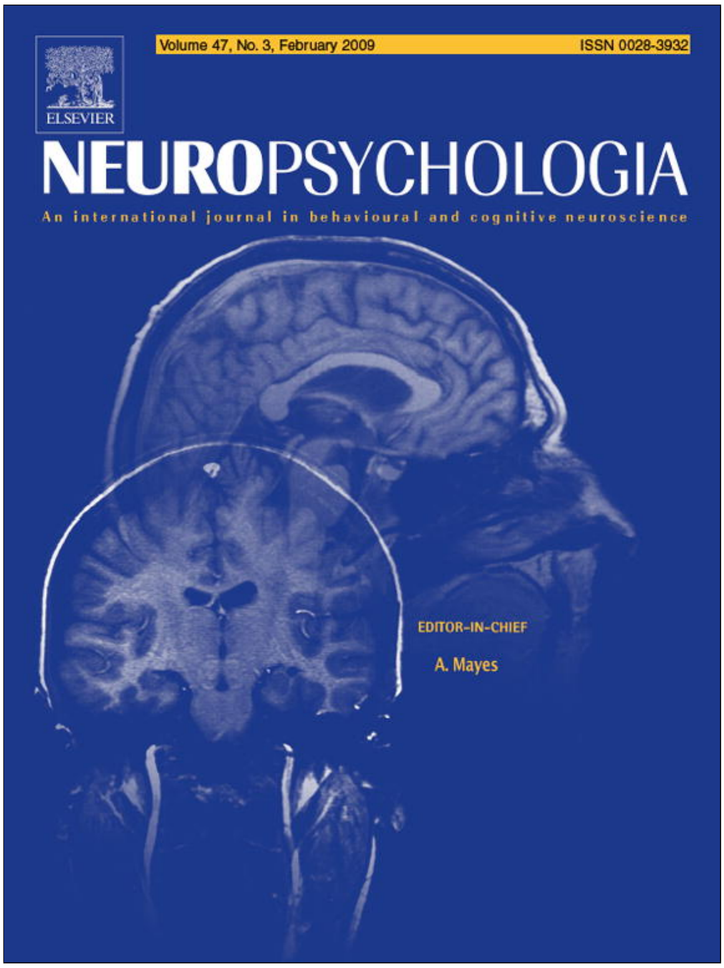
Volume 47, No. 3, February 2009
ISSN 0028-3932
ELSEVIER
NEUROPSYCHOLOGIA
An international journal in behavioural and cognitive neuroscience
EDITOR-IN-CHIEF
A. Mayes

Neuropsychologia 47 (2009) 639–643

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Early adaptation to repeated unfamiliar faces across viewpoint changes in the right hemisphere: Evidence from the N170 ERP component

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ARTICLE INFO

Article history:
Received 30 August 2008
Received in revised form 9 November 2008
Accepted 11 November 2008
Available online 24 November 2008

Keywords:
Face adaptation
N170
Face viewpoint
ERPs

ABSTRACT

Event-related potential (ERP) studies have shown that sensitivity to individual faces emerges as early as ∼160 ms in the human occipitotemporal cortex (N170). Here we tested whether this effect generalizes across changes in viewpoint. We recorded ERPs during an unfamiliar individual face adaptation paradigm. Participants were presented first with an adapting face (∼3000 ms) rotated 30° in depth, followed by a second face (200 ms) in a frontal view of either the same or a different identity. The N170 amplitude at right occipitotemporal sites to the second stimulus was reduced for repeated as compared to different faces. A bilateral adaptation effect emerged after 250 ms following stimulus onset. These observations indicate that individual face representations activated as early as 160 ms after stimulus onset in the right hemisphere show a substantial degree of generalization across viewpoints.

1. Introduction

One of the most interesting characteristics of the human visual system is its ability to recognize individual faces quickly and efficiently, and this despite changes of viewing conditions, such as lightning or viewpoint.

