus-to-response association (these associations were counterbalanced across subjects), subjects had to give a right response to digit 3, a left response to digit 4, and no response to digits 7 or 8.

Donders' C condition. On Go trials, participants had to respond with only one hand (the right one on half of the blocks, the left one on the other half). Participants had to produce the required key press in response to both the even and the odd "Go digits." For example, for a given stimulus-to-response association (counter-balanced across subjects), subjects had to give the only possible response to digits 3 or 4. They did not have to respond to digits 7 or 8.

These mapping rules ensured that in both the Donders' B and the Donders' C conditions one stimulus among four possible stimuli had to be identified. In other words, the uncertainty regarding the nature of the incoming stimuli was maintained constant across the conditions.

Reaction times were recorded to the nearest ms.

Trial Events

Following the Go stimuli, a key press on one of the two buttons on the response pad turned off the stimulus. The next response signal was presented 500 ms later. Participants were to respond within the next 800 ms. When they failed to respond within this time limit, the response signal (RS) was turned off and the next RS was delivered 500 ms later (that is, 1300 ms after the previously omitted RS). RTs below 130 ms or greater than 800 ms were considered as anticipations or omissions, respectively, and discarded. The participants were asked to respond as fast as possible and to minimize errors.

Following the "No-go digits," the participants had not to respond, and the next RS was delivered 1300 ms later.

Each participant ran 12 experimental blocks of 80 trials each, containing 40 Go and 40 No-go trials mixed in pseudo random order (the same stimulus could not be presented for more than 4 consecutive trials).

Half of the participants performed the Donders' B task first; the other half performed the Donders' C task first. They began with 80 practice trials of the Donders' B task and, then, performed 6 experimental Donders' B blocks. On average, a block lasted about 1 min and 30 s. A small rest was given between each block. This increased the likelihood that participants would not blink, swallow, or move their heads during a block. Once the 6 Donders' B blocks were over, participants were given a longer break. Participants then performed a practice Donders' C block (80 trials), followed by 6 experimental Donders' C blocks.
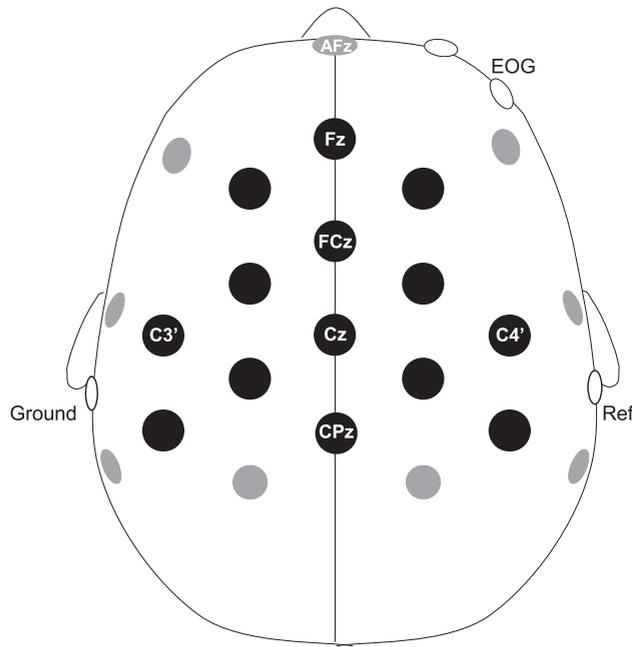
Figure 1. Electrodes placement. The array is symmetrical. The electrodes marked in black are the ones where surface Laplacian could be estimated by the source derivation method ('nodal electrodes'). The distance between neighboring electrodes is 1/20th of the sum of the distance separating the inion from the nasion plus the distance separating the right from the left tragus (3.7 cm on average). The angles between the segments joining a nodal electrode and the surrounding ones used to calculate the surface Laplacian are 120°. The midline Fz, FCz, Cz, CPz, and lateral C3'and C4' electrodes are explicitly indicated. EOG: electrooculogram, Ref: reference.

Electrophysiological Recordings

EEG was recorded from 23 Ag/AgCl scalp electrodes (see Figure 1). The reference and ground were on the right and left mastoids, respectively. Impedances were kept below 5 kΩ. The brain structures underneath the electrodes of interest were identified on the basis of Homan, Herman, and Purdy (1987) and Steinmetz, Fürst, and Meyer (1989).

Electrodes placement (Figure 1) and acquisition. In order to be able to estimate the time course of the surface Laplacian by the source derivation method (Hjorth, 1975),[3] as modified by MacKay (1983), we used an electrode configuration that partly differs from the standard 10–20 electrode placement system. This configuration permitted the Laplacian to be estimated at 14 electrodes, among which were FCz (i.e., over the SMAs), C3', and C4' (i.e., about 1 cm medial from C3 and C4, respectively; over the primary sensorimotor cortices). (See Vidal, Hasbroucq, Grapperon, & Bonnet, 2000, for a detailed description of the procedure.)

