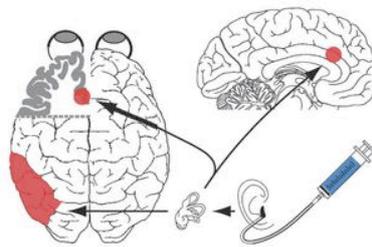


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Visual perception and neural correlates of novel ‘biological motion’

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Abstract

Studies of biological motion have identified specialized neural machinery for the perception of human actions. Our experiments examine behavioral and neural responses to novel, articulating and non-human ‘biological motion’. We find that non-human actions are seen as animate, but do not convey body structure when viewed as point-lights. Non-human animations fail to engage the human STSp, and neural responses in pITG, ITS and FFA/FBA are reduced only for the point-light versions. Our results suggest that STSp is specialized for human motion and ventral temporal regions support general, dynamic shape perception. We also identify a region in ventral temporal cortex ‘selective’ for non-human animations, which we suggest processes novel, dynamic objects.

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Keywords: Vision; Perception; Motion; fMRI; Biological motion

1. Introduction

Humans are highly skilled at seeing the motions of others. This is elegantly demonstrated by ‘point-light’ animations (Johansson, 1973), which display only the joints of an actor as moving dots. Despite the sparseness of these displays, observers can see the complex actions depicted in these ‘biological motion’ stimuli and can infer the gender, identity, and mood of the actor (e.g., Cutting, 1978; Cutting & Kozlowski, 1977; Dittrich, Troscianko, Lea, & Morgan, 1996; Loula, Prasad, Harber, & Shiffrar, 2005). Because single frames of point-light animations appear meaningless to observers, it has been argued that biological motion perception is constructed from the analysis of local motion trajectories (Hoffman & Flinchbaugh, 1982; Mather, Radford, & West, 1992; Neri, Morrone, & Burr, 1998).

Biological motion perception has neural correlates in several areas of human cortex, in particular the posterior superior temporal sulcus (STSp, e.g., Bonda, Petrides, Ostry, & Evans, 1996; Grossman et al., 2000; Howard et al., 1996). Located a few centimeters anterior to the

motion-selective hMT+ complex, the STSp is more strongly activated by point-light animations of humans than by motion-matched controls, arrays of randomly moving dots, dots forming rotating 3D shapes, and inverted point-light animations (Beauchamp, Lee, Haxby, & Martin, 2003; Bonda et al., 1996; Grossman & Blake, 2001; Grossman & Blake, 2002b; Peuskens, Vanrie, Verfaillie, & Orban, 2005). In addition, researchers have found neural correlates of biological motion in ventral temporal cortex, including inferior temporal cortex (Thompson, Clarke, Stewart, & Puce, 2005) and regions on the ventral fusiform gyrus (Grossman & Blake, 2002a; Vaina, Belliveau, des Roziers, & Zeffiro, 1998). Together these findings suggest a distributed network of cortical areas supporting the visual analysis of human action.

Some researchers have recently argued that perception of point-light biological motion is a form-driven process. For example, Beintema, Georg, and Lappe (2006) found that observers could reliably discriminate biological motion in point-light animations that had been carefully constructed to eliminate frame-to-frame local correspondences, short-circuiting local motion cues. Indeed, the effects of inverting displays of biological motion—impaired detection and discrimination of point-light animations

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(Pavlova & Sokolov, 2000; Sumi, 1984)—are not predicted from the simple integration of local motion cues.

The ability to dissociate the contributions of motion and form in the perception of biological motion in point-light displays is difficult because the structure of the human body remains constant during articulated motion. The majority of studies investigating biological motion use human actions, either in fully-illuminated or point-light forms with a smaller number of studies using highly familiar animal actions (e.g., Mather & West, 1993; Pavlova & Sokolov, 2003; Ptito, Faubert, Gjedde, & Kupers, 2003; Richardson & Webster, 1996). Little research has yet been conducted using novel stimuli unfamiliar to subjects, with a few notable exceptions (Jastorff, Kourtzi, & Giese, 2006; Pelphrey et al., 2003). Recognition of human actions may benefit from the unvarying form of the human body, a prediction explicit in recent models of biological motion perception (Giese & Poggio, 2003; Lange, Georg, & Lappe, 2006). An alternative hypothesis is that the perception of biological motion is constructed from other cues, such as joint kinematics (e.g., Mather et al., 1992; Neri et al., 1998). It remains unclear to what extent the perception of biological motion, and the associated cortical activity, is specialized for human actions or whether this network can be co-opted by non-human, biological events.

To clarify the importance of a specific body structure in biological motion perception, and to assess the specialization of the cortical network supporting biological motion perception, we have constructed a new set of stimuli, which we refer to as 'Creatures'. Creatures share a number of features with human bodies—for example, Creatures have articulated joints and a 'nervous system' that allow them to locomote through their environment. Because their body configurations are piece-wise rigid and articulated, point-light animations of Creature movements can be created in the same way as point-light animations of human actions. However, unlike humans, each Creature has a unique body structure, removing the confound of a single familiar form.

We have compared perception of Creatures to humans across several measures, including animacy and immunity to surrounding visual clutter. Human actions are readily recognized even when depicted as point-light animations (and thus without explicit body structure (Johansson, 1973)), and remain recognizable even when masked by substantial noise (taxing the perceptual construction of implied body structure (e.g., Hiris, Humphrey, & Stout, 2005)). We measured whether Creatures are readily perceived as animate when reduced to point-light depictions, and whether the perceptual integration is sufficiently robust to tolerate additional noise in the scene. We also measured neural activity during Creature perception in brain areas normally activated by human biological motion. The resulting patterns of activity dissociate brain areas specialized for human biological motion from those involved in the general recognition of dynamic objects.

2. General methods

2.1. Stimuli

2.1.1. 'Creatures'

The new set of 'biological motion' stimuli was generated using Framsticks artificial evolution and life simulation software (Komosinski & Ulatowski, 1999). Creatures' bodies were built from rod-like shape primitives linked by rigid and non-rigid joints and 'muscles', controlled by a simple neural network 'brain'. The Creatures' artificial environment simulates physical forces affecting the Creatures bodies such as gravity, elastic reaction between body parts, and the upward force and friction of the ground. Locomotion was the goal of the artificial evolution process that generated these stimuli. No specific constraints were placed on number of body parts, number of joints or body symmetry. Short sequences of locomoting Creatures were exported and converted to either fully-illuminated or point-light animations (Fig. 1). Point-light animations depicted joint positions as black dots against a gray background using Matlab (Mathworks, Inc.) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). In the fully-illuminated animations, the rods and joints of the Creatures' body structures were visible. Fully-illuminated animations were exported as image sequences, converted to grayscale and displayed using the Quicktime functions in Psychophysics Toolbox.