Electrophysiological recordings on the human scalp (event-related potentials, ERPs) indicate that individual unfamiliar faces can be discriminated as early as 160 ms following stimulus onset, i.e. at the level of the face-sensitive occipitotemporal N170 component (Bentin, Allison, Puce, Perez, & McCarthy, 1996; for a recent review, see Rossion & Jacques, 2008). The strongest evidence for this fast extraction of individual face representations comes from so-called adaptation or repetition suppression effects as observed in ERPs (e.g., Kovacs et al., 2006). Several recent studies have found that the N170 (or the M170 in magnetoencephalography, MEG) in response to a repeated face stimulus is reduced as compared to the response to an unrepeated stimulus (Ewbank, Smith, Hancock, & Andrews, 2008; Harris & Nakayama, 2007; Heisz, Watter, & Shedden, 2006; Jacques, d'Arripe, & Rossion, 2007). This observation indicates that individual face representations are extracted as early as 130–170 ms in the occipitotemporal cortex, at the level of the N170 (see also Jacques & Rossion, 2006 for evidence obtained in a continuous stimulation paradigm). The full processing of facial identity may be prolonged, as indicated by later effects of individual face repetition (i.e. on the N250r, Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002).

The N170 onset is thought to mark the early access to the face category in the human brain (Bentin et al., 1996; Rossion & Jacques, 2008). Thus, sensitivity to individual faces at this level is an important observation because it indicates that information about facial identity accumulates rapidly after the initial categorization of the stimulus as a face, in line with evidence from recording studies of face-selective neurons in the monkey brain (e.g., Sugase, Yamane, Ueno, & Kawano, 1999; Tovee & Rolls, 1995).

However, it is unclear whether this early sensitivity to individual face representations is robust enough to generalize across changes in viewpoint. It is known that the vast majority of face-selective neurons in the temporal lobe of non-human primates are viewpoint-sensitive but show a gradual rather than an abrupt decline of their activity for views progressively more rotated from one of their preferential views (Perrett et al., 1985, 1991). Hence, while being viewpoint-sensitive, these cells also show a large degree of generalization across views. Thus, while keeping in mind that the neural signal recorded from single neurons and field potentials may not be directly correlated, one would predict at least a certain degree of generalization across views at a more global level of measuring neural signal, i.e. on the scalp N170. Yet, using MEG, Ewbank et al. (2008) recently failed to report adaptation of the M170 when the viewpoint of the face was slightly changed during a block of identical faces. Accordingly, these authors concluded that the early mechanisms underlying face processing, reflected by the M170, depend on strict viewpoint-dependent neuronal representations. This observation is quite surprising, considering that

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doi:10.1016/j.neuropsychologia.2008.11.016

viewpoint changes were small (2–8°) in that study and the different viewpoints were generated artificially from the same full front image. However, stimuli were presented in block, so that participants knew in advance whether the exact same image would appear successively in a block or if different images would be presented, leaving open the possibility of different sustained attentional levels in distinct conditions. Perhaps most importantly, a short duration of presentation for each stimulus (400 ms), coupled with a long ISI between trials during a block, may have substantially reduced the sensitivity of the paradigm to disclose individual face adaptation effects across viewpoints (Harris & Nakayama, 2007).

Taking into account these issues, the goal of the present study was to readdress this question of individual face coding across viewpoint changes by recording ERPs during a sensitive event-related identity adaptation paradigm (Jacques et al., 2007) with unfamiliar faces presented under different viewpoints.

2. Methods

2.1. Participants

Twenty paid volunteers (12 females; mean age = 19.9 ± 2.3 years) participated in this experiment. All the participants were right-handed and had normal or corrected-to-normal vision.

2.2. Stimuli

Twenty-three unfamiliar faces without glasses, facial hair or make-up, and with neutral expression were used. Each face was presented from two different views (frontal, and 30° to the right). All faces' pictures were trimmed to remove background, clothing and hairline using Adobe® Photoshop® 7.0. Resulting cropped faces were equated for mean pixel luminance using the "image/adjustments/brightness" function in Photoshop. The stimuli were shown in full color and subtended approximately 2.8 × 3.7° of visual angle.

