What Does "Biological Motion" really mean?
Differentiating visual percepts of human, animal, and non-biological motions

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For well over 30 years, vision researchers have commonly used the term "biological motion" to refer to point-light displays of human movement. This phrase comes from Gunnar Johansson's classic 1973 article in which he explicitly tested whether his vector analysis model of visual motion perception (e.g., Johansson, 1950; 1964) applied to the perception of animal motion, in general. The stimuli in this 1973 article were point-light displays of human motion. However, this choice of stimuli appears to have reflected convenience rather than theoretical necessity. Indeed, Johansson explicitly stated on several occasions that he was searching for a perceptual mechanism that analyzed all categories of visual motion in the same manner (e.g., Johansson, 1976).

Johansson (1973) noted that observers in his studies described their visual percepts of point-light displays of human movement as particularly vivid and he attributed this vividness to observers' extensive previous visual experience with human motion. Johansson did not interpret his data as suggesting the existence of differentiated visual processes dedicated to the perception of human action. In sum, Johansson (1973) used the term "biological motion" to refer to the movements of living animals: both human and non-human. However, vision researchers have used the term, more often than not, to refer to point-light displays of human motion. As a result, in many post-Johansson articles, it is not clear whether researchers believe that the results of their point-light studies are specific to the perception of human motion or generalize to the perception of any dynamic biological entity. Thus, the current meaning of the term "biological motion" is ambiguous in the vision sciences. Would it be best for us to use the term "biological motion" to refer to the motions of all animals, as the phrase suggests and Johansson's original work assumed? Using the phrase "biological motion" in this way would be appropriate if both human and animal motions were analyzed in the same way. On the other hand, if human observers analyze human and animal movements differently, then vision researchers would be better served by modifying their use of this phrase so that it describes either the perception of human motion or the perception of non-human animal motion. The goal of this chapter is to examine the degree to which visual analyses of point-light displays of human movement overlap with, or are differentiated from, the visual analyses of point-light displays of animal movement and non-biological movement.

Animals versus objects

Obviously, one clear implication of the phrase "biological motion" perception is that biological stimuli should be, or at least could be, perceived differently from non-biological stimuli. Early evidence from studies of the visual perception of static objects supports the hypothesis that percepts of biological and non-biological objects are neurologically dissociable. In one such study, Tippett, Glosser, and Farah (1996) asked neurological patients and healthy controls to view and name line drawings of animals and non-biological objects. Patients with left temporal lobe damage exhibited significant impairments in their recognition of non-biological objects relative to their recognition of animals. Conversely, neither healthy controls nor patients with right temporal lobe damage exhibited differential recognition of line drawn animal and objects. In a related study, Farah, Meyer, and McMullen (1996) documented patients who exhibited selective deficits in their visual recognition of drawings of animals relative to their recognition of drawings of non-living objects.

These and subsequent results (e.g., Fuggetta, Rizzo, Pobric, Lavidor & Walsh, 2008) suggest that distinct neural regions are involved in the recognition of living and non-living entities, at least in the static domain.

Evidence that the visual recognition of human forms may be further differentiated from the visual recognition of animal forms comes from a sorting task in which visual representations of the static human body, as a class, were found to differ from visual representations of both static object and static animal shapes (Reed, McGoldrick, Shackelford, & Fidopiastis, 2004). Differences in inversion effects, a signature of configural processing, also suggest that static human body postures are perceived somewhat differently from static dog body postures (Reed, Stone, & McGoldrick, 2006). However, in a finding that foreshadows subsequent data and discussions, inversion effects also suggest that observers may be tapping their representations of possible human body postures during their percepts of dog body postures (Reed et al., 2006). Thus, Cathy Reed's research provides important evidence that the visual analyses underlying the perception of humans and non-human animals may differ by degree rather than kind, at least in the static domain. This question of qualitative versus quantitative differences in perception is raised again later in this chapter.

Cutting (1982) performed the first study of the perception of complex, point-light defined objects and found that observers could discriminate different types of wind blown foliage in these displays. Subsequent work demonstrated that aerodynamic and hydrodynamic events, including rolling balls, free-falling springs and splashing water, could be recognized from point-light displays (Bingham, Schmidt, & Rosenblum, 1995). Clearly observers can recognize physical events and non-living objects in point-light displays. Such findings are consistent with Johansson's (1973) hypothesis that the same motion perception processes underlie the perception of bouncing balls, falling leaves, walking cats, and swimming fish. However, the ability to recognize point-light objects does not directly address the question of whether percepts of biological and non-biological motions depend upon the same perceptual processes or reflect the same levels of sensitivity.

Many of us have conducted studies of visual sensitivity and/or neural responsiveness that compared coherent, canonically oriented point-light displays of human motion to scrambled and/or inverted point-light displays of human motion. Such studies have shown that inversion decreases visual sensitivity to human motion (e.g., Sumi, 1984; Bertenthal & Pinto, 1994; Pavlova & Sokolov, 2000) and decreases neural activity in those areas associated with the perception of coherent, canonically oriented human motion (e.g., Grossman & Blake, 2001). Often the results of such experimental comparisons are taken as evidence that the behavioral and neural responses to coherent, upright displays of human motion tell us something about the perception of human motion, in specific. Scrambled point-light displays of human motion clearly constitute informative control stimuli because they contain the same local motion information as coherent point-light displays. Inverted point-light displays of coherent human motion are also useful control stimuli because the same local and global motion information is available in upright and inverted displays. And yet, we tend to forget that scrambled and inverted depictions of human motion do not fully capture, or control for, other important characteristics of human motion. For example, inverted displays depict physically impossible motions and are perceived as at least partially, if not fully, incoherent. Furthermore, scrambled displays are not simply incoherent and physically impossible. They are also meaningless. Thus, interpreting data from comparisons of point-light displays of upright, meaningful, and physically possible motion with point-light displays of inverted, meaningless, and physically impossible motion is anything but clear cut. As a result, at least some of the results of our past studies may tell us more about the perception of coherent motion or the perception of meaningful motion than they tell us about the perception of human motion, in specific.