2.1.2. Human actions

Point-light human animations depicted human figures engaged in various activities such as kicking, throwing, jumping, and crawling (Fig. 1c). Joint positions were encoded as x, y positions and movement vectors, and were displayed as black dots against a gray background. Scrambled point-light motion sequences were created by randomizing the initial positions of dots, then allowing each dot to move as in the normal animation. Animations were displayed using Matlab and the Psychophysics Toolbox. Fully-illuminated human animations, imported from motion-captured data files (<http://www.bvhfiles.com>) depicted grayscale, featureless 3D mannequins (Fig. 1d; Poser, e frontier America, Inc.) performing a variety of actions.

2.2. Displays

Observers viewed animations in a darkened room on a CRT monitor (1280 h × 1024 v resolution, 85 Hz) connected to a Macintosh G4 computer running Matlab 5.2 and Psychophysics Toolbox. Viewing distance was fixed at 37 cm through the use of a chinrest, resulting in stimuli subtending approximately 14° of visual angle. Subject responses were collected on a standard keyboard.

3. Experiment 1: Creature animacy

The goal of Experiment 1 was to measure ratings of animacy for Creatures stimuli. As a comparison, observers also rated the animacy of human point-light animations. Observers viewed the animations in one of two forms: fully-illuminated or point-light. Point-light animations lack explicit information about a stimulus' underlying structure since only motion of the joints is present.

3.1. Methods

Twenty-seven University of California, Irvine students participated in this experiment and received course credit for their participation. All observers had normal or corrected to normal vision, and gave informed consent as

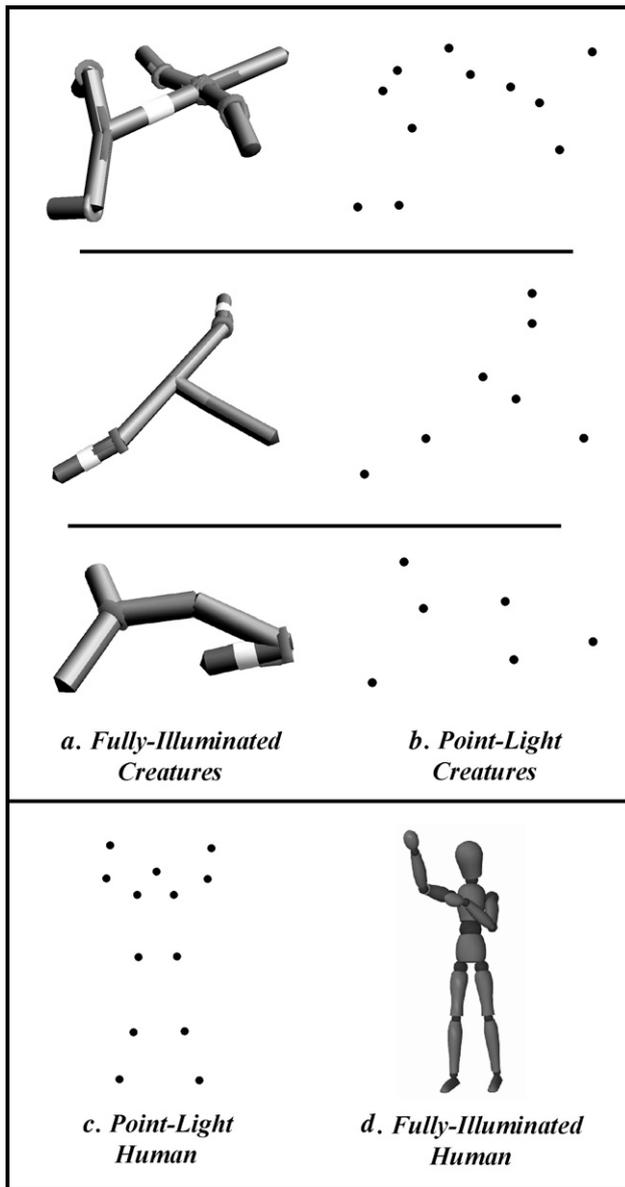


Fig. 1. Sample stimuli used in our experiments. (a) A single frame from three fully-illuminated Creatures. (b) Matching point-light counterparts to the three fully-illuminated Creatures. As with human point-light animations, dots are places at the joints and ends of limbs. (c) Sample single frame from a human point-light animation (a jumping jack and tossing an object). (d) Single frame of a fully-illuminated human animation.

approved by the University of California Irvine Institutional Review Board.

Observers viewed 35 different Creatures locomoting and 21 different human actions. Twelve observers viewed the animations as fully-illuminated and 15 different observers viewed the animations as point-light. Fully-illuminated animations were displayed for 2 s while point-light animations were displayed for 1.85 s. Trials were blocked by animation type and the order of presentation within each block was randomized. Observers' task was to provide a Likert rating indicating "How alive?" each animation appeared. Ratings were made on a five-point scale with a rating of one being "Not Alive" and a rating of five being "Very Alive". To

emphasize that the task was to rate animacy without the influence of other factors, observers were instructed not to base their rating on whether they were familiar with the stimulus (which they were not). Observers rated each animation three times.

3.2. Results and discussion

Group results are shown in Fig. 2a. On average, approximately half of the Creatures were rated as alive (mean rating of three or above). Of the 35 Creatures, 14 fully-illuminated and 18 point-light had a mean rating of three or above, indicating that observers perceived them as alive. Ratings for all but one point-light human animation were above three, with 17 of 21 animations being rated above four.

High animacy ratings for a subset of the Creatures indicate that stimuli with novel structure and motion can be perceived as animate by naïve observers. This result is perhaps not surprising given the success of television and film productions that animate novel objects (for example, the toys in Pixar's *Toy Story*), and the strong perception of social interaction that has been demonstrated using simple moving shapes (Blakemore, Sarfati, Bazin, & Decety, 2003; Heider & Simmel, 1944; Martin & Weisberg, 2003; Tremoulet & Feldman, 2000). That strong animacy is attributed to even point-light Creatures suggests that kinematics

