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Evidence for rapid prefrontal emotional evaluation from visual evoked responses to conditioned gratings

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ABSTRACT

The human brain's ability to rapidly identify emotional stimuli is subject of ongoing debate. The 'standard hypothesis' postulates a fast but coarse screening of the stimulus valence in subcortical regions, the amygdala in particular, followed by a precise, cortically driven analysis. Recent electrophysiological studies reported differential effects of conditioned faces in prefrontal regions as early as 60–80 ms after target onset, suggesting considerably faster cortical processing than traditionally assumed. Evidence for rapid prefrontal evaluation was provided specifically for complex and evolutionarily significant stimuli, i.e. faces. Here we used simple gratings in a conditioning paradigm, testing the generalization of these results. Event-related potentials and source reconstruction identified rapid (60–80 ms) enhanced processing of affectively conditioned gratings in occipital as well as prefrontal areas. Our results support the assumption of a general fast feed-forward sweep of information, partially activating an interconnected network of affective processing encompassing sensory, subcortical and prefrontal cortex regions.

1. Introduction

Threatening stimuli or stimuli indicative of danger to the individual draw its attention (Bröckelmann et al., 2011; Driver, 2001; Kastner & Ungerleider, 2000; Öhman, Flykt, & Esteves, 2001; Pourtois, Grandjean, Sander, & Vuilleumier, 2004). They seem to receive prioritized or enhanced processing (Pourtois et al., 2004; Schupp, Junghöfer, Weike, & Hamm, 2003; Stolarova, Keil, & Moratti, 2006; Vuilleumier, 2005; West, Anderson, Ferber, & Pratt, 2011). Electro- and magnetoencephalographic (EEG/MEG) studies report these amplification processes in response to emotional stimuli to manifest in increased neural activity in a distributed cortical network, encompassing sensory and prefrontal cortex areas (Junghöfer et al., 2006; Junghöfer, Schupp, Stark, & Vaitl, 2005; Lang, Bradley, & Cuthbert, 1998; Padmala & Pessoa, 2008; Pourtois et al., 2004; Royet et al., 2000; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005; Sander & Scheich, 2001). The high temporal resolution offered by EEG and MEG reveals that emotional relevance modulates event-related potentials (ERPs) or fields (ERFs) at many time points of stimulus processing: In late components (latencies of 300–400 ms) as well as mid-latency components (120–200 ms), responses to neutral and negative stimuli diverge (Herbert, Kissler, Junghöfer, Peyk, & Rockstroh, 2006; Junghöfer et al., 2006; Kissler, Herbert, Winkler, & Junghöfer, 2009; Peyk, Schupp, Elbert, & Junghöfer, 2008; Schupp et al., 2004). Furthermore, even early components (latencies of 50–80 ms) appear to be modulated by the emotional relevance of a stimulus (Keil, Stolarova, Moratti, & Ray, 2007; Pourtois et al., 2004; Steinberg et al., 2011; Stolarova et al., 2006). The traditional hypothesis, or 'standard hypothesis', as it was called by Pessoa and Adolphs (2010), suggests these early effects to be primarily caused by sensory areas and their connection to subcortical structures (for instance described by the dual-pathway model; LeDoux, 2000, 2007). The hypothesis predicts a coarse set of stimulus features to be rapidly forwarded to the amygdala via subcortical pathways ('low road'), triggering an initial evaluation of the stimulus' emotional valence or threat-predicting relevance. Delayed but elaborately processed cortical signals reach the amygdala via cortical pathways ('high route'), boosting or inhibiting the initial reaction to the stimulus. Functional imaging studies were able to provide support for the assumption of fast reactions of subcortical structures to affective stimuli (e.g. Garrido, Barnes, Sahani, & Dolan, 2012; Öhman, Carlsson, Lundqvist, & Ingvar, 2007; Williams et al., 2006). However, the strong emphasis the theory places on the amygdala and its role in affective processing are subject of debate. Experiments including patients with lesions to the amygdala reported intact rapid detection of fearful faces (Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009) and similar capture of

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attention by emotional stimuli as in healthy controls (Piech et al., 2011), challenging the assumption that the amygdala is mandatory for rapid threat detection. After reviewing anatomical and physiological data arguing against the standard hypothesis, Pessoa and Adolphs (2010) suggested the role of the amygdala in affective processing to be that of a coordinator for other cortical networks, with a multitude of connections to, e.g., the prefrontal cortex. Likewise, the pulvinar, assumed a relatively passive relay in the standard hypothesis, is granted a more important role by Pessoa and Adolphs. Connected to the all 20–30 known visual areas (e.g. Shipp, 2003) and the amygdala, the pulvinar seems to be involved in determining the behavioral relevance of a stimulus and the coordination of the flow of information in bidirectional thalamocortical and cortical loops (Pessoa & Adolphs, 2010). The revised role of the pulvinar in affective processing allows amygdala-independent, rapid detection of saliency. The standard hypothesis originated from the assumption of rather slow cortical processing, deducing the need of a separate, fast subcortical route to account for early effects of affective stimuli. The assumption of slow cortical processing has since been challenged and an involvement of frontal and prefrontal networks has been identified at far earlier stages of stimulus processing than the standard hypothesis predicts (Kirchner, Barbeau, Thorpe, Régis, & Liégeois-Chauvel, 2009; Liddell et al., 2005; for a review, see Van Gaal & Lamme, 2012). Liberated by the revised view on the speed of cortical processing and the multitude of cortical connections of the pulvinar, allowing information to be rapidly relayed through the brain, Pessoa and Adolphs (2010) suggest in their multiple-wave model a network of interconnected structures, including sensory, subcortical and cortical areas to be responsible for affective processing. Several 'waves' of activation are assumed to spread across the visual cortex and beyond, allowing multiple cortical structures to be engaged by affective or motivationally relevant stimuli. These waves are assumed to culminate in the conscious percept of the stimuli, while early waves already allow for rapid processing of affective or motivational relevance in cortical structures. This led Pessoa and Adolphs to advocate a shift of emphasis from the amygdala to cortical structures, especially the prefrontal cortex. The prefrontal cortex, classically associated with deliberate consciousness and cognitive control functions (e.g. Dehaene & Changeux, 2011; Rees, 2007) is, according to the current state of research, also involved in early, presumably nonconscious stages of most complex mental operations (Van Gaal, de Lange, & Cohen, 2012; Van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008; Van Gaal & Lamme, 2012). Similar to the multiple-wave model, Bullier (2001) proposed the integrated 'fast brain model', not limited to affective processing but to account for visual processing in general. In this computational model of hierarchically organized structures, strong emphasis is placed on feedforward and feedback pathways, connecting the stages of visual processing. He based his assumptions about the speed of these connections on cell recordings from the primate cortex, recording activity in the prefrontal cortex as early as 70 ms after stimulus onset.