Human motion versus object motion

Some researchers have directly compared visual analyses of human motion with visual analyses of meaningful object motion. The human body typically has many more degrees of freedom than objects and as a result, can produce relatively more complex patterns of motion. Thus, interpretations of studies comparing human motion and object motion are not without their own ambiguities. On the other hand, both human motions and object motions are meaningful, coherent, and physically possible. Comparisons of visual percepts across the categories of human motion and object motion suggest that, under some conditions, different processes may underlie the analyses of these stimuli. For example, over twenty years ago, Jennifer Freyd and Maggie Shiffrar measured perceived paths of apparent motion during the perception of photographs of people and objects briefly presented in a tachistoscope. Apparent motion percepts differed across human and object motion as a function of the temporal rates at which the photos were presented. When inter-stimulus intervals were short (i.e., photographs were presented in rapid alternation), observers consistently reported seeing the shortest possible paths of apparent motion for both people and objects, regardless of whether such paths were physically possible. However, when inter-stimulus intervals were extended, observers tended to report the perception of paths of apparent human motion that were consistent with the biomechanical limitations of the human body (Shiffrar & Freyd, 1990, 1993). These biomechanically plausible paths were reported even when they were not the shortest possible paths of motion. When objects were presented at the same long inter-stimulus intervals, observers still reported seeing the shortest possible paths of apparent motion. Such divergence of apparent motion perceptions suggests that something differentiates visual analyses of human motion and object motion.

Further evidence of divergent processing was found in studies of the visual analysis of line drawn objects and people moving behind apertures. While observers described their visual percepts of objects moving behind apertures as non-rigid and incoherent, line drawn depictions of upright human gait were described as coherent (Shiffrar, Lichtey & Heptulla-Chatterjee, 1997). When depictions of upright human gait were presented faster or slower than people can actually walk, then observers reported the perception of incoherent motion (Shiffrar et al., 1997). Taken together, these behavioral data suggest that the integration of motion signals across space occurs differently for human motion and object motion. Further behavioral evidence comes from a now classic task in which observers moved their limbs while judging whether two images of a person or two images of a cluster of blocks were the same or different (Reed & Farah, 1995). While the observer's own bodily motions impacted that observer's immediate perceptual memories for another person's bodily postures, observer movement did not impact memories for complex objects such as clusters of blocks (Reed & Farah, 1995). These results suggested that motor processes might help to differentiate visual analyses of human limb positions and object part locations. Patterns of movement acceleration may be especially important in differentiating human from object motion, or more generally, the movements of living things from the movements of non-living things (Chang & Troje, 2009; Troje & Westhoff, 2006; see also Troje this volume).

Several brain imaging studies have also directly compared visual analyses of meaningful human and object motions. For example, activity in the posterior region of the superior temporal sulcus, or STSp, is strongly associated with the visual analysis of human movement (see chapters in the neurophysiology section of this volume). Differences in STSp activity, as measured by fMRI, indicate that this region is sensitive to the distinction between human and object motion (see chapter by Pelphrey, this volume). Indeed, STSp responds more strongly to point-light displays of human movement than to point light displays of moving objects (Beauchamp et al., 2003). As typical children mature, STSp activity becomes increasingly tuned to human movement (e.g., Carter & Pelphrey, 2006; Pelphrey, this volume). In adult observers, MEG activity indicates that analyses of point-light displays of human movement and object movement diverge approximately 200 msec after stimulus onset when processes in the right temporal lobe, encompassing the STSp, are triggered during the perception of human movement but not during the perception of object movement (Virji-Babul, Cheung, Weeks, Kerns, & Shiffrar, 2007).

In addition to differences in STSp activation during the perception of human motion and object motion, motor processes also play a significant role in differentiating percepts of human motion and object motion. For example, the so-called action perception system, which includes the premotor cortex, appears to link action production with action perception (see chapters by Calvo-Merino and Saygin in this volume). This system responds during the visual perception of actions but not objects (see Rizzolatti, Fabbri-Destro, & Cattaneo, 2009 for review). Neural activity in the primary motor cortex and cerebellum also increases during the perception of possible human motion but not during the perception of object motion (Stevens et al., 2000).

Human motion versus animal motion

Taken together, the results summarized above are consistent with the hypothesis that the motions of biological and non-biological entities are analyzed differently by the human visual system. Of course, human motion constitutes just one type of biological motion. How does the human visual system analyze the movements of non-human animals? Are human and non-human subcategories of biological motion processed in the same way (see Troje chapter in this volume) or is their processing differentiated? If the movements of non-human animals and human animals are processed differently, then vision scientists should carefully consider whether, or when, the term "biological motion perception" should be used to refer to both.

Psychophysical Evidence

Mather and West (1993) conducted the first study investigating whether observers could accurately recognize different types of moving animals in point-light displays. They did so in a particularly elegant manner; that is, by animating Eadweard Muybridge's engaging stop-action photographs of animals and humans (Muybridge, 1979) and converting those animations into point-light displays. The stimuli included side views of walking bipeds (specifically, a man, ostrich and kangaroo) and quadrupeds (a baboon, camel, cat, dog, elephant, elk, goat, horse, lion, ox and pig). Recognition performance was compared across two conditions: static and dynamic. In the static condition, observers were able to identify, at levels significantly above chance, all three bipeds as well as some of the quadrupeds (the camel, cat and horse) from a single image. Once the point-light stimuli were set in motion, observers correctly identified 12 of the 14 animals. Because animal identification was significantly better in the dynamic condition than in the static condition, Mather and West (1993) concluded that the ability to interpret "biological-motion displays" generalized to non-human animal motion thus was not specific to human motion. Subsequent work indicates that the visual recognition of animals from point-light displays is as accurate as the recognition of animals from bodily shapes defined by luminance contrast (Bellefeuille & Faubert, 1998). Observers can also determine the size of a point-light defined dog from the frequency of the dog's gait (Jokisch & Troje, 2003). Interestingly, domestic cats (Blake, 1993), pigeons (Dittrich et al., 1998), and recently hatched chicks (Regolin et al., 2000) also demonstrate visual sensitivity to experimental manipulations of point-light animals.