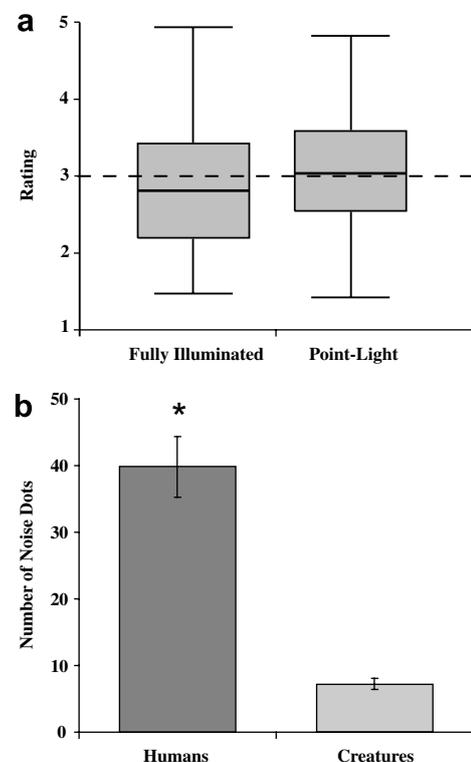


Fig. 2. (a) Box plots of mean animacy ratings for 35 fully-illuminated and point-light Creatures. Creatures with a mean rating of three or above (dotted line) were considered animate. (b) Noise-tolerance thresholds for humans and Creatures. Significance ($p < .0001$) is indicated by (*).

alone (without any explicit shape or social interaction) is sufficient to generate a percept of animacy. We observed no obvious qualitative or quantitative difference in features separating the two groups, although it should be noted that the two animations rated the least animate were non-articulating (i.e., rigid bodies with no joints).

4. Experiment 2: Detection of Creatures in noise

Previous experiments have demonstrated recognition of human actions from point-light animations even when the point-light figures are heavily masked (Bertenthal & Pinto, 1994; Grossman, Kim, & Blake, 2004; Hiris, Krebeck, Edmonds, & Stout, 2005; Pavlova & Sokolov, 2000). Adding noise dots to point-light animations interferes with frame-to-frame dot correspondences, forcing observers to rely more heavily on implied structure. Indeed, masks that retain structural components of the body (such as ‘arm’ and ‘leg’ dot triads) are the most effective in degrading perception of human actions (Bertenthal & Pinto, 1994). In this experiment we assess the strength of structural cues in Creature perception by measuring observers’ tolerance to noise when viewing point-light animations of the novel Creatures.

4.1. Methods

Eight University of California Irvine students participated in Experiment 2. All had normal or corrected to normal vision, and gave informed consent as approved by the University of California, Irvine Institutional Review Board.

Observers viewed 1.8 s animations of 11 point-light human actions and of the 11 most highly-rated point-light Creatures. On each trial, observers indicated whether the animations depicted a biological or motion-matched non-biological (‘scrambled’) stimulus. Stimuli were spatially jittered $\pm 4^\circ$ to prevent subjects from making discrimination judgments based on the spatial position of individual dots.

Observers first completed a practice block in which they discriminated biological from scrambled motion while viewing animations free of noise. In the subsequent experiment, noise-tolerance thresholds were measured for each stimulus type using a staircase design (blocked by stimulus type). Motion-matched noise was created by randomly positioning dots sampled from the trajectories of the same action depicted in the target animation. The number of noise dots in any given trial was determined by a double-interleaved, 3–1 staircase design which converged on 79.4% accuracy. The number of masking noise dots was increased (by three) following three sequential correct responses, and decreased (by three) following a single incorrect response. Two independent staircases were interleaved such that the number of noise dots was determined by one of two staircases, randomly selected on each trial. Staircases were terminated following 24 reversals (e.g., increases or decreases in noise levels), which typically

resulted in approximately 140 trials. Noise thresholds were computed as the average noise levels for the trials during the last 20 staircase reversals. Observers received feedback during the experiment.

4.2. Results and discussion

Observers were much more tolerant of noise added to the human animations than to the Creature animations (within subjects, paired *t*-test, $p < .0001$) (Fig. 2b). On average, observers completed the task with threshold accuracy when the human animations were embedded in 39.8 noise dots ($SD = 13.00$) and when Creatures were embedded in an average of 7.1 noise dots ($SD = .82$).

Motion-matched noise creates possible mismatches in the frame-to-frame correspondences of individual dots, thus having the effect of interfering with local motion computation in point-light animations (Bertenthal & Pinto, 1994; Hiris, Humphrey, et al., 2005). Robust tolerance to noise indicates that observers are able to overcome the motion interference by use of alternate cues or cognitive strategy. In the case of point-light human animations, prior knowledge of body structure may facilitate selection of dots likely to comprise the target form (the human body). Dots outside of this region can be largely ignored, effectively increasing noise tolerance. As further evidence for this, noise tolerance is approximately halved when the human figure is viewed in a non-canonical perspective, such as when turned upside-down (Pavlova & Sokolov, 2003). Thus noise tolerance indicates the extent to which observers use knowledge of implied body structure in discriminating point-light animations.

The addition of just a few noise dots to the point-light Creatures had the effect of disrupting discrimination performance, indicating observers had difficulty segregating the target dots from the noise arrays. Thus it appears that observers fail to fully determine the underlying body structure of the point-light Creatures.

5. Experiment 3: Neural correlates of viewing Creatures

Previous neuroimaging research has identified several brain areas active during perception of human biological motion. These areas include the posterior superior temporal sulcus (STSp, Grossman et al., 2004; Pelphrey et al., 2003), the inferior temporal sulcus (ITS, Peelen, Wiggett, & Downing, 2006; Thompson et al., 2005), and regions of the fusiform gyrus (Grossman & Blake, 2002a; Peuskens et al., 2005; Santi, Servos, Vatikiotis-Bateson, Kuratate, & Munhall, 2003; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001).

Here we compare neural activity during perception of Creature motion to neural activity during the perception of human motion. Our analysis targets the brain areas that have been previously implicated in biological motion perception and compares BOLD activation levels during perception of Creature and human motion. We also analyze

global patterns of brain responses during Creature perception as compared to human biological motion perception. The results from this study dissociate the brain areas selectively involved in the perception of human actions from those more generally involved in the perception of dynamic objects.

5.1. fMRI methods

5.1.1. Observers

Eleven observers (six women, five men) with normal or corrected to normal vision participated in the following neuroimaging experiments. All observers gave informed consent as approved by the University of California Irvine Institutional Review Board. Scanning was conducted using a 1.5 T Philips MR scanner located on the University of California Irvine campus.

5.1.2. Procedure

Regions of interest (ROIs) were identified using previously published procedures (e.g., Grossman et al., 2000; Kanwisher, McDermott, & Chun, 1997; Malach et al., 1995). Briefly, the STSp localizer contained alternating blocks of human point-light and scrambled point-light animations. The fusiform face area (FFA) was localized using alternating blocks of static faces and objects. For both localizer scans, blocks lasted 20 s and were separated by a 6 s fixation. Each block contained thirteen 1 s stimuli separated by 500 ms interstimulus intervals (ISI). Each condition was viewed seven times per run, and each run was repeated. Observers performed a one-back task (push a button whenever a stimulus was repeated) to maintain attention throughout the scan.