2.3. Procedure

After electrode-cap placement, subjects were seated in light- and sound-attenuated room, at viewing distance of 100 cm from a computer monitor. Stimuli were displayed using E-prime 1.1, on a light grey background. In each trial, two faces (adapting and test faces) were presented sequentially. The adapting face was oriented 30° to the right, and the test face was presented from a frontal view. The target face was presented full front for three reasons. First, a full front target face provides as much information in the left and right visual field, allowing testing more objectively for potential lateralization effects. Second, behavioral studies of face viewpoint adaptation used exactly this kind of paradigm: 3/4 profile face followed by a full front face (e.g., Fang & He, 2005; Fang, Ijichi, & He, 2007). Third, it is easier to generalize from a 3/4 profile view to a full-front view than the reverse for unfamiliar faces (Hancock, Bruce, & Burton, 2000; Hill, Schyns, & Akamatsu, 1997), so that this kind of design was judged as most sensitive to test our hypothesis. A trial started with a fixation point displayed at the center of the screen for 200 ms. Approximately 200 ms (randomized between 100 and 300 ms) after the offset of the fixation point, the first face (adapting face) appeared for ~3000 ms (randomized between 2800 and 3200 ms). After an interval of about 250 ms (150–350 ms), a second face (test face) appeared for 200 ms. The offset of the second face was followed by an inter-trial interval of about 1400 ms (1300–1500 ms) (Fig. 1). In half of the trials, the second face was of the same identity as the first face. To further avoid any possible pixel-based adaptation effect, the second face of each trial was 5% larger than the first face. Each face appeared equally often in the "same" and "different" conditions. Whenever the pairs of faces were different, the consecutively presented faces were always of the same gender. Participants performed an individual face matching task between the adapting and test faces, and gave their response by pressing one of two keys with their right hand (keys counterbalanced across subjects). They were instructed to maintain eye gaze fixation to the center of the screen during the whole trial and to respond as accurately and as fast as possible. Participants performed 69 trials per condition (23 faces repeated 3 times each). The order of conditions was randomized within each block. All participants underwent a training phase before being tested.

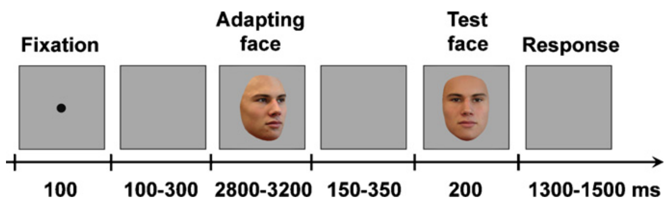

Fig. 1. Timeline of the stimulus sequence.

2.4. EEG recording

EEG was recorded from 128 Ag/AgCl electrodes mounted in an electrode cap (Waveguard, ANT). Electrode positions included the standard 10–20 system locations and additional intermediate positions. Vertical and horizontal eye movements were monitored using four additional electrodes placed on the outer canthus of each eye and in the inferior and superior areas the right orbit. During EEG recording, all electrodes were referenced to the left mastoid reference, and electrode impedances were kept below 10 kΩ. EEG was digitalized at a 1000 Hz sampling rate and a digital anti-aliasing filter of 0.27* sampling rate was applied at recording (at 1000 Hz sampling rate, the usable bandwidth is 0 to ~270 Hz). After a 30 Hz low-pass filtering of the EEG, time windows in which the standard deviation of the EEG on any electrode within a sliding 200 ms time window exceeded 35 μV were marked as either EEG artifacts or blink artifacts. Blink artifacts were corrected by subtraction of a vertical electrooculogram (EOG) propagation factor based on EOG components derived from principal component analyses. Incorrect trials and trials containing EEG artifacts were rejected, and the number of trials was equated between conditions. Subjects' averages were baseline corrected using the 100 ms pre-stimulus epoch and then re-referenced to a common average reference.

2.5. Statistical analyses

Correct response times and percentages of correct responses were submitted to a repeated-measures analysis of variances (ANOVA) with Adaptation (same vs. different identities) as a within-subject factor.

Two clear visual components elicited by the second (test) face were analyzed: the P1 (maximal at approximately 110 ms), and the N170 (maximal at approximately 170 ms). Amplitude values of these components were measured at 6 different pairs of occipitotemporal electrodes in the left and right hemisphere where they were the most prominent (see Fig. 2). Amplitudes were quantified for each condition as the mean voltage measured within 30 ms windows centered on the grand average peak latencies of the components' maximum. The mean amplitude of the N250r was also measured in the interval from 230 to 330 ms after stimulus onset at 7 pairs of occipitotemporal electrodes where this component was the most prominent. The amplitude values of each component were then submitted to separate repeated-measures analysis of variance with Adaptation (same vs. different identities), Hemisphere (right vs. left), and Electrode (6 or 7 levels) as within-subject factors. All effects with two or more degrees of freedom were adjusted for violations of sphericity according to the Greenhouse-Geisser correction. Polynomial contrasts were performed for post hoc comparisons.

