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Selective attention effects on early integration of social signals: Same timing, modulated neural sources

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ABSTRACT

Humans combine co-emitted social signals to predict other's immediate intentions and prepare an adapted response. However, little is known about whether attending to only one of co-emitted social signals impacts on its combination with other signals. Here, using electroencephalography, we address selective attention effects on early combination of social signals. We manipulated three visual cues: gaze direction, emotional expression, and pointing gesture, while participants performed either emotion or gaze direction judgments. Results showed that a temporal marker of social cues integration emerges 170 ms after the stimulus onset, even if the integration of the three visual cues was not required to perform the task, as only one feature at a time was task relevant. Yet in addition to common temporal regions, the relative contribution of specific neural sources of this integration changed as a function of the attended feature: integration during emotion judgments was mainly implemented in classic limbic areas but in the dorsal pathway during gaze direction judgments. Together, these findings demonstrate that co-emitted social cues are integrated as long as they are relevant to the observer, even when they are irrelevant to the ongoing task.

Introduction

The quality of our social interactions depends on correctly detecting co-emitted social signals and adapting our behavior accordingly. Of interest, once merged into a single percept, co-emitted social signals can take on new significance and certain combinations, notably those indicating the presence of threat, become more relevant than others. Typically, angry expressions are perceived as more threatening when associated with a direct gaze than with an averted gaze (Sander et al., 2007; N'Diaye et al., 2009; Sato et al., 2010; Conty et al., 2012). Despite the clear relevance of understanding the spatiotemporal characteristics of the mechanisms underlying the combination of social cues, the question of whether, when and how, directing one's attention towards a specific social signal impacts on its neural integration with other co-emitted social cues remains.

Indeed, the literature exploring the neural sources of gaze and expression integration reports incongruous results (Graham and Labar, 2012). One possible explanation is that the neural sources underlying social cues integration may be task demand-dependent (Graham and Labar, 2012; Dumas et al., 2013). While most of the functional magnetic resonance imagery (fMRI) experiments revealed that the amygdala integrated emotion and gaze when participants were required to attend to the emotional content of the faces or their gender (Sato et al., 2004, 2010; Sander et al., 2007; N'Diaye et al., 2009; Adams et al., 2012), the premotor cortex was involved in gaze and expression combination when participants were requested to attend to gaze direction (Conty et al., 2012). Electroencephalography (EEG) results also suggest that the temporal marker of such integration is susceptible to task demand influences: it emerges around 170 ms after stimulus onset when participants attend emotional expressions (Akechi et al., 2010), at around 200 ms when participants attend gaze direction (Conty et al., 2012), at 240 ms during passive viewing (Rigato et al., 2010), and later during an oddball task concerning gaze direction (Klucharev and Sams, 2004). Finally, other studies in the literature have reported that when observers orient their attention to only one feature at a time as requested by the task (i.e. judging the emotion or the gaze of emitters), co-emitted facial signals are processed independently (Bindemann et al., 2008) by anatomically and functionally segregated neural structures, at least initially (Klucharev and Sams., 2004; Pourtois et al., 2004).

To directly address how selective attention affects the time course and neural bases of early combination of social signals, we implemented an electroencephalography (EEG) experiment (evoked potentials and source reconstruction analysis). To parametrically modulate the self-relevance of perceived social signals, we manipulated three visual

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cues: emotion, gaze direction, and pointing gesture (as in Conty et al., 2012). Participants performed two tasks: one which requested them to attend only to the gaze direction cue and one which requested them to attend only to the emotional cue. Based on our previous study using the same stimuli (Conty et al., 2012), we expected an early combination (rather than parallel processing) of the social cues that clearly portrayed a relevant threat for the observer within the first 200 ms. Yet how the precise temporality and the sources of this integration were influenced by task demand was addressed in a hypotheses-free manner.

Methods

Participants

Eighteen healthy subjects (10 females; mean age, 24.0 ± 0.5 years) participated in the EEG experiment. All participants were right-handed, with a normal or corrected vision, and were free of current or past psychiatric or neurological disorders. The subjects gave their written informed consent and were paid for their participation. The study was approved by the local ethics committee and was conducted in accordance with the Declaration of Helsinki.

Stimuli

The stimuli used in the present experiment were developed by Conty and Grèzes (2011). They consisted of 192 photographs of 12 actors (six females) seen under 8 conditions: 2 emotions (anger/neutral) × 2 gaze directions (head and eye gaze directed toward the participant or averted to the right and left side: direct/averted) × 2 gestures (pointing/no pointing) (Fig. 1a). An "initial position" photograph depicts each of the actors with a neutral expression, arms by their sides, and an intermediate head and eye direction of 15°. More detailed description of the stimuli can be found in Conty and Grèzes (2011).