In a separate scan, observers viewed three different stimulus conditions: fully-illuminated Creature motion, fully-illuminated human motion, and fixation. Eight different Creatures rated as highly animate (mean fully-illuminated rating = 3.6, $SD = 1.0$) in Experiment 1 were shown locomoting in 2 s animations within each 20 s block (ISI = 500 ms). A 6 s fixation separated the blocks and the order of the conditions was randomized for each scan. Observers viewed each condition a total of 10 times (across two scans).

In another scan, observers viewed blocks of point-light Creatures, point-light humans, scrambled point-light humans, and fixation. Ten different Creatures rated as highly animate in Experiment 1 (mean point-light rating = 4.0, $SD = .4$) were shown locomoting in 1500 ms animations within each 20 s block (ISI = 500 ms). A 6 s fixation separated the blocks, and the order of the conditions was randomized for each scan. Each condition was repeated eight times across two scans.

Scan sessions lasted approximately 1.5 h. Observers viewed animations through MR compatible LCD goggles (Resonance Technologies Inc.; 800 h × 600 v, 60 Hz) connected to a Macintosh G4 computer in the scanner control

room running Matlab 5.2 and equipped with Psychophysics Toolbox.

High resolution whole brain images were acquired for each observer (T1-weighted 3D SPGR, 256 × 256 axial matrix, 1 mm slice thickness). Functional images were acquired using single-shot gradient-recalled echoplanar imaging (EPI, TR = 2000 ms, TE = 40 ms, flip angle = 90°, 22 axial slices 1.95 × 1.95 × 4 mm³, 0 mm gap). Scans lasted between 6.5 and 7.5 min.

After scanning, EPI images were reconstructed from raw k -space data and the first four volumes of each run were discarded to allow for stabilization of the MR signal. All volumes within a scanning session were motion corrected to the first image of the session using SPM2 (Wellcome Department of Cognitive Neurology, London, UK; Friston et al., 1995). The resulting corrected images were imported into Brain Voyager (Brain Innovations, Inc.) where they were corrected for linear drift and coregistered with the high resolution anatomical images.

ROIs were identified as those voxels from the localizer scans (biological versus scrambled, faces versus objects) significantly correlated with an ideal boxcar. Experimental scan timecourses were averaged by condition, and a percent BOLD signal change for each condition was calculated relative to the average BOLD response during fixation blocks.

5.2. ROI analysis

ROIs were identified within each individual (Fig. 3 and Table 1). Across observers, the localizer scans resulted in four brain areas in posterior cortex highly correlated with the perception of biological motion. Consistent with prior findings, STSp was identified as the cluster of voxels on the posterior extent of the superior temporal sulcus correlated with viewing point-light biological motion (FDR < .05) (Genovese, Lazar, & Nichols, 2002). STSp was identified in all our observers (bilateral in seven observers, right hemisphere only in four observers). We also identified a region selective for human biological motion in the inferior temporal sulcus (ITS) in all observers (FDR < .001; bilateral in four observers, right hemisphere only in seven observers). This region likely corresponds to an area previously identified as ITS, pITS and possibly the EBA (i.e., Downing, Jiang, Shuman, & Kanwisher, 2001; Peelen & Downing, 2005; Peelen et al., 2006; Thompson et al., 2005). A region on the posterior inferior temporal gyrus (pITG) was also selective for biological motion (FDR < .001; bilateral in seven observers, right hemisphere only in four observers). The pITG has been previously reported as selective for biological motion (Peuskens et al., 2005), and lies adjacent to cortex identified as being involved in general object recognition (e.g., Altmann, Deubelius, & Kourtzi, 2004; Grill-Spector, Kourtzi, & Kanwisher, 2001; Malach et al., 1995). Lastly, a region on the floor of ventral temporal cortex was also selective for human biological motion (FDR < .001; bilateral in six

