



Brief report

The N-40: An electrophysiological marker of response selection



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ABSTRACT

A frontocentral electrophysiological wave occurring before the response, the N-40, has been reported in response choice situations compared to no-choice situations. This was interpreted as reflecting response selection. The gradual sensitivity of the N-40 to the demands put on response choice was tested by manipulating stimulus–response (S–R) congruence so as to influence response selection processes. After Laplacian transformation, an N-40 clearly emerged and was larger for incongruent (more demanding) than for congruent (less demanding) S–R associations. The N-40, which possibly reflects SMA activation, thus provides information about the implementation of response selection in the brain.

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1. Introduction

In choice reaction time (RT) situations, about 40 ms before the contraction of the muscle involved in the required response, a phasic negative event-related potential was evidenced (Vidal et al., 2003). It was called the N-40.¹

On the basis of converging arguments, Vidal et al. (2011) suggested that the N-40 was an electrophysiological marker of response selection. Indeed, the N-40 (1) arises *before* the build-up of the motor command (Vidal et al., 2003), as revealed by the initial slope (Tarkka and Hallett, 1991) of the motor potential (Deecke et al., 1969); (2) the N-40 has a frontocentral topography and most likely originates from motor areas of the medial wall (Picard and Strick, 1996) whose contribution to response selection is also supported by metabolic neuroimaging in humans (see Rushworth et al., 2004, for a review); and (3) the N-40 is *present* when a choice between two alternative responses is required (in a between-hand choice RT task), but *absent* when no response choice is required (in a Go/No-go task) (Vidal et al., 2011). It is worth pointing out, as discussed by the authors, this difference could not be attributed to perceptual processes as, in the between-hand as well as in the

Go/No-go task, the nature, the number, and the probability of the imperative stimuli were the same. Moreover, in both tasks, participants had to identify the stimuli in order to react properly in both conditions.

If the N-40 is actually an electrophysiological marker of response selection, we should be able to predict that when the implementation of response selection is made more or less demanding, this should result in a modulation of the N-40.

The so-called “Simon task” provides an experimental context for manipulating the demands put on response selection (Kornblum et al., 1990; Ridderinkhof, 2002; van den Wildenberg et al., 2010). In the most common version of the Simon task, participants have to choose between a left- and a right-hand keypress according to the color of a visual stimulus presented a few degrees to either the left or the right of a fixation point. The performance expressed both in terms of error rate and RT is better when the required response corresponds spatially to the irrelevant stimulus location (congruent association) than when it does not (incongruent association). This effect is termed the “Simon effect” (Simon, 1990; Hommel, 2011). A widely accepted interpretation of the Simon effect is that the irrelevant stimulus location automatically engages a response impulse in the spatially corresponding hand while the relevant stimulus color must be translated into the required response according to the task instructions (De Jong et al., 1994; Kornblum, 1994; Proctor et al., 1995, but see Van der Lubbe et al., 2012). When the stimulus–response (S–R) association is congruent, the impulse triggered by the irrelevant stimulus location activates the required response, which facilitates response processing. In contrast, when the S–R association is incongruent, the impulse triggered by the irrelevant location activates the non-required response which must

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¹ The N-40 was evidenced by the Laplacian transformation. Indeed, acting as a highpass spatial filter, the Laplacian transformation strongly attenuates volume conduction effects (Babiloni et al., 2001) and has proven efficient in disentangling overlapping components (Vidal et al., 2003).

be suppressed and replaced by the required one. These additional operations occur at a cost and the performance is degraded.

Consequently, in the present study, we affected the response selection by using a Simon task. If the N-40 actually reflects the response selection process, we expect that the more the response selection is demanding, the larger the N-40 should be. The N-40 should, therefore, be larger for incongruent than for congruent S-R associations.

2. Methods

2.1. Participants

Twelve participants (six males; mean age: 26; range: 21–37; right-handed; normal vision) volunteered. They performed the task in standard conditions (reported), and for another purpose, after a 26 h period of wakefulness (not reported). The order of the two sessions was counterbalanced across participants. They were paid 200 euros. Informed written consent was obtained according to the declaration of Helsinki and the local ethics committee approved the experiment.

