International Journal of Psychophysiology 98 (2015) 35–43

Contents lists available at ScienceDirect

International Journal of Psychophysiology

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

Temporal dynamics of repetition suppression to individual faces presented at a fast periodic rate

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ARTICLE INFO

Article history:
Received 15 March 2015
Received in revised form 3 June 2015
Accepted 19 June 2015
Available online 22 June 2015

Keywords:
Face perception
Individual face discrimination
EEG
Adaptation
Repetition suppression
Fast periodic stimulation

ABSTRACT

Periodic presentation of visual stimuli leads to a robust electrophysiological response on the human scalp exactly at the periodic stimulation frequency, a response defined as a "steady-state visual evoked potential" (SSVEP, Regan, 1966). However, recent studies have shown that SSVEPs over the (right) occipito-temporal cortex are reduced when the same individual face is repeated at periodic rates of 3 to 9 Hz compared to when different faces are presented (Rossion, 2014). Here, we characterized the temporal dynamics of this repetition suppression effect. We presented different face identities at a rate of 5.88 Hz (stimulus onset asynchrony of 170 ms) for 15 s, followed by the repetition of the exact same face at this rate for 35 s. Compared to a stimulation sequence with different faces only, there was a large and specific decrease of the 5.88 Hz response when the same face was repeated at that rate. This effect was observed over the left and right occipito-temporal cortex, but not over medial occipital electrode sites where SSVEPs are typically measured. In the right hemisphere, this decrease occurred abruptly, i.e., within half a second following the introduction of the same-identity stimulation, with no further decrease until the end of the stimulation. These observations indicate that the SSVEP recorded over high-level visual areas to periodic stimulation is not steady but rather adapts immediately and fully following the repetition of the same individual face, supporting a bottom-up, stimulus-driven account of repetition suppression effects.

1. Introduction

Two important and complementary functions of the human brain are the ability to discriminate between different visual entities, and to generalize across different presentations of the same visual entity. For instance, the human brain is able both to discriminate people by their faces rapidly and efficiently and to generalize across different viewing conditions of the same face identity. A powerful way to understand visual discrimination and generalization is by taking advantage of the phenomenon of repetition suppression (RS), i.e., the reduced (adapted) neural response to repeated compared to unrepeated visual stimuli. In particular, this effect has been reported for face stimuli at the single neuron level in the monkey inferior temporal (IT) cortex (e.g. Baylis and Rolls, 1987; Fahy et al., 1993; Li et al., 1993; Miller et al., 1991; Ringo, 1996), at the neural population level in the human ventral occipito-temporal cortex with neuroimaging (e.g. Andrews and Ewbank, 2004; Ewbank et al., 2013; Gilaie-Dotan et al., 2008; Grill-Spector and Malach, 2001; Grill-Spector et al., 2006; Henson et al., 2002) and on the human scalp with visual event-related potentials (ERPs, e.g., Eimer et al., 2011; Jacques et al., 2007; Kovács et al., 2006; Walther et al., 2013).

Although the neural mechanisms of RS are unclear, the response difference between a repeated face stimulus and face stimuli differing by a carefully controlled characteristic reveals the sensitivity of the human brain to this characteristic. This response difference occurs at a given spatio-temporal scale determined by certain factors, e.g. a single neuron, a population of neurons or a functional brain region. RS effects for faces have been observed at multiple spatial, temporal and frequency scales, both in the human and nonhuman primate brain, as indicated above (see also Gruber et al., 2004; Merzagora et al., 2014). However, since these responses are widely distributed in time, space and frequency bands, adaptation effects that arise from the comparison of repeated to unrepeated stimuli can be nonspecific (i.e. not directly related to the stimulus). Moreover, they can potentially be attributed to several factors beyond visual discrimination (attention, arousal, change detection, model adjustment, novelty detection, prediction error) (Lieder et al., 2013).

One way to circumvent this limitation is by using a periodic rate of visual stimulation eliciting a periodic brain response exactly at this stimulation rate (Adrian and Matthews, 1934). Even if the rate is fast, for instance, three or more items are presented per second, the response can be identified exactly at the frequency of stimulation by means of techniques with a high temporal resolution, such as electroencephalography (EEG)

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http://dx.doi.org/10.1016/j.ijpsycho.2015.06.006
0167-8760/

or magnetoencephalography (MEG). In EEG, this periodic neural response is known as the "steady-state visual evoked potential" (SSVEP, Regan, 1966, 1989; Norcia et al., 2015 for a review).

Although the SSVEP has long been thought of, and defined, as a response that is constant in amplitude and phase over time (a "steady state" response), there is recent evidence that this response is sensitive to stimulus identity repetition. Specifically, when the same visual stimulus, a given face identity, is repeated at a relatively fast periodic rate (e.g., 3.5 Hz, or a stimulus onset asynchrony of 286 ms), it leads to a reduced response compared to the presentation of different face identities exactly at that rate (Rossion and Boremanse, 2011). Importantly, this RS effect is restricted to the frequency of interest (3.5 Hz) and observed on the scalp mainly over the right occipito-temporal cortex, a scalp topography characteristic of face-sensitive responses such as the well-known N170 potential (Bentin et al., 1996; Rossion and Jacques, 2011 for review). A robust RS effect can be obtained with this approach for stimulation frequency rates of 3 to 9 Hz (Alonso-Prieto et al., 2013; Rossion and Boremanse, 2011; Rossion et al., 2012; see also Gerlicher et al., 2013; Vakli et al., 2014; see also Jonas et al., 2014 for an RS effect at 6 Hz as recorded intracerebrally in the right lateral occipital cortex).