Procedure

Each trial started with a fixation screen (500 ms) consisting of a central red fixation point and four red angles, displayed on a uniform gray background. The participant was instructed to fixate the central point and to keep his/her attention inside the fixation area at the level of the central point throughout the trial, avoiding eye blinks and saccades. Because dynamic social displays are more ecologically valid (Sato et al., 2010; Schilbach, 2010), we created an apparent movement by presenting two photographs, one after the other (Conty et al., 2007, 2012). The first photograph always displayed the actor in the initial position during a random period of time, ranging from 1200 to 1500 ms. The second one immediately followed and displayed the same actor in one of the eight conditions of interest (Fig. 1b) for 1300 ms. Throughout the trial, the actor's face remained within the fixation area. Then, a response screen was presented for 1000 ms, followed by a black screen of 500 ms preceding the next trial. We delayed the responses to ensure that the participants responded at the end of the observation period.

The experiment was divided in 8 experimental blocks of 96 trials each. Two tasks alternated in separate blocks resulting in 4 blocks for each task. Participants were requested to focus either on the nature of

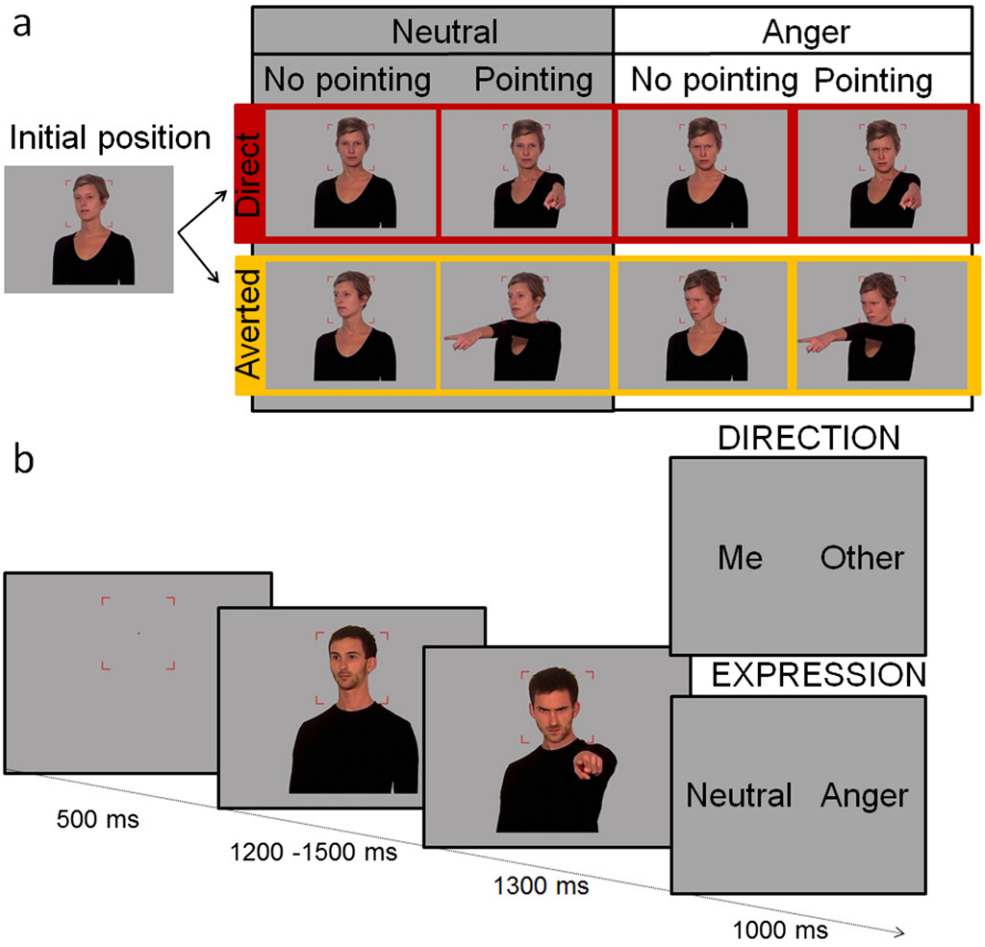

Fig. 1. Experimental procedure and stimuli examples. (a) From the initial position, gaze, emotion, and gesture were manipulated: stimuli displayed a direct or an averted gaze, an angry or a neutral expression, a pointing gesture or not. (b) Trial procedure: a central fixation area where the face of the stimuli later appears was presented for 500 ms. In the expression task blocs, subjects had to judge whether the actor displayed an angry or a neutral expression. In the direction task blocs, they had to judge whether the actor was addressing them or another.