2.2. Design and procedure

Participants were seated in a sound attenuated Faraday cage in front of a far-advised screen. They had to press a left or right key with the left or right thumb, respectively, as soon and accurately as possible after a response signal (RS). RSs were the digits 1, 2, 3, 4, 5 and 6² (62° visual angle). Participants had to respond right or left depending on the digit parity (this was counterbalanced across participants). RSs were randomly presented to the right or to the left of a fixation cross (1.24° visual angle). In the congruent condition, responses were required ipsilaterally to stimuli; in the incongruent condition, responses were required contralaterally. There were 16 blocks of 145 trials each. Between each block, there were short rest breaks during which participants were asked to be more accurate, if they had committed more than 10% of errors. Before recordings, participants performed one training block.

Trials began with RS onset. The RS was turned off after a key press or after 800 ms if no presses occurred. The next RS was displayed 500 ms later.

2.3. Electrophysiological recordings

Electroencephalogram (EEG), electromyogram (EMG), and electro-oculogram (EOG) were recorded continuously from preamplified Ag/AgCl electrodes (BIOSEMI Active-Two electrodes, Amsterdam). The signal was filtered and digitized online (bandwidth: 0–268 Hz, 3 db/octave, sampling rate: 1024 Hz).

For EEG, 64 recording electrodes were disposed according to the 10/20 system with CMS–DRL as reference and ground (specific to the Biosemi acquisition system). A 65th electrode on the left mastoid served to reference the signal offline.

Electrodes for vertical and horizontal EOG were at the Fp1 and below the left eye, and at the outer canthus of the left and right eyes, respectively.

For EMG, two electrodes were pasted onto the skin of the thenar eminence over the *flexor pollicis brevis* of each thumb, about two centimeters apart.

2.4. Data processing

Trials with RTs (measured from stimulus presentation to button press) shorter than 100 ms (anticipations), longer than 800 ms (omissions), errors and partial errors (correct key presses preceded by a subthreshold EMG burst on the incorrect response side: 9.5% of the trials) were excluded from analyses.

Electrophysiological data were numerically filtered offline (EEG, EOG: high-pass = .02 Hz, EMG: high-pass = 10 Hz). Bipolar derivations were performed for vertical and horizontal EOGs. Then, ocular artifacts were subtracted (Gratton et al., 1983). A trial-by-trial visual inspection of monopolar recordings allowed us to reject unsatisfactory subtractions and other artifacts.

Bipolar derivations were performed over each *flexor pollicis brevis*. Then, EMG onset was detected by visual inspection of each trial (Van Boxtel et al., 1993).

The data were segmented from –500 to 500 ms with the EMG onset as zero of time and averaged, time-locked to the EMG onset. No additional filtering was performed on the segmented data. The Laplacian transformation was applied to the monopolar averages, after spherical spline interpolation with 3 as the degree of spline and a maximum of 15 degrees for the Legendre polynomial (Perrin et al., 1987).

² The Spatial-Numerical Association of Response Codes (SNARC) effect does not interact with the Simon effect (Mapelli et al., 2003). Moreover, we checked this effect in the present study using an ANOVA with Simon (congruent vs. incongruent) and SNARC (congruent vs. incongruent) as within participants' factors. There was no SNARC effect, $F(1, 11) < 1$, $\eta_p^2 = .04$, there was a Simon effect $F(1, 11) = 10.94$; $p < .01$, $\eta_p^2 = .50$, and no interaction between SNARC and Simon, $F(1, 11) = 1.77$; $p = .21$, $\eta_p^2 = .14$.

We sought the generator of the N-40 (so far not localized) with the standardized Low Resolution Electromagnetic Tomography (sLORETA) method, which implements a normalized form of the minimum norm constraint (see Pascual-Marqui, 2002 for technical details). Source localization was performed at a single time point (35 ms before EMG onset) on the monopolar grand average for the incongruent condition in which the N-40 was the largest with a –200 to –100 ms baseline.