3. Results

3.1. Behavioral data

During the individual face matching task, subjects performed better for same (93 ± 1.5% (SE)) than for different (85 ± 1.9%) identities ($F(1,19) = 19.85$; $p = .0014$). They also responded more quickly for same (628 ± 29 ms) compared to different (683 ± 32 ms) trials ($F(1,19) = 13.09$; $p = .0018$).

3.2. Electrophysiological data

3.2.1. P1 component

At the level of the P1 component, there was a significant Electrode effect ($F(5,95) = 5.71$; $\varepsilon = .37$; $p = .008$), due to larger amplitudes on the PO5/6 and PO7/8 pairs of electrodes compared with the lower and more lateral channels (POO9 h/10 h, PO9/10, PPO9 h/10 h, and O1/2). All other effects were not significant ($p > 0.5$). Notably, there was no effect of adaptation ($F(1,19) = 2.91$; $p = .104$) on the P1 (Fig. 2).

3.2.2. N170 component

The N170 was larger in the right than in the left hemisphere ($F(1,19) = 7.22$; $p = .0146$) and on the lateral (PO9/10, P9/10, PPO9 h/10 h) electrodes compared to the more medial (POO9 h/10 h, PO7/8, P7/8) electrodes ($F(5,95) = 6.18$; $\varepsilon = .66$; $p = .0006$). Most importantly for our hypothesis, the amplitude of the N170 was larger in response to different than to same identities ($F(1,19) = 6.62$; $p = .018$). The significant interaction between