EEG and EOG signals were fed into Nicolet amplifiers, amplified (30,000 times) filtered and digitized (bandwidth: 0.016–100 Hz, 12db/octave, sampling rate: 256 Hz).

EOG was recorded bipolarly between electrodes situated above the right eye and at its outer canthus. No selective 'notch' 50 Hz filter or additional digital filtering was used. EMG was recorded from the *flexor pollicis brevis* of each hand, by paired surface Ag/AgCl elec-

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[3]Another method, described by Perrin, Bertrand, and Pernier (1987), can also be used. However, both methods are essentially equivalent to improve the spatial resolution of EEG traces as they yield virtually identical results (Tandonnet, Burle, Hasbroucq, & Vidal, 2005).

trodes (6 mm diameter), amplified (5000 times), filtered (high frequency cut-off 1 kHz), full wave rectified and integrated (integration window: 5 ms), and then digitized (sampling rate: 256 Hz).

Artifact rejection. Although the Laplacian transformation—because of its sensitivity to local sources—is considered to largely remove contamination by EOG signals (Law, Nuñez, & Wijesinghe, 1993), ocular artifacts were subtracted by a statistical method (Semlitsch, Anderer, Schuster, & Presslich, 1986). The principle of the method is to subtract a fraction of the recorded EOG signals from the recorded EEG activities, according to a coefficient of attenuation of EOG signals estimated for each channel separately.

Trials where the subtraction of ocular artifacts was judged unsatisfactory by visual inspection of monopolar recordings were manually rejected. The Laplacian transformation was applied on artifact free signals. We also carefully rejected local artifacts by visual inspection of the monopolar recordings (i.e., artifacts present at single electrodes; phasic artifacts as well as slow electrical shifts) because the use of the Laplacian transformation is very sensitive to them. After artifact correction and rejection, the remaining monopolar recordings were averaged and the Laplacians were calculated on the basis of these monopolar averages.

Trial selection, recording periods, and baseline. Brain activity was recorded continuously during the experiment. Response-related activities were averaged time-locked to EMG onset. The onset of EMG activities was detected by visual inspection of each trial (Hasbroucq, Possamaï, Bonnet & Vidal, 1999; Staude, Flachenecker, Daumer, & Wolf, 2001). Correct trials consisting of a correct response preceded by a small incorrect EMG activation on the "wrong" side (partial errors) were discarded from the present analysis in the Donders' B task since it has been demonstrated that information processing involves mechanisms somehow different from those involved on "pure" correct trials (Burle, Possamaï, Vidal, Bonnet & T. Hasbroucq, 2002). We thus only considered here the "pure" correct trials in our analysis in the Donders' B task.

In the Donders' C task, partial errors consisted of subthreshold EMG activation occurring, whereas no response was required (No-go trials). Therefore, partial errors (as well as errors) in the Donders' C task only occurred on No-go trials. Note that in the Donders' C task, partial errors (as well as errors) cannot occur on Go trials. Therefore, all these correct Go trials that we analyzed here are naturally "pure" correct ones.

Data analysis. We performed statistical analyses on the slopes of the curves (estimated by a linear regression analysis performed on the data) in specific time windows. Slopes particularly fit response-locked analysis since they are baseline-free, give morphological information, and are less variable than amplitude measures (Vidal et al., 2003). Two kinds of analysis were performed: comparisons to a norm (zero value) by the one-sample two-tailed Student's *t*-tests and comparisons of different means using analyses of variance.

Results

Behavioral and EMG Data

Errors and partial errors.

Errors. In the Donders' C condition, participants committed an error when they produced a response on No-go trials: the error rate was 3%.

In the Donders' B task, two types of errors were theoretically possible: a response given with the non-required hand, or a response on a No-go trial. However, only one participant produced 3 responses on No-go trials and the other ones never committed this type of error. This suggests that subjects could not anticipate the response signal because their response could not be prepared in advance.

The error rate (inappropriate hand response) was 3.6%, in the Donders' B condition.

Error rates were judged too small to allow further reliable analysis.

Partial errors. Participants committed a partial error when they produced an erroneous subthreshold EMG activity (not large enough to trigger an erroneous mechanical response) preceding the correct response.

In the Donders' C condition, the partial error (i.e., the subthreshold EMG activations on No-go trials) rate was 6.8%.

In the Donders' B condition, partial errors on No-go trials occurred in 1.9% of the cases, and participants committed a partial error with the inappropriate hand in 7.1% of the cases.

Reaction times. Chronometric indices were submitted to an analysis of variance with 2 within-subject factors: Condition (Donders' B vs Donders' C), and responding Hand (right vs left).