For a convergent and complementary approach, we used the Rap-Music algorithm (Mosher and Leahy, 1999) as implemented by Brain Electrical Source Analysis (BESA) in the –250 to 330 ms EMG-locked interval. Shortly, a principal component analysis (PCA) was first performed on the monopolar grand average of incongruent trials (largest N-40). We kept the first six dimensions for the signal space in which the sources would be identified. Within this subspace, we chose to identify four sources iteratively. It is worth pointing out that (1) we kept a rather large number of dimensions in the signal subspace to avoid missing any small activity and that (2) the choice of the number of sources does not influence, in any way, the amplitude or the time course of the source since this method is iterative: the method first identifies the strongest source, next discards the remaining signal (hence removing the contribution of this first source) and then identifies the second strongest source and so on.

3. Results

3.1. Behavior

RTs of correct trials and error rates were submitted to a repeated measures analysis of variance with Congruence (congruent vs. incongruent) as the within participants' factor and Order (standard session *before* sleep deprivation session vs. standard session *after* sleep deprivation session) as the between participants' factor.

There was no Order effect, $F_s(1, 10) < 1$, both for RTs, $\eta_p^2 = .01$, and for error rates, $\eta_p^2 = .03$, and no interaction between Order and Congruence, RTs: $F(1, 10) < 1$, $\eta_p^2 = .01$, error rates: $F(1, 10) = 1.26$; $p = .29$, $\eta_p^2 = .11$. Error rates did not differ between congruent (.074) and incongruent (.076) conditions, $F(1, 10) = 2.38$; $p = .15$, $\eta_p^2 = .19$. RT was longer in the incongruent (429 ms) than in the congruent condition (421 ms), $F(1, 10) = 10.45$, $p = .009$, $\eta_p^2 = .51$.

3.2. Electrophysiology

At the FCz electrode, the N-40 (Fig. 1) begins to develop about 100 ms and peaks about 35 ms before EMG onset. The slopes of the linear regression of this wave were computed for each participant from –100 to –35 ms and compared to zero, and between the congruent and incongruent conditions with a unilateral paired Student *t*-test. With response-locked data, slope analysis has certain advantages over amplitude analysis: slopes are independent of the baseline, they give morphological information on the polarity of the curves in delimited time windows and are less variable than amplitude measures (Vidal et al., 2003).

To verify the Order effect, slopes of the N-40 were submitted to a repeated measure analysis of variance with Congruence (congruent vs. incongruent) as within participants' factor and Order (standard condition *before* sleep deprivation condition vs. standard condition *after* sleep deprivation condition) as between participants' factor. There was no Order effect, $F(1, 10) = 1.64$, $p = .23$, $\eta_p^2 = .14$, and no interaction between Order and Congruence, $F(1, 10) < 1$, $\eta_p^2 = .03$. The slope was steeper in the incongruent than in the congruent condition, $F(1, 10) = 3.36$, $p < .05^3$, $\eta_p^2 = .25$. The slope of the N-40 was negative and different from zero, both in the incongruent condition ($-18 \mu\text{V cm}^{-2} \text{s}^{-1}$), $t(11) = 2.94$, $p < .01$, Cohen's $d = 1.21$ and

³ If there is only one degree of freedom in the numerator, the ANOVA F will be exactly equal to the square of the t computed on the same means and the F s will be absolutely equivalent to the t 's two-tailed p . So to test a directional hypothesis with ANOVA F and only two means, the ANOVA F 's p should be divided by two corresponding exactly to the same p one would obtain with a one-tailed p from t (Ley, 1979).

