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Interoceptive signals impact visual processing: Cardiac modulation of visual body perception

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ABSTRACT

Multisensory perception research has largely focused on exteroceptive signals, but recent evidence has revealed the integration of interoceptive signals with exteroceptive information. Such research revealed that heartbeat signals affect sensory (e.g., visual) processing: however, it is unknown how they impact the perception of body images. Here we linked our participants' heartbeat to visual stimuli and investigated the spatio-temporal brain dynamics of cardio-visual stimulation on the processing of human body images. We recorded visual evoked potentials with 64-channel electroencephalography while showing a body or a scrambled-body (control) that appeared at the frequency of the on-line recorded participants' heartbeat or not (not-synchronous, control). Extending earlier studies, we found a body-independent effect, with cardiac signals enhancing visual processing during two time periods (77–130 ms and 145–246 ms). Within the second (later) time-window we detected a second effect characterised by enhanced activity in parietal, temporo-occipital, inferior frontal, and right basal ganglia-insula regions, but only when non-scrambled body images were flashed synchronously with the heartbeat (208–224 ms). In conclusion, our results highlight the role of interoceptive information for the visual processing of human body pictures within a network integrating cardio-visual signals of relevance for perceptual and cognitive aspects of visual body processing.

1. Introduction

We live in a complex environment, receiving continuous multisensory information. Incoming signals are not limited to the external world (exteroceptive signals such as visual, auditory, or tactile signals), but also include information from the inside of our body (i.e. interoceptive signals) such as cardiac, respiratory and other visceral inputs. Up to now, data on how interoceptive and exteroceptive signals are integrated into the brain are still sparse. Previous neuroimaging research on multisensory integration has mainly focused on exteroceptive signals and extensively investigated how one sensory stimulus (e.g., a sound) influences the processing of another one (e.g., visual) (Stein and Stanford, 2008; van Atteveldt et al., 2014 for reviews). Studies in nonhuman primates described multisensory neurones in the inferior parietal sulcus responsive to combinations of visual, auditory and tactile stimuli (Andersen et al., 1997; Cohen and Andersen, 2004; Mazzoni et al., 1996; Schlack et al., 2005). Imaging studies in humans described multisensory responses in ventral premotor area and in parietal cortex, including inferior parietal and superior parietal lobules, as well as in primary cortices (such as primary visual cortex, Heschl's and superior temporal gyri) (Bushara et al., 1999; Calvert et al., 2000; Lewis and Van Essen, 2000; Bremmer et al., 2001; Calvert, 2001; Macaluso and Driver, 2001; Foxe et al., 2002; Pekkola et al., 2006; Martuzzi et al., 2007; Gentile et al., 2011). The importance of these brain regions for multisensory processing was extended by electrical neuroimaging studies, which investigated the spatio-temporal brain dynamics of visual-auditory, visual-tactile and audio-tactile integration. In favour of multisensory integration occurring within primary cortices, electroencephalography (EEG) studies found

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early integration effects starting at 60 ms after stimulus onset, and during a later time-window (180 ms) (e.g., Molholm et al., 2002, 2006; Schürmann et al., 2002; Teder-Sälejärvi et al., 2002; Foxe and Schroeder, 2005; Cappe et al., 2010; Quinn et al., 2014). Early and late responses to multisensory stimulation in these regions were further supported by intracranial recordings in humans (Molholm et al., 2006).

Compared to these findings, there is currently only limited evidence about multisensory perception and integration of exteroceptive and interoceptive signals. For example, visual evoked potentials in response to basic visual stimuli (i.e., flashes) are enhanced when the visual stimulus is presented time-locked to the heartbeat (i.e., at the diastole) (Walker and Sandman, 1982). Moreover, recent studies demonstrated that the amplitude of the heartbeat-evoked potential (i.e., the cortical marker of cardiac processing) (Schandry and Montoya, 1996) is associated with changes in visual perception (Park et al., 2014; see also Park et al., 2016), and that conscious access for visual stimuli depends on when the stimulus is presented with respect to the participants' heartbeat (Salomon et al., 2016). Other research found that cardiac information facilitated the detection of emotional stimuli, such as fearful faces (Garfinkel et al., 2014). Related findings were reported in the auditory domain: presenting sounds in synchrony with the heartbeat resulted in a modulation of the auditory evoked potentials (van Elk et al., 2014). Even if it has been shown that cardiac signals modulate the processing of visual stimuli, it is currently unknown if and how interoception influences the visual perception of human bodies.