In several articles, Lamme et al. (e.g. Lamme, 2010; Lamme & Roelfsema, 2000) suggested a comprehensive model for visual perception, also including the distinction of a fast feedforward sweep of information the multiple-waves model suggests and recurrent feedback processes that Bullier (2001) assumed, primarily to address conscious and nonconscious perception. The feedforward sweep is assumed to convey information necessary for coarse stimulus information and grouping. It is, however, not limited to subcortical structures but also encompasses higher cortical structures like frontal and prefrontal networks (Van Gaal & Lamme, 2012). The recurrent activity is assumed to be necessary for the activation of more widespread cortical networks, ultimately allowing the stimulus to enter consciousness. Nevertheless, empirical evidence for the capacity of the feedforward sweep to exert an influence on the subjects actions was provided e.g. by Vorberg et al., proving that fast, non-conscious information is sufficient to elicit priming effects (Schmidt & Vorberg, 2006, pp. 497–498; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003). In a recent review article, Van Gaal et al. (2012) concluded that unconscious information has been shown to affect various perceptual and high-level cognitive functions and the associated brain areas, including the prefrontal cortex".

We reviewed evidence for very early neural signatures of threat related processing, possibly in the absence of consciousness. The assumption of an evolutional preparedness to fast threat detection and preparation of subsequent action in humans in combination with the experimental evidence justify the hypothesis that the forward sweep of information also conveys emotional or threat-related information to the prefrontal cortex, priming the organism for action and causing the differential pattern of activation observed in previously mentioned EEG/MEG experiments.

In recent EEG/MEG face conditioning studies, Steinberg, Bröckelmann, Rehbein, Dobel, and Junghöfer (2013) were able to supply converging evidence for a rapid identification of affectively conditioned faces in human subjects. They found a significant amplification caused by emotion-associated faces in occipital but importantly also right prefrontal cortex regions already 60–80 ms after stimulus onset. Keil et al. (Keil et al., 2007; Stolarova et al., 2006) were able to show that even simple gratings, conditioned with aversive or neutral pictures, elicit differences in the occipital C1 component, a negative deflection reflecting the initial response of the primary visual cortex to a visual stimulus at a latency of 65–90 ms. While the latency of the effects is strikingly similar to the results reported by Steinberg et al. (2013), Stolarova et al. report no prefrontal effects. However, the focus of their analysis was on scalp potentials while Steinberg et al. used source localization techniques to identify the cortical generators of the measured event related potentials (EEG) and fields (MEG). While not superior in general to the analysis of scalp potentials, source reconstruction techniques proved advantageous in discovering modulations of distributed neural network activations. Nevertheless, the diverging results might be an effect of differences in stimulus material: Stolarova et al. used grating stimuli, Steinberg et al. face stimuli. This would imply a recruitment of prefrontal structures for affective processing of rather complex visual material and/or stimuli with assumed cultural or evolutionary significance (Mineka & Öhman, 2002; Schupp et al., 2004), while simple grating stimuli without innate biological preparedness experience affective processing confined to sensory areas. While fundamental in its impact on theories of affective processing mentioned above, experimental evidence elucidating the divergence between the results is missing. Expanding the research on early affective processing while consolidating the results of these two studies, in this experiment, we use grating stimuli, similar to the CS stimuli in the experiment by Stolarova et al. (2006). The resulting data was – as replication and extension of the study by Stolarova et al. – analyzed in sensor space, but similar to the data reported by Steinberg et al., additionally included localization of the origin of the electrophysiological differences by means of current density-based source reconstruction methods.

Hence, in this experiment we paired one of two differently oriented but otherwise physically identical gratings with an aversive auditory shock in a trace conditioning paradigm.

The stimuli were presented in a metacontrast masking paradigm (see e.g. Breitmeyer & Öğmen, 2006; Bruchmann, Breitmeyer, & Pantev, 2010), i.e. a short presentation of the conditioned stimulus, subsequently called the target and, in rapid succession, of a second stimulus closely surrounding but spatially not overlapping the first stimulus, called the mask (see Fig. 1). This paradigm allows