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Research Report

Induced gamma-band activity is related to the time point of object identification

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ABSTRACT

Object recognition is subserved by mechanisms that seem to rely on the activity of distributed neural assemblies coordinated by synchronous firing in the gamma-band range (>20 Hz). The present study relied on a novel EEG-compatible plane-rotation paradigm to elicit view-dependent processing leading to delays in the recognition of disoriented objects. The paradigm involved a covert naming task (grammatical gender decision). The task's suitability was first evaluated through a control experiment that contrasted covert with overt naming. The plane-rotation paradigm was subsequently employed in an EEG experiment. It was found that recognition delays for disoriented objects were accompanied by induced gamma-band activity's (GBA) peak latency delays, replicating Martinovic, Gruber and Müller (2007, *Journal of Cognitive Neuroscience*). Brain electrical tomography was performed to obtain further information on the intracranial current density distributions underlying the latency shifts. Induced GBA was found to be generated by a set of distributed prefrontal, temporal and posterior sources committed to representational processing. Their relative contribution differed between upright and disoriented objects, as prefrontal activity became more prominent with increased disorientation. Together these findings indicate that adaptive changes in dynamic coding of object identity occur during recognition of disoriented objects. Induced GBA is a marker of pronounced sensitivity to these changes and thus a robust neural signature of representational activity in high-level vision.

1. Introduction

Studies on mechanisms of high-level vision suggest objects are represented through formations of distributed feature-coding neural assemblies. Within and between these assemblies transient integrative activity is thought to occur through synchronous firing in the gamma-band frequencies (>20 Hz) (Gruber and Müller, 2005; Varela et al., 2001). This type of activity can be detected in the high frequency range (30–90 Hz) of the human electroencephalogram (EEG). It can be either evoked or induced depending on whether it is or is not time-and phase-locked to stimulus onset (Singer and Gray, 1995). In the visual domain it has been repeatedly demonstrated that evoked gamma-band activity (GBA), occurring at approx. 100 ms post-stimulus onset, is related to the processing and integration of features (Busch et al., 2004; Karakas and Basar, 1998). Meanwhile, induced GBA, occurring at approx. 200–400 ms post-stimulus onset, is a signature of cortical object representation (Kaiser et al., 2004; Lachaux et al., 2005; Tallon-Baudry and Bertrand, 1999; Tallon-Baudry et al., 2005); particularly the late representational processing

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that follows successful identification (Fiebach et al., 2005; Gruber et al., 2004; Gruber and Müller, 2005; Martinovic et al., 2007).

An abundance of evidence shows that increases in induced GBA amplitude accompany successful recognition of complex meaningful objects (Gruber et al., 2004; Gruber and Müller, 2005; Lachaux et al., 2005; Tallon-Baudry et al., 2005). However, its time course has not been successfully related to object identification until our recent study (Martinovic et al., 2007) demonstrated that delayed peak latency of induced GBA accompanied delayed covert naming of disoriented objects. In that study, participants had to covertly name images that could either be presented upright or disoriented in the picture plane. Covert naming was performed in the form of a phonological decision on the first letter of the object's name, with vowels as rare stimuli. The participants were instructed to press one button if the name of the object started with a consonant and another button if the name started with a vowel. This covert task produced naming delays for disoriented objects. Such naming delays in plane-rotation paradigms are generally considered to reflect delays in the recognition processes itself (Jolicoeur et al., 1998; Lawson and Jolicoeur, 1998; Lawson and Jolicoeur, 2003). Martinovic et al. (2007) found that while induced GBA showed latency shifts, evoked GBA and event-related potential (ERP) components remained unmodulated. However, the delays in behavioural and neurophysiologic measures failed to show a direct correlation. It has already been reported that repetition suppression in induced GBA amplitude relates to RT (reaction time) benefits obtained through visual priming, although the two measures do not correlate (Fiebach et al., 2005); same holds for BOLD responses from the ventral visual pathway (Maccotta and Buckner, 2004; Wig et al., 2005). Thus, in spite of the lack of correlation,our previous publication's findings provide further evidence in support of the Tallon-Baudry and Bertrand's (1999) representational hypothesis, which claims that induced GBA is a neural marker of object coding.

