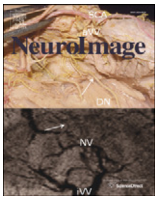
NeuroImage 63 (2012) 581–590

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



The responsiveness of biological motion processing areas to selective attention towards goals

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ARTICLE INFO

Article history:
Accepted 28 June 2012
Available online 14 July 2012

Keywords:
Biological motion
Selective attention
Superior temporal sulcus
Extrastriate body area
hMT+

ABSTRACT

A growing literature indicates that visual cortex areas viewed as primarily responsive to exogenous stimuli are susceptible to top-down modulation by selective attention. The present study examines whether brain areas involved in biological motion perception are among these areas—particularly with respect to selective attention towards human movement goals. Fifteen participants completed a point-light biological motion study following a two-by-two factorial design, with one factor representing an exogenous manipulation of human movement goals (goal-directed versus random movement), and the other an endogenous manipulation (a goal identification task versus an ancillary color-change task). Both manipulations yielded increased activation in the human homologue of motion-sensitive area MT+ (hMT+) as well as the extrastriate body area (EBA). The endogenous manipulation was associated with increased right posterior superior temporal sulcus (STS) activation, whereas the exogenous manipulation was associated with increased activation in left posterior STS. Selective attention towards goals activated a portion of left hMT+/EBA only during the perception of purposeful movement—consistent with emerging theories associating this area with the matching of visual motion input to known goal-directed actions. The overall pattern of results indicates that attention towards the goals of human movement activates biological motion areas. Ultimately, selective attention may explain why some studies examining biological motion show activation in hMT+ and EBA, even when using control stimuli with comparable motion properties.

Introduction

Posterior regions of the brain contain discrete areas involved in processing information about biological motion. The development of these areas has presumably served a critical evolutionary purpose—the identification and classification (predator, prey, kin) of moving animals. This capacity has reached its apogee in humans, where the perception of coherent body movement can provide exquisitely subtle information regarding other people's thoughts and intentions.

It is therefore not surprising that a number of basic visual information processing areas have been implicated in social perception. These areas include the human homologue of non-human primate area MT+ (hMT+). Because this area is active during the passive viewing of a variety of coherent motion stimuli (checkerboards, radial motion displays, random dot kinematograms, human movement, etc.), it is typically construed as a “bottom-up” processing area—i.e., responsive primarily to exogenous (stimulus-driven) visual events (Blake and Shiffrar, 2007; see Sani et al., 2010, for a consideration of hMT+ in the tactile experience of coherent motion). However, numerous studies show increased activation in this area for stimuli depicting biological motion relative to stimuli that share many critical movement parameters (global motion, velocity, etc.; Beauchamp et al., 2002; Grossman and Blake, 2002; Herrington et al., 2011a; Michels et al., 2005, 2009; Peelen et al., 2006; Pelphrey et al., 2004; Peuskens et al., 2005). Some of these studies do not refer to observed activation as encompassing hMT+, despite overlapping directly or extremely closely with hMT+ coordinates reported in multiple studies (for a consideration of hMT+ localization, see Dumoulin et al., 2000). The failure of biological motion studies to more clearly account for activation in this region likely reflects the fact that it is not a discrete functional module with respect to human movement.

However, accumulating evidence indicates that, although not a biological motion module per se, hMT+ may play an important role in human movement processes. For example, Herrington et al. (2011a) recently showed increased hMT+ activation for human movement stimuli compared to a control stimulus (a spinning wheel, which shared many critical motion parameters but differed in the complexity of configural motion). Using an fMRI adaptation paradigm, Jastorff et al.

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doi:10.1016/j.neuroimage.2012.06.077

(2009) associated hMT+ function with the discrimination of subtle changes in otherwise comparable human movement stimuli. Changes in hMT+ connectivity during biological motion perception have also been reported. For example, Nummenmaa et al. (2010), found increased connectivity between hMT+ and posterior superior temporal sulcus (pSTS, discussed below) during the perception of changes in eye gaze. Nummenmaa et al.'s finding suggests that hMT+ may support biological motion perception by providing motion information to pSTS. It is possible that a low-level visual information processing system such as hMT+ is differentially recruited for specific higher-order tasks that require the discrimination of subtle motion parameters (i.e., human movement perception). This possibility is the focus of the present study; are basic visual information processing systems responsive to selective attention towards the meaning of human movement, even when controlling for visual input to those systems?

hMT+ is one of a number of posterior visual areas shown to be active during human movement perception. It is directly adjacent to the extrastriate body area (EBA), which is responsive to both static and dynamic visual displays of the human form, as well as affordances of human forms (such as tool movement; Beauchamp et al., 2002, 2003; Downing et al., 2001; Grossman and Blake, 2002; Grossman et al., 2004; Michels et al., 2005, 2009; Santi et al., 2003; Spiridon et al., 2006; Wiggett and Downing, 2011). EBA may in fact respond in an obligatory way to human form input (see Jastorff and Orban, 2009). The spatial and functional distinction between EBA and hMT+ has been a recurring theme in the EBA literature since its inception (Downing et al., 2001, 2007; Peelen et al., 2006; Wiggett and Downing, 2011). EBA is often distinguished from hMT+ by virtue of its sensitivity to the static structural components of the human form (whereas hMT+ appears sensitive to dynamic human motion vectors; Downing et al., 2006). Although the case for the hMT+/EBA distinction has been clearly made, EBA has been shown to overlap spatially with hMT+ at the voxel level, to the point where the two areas can be difficult to separate even on a per-subject basis (Downing et al., 2001, 2007; Peelen and Downing, 2007; Peelen et al., 2006; Wiggett and Downing, 2011). Coordinates reported for EBA and hMT+ are in fact highly interdigitated between biological motion studies (for example, EBA coordinates from the references cited above are comparable to hMT+ coordinates from Michels et al., 2005; Peuskens et al., 2005; Spiridon et al., 2006). The spatial and functional relatedness of EBA and hMT+ suggests that, despite the fact that EBA does not appear to play a specific role for biological motion processes as distinct from general human form perception, they may nevertheless work in a coordinated manner during biological motion perception.