A few studies have directly compared visual sensitivity to human and non-human animal motions. For example, in her doctoral dissertation, Leslie Cohen (2002) found that observers were better able to detect the presence of coherent human motion than the presence of coherent seal motion or dog motion in masked point-light displays. Importantly, Cohen (2002) controlled for visual experience by running three different groups of observers: seal trainers, dog trainers, and Temple University undergraduates. While the seal and dog trainers had many years of daily or near daily visual exposure to seal motions or dog motions, respectively, these special observers showed the same patterns of visual sensitivity as typical observers. Across all three categories of observers, the greatest visual sensitivity was found for human motion and the lowest visual sensitivity was found with seal motion. Cohen's evidence supports the idea that visual analyses of human and animal motions may differ in graded fashion and that differences in visual sensitivity to the movements of people and animals may not be readily attributed to differences in visual experience. She further proposed that visual sensitivity to point-light displays of animal motion might reflect the degree of physical similarity between observed actions and the observer's own repertoire of performable actions. Certainly, it is much easier for humans to imitate dog gaits than the undulating whole-body flops of seal locomotion on land.

Additional psychophysical support for graded differences across analyses of human and animal motions comes from comparisons of the impacts of stimulus inversion and masking on visual sensitivity to the presence of coherent human gaits and coherent horse gaits. Patterns of coherent motion detection in this study suggested that while observers were more sensitive to human motion than to horse motion, the processes underlying the perception of these motion were both orientation dependent and spatio-temporally global (Pinto & Shiffrar, 2009). These results further support the hypothesis that the analyses underlying percepts of human motion and non-human, animal motions in point-light displays might differ in a graded rather than dichotomous fashion.

Neurophysiological Evidence

Pyles, Grossman and their colleagues (2007; see also chapter by Pyles & Grossman, this volume) conducted combined psychophysical and fMRI studies comparing the visual analysis of point-light human motion and point-light animal-like, creature motion. When asked to detect the presence of coherent motion within point-light masks of variable point densities, observers could tolerate substantially more mask noise during the detection of human motion than during the detection of animal-like creature motion. While the STSp was responsive during the perception of creature motion, significantly greater STSp activity was found during the perception of human motion than creature motion (Pyles et al., 2007). Importantly, patterns of STSp activity were positively correlated with psychophysical measures of visual sensitivity to human and creature motions (Pyles et al., 2007).

Percepts of animal and human motion may also be differentiated by motor system activity. For example, EEG data indicate that the visual perception of human movement engages components of the mirror neuron system while the perception of animal motion does not (Martineau & Cochin, 2003). Other neurophysiological work suggests that the role of motor processes may differ in more subtle ways during the visual perception of human and animal motions. For example, Giovanni Buccino and his colleagues (2004) recorded fMRI signals as human observers viewed human, dog and monkey actions that fall either within (e.g., biting) or outside (barking) the motor repertoire of human observers. Overall, both overlapping and divergent patterns of neural activity were found during the observation of simple human, dog, and monkey actions. For example, observation of the biting actions of a dog and of a human both produced similar patterns of neural activity in the rostral inferior parietal lobule. Yet, more motor system activity was found when observers viewed a dog performing an action that humans commonly perform (biting) than when observers viewed a dog performing an action that humans rarely, if ever, perform; namely, barking (Buccino et al., 2004). Consistent with these findings, PET data indicate that there is significant overlap in the neural areas responsive to point-light human locomotion and point-light horse and dog locomotion (Ptito, Faubert, Gjedde, & Kupers, 2003). Taken together, these results suggest that analyses of animal motions approximate analyses of human motion as a function of the degree to which observers are able to perform the observed actions.

Development and Experience

Infant research suggests that visual sensitivity to human motion and animal motion may initially depend upon very similar, if not identical, mechanisms that diverge during the course of early development (see chapter by Frankenhuis et al., this volume). For example, when infants viewed point-light displays of human and animal motions, their ability to differentiate phase perturbed from canonically timed displays changed over the course of their development (Pinto, 2006). At two days of age, human infants differentially orient to upright, as compared to inverted, point-light displays of chicken motion (Simion, Regolin & Bulf, 2008). Three months later, infants demonstrate equally sensitivity to phase differences in point-light human and animal motion (Pinto, 2006). That is, at least until the age of three months, infants respond similarly to the temporal parameters of human and animal motions. However, just 2 months later, five month old infants only respond to phase differences in upright human motion. This pattern of results suggests that some mechanism in the infant visual system becomes specialized or tuned for the detection of canonical human motion (Pinto, 2006). Neurophysiological evidence from the lab of Kevin Pelphrey suggests that this perceptual tuning may be associated with the tuning of the pSTS to human movement during early childhood development (see Carter & Pelphrey, 2006; Pelphrey, this volume).

Research and computational modeling indicate that some aspects of human visual sensitivity to point-light displays of human movement depend upon visual experience (Bulthoff, Bulthoff, & Sinha, 1998; Giese & Poggio, 2003). While visual experience likely is a significant contributor in defining visual sensitivity to human movement, psychophysical studies with adult observers suggest that its impact is relatively small (e.g., Jacobs, Pinto, & Shiffrar, 2004; Loula et al., 2005; Prasad & Shiffrar, 2009). Instead, it appears that perception-action coupling, or interactions between an observer's visual and motor systems, has a greater impact in shaping visual sensitivity to human motion (e.g., Wilson & Knoblich, 2005; van der Wel et al., this volume). For example, hemiplegic observers who have lost the ability to move one of their arms differ from typical observers in their visual sensitivity to point-light displays of human arm movements. This finding is relevant to the issue of visual experience because adults with late onset hemiplegia differ from typical adults in their current action execution abilities and not in their visual experience of other people's actions. More specifically, observers with hemiplegia show decrements in visual sensitivity to self-generated arm movements that appear to correspond to their compromised arm relative to movements that appear to correspond to their unaffected arm (Serino et al., 2010). Thus, hemiplegic observers demonstrate greater visual sensitivity to arm gestures that they can execute than to arm gestures that they cannot execute. Not surprisingly, typical observers show no asymmetry in their visual sensitivities to left and right arm movements. Importantly, observers with hemiplegia of either their left or right arm do not differ from one another in their identification of moving animals depicted in point-light displays (Serino et al., 2010). Such control data suggest that hemiplegia does not appear to cause generic decrements in visual sensitivity to point-light displays of human and animal motions. Additional evidence that differences in visual sensitivity to point-light displays of human action reflect motor experience, *per se*, comes from a psychophysical study in which participants learned to perform a particular gait while blindfolded and then showed increments in visual sensitivity to that felt but unseen gait but showed no changes in visual sensitivity to another gait type that they had not performed (Casile & Giese, 2006). These and other data (Calvo-Merino et al., 2006; Cohen, 2002) suggest that motor experience can dominate visual experience in defining visual sensitivity to point-light displays of human and animal motions.