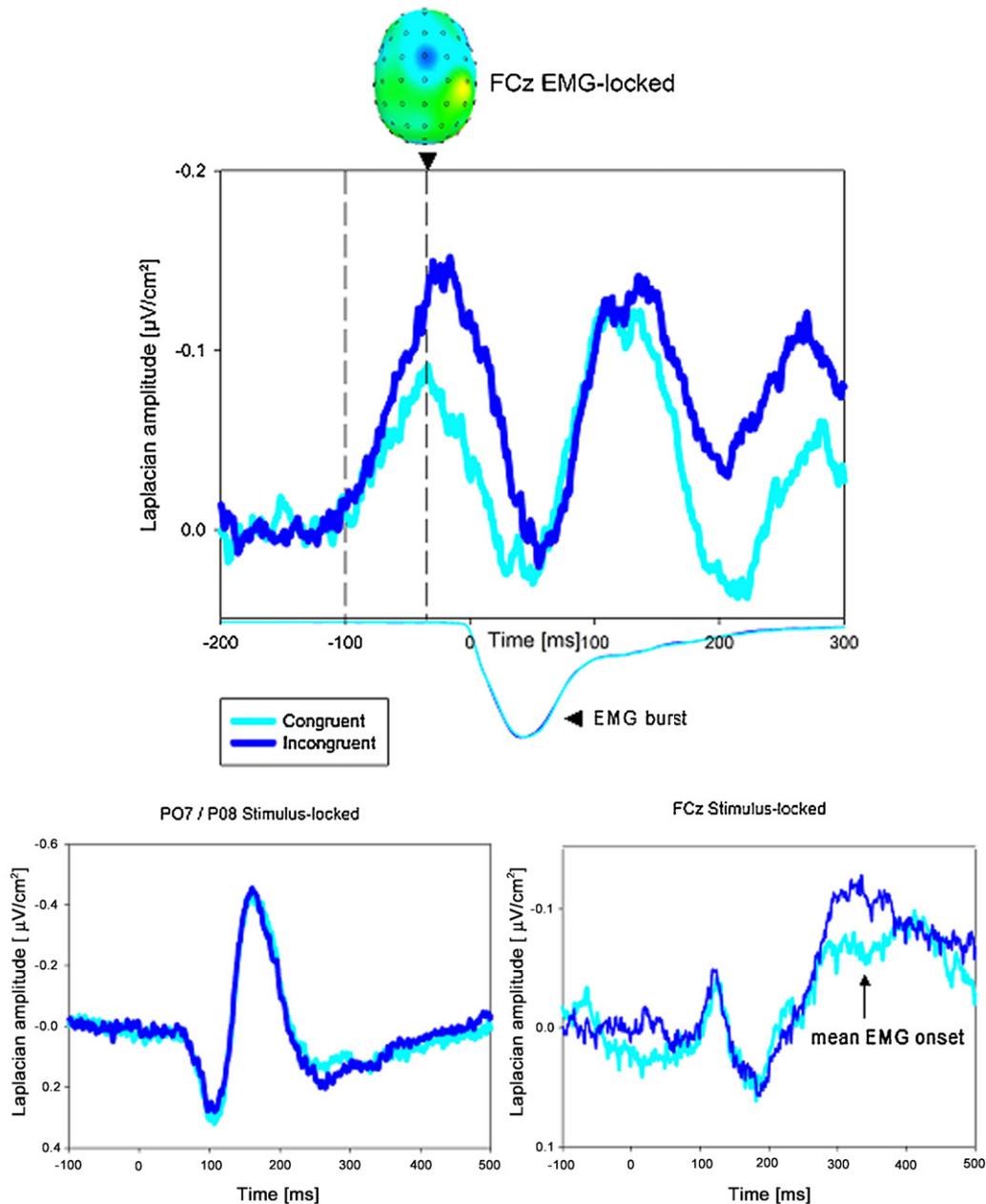


Fig. 1. Frame up: averaged Laplacian transformed EEG activities at FCz (ordinate in $\mu\text{V}/\text{cm}^2$) as a function of time (abscissa in milliseconds, zero of time corresponds to EMG onset). Dashed lines define the temporal windows in which statistical analyses of slopes were made (-100 to -35 ms). A Laplacian map, front of the head upward, corresponding to the incongruent condition is represented with a -0.15 (blue) to 0.3 (red) $\mu\text{V}/\text{cm}^2$ scale at -35 ms. The left side of the map corresponds to brain activities contralateral to the responding hand; the right side of the map corresponds to brain activities ipsilateral to the responding hand. Below the abscissa axis, EMG bursts for both conditions are represented in arbitrary units (-100 ms to EMG onset baseline). Frames down: right, the same data are represented, but stimulus-locked (zero of time corresponds to stimulus onset); left, stimulus-locked averaged Laplacian transformed EEG activities at parieto-occipital sites (PO7 and PO8) where activity was larger than at parietal and occipital sites. For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.

in the congruent condition ($-13 \mu\text{V cm}^{-2} \text{s}^{-1}$), $t(11) = 2.92$, $p < .01$, Cohen's $d = 1.15$.