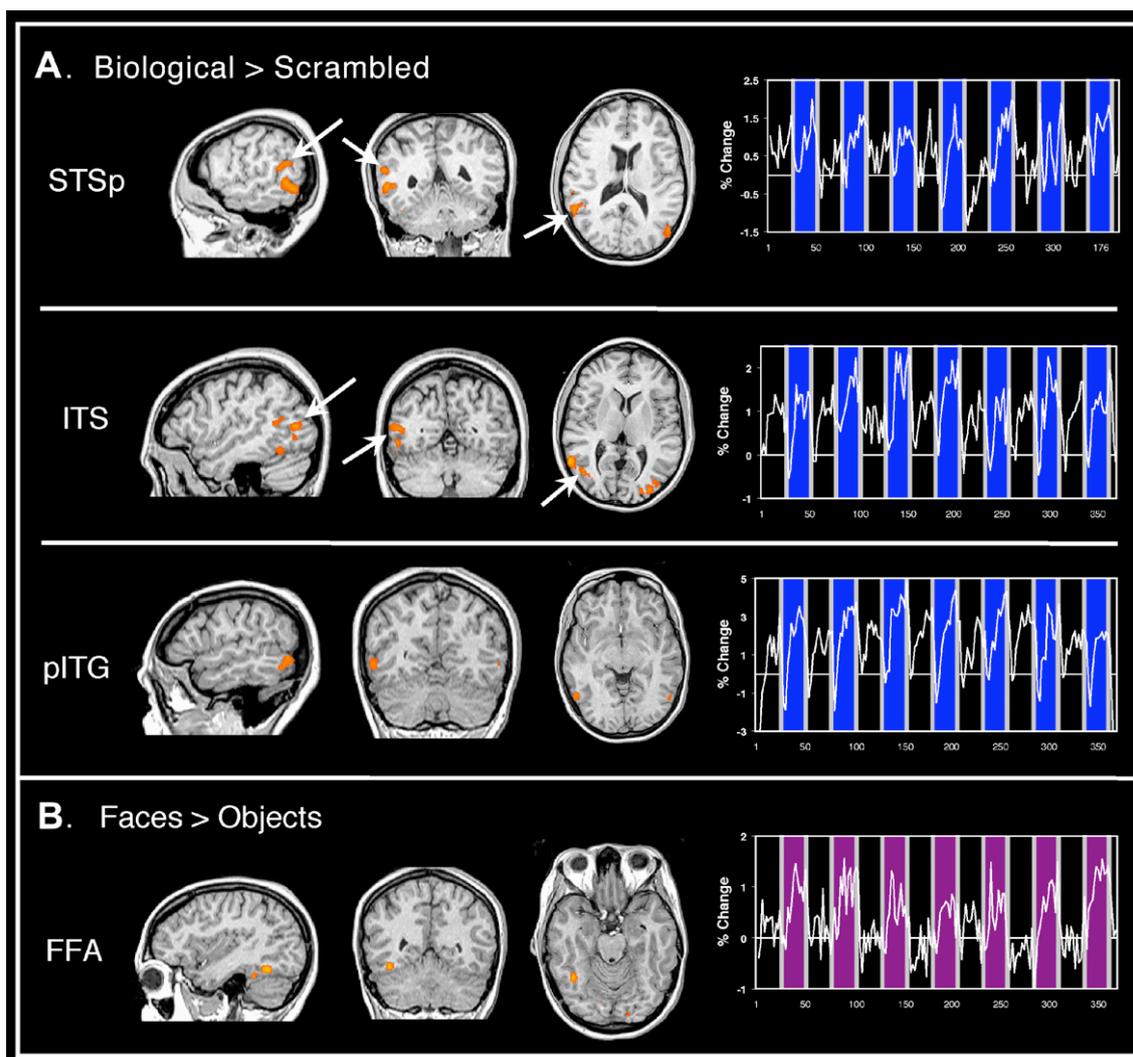


Fig. 3. ROIs and sample BOLD intensity timecourses from representative individual subjects in the biological motion (STSp, ITS, and pITG) and FFA localizer scans. A sagittal, coronal, and axial slice are shown for each ROI. Statistical maps are displayed at FDR < .001. BOLD intensity timecourses are shown as percent change from fixation, with time displayed on the x-axis in seconds. (A) ROIs identified in the biological motion localizer contrast: point-light human actions minus scrambled point-light human actions. Blue bars indicate biological motion epochs. Black bars indicate scrambled epochs. Gray bars indicate fixation intervals. (B) The fusiform face areas as identified with the faces > objects contrast. Purple bars indicate face epochs. Black bars indicate object epochs. Stimulus protocols have been shifted 4 s in this depiction to account for the hemodynamic lag.

Table 1
Average Talairach coordinates for the regions of in Experiment 3

ROI	Num observed hemispheres		Talairach coordinates					
	Left	Right	Left			Right		
			X	Y	Z	X	Y	Z
STSp	7/11	11/11	-47 (7.7)	-52 (9.0)	6 (5.0)	50 (5.5)	-47 (6.0)	7 (5.5)
ITS	5/11	11/11	-50 (5.2)	-68 (5.5)	3 (7.1)	47 (6.0)	-62 (5.6)	5 (4.7)
pITG	7/11	11/11	-47 (4.2)	-72 (4.8)	-7 (5.1)	46 (6.2)	-67 (6.5)	-9 (5.5)
FFA/FBA	5/11	10/11	-41 (3.1)	-54 (6.6)	-19 (2.8)	36 (3.8)	-50 (9.1)	-20 (2.9)
IOS	6/11	9/11	-43 (5.0)	-62 (7.3)	-9 (7.8)	44 (4.0)	-57 (4.7)	-13 (6.3)

Standard deviations are shown in parentheses.

Abbreviations: STSp, superior temporal sulcus, the posterior extent; ITS, inferior temporal sulcus; pITG, posterior inferior temporal gyrus; FFA/FBA, fusiform face/fusiform body area; IOS, inferior occipital sulcus.

observers, right only in four observers). This result is consistent with reports of fusiform activation during the per-

ception of biological motion and likely corresponds to the fusiform body area (FBA) (Peelen & Downing, 2005).

A recent report by Peelen et al. (2006) found the FFA and FBA to be sufficiently proximal that traditional localizers cannot distinguish the two (although voxel-by-voxel analyses can). In our observers, this ventral brain site was adjacent and overlapping with the functionally defined FFA (see below). Because these two brain areas are so close, and our results did not differ between the two, we report neural responses from the ROI defined in our FFA localizer.

The faces versus objects localizer yielded a cluster of voxels highly correlated with perception of faces ($FDR < .001$). These clusters were located on the ventral surface of the temporal lobe on the posterior fusiform, corresponding to published reports of the FFA (bilateral in five observers, right hemisphere only in five observers, not identified in one observer likely due to slice coverage insufficient to sample ventral temporal cortex).

5.3. Creature results and discussion

Mean timecourses for the STSp, ITS, pITG and FFA ROIs were extracted for each subject and the results are summarized in Fig. 4. There was a significant main effect of region of interest, and significant interaction between region of interest and condition ($p < .05$). Only in STSp

were BOLD signals higher for the fully-illuminated human animations versus the Creature animations ($p < .0002$). In the FFA, ITS and ITG the BOLD signals were equivalent for the two types of animations (FFA: human MN = 1.04%, Creature MN = .98%, $p = .44$; ITS: human MN = 1.64%, Creature MN = 1.52%, $p = .22$; pITG: human MN = 2.66%, Creature MN = 2.70%, $p = .74$).

When viewed as point-light animations, the BOLD signals in STSp were again stronger for humans than Creatures (main effects of ROI and condition, $p < .05$; human MN = .86%, Creature MN = .73%, $p < .005$). The same was true for ITS and ITG (ITS: human MN = 1.59%, Creature MN = 1.34%, $p < .01$; pITG: human MN = 2.74%, Creature MN = 2.41%, $p < .005$). In the FFA, the BOLD response showed a non-significant trend in the same direction (FFA: human MN = .78%, Creature MN = 0.60%, $p = .09$).

The weak BOLD response in the STSp for Creatures is further evidence for STS specialization in perception of human actions (e.g., Allison, Puce, & McCarthy, 2000; Pelphrey, Adolphs, & Morris, 2004). And given that the STSp responded weakly to Creatures despite the strong ratings of animacy for these stimuli, we conclude that perceived animacy alone is insufficient to optimally drive the STSp.