If we consider, for example, the grossly similar bodily structures of macaques and humans, it is easy to imagine that motor experiences and processes in one species could contribute to the perceptual interpretation of actions produced by the other species. Consistent with this, some neurons in the macaque's action perception system fire during the observation of human action (Rizzolatti, Fadiga, Fogassi, & Gallese, 2002). Indeed, neurons with mirroring properties were initially identified in macaques watching human grasping actions (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Similarly, neural responsiveness in single cells of the STSp during the observation of human movement was also first documented in macaques as they viewed the whole body actions of people (Perrett, Smith, Mistlin, Chitty, Head, Potter, Broennimann, Milner, & Jeeves, 1985). Conversely, human observers show similar patterns of neural activity in the action perception system during the observation of a person and of a monkey performing similar actions (Buccino et al., 2004).

The above review summarizes several studies that have investigated how and how well macaques and humans perceive the actions of themselves and other animals. The results of these studies seem to suggest that the visual perception of human and non-human animal motions differ from one another in a graded fashion rather than a dichotomous one.

Is "Biological Motion" a perceptual category?

Taken together, the results summarized above suggest that the visual percepts of human motion and object motion typically differ from one another dichotomously while the percepts of human motion and non-human, animal motion vary smoothly along some continuum. That continuum appears to be graded in a manner that reflects the degree of similarity between an observed event and the observer's ability to produce that event with his or her own body (e.g., Wilson, 2001; Cohen, 2002). Such results are consistent with the existence of a perceptual category that might be called "biological motion" that includes at least people and animals but not human made objects. Within this proposed category of "biological motion", human movement appears to constitute the best or prototypical stimulus that yields the greatest neural activity within the action perception system as well as relatively elevated perceptual sensitivity. This descriptive model of a potential "biological motion" category makes several predictions. First, the human body, and its motion, should have a special status, if not rein supreme, in human visual perception (e.g., Wilson, 2001; Viviani, 2002; Shiffrar, 2010). One test of this prediction would be to examine whether human observers consistently demonstrate greater levels of visual sensitivity to performable human actions than to motions of either animal or objects.

A second prediction from the above model concerns the relative levels of visual sensitivity to biological and non-biological motions. Previous studies have compared perceptual sensitivity and/or neural activity during the observation of human movement and animal movement and during the observation of human movement and object movement. However, none of the studies noted above compared all three types of motion simultaneously (see chapter by Kaiser & Shiffrar, this volume, for a recent exception). If biological motion and non-biological motion truly reflect different perceptual categories and if performable human actions constitute a prototype within the category of biological motion and if the perception of biological motions is selectively enhanced by STSp and motor processes, then observers should show greater visual sensitivity to human movement than to animal movement and they should show greater sensitivity to human and animal motions than to object motion.

To begin examining these predictions, we conducted a pair of simple perception studies in which naïve participants viewed and categorized point-light videos of people, animals and objects in motion. Most, but not all, previous studies of visual sensitivity to point-light displays of human motion have used stimuli depicting simple actions (see Blake & Shiffrar, 2007 for review). Human gait is by far the most common stimulus used in studies of "biological motion" perception. But what happens when observers view more challenging human actions? Not impossible actions, but actions that are relatively difficult to perform? Is visual sensitivity to human motion uniform across all types of performable human actions? Or, does it vary with the effort needed to perform an action? Previous work by Winand Dittrich (1993) indicates that observers demonstrate more visual sensitivity to human locomotor actions than to social or instrumental (e.g., stirring the contents of a bowl) actions. This result suggests that visual sensitivity varies across even easy to perform human actions. In the following studies, visual sensitivity was measured as a function of action difficulty with experimental stimuli including point-light displays of easy and challenging human actions.

Another issue examined in the studies below was the relative levels of visual sensitivity of human observers to the movements of non-human bipeds. Most studies of the visual perception of animal motion have employed stimuli depicting the gaits of animals with four limbs (e.g., Buccino et al., 2004; Jokisch & Troje, 2003; Kaiser & Shiffrar, this volume; Mather & West, 1993; Martineau & Cochin, 2003; Ptito, Faubert, Gjedde, & Kupers, 2003; Pinto & Shiffrar, 2009). A few studies have included the actions of bipedal animals; including a chicken (Simion, Regolin & Bulf, 2008), ostrich and kangaroo (Mather & West, 1993). Obviously, human locomotion is predominantly bipedal. How does visual sensitivity to human motion compare to visual sensitivity to bipedal, and thus more human-like, animal motion? As Niko Troje's chapter in this volume makes clear, the trajectories of feet during gait are highly informative. With this question in mind, we also wondered how well observers could detect the presence of moving animals lacking feet. To that end, our stimulus set included apedal animal motions.

Lastly, to create a larger context for understanding relative levels of visual sensitivity to human and animal motions, the stimulus set also included point-light displays of mechanical actions. Past research had not directly compared percepts of human, animal, and object motions within the same study (see Kaiser & Shiffrar chapter in this volume for an exception). Such a comparison is needed to examine whether observers demonstrate equal or different levels of visual sensitivity to "biological" (i.e., people and animals) and "non-biological" (i.e., object) motions.