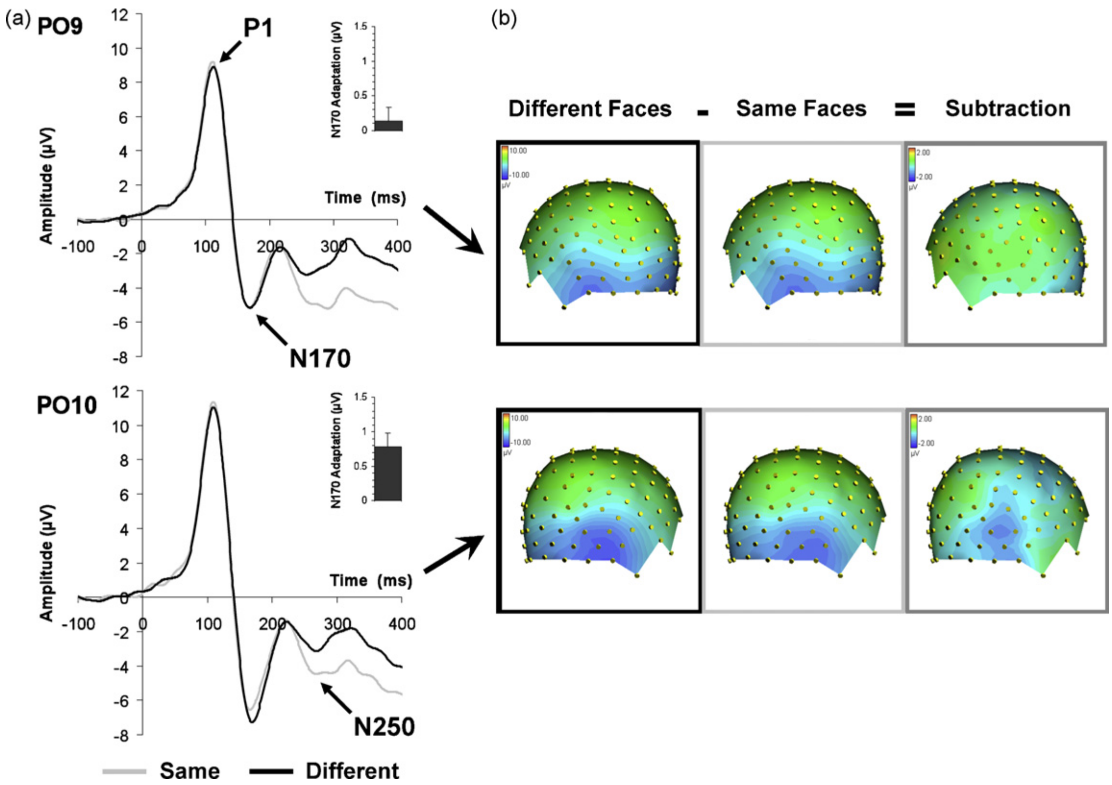

Fig. 2. (a) Grand average ERP waveforms elicited by the second (test) face at two occipitotemporal electrodes (PO9 and PO10) for the different and same conditions. Histograms represent the amount of adaptation (amplitude in same minus in different conditions) in the N170 time window. (b) Topographical maps of the N170 (170 ms) for the different and same conditions, and for the difference between these two conditions.

Adaptation and Hemisphere ($F(1,19) = 2.91$; $p = .0052$), indicates an adaptation effect in the right hemisphere ($F(1,19) = 18.37$; $p = .0004$), but not in the left hemisphere ($F(1,19) = .55$; $p = .465$) (Fig. 2).

3.2.3. N250r component

There was a significant Electrode effect ($F(6,144) = 9.82$; $\varepsilon = .40$; $p = .00013$), due to larger amplitudes on the more lateral (TPP9 h/10 h, P9/10, PO9/10, I1/2) electrodes than on the other channels (POO9 h/10 h, PPO9 h/10 h, OI1 h/2 h). The Hemisphere factor failed to reach significance ($F(1,19) = 3.91$; $p = .063$). As for the N170, there was also an identity repetition effect on the N250r component ($F(1,19) = 23.17$; $p = .0001$), in line with previous observations (Jacques et al., 2007; Schweinberger et al., 2002).

4. Discussion

Using a face identity adaptation paradigm, we found significantly reduced N170 amplitude in the right hemisphere during consecutive presentation of same as compared to different identities. These results confirm previous evidence showing an early identity adaptation effect for unfamiliar faces (Ewbank et al., 2008; Harris & Nakayama, 2007; Jacques et al., 2007), which indicate that the extraction of individual face representations takes place early during the time course of face processing, i.e. at around 170 ms post-stimulation in the occipitotemporal cortex (see also Jacques & Rossion, 2006).

The present study goes beyond these findings by showing for the first time that the adaptation effect to face identity on the N170 component is robust enough to generalize across changes in viewpoint. These data corroborate behavioral findings showing that the face adaptation effects is not only resistant to changes of size, orientation and location (Anderson & Wilson, 2005; Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003), but also to a substantial change in viewpoint (Jiang, Blanz, & O'Toole, 2006). Since we modified the size between the two consecutively presented stimuli, and the images differed by 30° of angle, this finding of an early adaptation effect could hardly be explained by low-level visual features. Moreover, the absence of individual face adaptation effect on the earlier visual P1 component, which may show face-sensitivity due to low-level features (e.g. spatial frequencies of faces vs. other categories, Tanskanen, Näsänen, Montez, Päällysaho, & Hari, 2005; see Rossion & Jacques, 2008), concurs to reject a low-level interpretation.

Contrary to our results, Ewbank et al. (2008) did not find a reduction of the M170 amplitude in their MEG study when images of the same face were presented under different viewpoints. This is even more surprising given that this study used small (<10°) changes in viewing angles. However, each image was presented for a relatively short duration (400 ms), whereas here we used a long duration for the adapter face, in line with behavioural studies of face adaptation (Leopold, Rhodes, Muller, & Jeffery, 2005; Webster, Kaping, Mizokami, & Duhamel, 2004). In fact, short durations of adapting face stimuli have not always led to identity repetition effects on the N170 component, even when there was no viewpoint change between the adapter and the target (Henson et al., 2003). Other studies, using ERPs or fMRI, have shown that the long or short duration of the adapter could be a critical parameter in disclosing face adaptation effects (Fang, Murray, & He, 2006; Kovacs, Zimmer, Harza, & Vidnyanszky, 2007).