A third area – pSTS – shares functions associated with both hMT+ and EBA. PSTS appears selective for the processing of human movement, compared to stationary human forms or non-human movement (for a review see Puce and Perrett, 2003). The proximity of pSTS with hMT+ and EBA, and their co-activation in some biological motion paradigms (for example, Herrington et al., 2011a; Jastorff et al., 2009), suggests that they implement unique but overlapping aspects of human movement perception—hence the term "STS complex" coined by Puce and Perrett (2003; Puce et al., 1998). Although a few studies have examined the respective roles of each area within the complex, the pattern that emerges from the literatures reviewed above suggests that 1) hMT+ processes information related to human configural motion, 2) EBA processes information related to human form, whether moving or not, and 3) pSTS integrates these and possibly other lower-level visual inputs to form the percept of a moving human. Findings on pSTS (but not EBA) suppression during the perception of incongruous motion (i.e., altered videos of one's own movement) suggest that pSTS is integrated with higher order processing structures in a manner that EBA (and by extension hMT+) is not (Kontaris et al., 2009). PSTS thereby serves to integrate visual information processes related to human movement, and to interface with other human movement processing systems during biological motion perception (for example, parietal and frontal motor systems; Carr et al., 2003; Iacoboni et al., 200 l; Kontaris et al., 2009).

It is now widely held that some social information processes may be implemented in part by the STS complex (henceforth called STSC, including pSTS, hMT+, and EBA; Puce and Perrett, 2003). Empirical support for this claim comes from a variety of studies comparing goal-directed human movement to either non-coherent, scrambled motion displays (e.g., Bonda et al., 1996; Grossman and Blake, 2002; Michels et al., 2005; Peuskens et al., 2005; Saygin, 2007; Saygin et al., 2004), or coherent human movement without a salient or predictable goal (Campbell et al., 2001; Pelphrey and Morris, 2006; Pelphrey et al., 2003, 2004; Saxe et al., 2004; Wyk et al., 2009; also see Blake and Shiffrar, 2007). Although it is a widely held view that STSC (particularly pSTS) is involved in the *understanding* of human movement (i.e., Mosconi et al., 2005; Pelphrey and Morris, 2006), a close examination of the paradigms used in this literature reveals some challenges in making this inference. Many studies eliciting robust STSC activation have used human movement stimuli without any manipulation of the endogenous processing of movement meaning or understanding. In other words, whether articulated or not, studies on human movement perception often ignore endogenous processes and assume that human movement processing systems activate in a more or less obligatory manner to the perception of coherent human movement, which is why they are sensitive to basic contrasts of coherent versus non-coherent human movement, or human versus non-human movement. A similar assumption is that these systems will be differentially sensitive to goal-directed movement versus random but legitimate human movement, even when participants are not directed by task demands to attend to goal orientation per se (e.g., Pelphrey et al., 2003, 2004; Saxe et al., 2004).

However, increasing evidence indicates that STS is sensitive to selective attention towards biological motion (Thompson and Parasuraman, 2012). For example, Safford et al. (2010) found increased activation in STS when participants attended to a biological motion stimulus within a display also containing non-biological stimuli (tools). There is also some evidence for attentional modulation of hMT+/EBA. In particular, Luks and Simpson (2004) found increased preparatory activation of hMT+ when prompted to detect the movement direction of a random dot kinematogram before it was actually presented (i.e., in the absence of any visual input). This finding represents very strong evidence that putatively "bottom-up" visual motion areas are modulated by attentional resource allocation. Further evidence also comes from Engel et al. (2008), who found increased activation in the occipito-temporal junction (likely overlapping with hMT+/EBA) during the perception of trained movements (learned immediately prior to scanning), which may relate to heightened attentional resources paid to these movements (in addition to increased input from motor cortices).

The present study tested whether STSC is modulated by selective attention towards or away from the goals of a moving figure (henceforth referred to as goal orientation). Selective attention, in this context, does not refer to attention towards distinct aspects of a single visual display, but to distinct features of a single stimulus (as in, for example, a Stroop task, where selective attention can be paid towards either the color ink or color name of a single word). It is becoming increasingly clear that multiple visual processing areas are modulated by selective attention (Bar et al., 2006; Luks and Simpson, 2004; Miyashita and Hayashi, 2000; Ranganath et al., 2004; Vuilleumier et al., 2001, 2004). However, few studies to date have examined whether STSC and adjacent movement processing areas are among these regions. To our knowledge, no studies to date have tested whether attention to movement goals affects STSC function, independent from changes in perceived stimuli.

This study uses point-light biological motion stimuli to examine the role of selective attention in modulating STSC function. Point-light