To compare the EMG of the prime mover (i.e. the flexor pollicis brevis) on congruent and incongruent conditions, the amplitude of averaged and rectified EMG bursts was measured from 0 (EMG onset) to 100 ms with a baseline from -100 to 0 and, then compared using a paired-samples t test. EMG bursts did not differ between conditions, $t(11) < 1$, $p = .48$, Cohen's $d = .01$. This indicates that the response execution is very similar on both conditions.

The sLORETA solution obtained points to a source for the N-40 within the superficial part of Brodmann area 6 (Talairach coordinates $(x, y, z) = 3, -11, 53$) (Fig. 2).

The time course of the second source identified by the Rap-Music algorithm fits fairly well with the time course of the N-40 obtained after Laplacian transformation (Fig. 2). Moreover, the scalp distribution of this source (by projecting back the source on the scalp through the direct problem) (Fig. 2) shows a fronto-central topography comparable to the Laplacian map (Fig. 1). The Talairach coordinates $(x, y, z) = 8, -25, 53$ point to a source within the superficial part of Brodmann area 6.

Although not directly within the scope of this study, the first source identified by Rap-Music (Source 1, Fig. 2) deserves some comments. Indeed, it is a relatively powerful source which is similar to the deep source evidenced with sLORETA (Fig. 2).