As expected, there was a clear effect of Condition on RT (407 ms vs 354 ms for Donders' B and Donders' C tasks, respectively, $F(1,11) = 67$, $p < .0001$), an effect of the responding hand ($F(1,11) = 18.4$, $p < .01$), and no Hand × Condition interaction ($F(1,11) < 1$). To better describe the locus of the task effect, we split the RT into two independent intervals: the premotor time (PMT, i.e., the time separating the occurrence of the RS from EMG onset) and the motor time (MT, i.e., the time separating EMG onset from the mechanical response). The effect of task on RT was largely due to an effect on the PMT, which was longer in the Donders' B (333 ms) than in the Donders' C (283 ms) condition ($F(1,11) = 47.57$, $p < .0001$). There was no effect of the responding hand ($F(1,11) = 3.03$; $p > .10$), and no Hand × Condition interaction ($F < 1$) on this index. However, a main effect of task also showed up on the MT, which was longer in the Donders' B (73 ms) than in the Donders' C (66 ms) condition ($F(1,11) = 5.59$, $p < .04$). There was an effect of the responding hand ($F(1,11) = 5.17$, $p < .05$): The right hand was, on average, 6.8 ms faster than the left one, but there was no Hand × Condition interaction ($F < 1$). Those data indicate that, if the task to perform largely affects the premotor components of the RT, it also affects the motor component of the RT. We shall come back to that point in the discussion.

EEG Data

Activities recorded over the SMAs. Figure 2 shows the Laplacians obtained at FCz (i.e., over the SMAs) in the Donders' B and in the Donders' C conditions. In the initial part of both traces, a slow negative wave develops. In the Donders' B condition, a phasic negative-going wave superimposes the slow one. This additional component precedes the M1 negativity contralateral to the response by about 50 ms and corresponds to the N-40. In contrast, in the Donders' C condition, such a phasic negative-going wave is absent. Finally, sharp negative waves follow EMG onset in both conditions. These correspond to error-negativity-like waves, which have been shown to be present on correct responses (Vidal et al.,
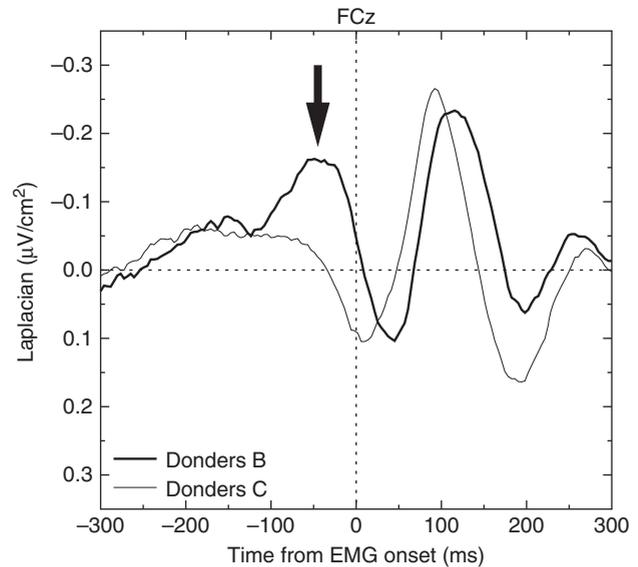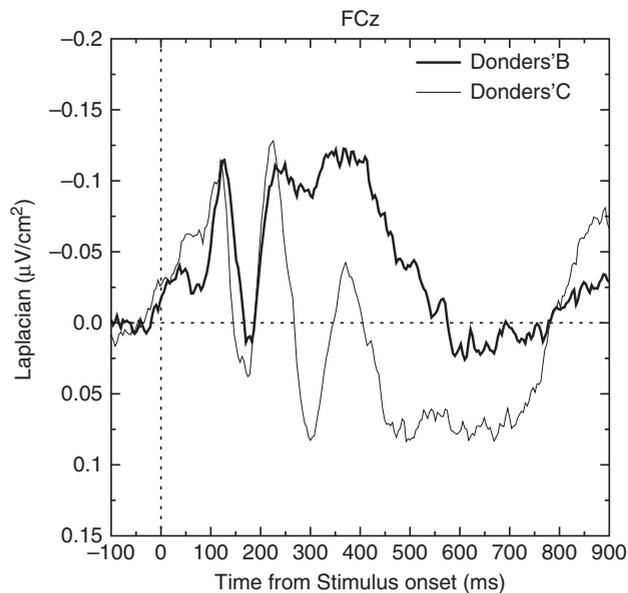

Figure 2. Amplitude of the surface Laplacian (microvolts per square centimeter, ordinate) as a function of time (milliseconds, abscissa) estimated over the supplementary motor areas obtained in the Donders' B condition (bold line), and in the Donders' C condition (thin line). Averages are time-locked to EMG onset (zero of times: dotted vertical black line) of the responding hand. The black arrow indicates the peak of the N-40.