The plane-rotation paradigm by Martinovic et al. (2007) used a covert naming task in order to elicit delays in the recognition of disoriented objects. Such view-dependent recognition effects have long been known and studied in behavioural literature. Picture-plane rotated two-dimensional (2D) images of familiar objects with a predominant environmental orientation (e.g., horse, table, chair, etc.) generally require more time to be *overtly named* than upright images (Jolicoeur, 1985; McMullen and Jolicoeur, 1990; Murray, 1995a). Such orientation effects are observed in speeded naming tasks performed on large and diverse stimulus sets, therefore demanding recognition to occur at the entry-level of recognition. Objects can be identified at a general (superordinate, e.g., animal), intermediate (basic, e.g., bird), and specific (subordinate, e.g., sparrow) level. Another level of identification is entry level: the level of identification at which objects are named in everyday life. This generally occurs at the basic level except for certain visually distinct exemplars, for example, a sparrow would be identified as a bird, whereas a penguin would be identified as a penguin. Object recognition at the superordinate level of identification has been shown to be viewpoint-invariant (Hamm and McMullen, 1998). Identification at entry level, on the other hand, mainly relies on viewpoint-dependent mechanisms (Murray, 1998).

Overt naming delays for disoriented objects obtained with plane-rotation paradigms are generally considered to reflect delays in recognition processes themselves. These delays are thought to arise due to a nonlinear image normalisation that is needed for the initial identification of the object (Jolicoeur et al., 1998; Lawson and Jolicoeur, 2003; Willems and Wagemans, 2001). An alternative view claims that the viewpoint costs do not occur during initial identification. This account, based on attentional blink and repetition blindness paradigms, claim that costs are incurred when representations become consolidated in visual memory (Dux and Harris, 2007; Harris and Dux, 2005). The early versus late viewpoint-effect distinction from behavioural literature does not challenge the findings of our previous study. As induced GBA is related to late representational processing, the delay that is observed in its peak latency could be due to an intervening process at either the initial or the consolidated representation stage.

The aim of the present study was to replicate and extend the findings by Martinovic et al. (2007) on the relatedness of induced GBA to the time point of object recognition. Compared to our previous publication, the present study introduces three major new elements. First of all, modifications were introduced to the plane-rotation paradigm in order to increase the quality of the data. The assignment of stimuli to the upright and disoriented conditions was counterbalanced across the sample instead of being fixed to condition as in our previous publication. Also, a more stringent gender decision task was used instead of the phonological decision that was employed in the previous study[1].

Secondly, in order to assess the validity of covert tasks a control experiment was conducted. It contrasted overt and covert naming (i.e. gender decision) in eliciting object recognition delays with a plane-rotation paradigm. Martinovic et al. (2007) implicitly posited that tasks based on covert naming directly correspond to overt naming. However, the comparability between overt and covert naming should be experimentally examined. Convergence of covert and overt RTs would allow us to confidently relate RT delays from covert tasks to the timing of recognition processes.

Lastly, the EEG experiment was more extensive than in Martinovic et al. (2007). In addition to behavioural, ERP and event-related GBA analyses it included brain electrical tomography (BET) of induced GBA. This was done in order to ascertain if shifts in latency would also be accompanied by changes in the activity of generating cortical structures. A distributed set of prefrontal, temporal and posterior regions, committed to object recognition, were expected to be the sources of GBA induced by entry-level object recognition (for previous findings using a categorisation task, see Gruber et al., 2006; for a detailed model describing regions involved in object identification, see Bar, 2003). If induced GBA was indeed a marker of dynamic object coding, as we had proposed in the conclusion of our previous publication, adaptive changes that lead to latency shifts should also be visible from the pattern of activity within these distributed sources. In line with Bar's (2003) model, prefrontal generators should become more prominent with increased rotation through additional or prolonged top–down

[1] In the Discussion, you can find further information on the importance of stimulus counterbalancing in plane-rotation studies. It also provides the relevant information on the advantages of a grammatical gender decision task.