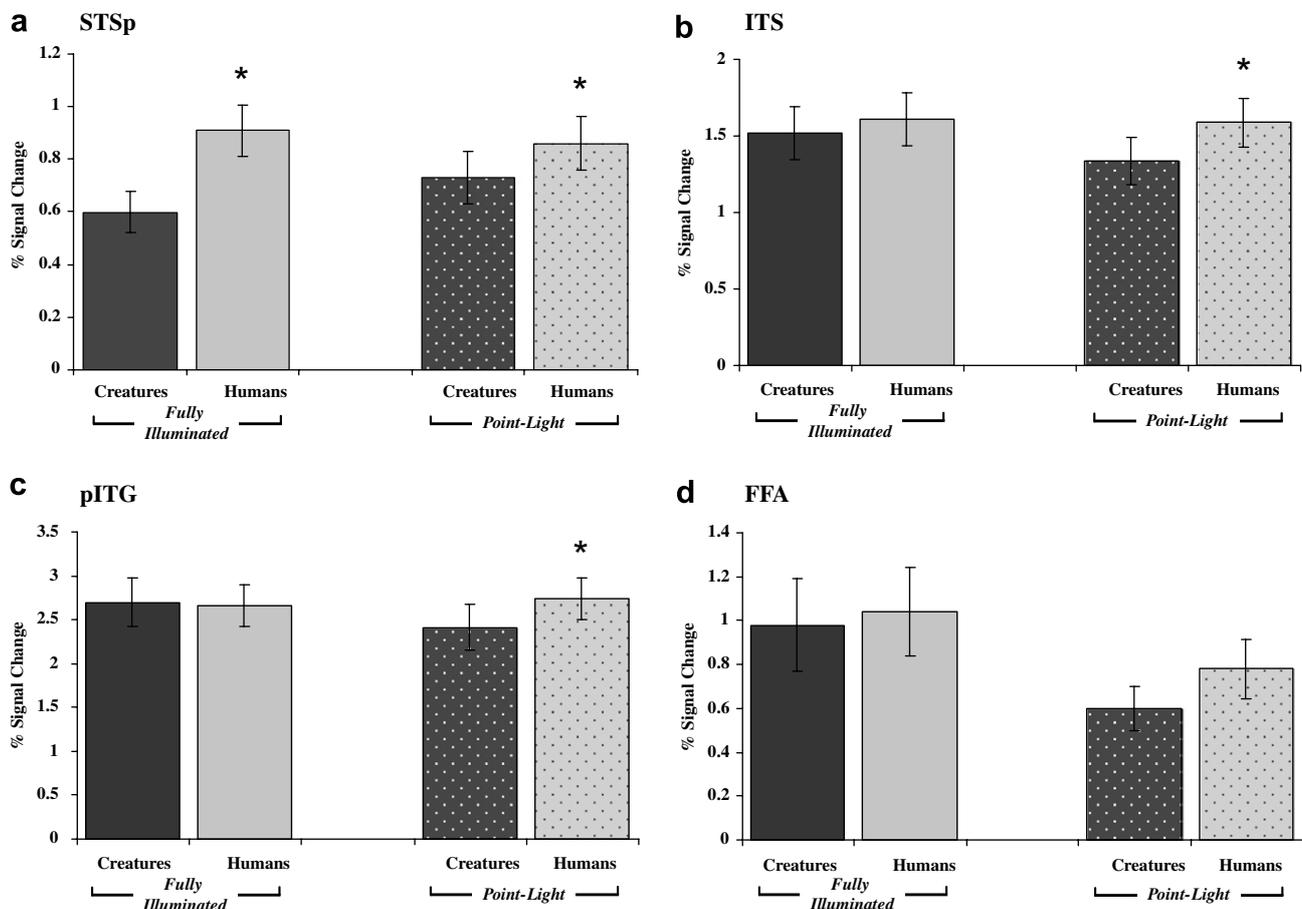


Fig. 4. Percent signal change relative to fixation change averaged across observers for our four ROIs. *Indicates statistical differences between BOLD responses for human and Creatures.

In contrast, BOLD responses in the more ventral ROIs did not differentiate between the fully-illuminated humans and Creatures. Thus we interpret the pITS, ITG and FFA/FBA as being recruited more generally in perception of articulated objects. Because the BOLD response is attenuated when Creatures are viewed as point-lights, conditions which we know from our psychophysical study mask the underlying body structure, we argue that the recognition of body form, not stimulus category or perceived animacy, is driving these neural responses.

5.4. Creature localizer?

In a further analysis, we investigated whether there were any common areas across our subjects that respond more for Creatures than humans. Using a general linear model, we probed the entire brain for regions that respond significantly more during the fully-illuminated Creature condition as compared to the human animation condition.

We found a brain area that preferentially activates for Creatures over human actions (Fig. 5A) in nine of eleven subjects (FDR < .05; bilateral in three observers, right hemisphere only in six observers). This area is ventral and slightly anterior to pITG, often extending into the region of cortex described as the lateral occipital complex (e.g., Grill-Spector et al., 1998; Malach et al., 1995).

Because we did not acquire LOC localizers on these subjects, and because of the proximity of this region to the inferior occipital sulcus, we have labeled it the IOS (see Table 1 for Talairach coordinates).

It is noteworthy that the IOS did not overlap with the previously defined ROIs (STSp, ITS, pITG, and FFA) in any of our subjects. However we did find partial overlap of the IOS with object-selective brain areas. Using our FFA localizer data, we identified brain areas with neural responses selective for objects over faces. This comparison revealed large areas of object selectivity on the medial fusiform in all of our subjects, including in the vicinity of the IOS (Fig. 5B). Further analysis revealed that these object-selective regions partially overlap the IOS Creature area, with the Creature selective IOS always extending more anterior.

The IOS was localized using the BOLD responses when observers viewed the fully-illuminated animations. The same pattern of selectivity was found when analyzing BOLD responses from the IOS when observers viewed the point-light animations. The IOS responded more strongly for Creatures as over human actions even when viewed as point-lights ($p < .0001$).

Because Creatures depict events not seen in the natural world, it is unlikely that the IOS responds selectively just to these stimuli. This is notable because many regions in