The processing of visual images of the human body has been linked to a dedicated network consisting of the extrastriate body area and the fusiform body area in the temporo-occipital cortex. These two regions respond strongest to the appearance of human bodies or human body parts compared to other stimuli such as houses (Downing et al., 2001; Peelen and Downing, 2007; Downing and Peelen, 2011), and process bodily features as shape and posture (Downing and Peelen, 2016). In addition to functional magnetic resonance imaging (fMRI) studies, important data about temporal and spectral aspects of the body-specific processing in the extrastriate cortex has been provided by magnetencephalography and EEG studies. Thus, a first activation occurs during the categorization of the bodily image (at 100 ms: P1) (de Gelder et al., 2010), followed by activations that are associated with a more refined structural body-specific processing, occurring between 150 and 250 ms after stimulus onset (N190) (Thierry et al., 2006; Ishizu et al., 2010). These activations are found within the temporo-occipital cortex, likely overlapping with the extrastriate body area (see Barraclough et al., 2006; Pourtois et al., 2007). Although several studies have supported the role of the extrastriate body area in multisensory (e.g., visuo-auditory) integration (Beer et al., 2013; Limanowski and Blankenburg, 2016), it is debated if this area is a unimodal visual area or an important region for multisensory bodily processing (Downing and Peelen, 2011). Moreover, to date no EEG study has reported interoceptive modulation during the visual processing of human bodies, and such processing has recently been linked to self-related brain processes (Blanke, 2014). Thus, behavioural data showed that seeing a body/body-part image flashing at the same frequency of the subject's heartbeat (i.e., cardio-visual stimulation) induces an alteration in the sense of body ownership and self-location. This was found in healthy subjects (Aspell et al., 2013; Suzuki et al., 2013) and a neurological patient (Ronchi et al., 2015).

Extending these findings, we asked whether brain activity related to the processing of the human body can be modulated by interoceptive information. This is a topic of particular relevance for at least two reasons: i) our sense of self, and the link between bodily processing and the sense of self, is based on the integration of exteroceptive and interoceptive bodily signals (Craig, 2002; Blanke, 2012), and ii) only little is known about the neural mechanisms of this integration. Here, we investigated whether an interoceptive signal, the heartbeat, modulates brain activity related to the visual processing of a human body and sought to determine the electrophysiological brain mechanisms of such cardio-visual processing. We recorded 64-channel EEG and analysed visual evoked potentials (VEPs) during the presentation of visual body images synchronised (or not) with participants' own online detected heartbeat. According to previous evidence, we predicted that cardio-visual synchrony would affect VEPs in response to human bodies. The specificity of cardio-visual effects on the visual processing of bodily stimuli was tested by repeating the same conditions for scrambled bodies.

2. Materials and methods

2.1. Participants

Sixteen healthy right-handed participants (2 females, mean age: 26.8 ± 2.8, range: 23–31) took part in this experiment, approved by the Ethical Committee of the Brain and Mind Institute at EPFL, Lausanne. Two participants were excluded due to excessive muscle artefacts contaminating the EEG signal, leaving 14 participants for the analyses. All participants gave their written informed consent prior to study participation.

2.2. Procedure

Participants were seated in a dark and sound attenuated room at a distance of 60 cm from an LCD screen (27-inch monitor, refresh rate of 120 Hz). Participants' electrocardiogram (ECG) was recorded for the entire session. ECG data were acquired by an Arduino™ microcontroller with a mounted e-Health Sensor Shield V2.0 from Libelium™ through three electrodes placed on the chest (two at the level of the left and right clavicles, the third one on the left side at the last rib). The in-house software detected, in real time, the R peak of the QRS complex (amplitude change over 80% of the difference between the exponential moving averages of the maxima and minima of the raw signal).

The experiment was composed of a total of 22 blocks. At the beginning of each block, the monitor displayed a black background and a red fixation point (visual angle: 0.3°) positioned in the centre of the screen. Participants were instructed to fixate the red dot throughout the whole block. The visual body stimuli were presented centrally on which a red fixation dot was presented, such that the fixation dot was always in the same location on the screen. The visual stimuli were of two categories: 1) Body-intact: a picture of a body from behind; and 2) Body-scrambled: the same picture of a body from behind but in a scrambled version, i.e. with the body divided into 5 parts (see Soria Bauser and Suchan, 2013). In the scrambled version, body parts were maintained in the original upright position (see Fig. 1). Both intact and scrambled body images were presented on the screen in one of the two following categories with respect to the heartbeat: 1) Synchronous (S): the body appeared synchronously with respect to the QRS complex (with a constant delay of 40 ms after detection of the R peak); 2) Non-Synchronous (NS): the body appeared randomly and out of phase with respect to the QRS complex of the participant. The stimulus was presented at a time interval of 900 ± 200 ms, accordingly to the control condition of a previous study about cardio-auditory integration (van Elk et al., 2014). We performed a two by two factorial design, with Factor 1: Stimulus (i.e. intact or scrambled), and Factor 2: Heart (i.e., S or NS), for a total of four experimental conditions. Each block of the four conditions lasted one minute and was repeated five times, for a total of 20 experimental blocks. The order of the 20 blocks was randomised across participants. Every stimulus presentation lasted 249 ms. The visual image subtended a maximum of 12° of visual angle. In addition to the above-described 20 blocks, two resting blocks (duration: 2.5 min each) were performed before and after the experiment (total duration: 5 min, as each experimental condition). During the resting block, no visual stimuli were presented (except for the red fixation dot); the participants' EEG was recorded while they were asked to look at the black monitor. The inclusion of the resting blocks was necessary to remove the cardiac artefact present in the EEG signal (Montoya et al., 1993; van Elk et al., 2014). Fig. 2 shows the schematic diagram of the experiment.