A simple study

We asked fifty undergraduate students from Rutgers-Newark to participate in our initial experiment for class credit. None had previously seen or studied point-light displays. All had normal or corrected to normal visual acuity and provided written informed consent.

The stimuli consisted of 22 point-light displays of human, animal, and mechanical movements. These displays included five easy human actions, five challenging human actions, seven animal actions, and five mechanical actions. The five easy human actions were walking, picking up a light object, picking up a moderately heavy object, crawling, and a performing a "high-five." The five challenging human actions were performed by a yoga instructor and consisted of the movements into and out of the following yoga poses: plow, warrior-3, freehand head bridge, downward dog, and half fish. Because previous studies have thoroughly investigated the perception of point-light defined quadruped animals (e.g., Mather & West, 1993), only bipedal and apedal animals were depicted in the current study. The bipedal animals included an ostrich, a flamingo, a swimming penguin, and a walking penguin. The apedal animals included 2 fish and a corn snake. These animals were digitally videotaped in their habitats at Camden Aquarium and Six Flags Wild Safari in New Jersey. Finally, a selection of jointed mechanical objects was used to create point-light displays of mechanical actions. The mechanical objects included a car, tractor, toy crane, toy car, and jack-in-the-box each undergoing its most typical action.

To create the point-light displays, reflective markers (either tape or cream) were attached to the major joints and/or moving parts of each stimulus. For all of the human stimuli except one, a reflective point was placed on each major joint and the head of the actor, following the classic procedure (Johansson, 1973). The exception was the human walker movie in which only two points were shown, one on each foot. The motion of the feet is particularly salient feature in gait detection and can be sufficient for the detection of human motion (Troje & Westhoff, 2006). For the mechanical stimuli, three point-lights were placed on each moving object part and one point-light was placed on each joint. This ensured that each mechanical object contained the same number of point-lights as a matched animal stimulus. To create the animal motion stimuli, round patches of reflective cream were applied to the animals by their trainers. As with the human stimuli, markers depicted each joint and the head of each bipedal animal. Since apedal animals have a very large number of joints along a single axis, the apedal stimuli depicted several points along this major axis as well as points on each side of this axis and on the animal's head. We biased the number of markers per body area so that the animal and object stimuli contained many more markers per unit of body surface area than the human stimuli.

Using a Canon Optura digital camera, each action was filmed for two seconds. Each resultant movie clip was then exported onto an iMac computer and filtered using iMovie software so that only the markers remained visible in the resultant displays. Each of the two-second movie clips was looped five times to create a 10-second movie for each stimulus. During testing, these 10-second movies were displayed sequentially in random order.

Observers were tested in groups of five to fifteen. In each group, participants were positioned so that each person could clearly see the display monitor. After obtaining participants' consent but before the stimuli were shown, each participant was given a response sheet. The sheet contained a vertical column of stimulus numbers (1 – 22) and to the right of each number was a row of four words: human, animal, mechanical, and other. At the end of each of the 22 movies, a blank screen was displayed until all of the participants made their perceptual judgment about that movie. Participants were instructed to circle the word, from the four possible responses, that best described the event they had just seen. Following this, the next point-light movie was shown. Two experimenters remained in the room during testing to control stimulus presentation and to ensure that participants did not discuss their percepts or responses.

At the conclusion of this categorization task, observers completed a questionnaire regarding their physical activity. Because past research indicates that athletes, relative to non-athletes, demonstrate enhanced levels of visual sensitivity to the effortful gaits of point-light walkers (Jacobs & Shiffrar, 2004), participants in the current study were asked to indicate the duration, frequency, and type of their athletic activity.

Results

Percent correct categorization was analyzed using a repeated-measures analysis of variance. Since this was a 4-alternative forced choice classification task, chance performance was 25% correct. Stimulus category (easy human action, difficult human action, bipedal animal, apedal animal, and mechanical object) served as a within-subjects variable. The ANOVA revealed a significant main effect of category, $F(4,49) = 38.50$, $p < .0001$. As illustrated in Figure 1, observers were most accurate in their classification of the easy human actions ($M = 80.5\%$ correct) and least accurate in their categorization of apedal animal movements ($M = 10.3\%$ correct). As an aside, recall that the easy human action stimuli contained only one gait and that gait was depicted with only two point-lights, one on each foot. This likely explains why categorization performance with the simple human actions used in this study was below ceiling levels of recognition typically found during the observation of long duration displays of point-light walkers. Furthermore, below ceiling categorization performance with simple human actions other than walking is consistent with Dittrich's (1993) finding that observers are most sensitivity to human gait.

Classification accuracies for bipedal animal actions (M = 41.5%), challenging human actions (M = 37.7%), and mechanical object movements (M = 45.7%) were intermediate (Figure 1), and did not significantly differ from one another (all ps > 0.05). One sample t-tests revealed that the point-light displays of easy human actions [t(49) = 10.74, p < .001], difficult human actions [t(49) = 2.98, p < .001], bipedal animal actions [t(49) = 5.35, p < .001], and mechanical object movements [t(49) = 4.92, p < .001] were categorized at levels significantly above chance performance. Categorization performance with the apedal animal actions was significantly lower than chance, [t(49) = -5.22, p < .001]. Categorization accuracy with the easy human actions was significantly higher than accuracy with any other category of stimuli (all *p*s < 0.01).

To examine the categorization trends within each stimulus class, a repeated-measures ANOVA was conducted to compare the percentage of trials in which observers categorized each stimulus as human, animal, mechanical, and other. This analysis revealed a significant interaction between categorization response and stimulus class, F(12,147) = 42.04, p < .0001. To examine the basis of this interaction, responses to each stimulus class were considered individually. As depicted in Figure 2, on most trials, observers correctly classified easy human actions as "human" (M = 80.5%). On the other hand, although difficult human actions (yoga moves) were rarely mistaken for animals (M = 16.3%) or unidentified (M = 9.0%), they were mistaken for mechanical objects (M = 37.0%) as often as they were correctly classified as human (M = 37.7%). Although bipedal animals were rarely categorized as mechanical (M = 10.0%), bipedal animals were misclassified as human (M = 38%) as often as they were correctly categorized as animal (41.5%). Apedal animal movements were rarely classified correctly (M = 10.3%), and were most likely to be judged to be "other". Relative to this, observers demonstrated superior and relatively unbiased categorization accuracy with the mechanical stimuli (M = 47.5%).