Another critical parameter may be the duration of the interval between the adapter and the target face. Harris and Nakayama (2007) reported that the adaptation of the M170 strongly increased when the two stimuli were presented in close succession, as in the present study (ISI of ~250 ms). The use of a long time interval (1100 ms) between stimulus presentations during a block by Ewbank et al. (2008) may also have prevented the observation of face identity effects across small viewpoint changes at the level of the M170.

Admittedly, one remaining limitation of the present paradigm is that one cannot fully exclude that the release from adaptation observed here is due to the adapting 3/4 profile face activating a viewpoint-dependent full-front face representation before the presentation of the target face, leading to the observed adaptation effects. Moreover, a full design with a full-front face as adapter and a 3/4 profile face as target could have strengthened our conclusions about the generalization across different views of N170 face identity adaptation effects.

However, the present observations of a significant degree of generalization across changes in viewpoint for face identity coding at the level of the N170 are consistent with the response properties of single-unit recording studies in the monkey brain, which show a gradual rather than a sharp decline of their activity for face views rotated progressively from their preferential view (Perrett et al., 1985, 1991). For instance, a rotation of 60° from the optimal view reduces neurons responses by approximately 1/2. This type of tuning function characterizes 83% of all face-selective neurons (Perrett et al., 1991). This physiological evidence suggests that face identity adaptation effects should transfer at least partially across a change of viewpoint.

In agreement with physiological evidence, a number of studies using fMRI-adaptation have also found that the response to faces in face-selective regions, such as the so-called “fusiform face area” (FFA), is viewpoint-dependent (Fang et al., 2007; Grill-Spector et al., 1999). Fang et al. (2007) observed with long adaptation duration (5 s) that the nature of the adaptation effects was dependent on the angular difference between the adaptor and test faces. The face-selective areas (right FFA and right posterior superior temporal sulcus) exhibited viewpoint tuned adaptation. As the angular difference (0, 30 and 90°) between the adapter and test stimulus increased, the blood oxygen level-dependent (BOLD) signal evoked by the test stimulus gradually increased as a function of the amount of rotation. This suggests that the strength of viewpoint adaptation in these regions – which are likely to contribute to the scalp N170 component (e.g., Horovitz, Rossion, Skudlarski, & Gore, 2004; Iidaka, Matsumoto, Haneda, Okada, & Sadato, 2006) – depends on the angular difference between the adapting and test faces, in agreement with single-unit recording studies and the present findings.

This partial transfer across viewpoints may account for the fact that we found a face identity adaptation effect that was less substantial here than when there was no change of viewpoint between adapter and target faces in the same paradigm (Jacques et al., 2007). In fact, while bilateral identity adaptation effects on the N170 were found previously (Ewbank et al., 2008; Harris & Nakayama, 2007; Jacques et al., 2007, with a right hemispheric advantage), this effect remained significant only in the right hemisphere here. This observation reinforces the dominant role of the right hemisphere in coding for individual face representations, as supported by a wide range of evidence from divided visual field studies (e.g., Hillger & Koenig, 1991), acquired prosopagnosia (e.g. Barton, Press, Keenan, & O'Connor, 2002; Sergent & Signoret, 1992), or neuroimaging (e.g. Rossion, Schiltz, Robaye, Pirenne, & Crommelinck, 2001). Bilateral sensitivity to individual faces as shown by adaptation effects emerged at approximately 250 ms following stimulus onset here (N250r), as shown previously (Jacques et al., 2007; Schweinberger et al., 2002). While the N170 effect may reflect the early stage at which sufficient information has been accumulated in the system to discriminate individual faces (Jacques & Rossion, 2006; Jacques et al., 2007), the N250r has been tentatively associated to the recognition of facial identity linked to face memory (Schweinberger et al., 2002). Thus, altogether, these observations indicate that the sensitivity to individual face representations across viewpoints starts at around 170 ms in the right occipitotemporal cortex and builds up during the time course of face processing, gradually involving both hemispheres.

Acknowledgements

This study was supported by a research grant (ARC 07/12-007, Communauté Française de Belgique-Actions de Recherche Concertées). SC, BR, MR and CJ are supported by the Belgian National Fund for Scientific Research (FNRS). We thank two anonymous reviewers for the careful reading and constructive comments on a previous version of this paper.

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