2000) in choice but also in simple RT tasks (Vidal et al., 2000). These activities being out of the scope of the present article, we will not discuss them further.

Figure 3 shows the same data before they were Laplacian transformed, that is, the corresponding monopolar data. One can see that the N-40 hardly shows up on these averages in the Don-
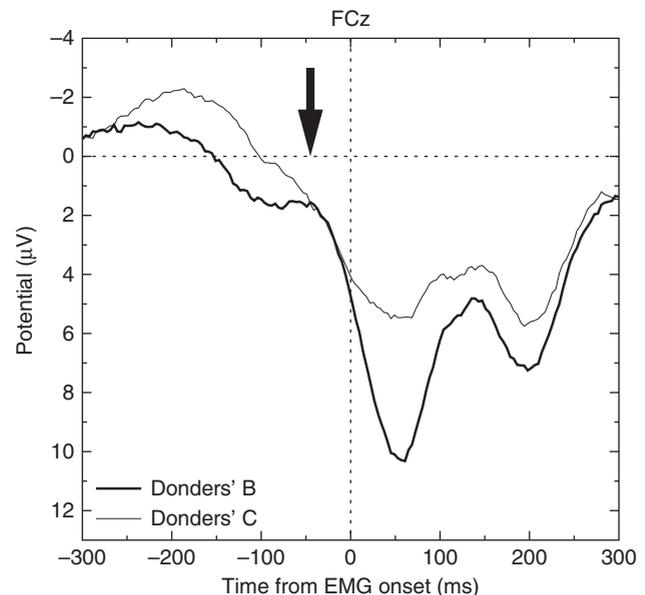
Figure 3. Amplitude of the potential (microvolts, ordinate) as a function of time (milliseconds, abscissa) recorded over the supplementary motor areas obtained in the Donders' B condition (bold line), and in the Donders' C condition (thin line). Averages are time-locked to EMG onset (zero of times: dotted vertical black line) of the responding hand. The black arrow indicates the occurrence of the peak of the N-40.

Figure 4. Amplitude of the surface Laplacian (microvolts per square centimeter, ordinate) as a function of time (milliseconds, abscissa) estimated over the supplementary motor areas obtained in the Donders' B condition (bold line), and in the Donders' C condition (thin line). Averages are timelocked to the stimulus (zero of times: dotted vertical black line).

ders' B condition, as already shown on Figure 4 and Figure 5 of Vidal et al. (2003) and Carbonnell et al. (2004), respectively.

Statistical analysis confirmed the observations made on the basis of the Laplacian transformed data: we measured the slopes of those activities, in the two tasks, in a window ranging from -100 to -50 ms (i.e., preceding EMG onset). These measures were submitted to an analysis of variance with the Condition (Donders' B vs Donders' C) and responding Hand (right vs left) as within-subject factors. The analysis revealed an effect of Task ($F(1,11) = 8.31$, $p < .02$), no effect of Hand ($F < 1$) and no Task × Hand interaction ($F < 1$).

To further refine this analysis, we evaluated whether the N-40 exists on the two tasks. To do so, we evaluated whether the slopes in the above time windows differed from zero. In the Donders' B condition, the slope significantly differed from zero ($t(11) = 3.15$, $p < .01$), whereas in the Donders' C condition, the slope showed a small (non-significant: $t(11) = 0.77$, $p > .10$) positive trend. An N-40 was thus present in the Donders' B condition only.

Figure 4 presents the same data time locked to stimulus onset. N100 and N200-like waves show up on these averages. On both conditions, a third negativity peaks about 370 ms after stimulus onset. It appears as a sharp peak in the Donders' C condition and as a smoother one in the Donders' B condition.

Activities recorded over M1. Although contra M1 and ipsi M1 activities elicited by right responses might not necessarily be symmetrical to those elicited by left responses, statistical analysis performed on the slopes of the curves yielded no significant effect of the responding hand (neither as a main effect nor as a component term in an interaction, see below). The left and right hand responses thus elicited symmetrical activities that were thus merged together.