Motor ability and action perception

To examine the role of observers' motor ability on stimulus perception, categorization performances by athletic and non-athletic participants were compared. Prior research suggests that observers' physical fitness levels impact their visual sensitivity to effortful human actions (Jacobs & Shiffrar, 2004). To that end, the results of participants whose responses fell at either end of our athletic training questionnaire were separated for further analysis. Half of these (nine participants) reported having over ten years of continuous as well as current athletic training. Their areas of athletic expertise included swimming, weight lifting, and running. The other half of the participants (again nine) reported having no significant athletic training. None of the participants in either group had more than two months of introductory yoga experience. A repeated-measures ANOVA was used to determine whether these athletic and non-athletic participants differed in their categorizations of the challenging yoga moves. The results of this analysis indicated a significant main effect of observers' physical fitness level on the categorization of difficult human actions F(1,16) = 4.89, p < .05. Athletic observers (M = 50.0%) were more likely than non-athletic observers (M = 18.5%) to correctly categorize the difficult human actions as human. Conversely, ANOVAs showed no main effect of observer fitness on the categorization of any other stimulus class, considered individually. Specifically, athletic and non-athletic participants did not significantly differ (all *p*s > 0.30) in their percentage of correctly categorized point-light displays of easy human actions [$M_{athletes}$ = 80.6%, M_{non} = 94.4%], apedal animals [$M_{athletes}$ = 7.4%, M_{non} = 11.1%], bipedal animals [$M_{athletes}$ = 36.1%, M_{non} = 47.2%], or mechanical objects [$M_{athletes}$ = 42.6%, M_{non} = 55.6%].

To ensure that performance differences between stimulus categories could not be simply explained by subtle differences in the number or distribution of reflective markers, a separate analysis was conducted on the walking human and a swimming fish stimulus. While the walking human stimulus was depicted with only two points, participants were much more likely to correctly classify it as human (M = 78%) than they were to correctly classify the swimming fish, with nine points, as animal (M = 10%), t(49) = 8.19, p < .0001. Thus, the number of distribution of point-lights cannot account for the current results.

The results of this preliminary study suggest that the human visual system is not uniformly sensitive to all human movements. Instead, the results are consistent with the hypothesis that an observer's ability to perform an observed action plays a defining role in that observer's visual sensitivity to the observed action (e.g., Funk, Shiffrar, & Brugger, 2004; Knoblich & Flach, 2001; Prinz, 1997; Shiffrar & Pinto, 2002; Viviani, 2002; Wilson, 2001). When an observed human action is difficult to perform (e.g., yoga), visual sensitivity to that action is relatively poor, especially for individuals with low levels of athleticism. Thus, the human visual system does not demonstrate the same level of sensitivity to all human motions (Dittrich, 1993). One possibility that our lab is investigating is whether observers demonstrate the greatest levels of visual sensitivity to point-light displays of human actions that are largely symmetric about the vertical or gravitational axis. If so, this might explain why observers are most sensitivity to point-light walking.

The results of this study also suggest the existence of marked differences in visual sensitivity to bipedal and apedal animal motions. While observers demonstrated the greatest visual sensitivity to easy human actions, their judgments of bipedal animal motions were substantially more accurate than their judgments of apedal animal motions. Poor categorization performance with apedal animal motions supports the importance of feet trajectories in the visual perception of point-light displays of animals (see Troje chapter this volume). Categorizations of bipedal animal motions were biased in a particularly interesting way. Observers were equally likely to categorize the locomotor actions of bipedal animals (penguins, an ostrich, and a flamingo) as animal (41.5%) or human (38%).

This above combination of results suggests several things. First, these data support the hypothesis initially put forth by Leslie Cohen (2002) that visual sensitivity to point-light displays of human and animal motion is defined by the degree of physical similarity between observed animals and their human observer. Within this theoretical framework, it makes sense that bipedal human observers would show greater visual sensitivity to bipedal animal motion than to apedal animal motion. While humans are capable of slithering on the ground like a snake and swimming like an apedal fish, anyone who has tried to learn the swimming stroke known as the butterfly can attest to the fact that trying to move ones' legs and torso together in a coordinated apedal fashion is very difficult. Second, the finding that observers frequently categorized bipedal animal motion as human motion provides support for the hypothesis that observers essentially "project" their own motor capabilities onto seen motor events (Viviani, 2002; Viviani & Stucchi, 1992). Indeed, this finding mirrors earlier research by Cathy Reed and her colleagues (2006) in which observers attempted to discriminate pairs of static body postures depicting people or dogs in upright or inverted orientations. The results of that work suggested that the visual perception of dog postures depends upon at least some of the same motoric representations that observers typically used during their visual percepts of human postures.

Finally, the results of this simple experiment suggest that visual analyses of human movement cannot be understood as uniformly superior to or more sensitive than visual analyses of complex animal or object movement. Indeed, observers were more accurate in their classifications of the movements of mechanical objects than they were in their classifications of moderately challenging yoga moves. It is also difficult to understand how the current results could be used to support the hypothesis that "biological motions" as a class are analyzed by a dedicated motion process that yields enhanced visual sensitivity to the movements of people and animals. While the locomotor actions of apedal fish and snakes most certainly fall within the category of "biological motion," observers were largely unable to classify these actions as animal, or even as biological (animal or human). Indeed, observers were much more accurate in their categorizations of mechanical objects than of apedal animals.

Taken together, categorization judgments in this simple experiment suggest that biological motions cannot be understood as a separate, homogeneous, or bounded perceptual category. Indeed, categorization data from the bipedal and apedal animal motions suggest that not even the motions of all large body animals fall readily into one uniform perceptual category.