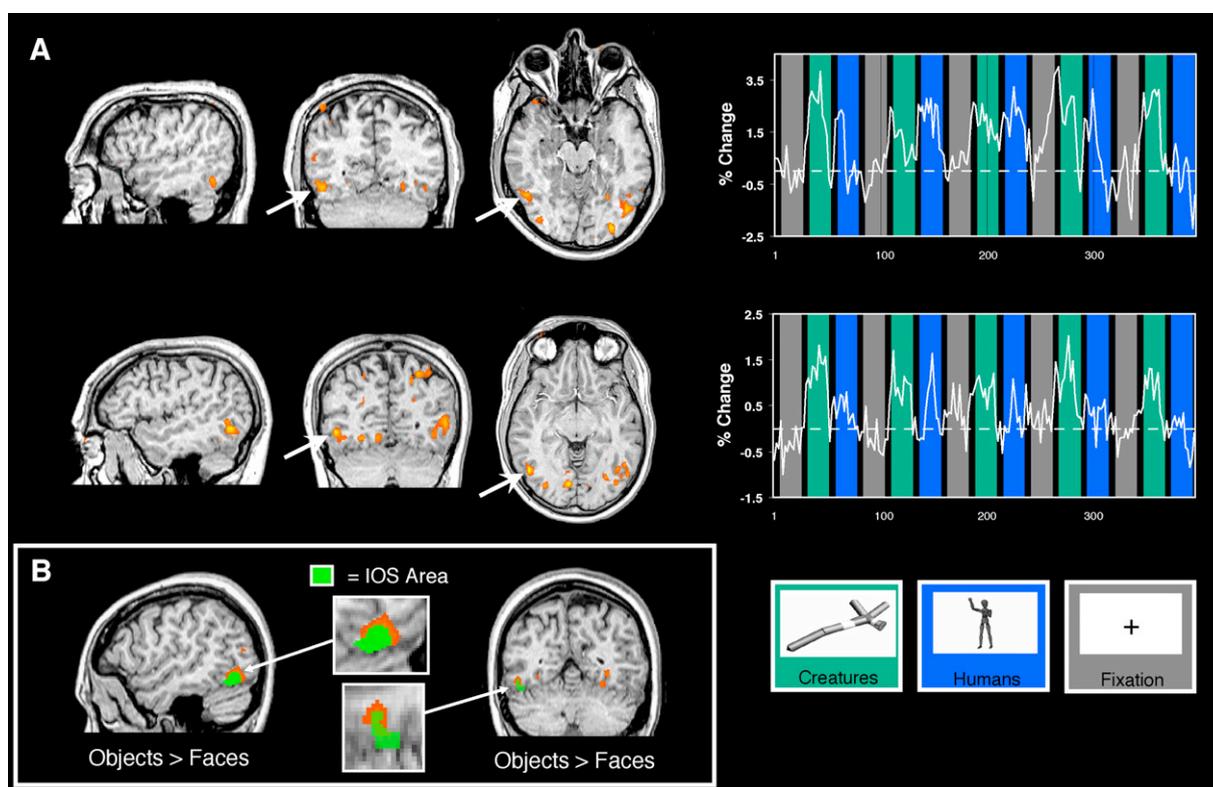


Fig. 5. (A) The IOS area and timecourses in two of our nine observers. Statistical maps are the result of a general linear model contrast subtracting humans (blue bars) from Creatures (green bars) performed on the fully-illuminated data. Maps thresholded at FDR < .001. Timecourses of the IOS BOLD signal percent change relative to fixation (gray bars). Dotted line indicates the mean fixation baseline. Protocols have been shifted to account for hemodynamic lag (4 s). (B) Overlap of the identified IOS ROI with object-selective areas. Statistical maps (in orange-yellow) show results of the objects minus faces contrast performed on our FFA localizer data. The IOS area (localized as above) is indicated in green.

the vicinity of IOS appear to prefer certain categories of natural objects (e.g., faces, bodies, or objects). Because the BOLD response in the IOS is weaker for human actions than Creatures, we do not attribute neural activity in this region to perceived animacy. We conclude that neural activity in IOS reflects a general mechanism involved in the perception of novel and dynamic objects.

6. Conclusion

Studies of biological motion have argued for the existence of specialized perceptual and neural machinery supporting the perception of human actions. Few studies, however, have tested sensitivity to non-human biological motion, and thus it was unclear to what extent the mechanisms involved in human action perception could be co-opted for non-human, dynamic motion. These experiments assessed the specialization of this system by examining behavioral and neural responses to novel stimuli depicting complex, articulating and animate motion unlike typical biological motion stimuli.

We found that artificially evolved Creatures can effectively portray animate events, even when depicted only as point-lights. This is perhaps not surprising given that inanimate objects are often anthropomorphized in popular television and cinema, the effects of which are very compelling (e.g., Pixar's *Cars*). Our study demonstrates that the perceived animacy of Creatures is retained when the stimulus is reduced to the movements of the joints, and is independent of the surface qualities of the object.

Perceived animacy, however, was insufficient to optimally drive neural activity in the human STSp, the brain area most commonly associated with biological motion perception. This is in contrast to prior findings of STS activation during perception of complex, dynamic events that are perceived as animate. For example, the STS is strongly activated by simple shapes that are moved to imply a social interaction, such as chasing, or a parent–child relationship (Castelli, Happe, Frith, & Frith, 2000; Martin & Weisberg, 2003; Schultz, Friston, O'Doherty, Wolpert, & Frith, 2005). Notably, these studies depict animacy through interactive dynamics, not articulated kinematics. For example, Schultz et al. (2005) find that increases in the speed and correlated motion of two small dots has the effect of increasing perceived social animacy in the dot animations. In our experiments a novel, locomoting object is viewed in isolation. And although observers rated the Creatures as highly animate (indeed, the subset of Creatures used during the neuroimaging experiments was chosen because of high observer animacy ratings), these stimuli were still not as effective in driving STSp as viewing human actions.

An additional study has argued that neural activity on the STS reflects the perceived 'intentional' state of an actor, not the actual body kinematics portrayed (Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). This proposal follows earlier reports from the monkey literature that STS neurons may be jointly tuned to body kinematics and per-

ceived intentional states of the actor (Jellema, Baker, Wicker, & Perrett, 2000). Clearly, both the human and Creature animations depicted articulated body kinematics, and to the extent that locomotion can convey an intentional activity, they both depicted goal-directed activity. Thus, in this scenario, the reduced BOLD response in STSp reflects an interaction between perceived intentionality of the figure with the unfamiliar body structure of the Creatures. Again, these results are evidence for specialized neural processing for human kinematics in the STSp.

One final caveat in interpreting the role of STS in perceived animacy, goal-directed behaviors and body structure is the uncertainty in comparing regions of interest across studies: are these studies investigating the same brain area or adjacent regions in this large expanse of cortex? Our results demonstrate that perceived animacy alone is insufficient for the STSp, the brain region that is highly responsive during perception of human actions.

In addition to the supporting the perception of animacy, the human STS has also been identified as a component of the human mirror neuron system, the neural network believed to facilitate motor learning, action imitation and action understanding (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Neuroimaging studies investigating action understanding have identified the human premotor cortex, posterior parietal regions, and the human STS. However, neuroimaging studies investigating biological motion perception using point-light animations have rarely identified frontal regions (for an exception, see Saygin, Wilson, Hagler, Bates, & Sereno, 2004). This discrepancy remains largely unaddressed in the literature, and may be related to the visual sparseness of the point-light animations. Whatever the reason, we were unable to identify premotor or parietal action regions using our localizer stimuli. Although this remains to be tested explicitly, one would not expect the novel Creatures activate our mirror system, as these stimuli have sufficiently unusual and unfamiliar structure such that they are unlikely to be embodied.