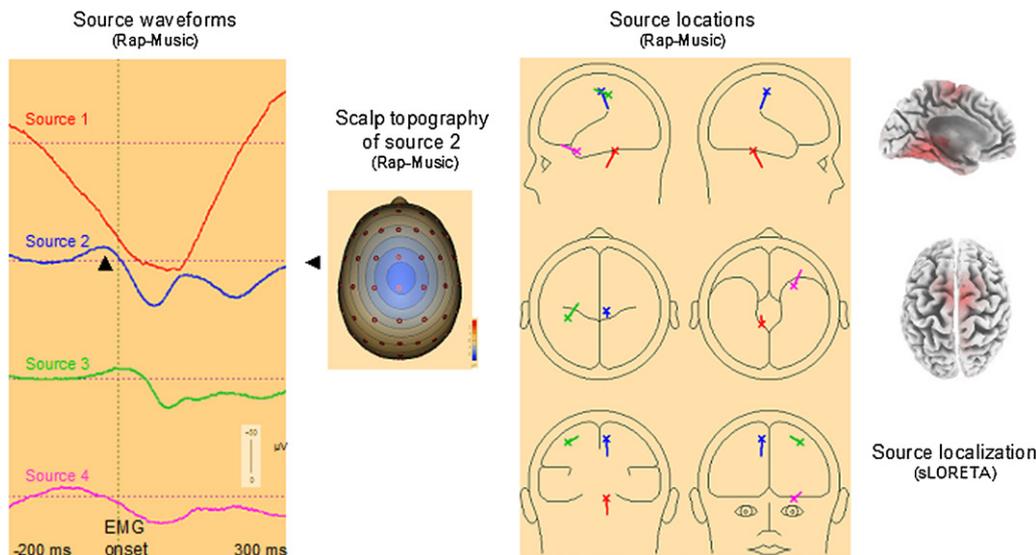


Fig. 2. Decomposition of the brain electrical signal based on monopolar recordings with the Rap-Music algorithm as implemented in BESA. Source waveforms (Rap-Music): four principal sources have been identified iteratively and without any a priori (see Section 2.4). Source 2 seems to correspond very well to the N-40; the time of the pre-EMG negativity peak indicated by the arrow fits with the time of the N-40 peak. Scalp topography of source 2 (Rap-Music): scalp distribution of the source shows a frontocentral topography. Source locations (Rap-Music): topographies of these four sources. Talairach coordinates of Source 2 are $(x, y, z = 8, -25, 53)$ within the superficial part of Brodmann area 6. Source localization (sLORETA): source localization for the N-40 at -35 ms in the incongruent condition. On the hemispheres seen from above, brain activities contralateral to the responding hand are represented on the left side and brain activities ipsilateral to the responding hand are represented on the right one; the activities contralateral to the responding hand are represented on the medial view of the left hemisphere. Talairach coordinates $(x, y, z = 3, -11, 53)$ of the solution indicate a source for the N-40 within the superficial part of Brodmann area 6. For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.

The stimulus-locked monopolar derivations (not shown here) show a large positivity peaking at about 370 ms and maximal at parietal and centro-parietal sites. This positivity disappears after Laplacian transformation suggesting that it probably comes from a deep source(s), as Laplacian is practically insensitive to deep sources (Pernier et al., 1988). This positivity probably corresponds to a P300, a wave mainly associated with attention and memory operations (Polich, 2007). Taking into account the time course and topography of Source 1 and of the P300, it is quite reasonable to assume that Source 1 is the main source of the P300.

To sum up, although based on different principles, both sLORETA and Rap-Music identified two principal solutions and in a convergent manner, one pointing to a deep and powerful source, probably that of a P300 and one, of interest for the present study, pointing to a weaker source at the level of the SMAs. This finding lends support to the idea that both sources have their own existence, each involved in specific processes.

4. Discussion

As predicted, the Laplacian estimation revealed a frontocentral pre-response negativity peaking about 40 ms before EMG onset. Its topography, shape and latency indicate that it corresponds to an N-40 (Vidal et al., 2003). In the present study, we modulated the response selection process *within* the same task, contrary to Vidal et al. (2011) who compared two different tasks (no choice versus choice task, which presents some shortcomings: different contexts, different moments, operation insertion). The response selection process was affected by the spatial S-R congruence: On incongruent trials, the demands put on the response selection process were greater than on congruent trials because, for the selection process to be achieved accurately, additional operations are needed on incongruent as compared to congruent trials (see Section 1). As predicted, the N-40 was larger on incongruent than on congruent trials.

Another interpretation is that the Simon effect could also be due, at least in part, to a kind of attentional reorienting response, which would be higher for incongruent stimuli because attention for the required button press would be directed at the wrong spot (Van der Lubbe et al., 2012). However, if the N-40 reflected an attentional reorienting response, it would be expected to occur earlier. Firstly, the N-40 showed up better when EMG-locked as compared to stimulus-locked (Fig. 1). Secondly, no modulation of stimulus-related activities showed up as a function of congruence, neither at parieto-occipital sites, nor at fronto-central sites. This suggests that the effects observed on the N-40 occurred downstream from perceptual operations.

It has been shown that the N-40 develops before, that is, upstream from the build-up of the motor command (Vidal et al., 2003), as revealed by the Motor Potential (Deecke et al., 1969; Tarkka and Hallett, 1991). This suggests that the N-40 is related to response selection.

We also verified that the N-40 does not correspond to a motor-command process which could differ between congruent and incongruent trials. Indeed, EMG bursts whose shape reflect the motor command, were almost identical for both conditions (which was not the case for the N-40). Moreover, contrary to the Motor Potential (Deecke et al., 1969; Tarkka and Hallett, 1991), when a motor response is emitted in a RT task, the N-40 is not mandatory: on Go responses of a Go/No-go task, there is no N-40 whereas, of course, there is a motor command (Vidal et al., 2011).

After EMG-onset, an Error Negativity-like (Ne-like: Vidal et al., 2000) can be observed (Fig. 1). Luu et al. (2004) proposed that the Error Negativity (Ne: Falkenstein et al., 1991) and the Ne-like, its analog on correct trials, belong to a functionally unitary theta oscillation complex. In this vein, the N-40, as well as the Ne/Ne-like, could also belong to this complex. Admittedly the N-40 which, contrary to the Ne/Ne-like, occurs *before* EMG-onset, could constitute the initial part of this complex.

