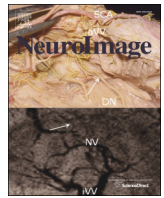




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Neural correlates of apparent motion perception of impoverished facial stimuli: A comparison of ERP and ERSP activity

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ABSTRACT

Our brains readily decode human movements, as shown by neural responses to face and body motion. N170 event-related potentials (ERPs) are earlier and larger to mouth opening movements relative to closing in both line-drawn and natural faces, and gaze aversions relative to direct gaze in natural faces (Puce and Perrett, 2003; Puce et al., 2000). Here we extended this work by recording both ERP and oscillatory EEG activity (event-related spectral perturbations, ERSPs) to line-drawn faces depicting eye and mouth movements (Eyes: Direct vs Away; Mouth: Closed vs Open) and non-face motion controls. Neural activity was measured in 2 occipito-temporal clusters of 9 electrodes, one in each hemisphere. Mouth opening generated larger N170s than mouth closing, replicating earlier work. Eye motion elicited robust N170s that did not differ between gaze conditions. Control condition differences were seen, and generated the largest N170. ERSP difference plots across conditions in the occipito-temporal electrode clusters (Eyes: Direct vs Away; Mouth: Closed vs Open) showed statistically significant differences in beta and gamma bands for gaze direction changes and mouth opening at similar post-stimulus times and frequencies. In contrast, control stimuli showed activity in the gamma band with a completely different time profile and hemispheric distribution to facial stimuli. ERSP plots were generated in two 9 electrode clusters centered on central sites, C3 and C4. In the left cluster for all stimulus conditions, broadband beta suppression persisted from about 250 ms post-motion onset. In the right cluster, beta suppression was seen for control conditions only. Statistically significant differences between conditions were confined between 4 and 15 Hz, unlike the occipito-temporal sites where differences occurred at much higher frequencies (high beta/gamma). Our data indicate that N170 amplitude is sensitive to the amount of movement in the visual field, independent of stimulus type. In contrast, occipito-temporal beta and gamma activity differentiates between facial and non-facial motion. Context and stimulus configuration likely plays a role in shaping neural responses, based on comparisons of the current data to previously reported studies. Broadband suppression of central beta activity, and significant low frequency differences were likely stimulus driven and not contingent on behavioral responses.

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Introduction

Visually equipped organisms must interpret movements of conspecifics and other organisms in their surroundings so as to adjust behavior for the current situation. Motion perception is an old information source that species spanning the evolutionary ladder have as a tool for survival (Frost, 2010). Since many species must deal with complex and coordinated social life, facial and body motion and vocalizations have become important sources of information (Blake and Shiffrar, 2007).

Biological motion is motion that originates from animate beings or living organisms, and from the pioneer work of Gunnar Johansson, a 'biological motion' stimulus became synonymous with a schematic depiction of this articulated motion with point-light displays (Johansson, 1973). It is well known that it is possible to induce the perception of animacy through a simulation of the motion of many different human actions in these point-light displays (Dittrich, 1993). Human infants show distinct preferences for biological motion stimuli relative to other forms of visual motion (Bertenthal et al., 1984; Simion et al., 2011). Remarkably, cats decode biological motion displays depicting the locomotion of other cats (Blake, 1993), and monkeys recognize the human walking as depicted with either point-light or line-drawn displays (Oram and Perrett, 1994, 1996). This type of visual

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perception indicates that the visual system is sensitive to invariant higher-order stimulus information imbedded in the motion pattern (Blake and Shiffrar, 2007). The invariance in biological motion perception allows relevant information to be extracted regarding an individual's identity (Cutting and Kozlowski, 1977) and gender (Barclay et al., 1978; Troje, 2002). Emotional expression can be gleaned from point-light displays of the whole body (Clarke et al., 2005) or from isolated body parts such as arms (Pollick et al., 2002) or face (Bassili, 1978).

Human neuroimaging studies and non-human primate neurophysiological studies indicate that dynamic stimulus attributes are mainly processed by brain regions considered to be part of the dorsal visual system, and that processing of progressively more complex motion information occurs within this system (Giese and Poggio, 2003; Jastorff and Orban, 2009; Thompson and Parasuraman, 2012). In a region of macaque superior temporal sulcus known as STPa, sensitivity of single neurons to direction of biological motion as shown by human figures walking in profile (Oram and Perrett, 1994) is seen, in addition to responses to (static) heads and bodies (Oram and Perrett, 1994). STPa has been proposed to integrate form and motion information (Oram and Perrett, 1996).

In the human brain, motion sensitive loci such as hMT+, which reside in highly folded cortex on the lateral aspect of the occipito-temporal junction, respond vigorously to coherent motion of linear and non-linear forms e.g. optic flow (e.g. Grossman et al., 2000). A nearby region in the posterior superior temporal sulcus is selectively sensitive to biological motion as depicted by point-light displays (Bonda et al., 1996; Grossman et al., 2000) or by natural images that depict motion of the face, hands or body (Puce et al., 1998; Wheaton et al., 2004). This region is also thought to integrate form and motion information (Beauchamp, 2005; Kourtzi et al., 2008; Puce and Perrett, 2003) and is active to static stimuli that depict different forms of implied human motion (Kourtzi and Kanwisher, 2000; Kourtzi et al., 2008). Neuropsychological investigations in rare cases with lesions to the superior temporal region have also reported difficulties with processing biological motion relative to other forms of motion perception (Vaina and Gross, 2004). The putative mirror neuron, which includes the cortex of the anterior intraparietal sulcus as well as premotor cortex, is also known to activate to viewing the articulated motion of others (see Van Overwalle and Baetens, 2009 for a meta-analysis).