Figure 5 shows the Laplacians, time-locked to EMG onset, obtained over the primary motor areas contralateral to the re-
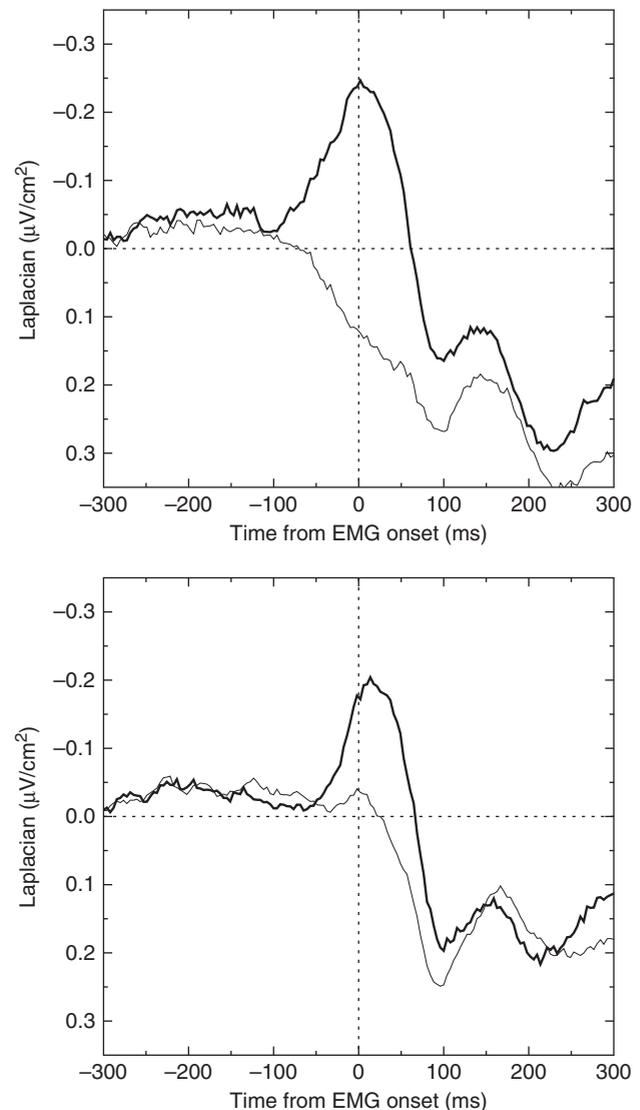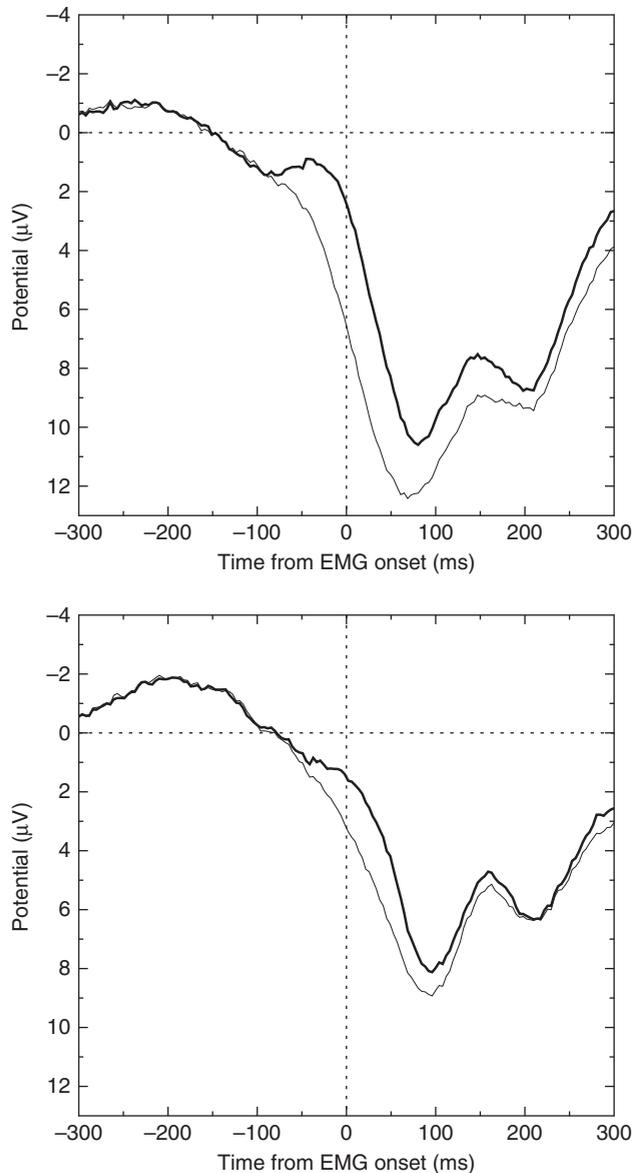

Figure 5. Amplitude of the surface Laplacian (microvolts per square centimeter, ordinate) as a function of time (milliseconds, abscissa) estimated over the primary cortex contralateral (bold line) and ipsilateral (thin line) to the responding hand obtained in the Donders' B (top) and in the Donders' C (bottom) conditions. Averages are time-locked to EMG onset (zero of times: dotted vertical black line) of the responding hand.

sponding hand (contra M1) and the primary motor areas ipsilateral to the responding hand (ipsi M1).[4]

In the Donders' B condition, the typical activation/inhibition pattern was observed before EMG onset: a negative wave over contra M1, and a positive deflection in the same latency range over ipsi M1. This contralateral-negative/ipsilateral-positive pattern was maximal over the primary motor areas.