A modified replication

In the study described above, observers were run in groups. This raises the possibility that the presence of other people might have influenced observers' judgments somehow. Furthermore, the stimuli in the previous study were always shown in the same random order. To address these two methodological weaknesses, a slightly modified replication of the previous experiment was run. This time, the order of movie presentation was randomized anew for each observer and observers were run individually. The movies in this study were identical to those used in the previous study.

A PsyScope program running on a Mac4 computer controlled stimulus presentation and recorded the responses of another 50 naïve observers. Each observer was positioned at 57cm from the display monitor. After obtaining observers' consent, the same percept categorization task was briefly explained and the experiment started. No practice trials were given. Each participant watched each of the 22 movies in random order. Immediately after each 10 second movie ended, a display appeared to prompt the observer to press one of four marked keys on a keyboard to indicate whether the motion was "human", "animal", "mechanical", or "other". Following each response, the next movie appeared after a 500msec delay. As before, at the conclusion of this categorization task, observers completed a questionnaire regarding their physical activity.

Percent correct categorization was again analyzed with a repeated measures ANOVA. Stimulus category (easy human motion, difficult human motion, bipedal animal motion, apedal animal motion, and mechanical motion) served as a within subjects variable. The ANOVA revealed a significant main effect of category, $F(4,49) = 57.10$, $p < .0001$. As in the previous experiment, observers were most accurate in their classification of the typical human actions ($M = 70.4\%$) and least accurate in their categorization of apedal animal movements ($M = 10.7\%$). As before, classification accuracies for bipedal animal actions ($M = 46.5\%$) and mechanical object movements ($M = 49.3\%$) did not significantly differ from one another. Unlike the previous experiment, categorization accuracy with difficult human actions was significantly less ($M = 26.3\%$) than accuracy with bipedal animals ($M = 46.5\%$) and mechanical objects ($M = 49.3\%$) (both ps <0.01). One sample t-tests revealed that the point light displays of easy human actions [$t(49) = 15.51$, $p < .001$], difficult human actions [$t(49) = .424$, $p < .001$], bipedal animal actions [$t(49) = 6.01$, $p < .001$], and mechanical object movements [$t(49) = 7{,}41$, $p < .001$] were categorized at levels significantly above chance performance (25% in this 4AFC task). Categorization performance with the apedal animal actions was significantly lower than chance, $t(49) = -4.08$, $p < .001$. Categorization accuracy with the easy human actions was significantly higher than accuracy with any other category of stimuli (all ps < 0.01).

Examining the types of errors that observers made in this simple experiment (Figure 3) again proved interesting. On most trials observers correctly classified easy human actions as "human" ($M = 70.4\%$). Difficult human actions, however, were mistaken for mechanical objects ($M = 41\%$) more often than they were correctly categorized as human ($M = 26\%$). Although bipedal animals were most commonly and correctly categorized as animal (47.5%), apedal animal movements were incorrectly categorized the vast majority of the time ($M = 10\%$). In this light, observers demonstrated superior and unbiased categorization accuracy with the mechanical objects ($M = 49.3\%$).

Unfortunately, the sample size of athletic observers was so small that there was insufficient statistical power to investigate the impact of physical ability on the categorization of difficult human movements in this study. Nonetheless, the results of this study largely replicate those of the earlier study. Observers readily identified easy human movements, although at levels of accuracy significantly below ceiling. Difficult human movements, however, were more likely to be identified as mechanical than as human. Furthermore, observers were significantly more accurate in their categorizations of the movements of bipedal animals than the movements of apedal animals. And again, observers were better able to categorize the movements of mechanical objects than the movements of apedal animals or even difficult human movements.

These results provide additional support for the conclusions drawn from the previous study. Furthermore, the current results raise the distinct possibility that vision researchers have significantly and repeatedly overestimated visual sensitivity to human movement by restricting ourselves, by and large, to the study of point-light walkers (Emily Grossman's lab provides a wonderful counterexample). The current results, along with past results (Dittrich, 1993) indicate that human observers demonstrate greater visual sensitivity to human gaits than to other categories of human motion. Enhanced visual sensitivity to the walking motions of other people likely reflects the extensive visual and motor experience that humans have with walking motion. It may also reflect the extensive vertical symmetry associated with upright gait. In any case, it seems increasingly clear that if researchers had adopted point-light depictions of other types of human movement, lower levels of visual sensitivity would have resulted.

In Conclusion

The results of the simple categorization studies described above are subject to important interpretative caveats. Indeed, anytime researchers try to compare the perception of "apples and oranges", or in this case, people, animals, and objects, it is prudent to tread lightly when drawing precise conclusions. Nonetheless, it seems safe to conclude the current data are inconsistent with the hypothesis that "biological motion" represents a bounded, clearly defined perceptual category. In other words, the current data do not support the hypothesis that the human visual system has a mechanism that is dedicated to the analysis of "biological motion" and is wholly independent of some other mechanism dedicated to the analysis of "non-biological motion."

Cognitive research on object categorization has long argued against the idea that objects are internally represented within categories that are rigidly defined by sharp boundaries (e.g., Rosch, 1973). Instead, category membership is understood as graded (e.g., Rosch, 1999). Consistent with this line of thought, the current results suggest that the visual analyses of human movement and non-human movement may differ along a gradient. As other have suggested, this gradient may be defined by the degree of bodily similarity between the observer's own body and observed bodies. Relatedly, this proposed gradient may be understood a reflecting an observer's ability to perform, or use their motor system to simulate, observed motions. Such a conclusion would be consistent with data from research with patients which suggest that visual sensitivity to human action drops when observers are unable to perform a seen action because of hemiplegia (Serino et al., 2010) or congenitally absent limbs (Funk et al., 2004). In sum, the current results do not support the existence of categorically independent processing of biological (i.e., human and animal) and non-biological (i.e., human made objects) motions.

