Cortical and subcortical responses to biological motion

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ABSTRACT

Using fMRI and multivariate analyses we sought to understand the neural representations of articulated body shape and local kinematics in biological motion. We show that in addition to a cortical network that includes areas identified previously for biological motion perception, including the posterior superior temporal sulcus, inferior frontal gyrus, and ventral body areas, the ventral lateral nucleus, a presumably motoric thalamic area is sensitive to both form and kinematic information in biological motion. Our findings suggest that biological motion perception is not achieved as an end-point of segregated cortical form and motion networks as often suggested, but instead involves earlier parts in the visual system including a subcortical network.

Introduction

The introduction of point-light motion displays (Johansson, 1973) has helped reveal the exceptional efficiency with which the human visual system can interpret animate (biological) motion devoid of other obvious contextual cues (e.g., the shape of the agent). Of course, form information is still readily available through the deformation of the motion pattern itself, and indeed observers use such global structure-from-motion information to interpret biological motion (Troje, 2002). It is clear now, however, that the global shape arising from deformation of the motion pattern is not the only cue available to the observer. Extensive behavioral data suggest that the visual system is also remarkably sensitive to local kinematic information, and particularly responds to the gravitational acceleration of the feet and the way they strike the ground (Beintema and Lappe, 2002; Troje and Westhoff, 2006; Chang and Troje, 2009). We refer to these two sources of information as "global" (structure from motion) and "local" (kinematics of individual dots) cues.

Neuroimaging, neurophysiology, and neurostimulation studies have identified a network of areas in the cortex that responds to biological motion. Relevant areas include ventral extrastriate regions such as the posterior superior temporal sulcus (pSTS), posterior inferotemporal sulcus (pITS), fusiform gyrus, extrastriate and fusiform body areas (EBA, FBA), but also portions of the frontal and parietal cortex (Bonda et al., 1996; Grossman and Blake, 2002; Peuskens et al., 2005; Saygin et al.,

2004; Peelen et al., 2006; Saygin, 2007; Jastoff and Orban, 2009; Grosbas et al., 2012; Thompson and Baccus, 2012; van Kemenade et al., 2012). However, these studies have generally isolated the areas involved in the perception of biological motion by contrasting an intact walker with one that is spatially scrambled. This contrast addresses the effects of global structure on the neural responses well, but since the kinematic information conveyed by the individual local dots are the same between the two stimuli, it is not appropriate to search for the neural representations of local cues. Studies thus far that have tried to tease apart the separate contributions of shape and kinematics have promisingly shown some dissociation in terms of the cortical networks involved. Notably, the dorsal cortex seems to be critical for the perception of kinematics, and the ventral stream critical for the perception of shape (with information from the two streams proposed to be integrated in the occipito-temporal cortex) (Casile and Giese, 2005; Thompson et al., 2005; Jastoff and Orban, 2009; Vangeneugden et al., 2014; Gilaie-Dotan et al., 2015). While the majority of these studies have reduced biological motion into point-light representations, these same regions are implicated in more naturalistic contexts. For example, videos and static images of bodies similarly elicit responses in ventral body areas EBA and FBA (O'toole et al., 2014).

There is reason to believe that surveys of the brain regions relevant to biological motion perception would benefit from moving beyond the cortex, considering the roles of subcortical loci. The neural substrates underlying the perception of local kinematics, in particular, has garnered

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much intrigue as it is posited that the relevant mechanisms are phylogenetically more primitive, and hence likely to involve older parts of the visual system (Troje and Westhoff, 2006; Johnson, 2006). In light of a growing body of developmental data showing that sensitivity to biological motion is present early in development (Fox and McDaniel, 1982; Bertenthal, 1996; Hirai and Hiraki, 2005; Méary et al., 2007; Reid et al., 2008), it would not be surprising if biological motion perception is governed in part by deeper structures such as the brainstem or thalamus. This line of thought is also strengthened by work in non-human species - newly hatched chicks - for orienting towards biological motion (Vallortigara et al., 2005; Vallortigara and Regolin, 2006). These findings in chicks, which have very different brain organization as compared to primates, though they do have circuits elsewhere with functions homologous to those governed by the mammalian six-layer cortex (Wang et al., 2010), should challenge our traditional understanding that high-order "biological motion" perception in humans is solely reliant on the cortex.

While the thalamus has been long-considered a sensory relay center, an increasing body of literature is indicating a regulatory role for this region, contributing to wide-ranging aspects of cognition. For example, it has been shown that fMRI responses in the human lateral geniculate nucleus (LGN) can be modulated by actively directing subjects to attend to or ignore a stimulus (O'Connor et al., 2002). Attentional modulations of single-unit responses in the LGN have also been shown in the macaque (McAlonan et al., 2008). Moreover, lesions in the thalamus, and in particular of the pulvinar and mediodorsal nucleus, can result in attention and memory impairments (e.g., Baxter, 2013; Jankowski et al., 2013). Considered together, these findings challenge traditional notions that attentional modulations have sole cortical origins. Beyond attentional processes, thalamic nuclei have been implicated in other high-order functions including learning (Bradfield et al., 2013; Habib et al., 2013), language (Klostermann, 2013), and movement control (e.g., Prevosto and Sommer, 2013) – extending to anticipations of perceptual consequences of ocular movements (Ostendorf et al., 2013). Hence, it would not be surprising if the thalamus, and potentially other subcortical centers may also be implicated in biological motion perception.