Neurophysiological investigations in humans using motion stimuli have typically used dynamic grating or checkerboard stimuli with fairly large visual fields for stimulation e.g. 20° of visual field (Kuba and Kubova, 1992). Typically, the elicited event-related potentials (ERPs) occur over the posterior scalp and consist of a triphasic positive-negative-positive complex with the most prominent and robust ERP component being the negativity, which occurs at around 150–160 ms post-motion onset.

To date very few neurophysiological investigations of biological motion and motion from faces, hands and bodies in natural images have been performed in humans. Robust motion sensitive ERPs from the bilateral occipito-temporal scalp have been elicited to viewing dynamic images of face, hand and body, and over the centroparietal scalp for the hand and body (Wheaton et al., 2001). A prominent negativity at around 170–220 ms (N170) post-motion onset is seen in the posterior scalp to apparent motion of a natural face (Puce et al., 2000) or a line-drawn face (Puce et al., 2003). A corresponding magneto-encephalographic response, the M170, has also been described to the apparent motion of natural faces (Watanabe et al., 2001) or to facial avatars (Ulloa et al., 2012). Larger and earlier N170s occurred to gaze aversions relative to direct gaze movements in both natural faces and isolated eyes, and to mouth opening relative to mouth closure (Puce et al., 2000). Similar results have been demonstrated by using images of line-drawn faces making mouth movements (Puce et al., 2003). These findings likely reflect the potential salience of a diverted gaze or opening mouth: diverted gaze signals a change in social attention away from the viewer, and an opening mouth may signal an impending

vocalization (Puce and Perrett, 2003). A point-light walker also elicits larger N170 activity to upright relative to inverted walkers or scrambled motion, and a subsequent positivity that was greatest to the point-light walker in either orientation relative to the scrambled control (Jokisch et al., 2005). Taken together, the small ERP literature describes a neural differentiation where N170s are: (i) significantly larger to biological motion relative to a scrambled control; and (ii) can be significantly different across biological motion conditions.

Traditionally, human neurophysiological investigations have focused on task and condition effects on ERPs. ERPs are phase-locked neural responses that are identified by averaging across multiple trials of the same condition, so that any (evoked) activity that is not phase-locked to the stimulus will be diminished in the average. However, this neural activity constitutes only part of the total neural response to a delivered stimulus: stimulus induced, but non-phase-locked (induced) activity can also be extracted as a function of frequency over the duration of the experimental trial (Galambos, 1992; Herrmann et al., 2005; Makeig, 1993; Tallon-Baudry et al., 1996). Total and induced activity is most typically displayed as a time-frequency analysis in the form Event Related Spectral Perturbation (ERSP) plots (Delorme and Makeig, 2004; Herrmann et al., 2005; Tallon-Baudry et al., 1996). Changes in alpha, beta, and gamma EEG frequency bands have been described in a number of tasks and conditions. Changes in a given frequency band may come about from more than one process or underlying mechanism. Simplistically speaking, decreases in alpha band activity have been related to attentive processing of stimuli, increases in the beta band to maintenance of the current brain state, and increases in the gamma band to facilitation of cortical processing (Engel and Fries, 2010; Foxe and Snyder, 2011; Herrmann et al., 2010; Palva and Palva, 2007). In reality, a more complex picture is emerging where interactions within and between frequency bands might represent multiplexing mechanisms for information processing and communication (Akam and Kullmann, 2010; Canolty and Knight, 2010; Schyns et al., 2011; Varela et al., 2001).

A number of studies have compared EEG changes to viewing point-light and real human motion stimuli and have typically focused their analyses on EEG power in the 8–13 Hz range [alpha, and one part of the mu rhythm] in central electrodes overlying the sensorimotor scalp. Mu rhythm is a complex rhythm seen typically over the sensorimotor scalp with components spanning both alpha and beta EEG bands (Hari, 2006). Typically, 8–13 Hz power in the central scalp is typically suppressed relative to the pre-stimulus baseline more when biological motion is viewed, as opposed to viewing non-biological motion (e.g. Oberman et al., 2005; Ulloa and Pineda, 2007). Additionally, this suppression is augmented for social versus non-social tasks (Oberman et al., 2007; Perry et al., 2010a), and when oxytocin is given to participants, as opposed to placebo (Perry et al., 2010b). Interestingly, 8–13 Hz activity suppression appears to be greater over the central scalp for viewing conditions depicting (hand) action, and greater over the occipital scalp for conditions presenting non-action related visual material (Perry et al., 2011). Suppression in the beta band power has also been reported for viewing hand motion relative to moving scenery (Darvas et al., 2013). In contrast, activity in the gamma band has been reported to be augmented to viewing biological motion relative to non-biological motion in occipital cortices within 100 ms of motion onset (Pavlova et al., 2004, 2006). Attentional task demands will produce subsequent gamma band increases when viewing biological motion (Pavlova et al., 2006). Importantly, oscillatory EEG changes can occur across a number of frequency bands to viewing hand motion stimuli (Perry et al., 2011), as well as to executing hand movements (Waldert et al., 2008).

Other studies using static faces have shown that oscillatory activity in the beta band is increased to viewing a familiar face relative to an unfamiliar one (Ozgoren et al., 2005), and differential frontocentral activity to some emotions, as displayed by static faces, has been observed in alpha, beta (Guntekin and Basar, 2007) and gamma (Balconi and

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