Neural activity in the more ventral brain areas (ITS, pITG and FFA/FBA) was more clearly linked to the structure of the visual stimuli than to human or Creature categories of action. The ITS and pITG brain areas have been identified in studies investigating object perception, including biological motion perception. When the animations are viewed as fully-illuminated, the BOLD signals in these brain areas do not discriminate between our two categories of dynamic stimuli (humans and Creatures). This is evidence against ITS and pITG specialization for human action perception. However, BOLD responses in these two brain areas are reduced when Creatures are depicted by point-lights. We believe that this finding is best understood in the context of our behavioral results.

We measured noise tolerance for the point-light Creature animations, such as has been done for human point-light biological motion (Bertenthal & Pinto, 1994; Grossman, Battelli, & Pascual-Leone, 2005). Observers are extremely tolerant of masking noise on point-light human

animations (Hiris, Humphrey, et al., 2005). In contrast, observers' ability to identify point-light Creatures suffered as a result of adding only a few masking dots (subjects tolerated, on average, only seven noise dots, a fraction of the total number of dots that comprise the Creature itself). In this task, prior knowledge of body structure is an effective cue for eliminating noise dots as potential signal dots. Thus we take our results as evidence that observers were unable to use a priori knowledge about body structure to facilitate point-light Creature recognition, due to unfamiliarity with this stimulus class.

Because the kinematic information is identical between the fully-illuminated and point-light depictions, and in light of our behavioral findings evidencing poor noise tolerance, we interpret reduced neural activity in the ventral stream brain areas as evidence for impaired shape processing during point-light Creature perception. Note that the BOLD signals in the ITS and pITG are equivalent for fully-illuminated and point-light human action perception. Again, kinematics are identical between the two depictions, and evidence suggests that observers are very effective at estimating the underlying body structures in the point-light human displays (e.g., robust noise-tolerance thresholds and the ease with which actions in these animations are recognized). Thus it appears that implicit shape recognition effectively drives these brain areas.

Note, too, that body structure is much more informative for human point-light animations in which the same body configuration can be anticipated regardless of the action depicted. Prior assumptions regarding body structure will be less informative for the Creature trials as compared to the human trials. Each Creature trial depicts a different, randomly selected exemplar. Thus observers must build the body representation from the implied cues in the joint kinematics. Low noise tolerance for point-light Creatures indicates that the computational processes that extract novel body forms from the joint kinematics are relatively fragile. Our neuroimaging findings, therefore, may reflect the observer's strategy to rely less on form cues to complete the one-back task during the point-light Creature animations.

Observers' familiarity with the motion patterns of human actions may have contributed to improved noise tolerance for human point-light stimuli. Previous work has argued for the existence of motion templates (Cavanagh, Labianca, & Thornton, 2001; Davies & Hoffman, 2003), which would operate for highly familiar and predictable motions (such as human actions), but not Creature locomotion (although some fragments of human locomotion could be shared in the subset of Creatures with symmetric limbs). For example, Jastorff et al. (2006) demonstrate that observers can learn to discriminate novel, non-biological point-light animations as well as human point-light animations, provided the novel animations are governed by an underlying structure. Neural selectivity for these motion patterns is also enhanced as a function of training (Jastorff, Kourtzi, & Giese, 2005). Our results

also show that the ability to construct the underlying body structure is critical in the recognition of novel stimuli when viewed in point-light form. It is possible that neural selectivity would emerge after a substantial period of training on these novel Creatures, which would presumably be accompanied by enhanced awareness of the underlying body structure.

The perceptual benefits of visual routines and familiar body structures are also reflected in computational models of biological motion (e.g., Giese & Poggio, 2003; Hoffman & Flinchbaugh, 1982; Lange & Lappe, 2006). In one such model, biological motion perception is proposed to rely on the dynamic integration of key postures embedded within human actions, a process thought to be subserved by the superior temporal sulcus (Giese & Poggio, 2003). In these schemes, inferior temporal regions serve to extract 'snapshots' of body shapes from the animations, which are compared against stored representations of various body postures. Our findings demonstrate specialized neural activity for human actions on the STSp, but not in the ventral ITS and pITG. The ITS and pITG are likely candidates for neural areas performing more general shape computations, which may feed forward into STSp.

One of the most surprising findings from these investigations was the consistent Creature selectivity we found in the inferior occipital sulcus of our observers. There is no a priori reason to expect a cortical region dedicated to Creatures, a category for which observers have no prior familiarity. However, we were able to identify an IOS area in 9 of our 11 subjects by comparing BOLD responses for fully-illuminated Creatures to BOLD responses for human actions. Even more surprising, Creature selectivity persisted in the point-light condition—BOLD responses were stronger during perception of point-light Creatures as compared to point-light humans.

One possible explanation for our IOS finding is that this region is being driven by the diversity of unique body structures in the Creature condition. For example, the human actions all depict the same human form, while each Creature exemplar has a unique body structure. This is an interesting hypothesis because it would imply that diversity of body structure, but not kinematics (which varies across exemplars in both stimulus classes) is driving neural activity in this area. The implication would be that the IOS is invariant across articulation, but not across body structures. Further studies are required to determine if such a hypothesis explains our findings.

A second plausible explanation for our IOS finding is that although Creatures are novel in the sense that they do not exist in the natural world, these animations may appear similar to animals (albeit unusual ones), and the neural activation we observe is simply categorical selectivity for animals. Indeed, one study has identified a region of the LOC as more selective for stationary images of animals as compared to tools in the relative vicinity of the IOS (Chao, Martin, & Haxby, 1999). In preliminary studies we have found inconsistencies in the overlap between acti-

vation for images of animals and the dynamic Creatures (Pyles, Garcia, Hoffman, & Grossman, 2006), however a more direct comparison between dynamic animals and Creatures would be informative.

We argue, however, that because IOS is located in ventral and lateral temporal cortex, and in four of our observers overlaps with object-selective regions, our results are evidence for Creatures being processed in cortex usually recruited for objects. And because our subjects have no prior experience with the Creature stimulus set, we interpret our findings as evidence of flexible machinery that is engaged during dynamic, novel object perception.

Our study provides evidence that perception of articulated actions benefits from the regularities present in the human body structure. Shape recognition appears to be an important component in the recognition of biological motion, and is likely subserved by brain areas recruited for perception of non-biological objects (e.g., ITS and pITG). In contrast, perceived animacy can be strongly linked to body kinematics, whether natural and familiar (i.e., human actions) or unique and unfamiliar (i.e., Creatures). Perceived animacy alone, however, is not sufficient to engage the cortical network supporting perception of human actions. The specialization for human actions we observe in the STSp is in contrast to the flexible mechanism we identified in the IOS. Both appear to be engaged during dynamic and biological event perception, but clearly serve different functions. Further studies are required to investigate the differential networks that are engaged during social perception, both of human and non-human actions.

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