To our knowledge, only one study to date has implicated a non-cortical area (the cerebellum) in the processing of biological motion (Sokolov et al., 2012). These findings are particularly interesting at it has become increasingly clear that the cerebellum should no longer be considered a solely motor structure. For example, the cerebellum has been shown to be involved in language processing (e.g., Xiang et al., 2003), visuospatial reasoning (e.g., Bonda et al., 1995; Creem-Regehr et al., 2007), and executive functions (e.g., Tomasi et al., 2007). Whether additional subcortical components of the motor loop may be involved in a broader range of functions, including, of more immediate relevance, the perception of biological motion, is unclear.

Here, using whole-brain, high-resolution, multiband fMRI, along with a multivariate approach (multivoxel pattern analysis, MVPA), we aimed to achieve a survey of the cortical and subcortical areas for the perception of global structure-from-motion and local kinematic information in biological motion that may have been overlooked in traditional univariate approaches. We focus on global and local cues containing information about the intended walking direction of a stationary point-light walker. The facing-direction task has been used widely to show the importance of both form-related processes (Beintema and Lappe, 2002; Miller and Saygin, 2013) and kinematics-related processes (Troje and Westhoff, 2006; Hirai et al., 2011) in biological motion perception. We introduced three main types of manipulations in order to isolate stimuli that contained solely global form from motion information, solely kinematics, or neither global form nor natural kinematics information. To isolate representations of global structure-from-motion we generated novel walkers that carried the structure of an intact walker but no informative local cues as to walking direction ("global only" walkers). These stimuli were generated by replacing each local trajectory with the average of its original trajectory and its left/right mirror-flipped variants. While the

overall spatial arrangement of the dots was preserved, this manipulation rendered individual local motions that were symmetric along the anterior-posterior axis, and critically carried no horizontal asymmetry. In order to create a stimulus that isolates local cues to facing direction, stimuli were deprived of structural cues to direction by taking the veridical walker (Troje, 2002) and randomly reallocating the positions of the individual dots along the horizontal dimension. We call this stimulus the "local natural" walker. We then took this latter stimulus and modified it further in order to also deprive it from the acceleration patterns that we had earlier shown to be the critical feature of the "life detector" (Chang and Troje, 2009). This last type was achieved by both scrambling the horizontal positions of the individual dots thereby destroying global structure, and manipulating kinematics such that the individual dots traveled along the original traces at constant speed (Chang and Troje, 2009). We call this stimulus the "local modified" walker (see Methods for further details on the stimulus manipulations). The three types of walkers were presented both upright and upside-down. We included an 'inversion' manipulation to help validate any dissociations between structure-related and kinematics-related regions, in light of behavioral literature that have suggested very different sources underlie inversion-related perceptual impairments for the two types of stimuli. The source of the first inversion effect appears to be similar to that observed in the face literature (Freire et al., 2000), relating to the inversion of the familiar (body) structure. The inversion effect observed with kinematics-only stimuli, however, appears to relate to the orientation of velocity gradients within the individual dot-motions, and specifically those of the feet, but is also curiously modulated by visual field position (Chang and Troje, 2009; Hirai et al., 2011). Inclusion of the upside-down variants, thus probe for differential modulations of the relevant regions with inversion and may thereby help verify any dissociation between structure-related and kinematics-related regions.

Methods

Participants

Nineteen observers (mean age of 26.4 years, 13 males) participated in this study. All had normal or corrected-to-normal vision, and provided written informed consent in line with ethical review and approval of the work by the ethics committee of the National Institute of Information and Communications Technology (NICT), Japan.

Stimuli

Stimuli were point-light biological motion sequences based on motion capture data of an average walker computed from 50 men and 50 women, that can be represented as a simple fourier series characterizing the position of each dot motion in three dimensions (Troje, 2002). Each walker in this particular experiment was represented by a set of 11 dots shown in sagittal view (facing either rightward or leftward) with a gait frequency of 0.93 Hz. Overall translation was subtracted. Dots were white (153.7 cd/m^2) on a black background (0.92 cd/m^2).

The average walker in its original form contains both full structure from motion information (through the presence of the familiar body shape) and kinematic information (as carried by horizontal and vertical asymmetries, such as acceleration). In order to tease apart the contributions of these differing types of information, we did not present the walker in this original form, but rather derived six variations of the stimulus, manipulating the presence or absence of structural organization (intact or absent), the kinematic information contained in the individual local trajectories (veridical kinematics, mirror-symmetric motion, or perturbed-constant speed), and orientation (upright or inverted). As these manipulations cannot be neatly characterized in terms of a factorial-type design, we provide schematic samples of the stimuli (Fig. 1a), as well as summarize the information contained in the stimulus in accordance with our stimulus labels, both in terms of global structure