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[4]Although the spatial resolution of the Laplacian-transformed data is not precise enough to separate unambiguously the activities arising from M1 from those arising from the primary somatosensory area, it has been argued in the introduction that the activities reported here correspond to an activation/inhibition pattern of contralateral and ipsilateral M1s, respectively. This is why we refer to M1s instead of SM1s when we describe the present data.

Figure 6. Amplitude of the potential (microvolts, ordinate) as a function of time (milliseconds, abscissa) recorded over the primary cortex contralateral (bold line) and ipsilateral (thin line) to the responding hand obtained in the Donders' B (top) and in the Donders' C (bottom) conditions. Averages are time-locked to EMG onset (zero of times: dotted vertical black line) of the responding hand.

In the Donders' C condition, the pattern of results clearly differed: although a negative wave could be observed over contra M1, no positive deflection developed over ipsi M1 before EMG onset. Furthermore, comparison of the activity recorded over contra M1 in the two conditions suggests that the activity rises later for the Donders' C task; that is, closer in time to EMG onset (let us remember that this activity is averaged EMG-locked).

On Figure 6, one can see that the activation/inhibition pattern hardly shows up on monopolar recordings, as already shown by Vidal et al. (2003, Figures 4 and 5) and Carbonnell et al. (2004). Moreover, a small transient "upward" peak occurs over contra M1 about 40–50 ms before EMG onset. On the contrary, Figure 5 shows no special event over M1 at this moment, which corresponds roughly to the middle of the rising phase of the motor potential. This can be explained by the spatial averaging, on monopolar recordings at central contralateral sites, of SMAs and M1 activities because of volume conduction effects (Vidal et al., 2003). On the Laplacian transformed data, however, the spatial filtering property of the Laplacian transformation has removed the influence of SMAs activity (N-40) at contralateral central sites, and no special event appears over contra M1 during the rising phase of the motor potential.

To assess the observations made on the basis of Laplacian transformed data, statistical analyses were performed on the slopes of the signal in various time windows.

We first performed an analysis of variance on the slopes during the last 50 ms preceding EMG onset (i.e., in the time window where the slopes are the steepest and the least variable) with 3 factors: Condition (Donders' B vs Donders' C), responding Hand (right vs left) and Electrode (contralateral vs ipsilateral). There was a Condition effect: $F(1,11) = 6.77$; $p < .025$, an Electrode effect ($F(1,11) = 60.62$; $p < .0001$) and no Hand effect ($F < 1$). The Hand factor did not interact with the other factors (Hand $\times$ Condition: $F < 1$; Hand $\times$ Electrode: $F < 1$; Hand $\times$ Electrode $\times$ Condition: $F(1,11) = 2.75$). This is why, as mentioned earlier, the data issued from each hand could thus be merged on Figure 5.

The Condition $\times$ Electrode interaction was significant ($F(1,11) = 6.21$, $p < .03$): there was no Condition effect at contralateral electrode ($F < 1$) whereas there was a significant Condition effect at ipsilateral electrode ($F(1,11) = 10.83$, $p < .01$).

The contralateral negative slope was significantly different from zero in both the Donders' B ($t = 4.63$, $p < .001$) and the Donders' C ($t(11) = 4.80$, $p < .001$) conditions.

In the Donders' B condition, the ipsilateral positive slope differed from zero ($t(11) = 3.39$, $p < .01$). In the Donders' C condition, there was no positive slope before EMG onset. Figure 5 even shows a small (non-significant: $t(11) = 1.06$, $p > .10$) negative trend for the ipsilateral slope in the Donders' C condition.

Inspection of Figure 5 suggests that contralateral activation begins earlier in the Donders' B condition than in the Donders' C one. Statistical analysis confirmed this visual impression: In a -100 to -50 ms window before EMG onset, the slope of contralateral activation was significantly different from zero in the Donders' B condition ($t(11) = 3.00$, $p < .02$), whereas it is was close to zero and far from being significant in the Donders' C condition ($t(11) = .12$, $p > .10$).

Discussion

In his seminal report, Donders (1868/1969) paved the way for chronometric exploration of mental processes by setting the three core RT tasks of experimental psychology, namely, Donders' task A (simple RT), Donders' task B (choice RT), and Donders' task C (Go/No-go). He was also the first to propose a method for inferring the speed of mental processes, through his so-called subtractive method.

Donders' subtractive method relies on two main assumptions: (1) mental processes can be inserted or suppressed between tasks, and (2) such insertions or suppressions leave the other processes unaffected. This second assumption is often called "pure insertion."

Knowing whether insertions can or cannot take place is an important issue as it would clarify the modularity debate (Sternberg, 2001). Moreover, the subtractive method, although largely criticized in the RT literature, is still largely used in neuroimaging, although it presents serious drawbacks in fMRI studies (Friston et

al., 1996), and must be used cautiously in EEG and MEG studies (van Boxtel, 2004). In the present study, we evaluate such insertion by analyzing two EEG activities that have been related to response selection and response execution, namely the N-40 and the activation/inhibition pattern, respectively.