However, although the N-40 and the Ne-like develop in the theta frequency band, this observation alone is not sufficient to conclude

that they belong to a functionally unitary theta band oscillation. Firstly, in the present data, although Source 2 identified by the Rap-Music algorithm seems to capture very well the N-40, it does not identify any clear oscillatory complex. Secondly, even if both components are part of a theta oscillatory complex, this complex does not seem to be unitary. Indeed, if such were the case, both the N-40 and the Ne/Ne-like would be similarly affected by experimental manipulations. However, previous data indicate that this is not the case. Vidal et al. (2011) showed that the N-40 was absent in a Go/No-go task, where no response choice was required, and present in a choice RT task, whereas the Ne-like was clearly present in both tasks (Vidal et al., Fig. 2). Comparable functional dissociations between the N-40 and the Ne/Ne-like were replicated twice. Using a priming paradigm, Meckler et al. (2010, 2011) showed that, in the case of correct responses, the N-40 was absent for validly primed responses and present for unprimed or invalidly primed responses (Meckler et al., 2010). However, the Ne-like was present in all conditions (Meckler et al., 2011). In the case of errors, the N-40 was present on unprimed trials, but absent on invalidly primed trials, while, a large Ne, in contrast, was always present in both conditions (Meckler et al., in press). In sum, even though the Ne/Ne-like and the N-40 develop in the theta band, it seems unlikely that they reflect the same process. Should it be the case, then, the present results would indicate that the initial part of this theta oscillation (that we called here, N-40) is sensitive, before the build up of the motor command, to the nature of response selection processes. Such an account would not challenge the existence of an electrophysiological index of response selection processes. Finally, it is very likely that pre-response and post-response activities reflect complementary processes. The N-40 (or an initial part of a theta oscillation), starting before EMG onset, would reflect response selection, while the Ne/Ne-like (or a later part of a theta oscillation), starting after EMG onset, would be related more so to the evaluation of the selected responses.

It is noteworthy that, although larger on incongruent than on congruent trials, the N-40 is not specific to interference effects, since the N-40 was evidenced in tasks free of congruence manipulations (Carbonnell et al., 2004; Vidal et al., 2011). In the framework of current models (Kornblum et al., 1990; Ridderinkhof, 2002; van den Wildenberg et al., 2010), this increase on incongruent trials reveals the implementation of operations required by incongruent associations.

Response selection, from metabolic neuroimaging studies, appears to be implemented in neuronal networks including the medial-frontal cortex (Rushworth et al., 2004). Although the Laplacian transformation yields a good approximation of the corticogram (Gevins et al., 1987; Gevins, 1989), it does not solve the inverse problem. However, given that Laplacian transformed data are poorly sensitive to deep sources (Pernier et al., 1988), it is likely that the N-40 originates mainly from SMAs. This opinion is supported by the sLORETA (Pascual-Marqui, 2002) and Rap-Music algorithm (Mosher and Leahy, 1999) solutions obtained for the grand average. Indeed, although the localization of the dipoles by these methods must be taken cautiously, both sLORETA and Rap-Music algorithm's solutions are convergent and point to a superficial source for the N-40 in Brodmann area 6, probably situated in the SMAs (Talairach coordinates: Rap-Music: $x, y, z = 8, -25, 53$; sLORETA: $x, y, z = 3, -11, 53$). Although we cannot exclude the possibility, given the current state of knowledge, that the anterior cingulate cortex located just below SMAs may also contribute to the N-40, three independent methods, relying on different mathematical principles suggest that the N-40 originates mainly from the medial frontal cortex and very likely from its more superficial part, i.e. the SMAs. If one can be quite confident that the SMAs constitute the main source for the N-40, our data provides further anatomofunctional arguments in favor of the idea that the N-40 is tightly related to

response selection. Indeed, there are several lines of evidence supporting the SMA's prominent role in response selection processes (for reviews see, Mostofsky and Simmonds, 2008; Picard and Strick, 1996; Rushworth et al., 2004).

To conclude, the N-40 seems to constitute a good marker of response selection and could be used in the future to clarify the mechanisms underlying this process.

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