One might argue that observers were simply better at categorizing patterns of motion that they have seen frequently (e.g., human gait). Indeed, motor exertion and movement production are coupled such that less effortful actions are produced more frequently (Hreljac, 1993; Hreljac & Martin, 1993; Perry, 1992). Consistent with this, categorization accuracy was significantly higher with frequently seen actions (e.g., walking) than with rarely seen actions (e.g., yoga). This alternative interpretation, that categorization accuracy reflects visual experience rather than motor experience, is difficult to reconcile with the analysis of athletic experience on categorization accuracy. In our first experiment, athletes were significantly more likely than non-athletes to correctly categorize the difficult human actions as human. Importantly, the athletes were not yoga experts and the two groups of observers did not differ in their visual experience of yoga. Moreover, categorization performance by athletes and non-athletes did not differ in any other stimulus category. Furthermore, categorization performance with bipedal animals was significantly more accurate than that with apedal animals. This occurred even though the animal stimuli were selected so that the apedal animals (fish and snakes) are more frequently seen than the bipedal animals (penguins and flamingos). These findings are consistent with previous evidence that, regardless of one's perceptual experience, visual sensitivity to human locomotion is greater than visual sensitivity to animal locomotion (Cohen, 2002). Instead, what appears to be the key factor differentiating human and animal motion perception is the degree to which the observer can easily perform an observed action (Cohen, 2002; Wilson, 2001).

In conclusion, current and previous results suggest that "biological motion perception" does not reflect a uniform or bounded perceptual category. Indeed, observers in the simple studies described here consistently demonstrated greater visual sensitivity to some non-biological entities, such as cars, than to some biological entities, such as apedal fish and snakes. Interestingly, when non-biological objects, such as wooden blocks, are positioned so as to mimic the structure of the human body, observers tend to interpret the movements of those non-biological objects as if they were actually human movement (Heptulla-Chatterjee et al., 1995).

It is entirely possible that not even the visual perception of human motion constitutes a special perceptual category. As discussed in the chapters by Pelphrey and Kaiser, some observers do not differ in their neural analyses of or visual sensitivities to human and object motions. Furthermore, even typical observers vary in their visual analyses of different socially defined categories of people. For example, Harris and Fiske (2006) have shown that typical observers demonstrate reduced levels of neural activity in many of the brain areas associated with person perception when these observers view pictures of homeless people and drug addicts than when they view pictures of rich people and business people. Such evidence suggests that the visual systems of all observers may be capable of processing the postures, and likely the actions, of other people in a dehumanized manner. Such results challenge the hypothesis that human movement can be understood as a consistently and uniformly unique stimulus category.

The goal of this chapter was to examine how the term "biological motion" could be most accurately employed by vision scientists. When Johannson (1973) originally introduced the term, he understood it as applying to the visual perception of all animal motion, whether human or non-human. Because research on the perception of "biological motion" has most frequently employed only point-light human motion, and even then, most frequently human gait, it has been far from clear whether most experimental results can be generalized to the visual analyses of the movements of all animals or to all human motion or just to human gait. A review of the literature and some novel preliminary evidence point away from the idea that the perception of human and animal motions constitutes a rigid perceptual category that might be called "biological motion." Instead, when taken together, the evidence seems to suggest that the visual perception of easily performable human actions, and non-human actions that approximate performable human actions, triggers processes that differentiate those actions from other categories of movement. Thus, it appears that vision sciences need to reconsider, or at least more carefully define, how they employ the term "biological motion" perception. Given the findings described above, one fitting replacement for "biological motion" perception might be "body centered" perception.

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Figure Captions

Figure 1. Categorization accuracy, measured as overall percent correct, as a function of stimulus category for the first experiment (observers run in groups). Categorization was most accurate for the easy human actions and least accurate for the apedal animal actions. Note that accuracy levels for difficult human motion, bipedal animal motion and mechanical motion did not significantly differ. These data challenge two common assumptions; namely, that (1) the visual system is optimized for the detection of all human actions as a class and that (2) visual sensitivity to biological and non-biological stimuli necessarily differ.

Figure 2. A confusion matrix from the data of the first experiment. The percentages (collapsed across observers) indicate how observers categorized each of the five types of stimuli: easy human, difficult human, bipedal animal, apedal animal, and mechanical. Correct categorizations are indicated in the gray boxes while incorrect answers are in the white boxes.

Figure 3. A confusion matrix from the data of the second experiment in which observers were run individually. As in Figure 2, the vertical columns indicate the percentage of trials during which observers judged each of the five classes of stimuli as depicting human, animal, mechanical or other patterns of motion. Correct categorizations are shown in the gray boxes.

Figure 1

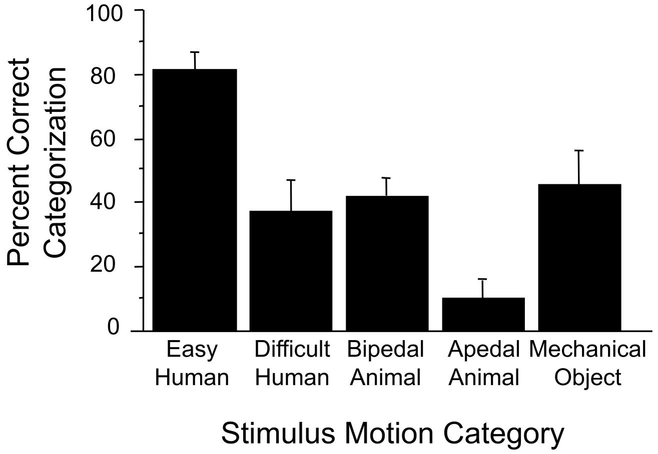

Figure 2

Observer Categorization Responses	Experiment 1: Stimulus Category				
	Easy Human Actions	Difficult Human Actions	Bipedal Animal	Apedal Animal	Mechanical Object
Human	80.5	37.7	38	14	10.3
Animal	21.5	16.3	41.5	10.3	25
Mechanical	6.8	37	10	18.7	47.5
Other	1.2	9	10.5	57	17.2

Figure 3

Observer Categorization Responses	Experiment 2: Stimulus Category				
	Easy Human Actions	Difficult Human Actions	Bipedal Animal	Apedal Animal	Mechanical Object
Human	70.4	26	9.5	7.3	4.4
Animal	23.6	22	47.5	10	29
Mechanical	4	41.1	15	20.7	49.3
Other	2	10.9	28	61.3	17.3