An N-40 shows up in the Donders' B condition but not in the Donders' C one. Before commenting further on these results, one can wonder if the averaging procedure used here (i.e., response-locked) may have affected the results. Could it be possible that the present data simply represent a contamination due to (ill-averaged) classical stimulus evoked potentials such as the N100 or the N200? Examination of Figure 3, where the stimulus-locked data are plotted, suggests it is not the case: Reminding that PMTs are 333 and 283 ms in the Donders' B and Donders' C conditions, respectively, it is clear from this figure and from its comparison to Figure 2 that the N100 and N200 have disappeared on the response-locked data. Indeed, if we consider the Donders' C condition, on response-locked data, there is no evidence of any N100 or N200-like waves although this condition yields the shortest PMTs. *A fortiori*, in the Donders' B condition where PMTs are longer, these two waves cannot show up either on response-locked data. As a consequence, these two waves cannot account for the N-40. On both conditions, a third negativity peaks about 370 ms after stimulus onset. Peaking, on average, *after* EMG onset in both conditions (whereas the N-40, when present, peaks *before* EMG onset), this third negativity cannot account either for the N-40. This third stimulus-locked negativity is more phasic in the Donders' C than in the Donders' B condition. It is likely that, in the latter, the ill-averaged N-40 is partly superimposed on a stimulus-locked negative peak (probably similar to the one observed in the Donders' C condition) smoothing it in such a way that it appears wider and less phasic. Therefore, in line with Vidal et al. (2003) conclusions, it seems safe to assume that the N-40 "... cannot be accounted for by stimulus-locked contamination of response-locked activities" (p. 801).

The observation that an N-40 was present while the subjects performed the Donders' B task, but not while they performed the Donders' C one, provides support for the proposition that mental processes can be inserted or suppressed between tasks (assumption 1 of Donders). Indeed, whatever the processing operation reflected by this component (see below), this result shows that some brain activity is present for the Donders' B task and absent for the Donders' C task. According to Donders' view, the operation inserted in Donders' B tasks should be the response decision operation. Note that this difference might not be the only one. Indeed, our montage of electrodes concentrated over the regions of interest. Other activities related to the Donders' B vs Donders' C differences may have taken place in other regions where no recording electrode was available. Moreover, although it presents several advantages, the Laplacian transformation is fairly blind to deep sources, whose influence can be picked up by monopolar recordings. Therefore, we cannot exclude either that "deep" structures may also be sensitive to the Donders' B vs Donders' C differences. However, the observation of *at least one* insertion suffices to show that such an insertion is possible.

Interestingly, the inserted component is clearly localized over fronto-central areas, with a likely source in the SMAs (Carbonnell et al., 2004; Vidal et al., 2003). This is consistent with the view that SMAs are critical for the implementation of response selection and/or programming processes (e.g., Carbonnell et al., 2004; Goldberg, 1985; Ikeda et al., 1999, Mostofsky & Simmonds, 2008; Roland, Larsen, Lassen, & Skinhøj, 1980).

These data also provide insight in Donders' "response decision." Indeed, at variance with Donders' initial assumption regarding response decision, it has been argued that deciding either to execute a prepared response or to withhold it (as needed in the Donders' C condition) involves the same (Gomez, Ratcliff, & Perea, 2007; Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003) or an analogous (Verleger, Paehge, Kolev, Yordanova, & Jaśkowski, 2006) kind of motor decision as deciding which, among several, response to produce as is the case in Donders' B task. However, in the present study, no N-40 appeared over the SMAs in the Donders' C condition, and the N-40 developed *only* in the Donders' B condition. This component seems therefore specific to motor decisions implicating (at least) two *movements*; in other words, it is specific to situations requiring what Donders called a "response decision" (Donders' B tasks) and confirms that the Donders' C task is not just a variant of the Donders'B tasks.[5]

In the present experiment, although Go and No-go trials were equiprobable, behavioral data indicate that participants did prepare the only possible response in the Donders' C condition: participants were 59 ms faster in the Donders' C than in the Donders' B condition. This difference cannot be attributed to perceptual processes as (i) the nature, the number, and the probability of the imperative stimuli were the same in the Donders' C and in the Donders' B conditions, and (ii) participants had to identify the stimuli in order to act properly in both conditions. This indicates that, although No-go responses were not rare, participants did prepare their unique possible response in the Donders' C condition, such a preparation being impossible in the Donders' B condition (Carlsen, Chua, Inglis, Sanderson, & Franks, 2004). These RT effects are in agreement with the notion that response decision takes place before the RS in the Donders' C condition (Carlsen et al., 2004; Vidal, Bonnet, & Macar, 1995) and that, as a consequence, this operation is not implemented between the stimulus and the response (Lépine, Glencross, & Requin, 1989). If the N-40 is an electrical signature of response decision, it should be elicited between the stimulus and the response in the Donders' B condition since, in this condition, response decision necessarily occurs after the response signal. Now, if response decision has already taken place before the RS, as in the Donders' C condition, no N-40 should be elicited during the RT period. Accordingly, an N-40 should be elicited when and only when a response decision must be implemented during the RT. Therefore, the presence of an N-40 in the Donders' B condition and its absence in the Donders' C condition indicate that this component is a physiological index of response decision.