Recording SSVEPs offers several advantages for exploring RS effects. First, the RS effect is confined to a very narrow frequency band corresponding to the stimulation frequency defined by the experimenter, so that the effect can be directly identified and quantified. Second, the SSVEP has a very high signal-to-noise ratio because the signal falls in a specific frequency band, which can be defined outside the range of frequencies associated with high levels of noise (i.e., low frequencies, alpha band). Moreover, the technique is relatively immune to artifacts (e.g. blinks, eye movements or muscular artifacts), since these artifacts spread over a wide range of frequencies while the signal is concentrated on a small stimulation frequency band (Regan, 1989; Norcia et al., 2015). This allows for robust effects to be obtained in a very short time. Third, the measure is implicit or behavior-free, since it can be obtained without performing an explicit task related to the process of interest (i.e., here, individual face discrimination, Rossion, 2014).

However, the temporal dynamics of the face identity RS effect to fast periodic stimulation remains largely unknown. Here, by "temporal dynamics", we do not mean the exact onset latency of the RS effect, which is difficult to define precisely (i.e., at the millisecond range) when a fast periodic train of stimuli is presented in a SSVEP paradigm. Rather, temporal dynamics refers here to the time taken by the periodic visual response to show suppression following the onset of stimulus repetition within a few hundreds of milliseconds, the time taken for this response to reach its minimal level, and the nature of this decay (i.e., a slow linear decrease or an abrupt decrease to its minimal level within a few hundreds of milliseconds). This issue is important to clarify in order to relate the RS effects obtained with periodic visual stimulation to other approaches and to help understand the nature of this effect. In addition, clarifying the temporal dynamics of the RS of an SSVEP response can have important practical consequences, allowing optimization of the paradigms used to capture this response. For instance, if RS is completed within a few hundreds of milliseconds, shorter trials could be used to measure this phenomenon.

Previous studies with low level visual stimuli have shown only a relatively slow RS effect on the SSVEP response. Heinrich and Bach (2001) showed an initial increase in SSVEP amplitude during the first 6 s of a checkerboard reversal stimulation, followed by an exponential decrease for about 10 s and a constant (linear) decline until the end of the 60 s trial. Peachey et al. (1994) presented vertical sinusoidal gratings that reversed contrast (70%) in a square-wave fashion for 20 s (preceded by a 10 s baseline of either a uniform adapting field or an adapting grating). With very low spatial frequencies, SSVEP amplitude remained stable throughout the trial, but higher spatial frequencies initially increased from 6 to 12 s, and then substantially linearly decreased to levels that were about 50% of the amplitude reached earlier in the trial. However, these latter studies used simple visual stimuli only. Moreover, they considered the absolute amplitude of the SSVEP over time, without comparing the amplitude between repeated and non-repeated stimulus sequences, and so could not disentangle the effects of specific stimulus repetition from general habituation responses. A recent study reported a decrease of the 12 Hz SSVEP response over low-level visual areas for repeated compared to novel complex stimuli (Martens and Gruber, 2012); however, the SSVEP response was only obtained with a single 3000 ms trial, i.e., a trial containing only 36 stimulus presentations. Hence, this study, or other studies to the best of our knowledge, did not address the question of the temporal dynamics of the RS effect for visual shapes presented at a fast periodic rate.

Here, to address the issue of the temporal dynamics of RS to periodic visual stimulation, we presented a periodic train of different faces at the optimal frequency rate for face discrimination (i.e., 5.88 Hz; Alonso-Prieto et al., 2013), for 15 s, in order to reach a large 5.88 Hz (1 F) periodic visual response. Then, from the 16th second of stimulation onward, the exact same face identity was repeated for 35 s. The expected reduction of the response at the frequency of stimulation was compared to a 35-second sequence in which different faces were presented at each stimulation cycle throughout the entire stimulation sequence.

2. Materials and methods

2.1. Participants

Fifteen healthy adult participants (age 20 to 42, 5 males) with normal or corrected vision participated in the study for payment. All participants were right-handed with the range of Edinburgh handedness inventory (Oldfield, 1971) score of 41–50. All participants demonstrated unimpaired face recognition performance (all scores were above 41/54) in the Benton facial recognition test (Benton et al., 1983). They were all Caucasians, as the face stimuli used in the study, except two participants who reported living in Belgium for at least 10 years prior to the experiment. Written informed consent was obtained from all participants prior to the experiment.

2.2. Stimuli

The stimuli consisted of ninety full-front color pictures of Caucasian faces (45 male) selected from a set of the face photographs (Laguesse et al., 2012). The faces were not familiar to the participants.

2.3. Procedure

After the completion of laterality and face recognition tests, the participants were seated in a light- and sound-attenuated room at a distance of 100 cm from the computer monitor. Stimuli were displayed using a custom-made application (SinStim) running on Matlab (The Mathworks), on a light gray background. Each stimulation sequence consisted in an initial 15 s baseline sequence of where different identities were presented, followed by a 35 s sequence of either the same or different identities (i.e., 2 conditions). The frequency of the stimulation was 5.88 Hz (1 F), chosen based on previous observations that this frequency rate provides the largest difference between sequences of different and repeated faces (Alonso-Prieto et al., 2013). The stimulation function was sinusoidal, so that each pixel reached the full luminance value of the face stimulus after half a cycle ((1000/5.88)/2). Since the refresh rate of the CRT monitor was 100 Hz, a full cycle consisted of 17 screen presentations.

In the *same* face condition, the same face, chosen randomly for each participant, was presented repeatedly. During *different* faces sequence, the 45 individual faces of the same sex were used and presented in a new random order in each sequence, from the 16th second until the end of the sequence (50 s in total, Fig. 1). Given that 45 pictures of faces were used and that the number of faces presented was high (i.e.