Altogether, the above arguments support the notion that response decision is inserted in Donders' B tasks as compared to Donders' C tasks.

While supporting assumption 1 (insertion), the present data invalidate assumption 2 according to which inserting or deleting an operation leaves the other processes unaffected. Indeed, the motor processes were clearly affected by the task to be performed—the MT was more than 10% longer in the Donders' B than in the Donders' C task. These MT effects extend those of

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[5]Let us point out, however, that Gomez et al. modeling relied on data using Donder's original procedure, where the Go/No-go option was replaced by a choice between two overt responses. In our variant of the Donder's B task, a choice between two overt responses was added to (and not replaced by) the Go/No-go option. It remains therefore possible that our divergent conclusions are a consequence of these differences in the realized experimental manipulation.

Ulrich, Mattes, and Miller (1999) who showed that Donders' C tasks yield more forceful responses than both simple RT (Donders' A) and Donders' B tasks. Both results demonstrate that the motor processes differ between Donders' C and Donders' B tasks, which falsifies Donders' original assumption.

An even more direct index of response implementation can be found at the central level with the negative wave developing over the contrateral MI just before EMG onset. The functional interpretation of this activity is straightforward: its temporal relation with EMG onset, its spatial distribution and the physiological arguments presented in the introduction, provide good evidence that it represents the activation of the motor cortex contralateral to the responding hand (Meynier, Burle, Possamaï, Vidal, & Hasbrouck, 2009; Tandonnet, Burle, Vidal, & Hasbroucq, 2003). In the present study, this central motor component was also affected by the task. Indeed, this activity started later, on average, (i.e., closer to EMG onset) in the Donders' C task, suggesting not only that the duration of peripheral motor processes was reduced, but also that the motor cortical components are also affected. Thus, a substantial part of the chronometric effect observed on the PMT might well be due to central motor stages. Altogether, those results show that, although a response decision process was indeed inserted in the Donders' B task (assumption 1), such an insertion had a clear impact on downstream processes, indicating that the insertion was not "pure."

Besides affecting the contralateral negativity, tasks also had a strong impact on the ipsilateral positivity. Based on previous stimulation studies (Burle, Bonnet et al., 2002; Hasbroucq et al., 2000), this positivity has been interpreted as reflecting an inhibition of the incorrect response. Nonetheless, the status of this ipsilateral inhibition remained unclear. The present data shed light on its functional significance.

Although the existence of interhemispheric transcallosal inhibitory connections between the two motor cortices has been demonstrated in cats (Asanuma & Okuda, 1962) and in humans (Ferbert et al., 1992), the present data definitely discard the idea that the ipsilateral inhibition described here is a mere "hard-wired" consequence of the contralateral activation. Indeed, this inhibition critically depends on the context of the task being absent when no between-hand choice is required.

Why should inhibition of alternative responses be necessary in the Donders' B condition? We have previously proposed (Burle et al., 2004; Carbonnell et al., 2004; Vidal et al., 2003) that this inhibition could help, functionally, to prevent the occurrence of errors. To prevent an error in the context of a speeded between-hand choice, the participant's interest is to activate the involved motor cortex and concurrently to inhibit the cortex involved in the alternative response to ensure that only the correct response will be triggered. The present data are in line with this view: In the Donders' C condition, where only one response was possible, the risk of committing a response error (giving the response with the non-required hand) was null, and, as a matter of fact, participants did not produce this kind of error. In this situation, no ipsilateral inhibition shows up either. Accordingly, the ipsilateral inhibition could represent a proactive control of errors.

It is also noteworthy that the presence or absence of ipsilateral inhibition is paralleled by the presence or absence of an N-40, respectively. This could indicate that there is a tight functional link between the need for inhibiting inappropriate responses in speeded situations, the elicitation of the N-40, and response decision. Although speculative, this view provides an illustration of why insertion cannot be pure: if one accepts that the N-40 implements response decision and that the ipsilateral positivity reflects a strategic control of errors, it appears that response decision does not only specify which response is to be activated, but that it also specifies which response must be inhibited. If such were the case, insertion of a response decision process in speeded situations is necessarily accompanied by a response inhibition process during response execution. In other words, inserting the former necessarily implies to concurrently insert the latter at the next stage.

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