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Perception of Human Motion

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action-perception linkage, posterior superior temporal sulcus

Abstract

Humans, being highly social creatures, rely heavily on the ability to
perceive what others are doing and to infer from gestures and expres-
sions what others may be intending to do. These perceptual skills are
easily mastered by most, but not all, people, in large part because hu-
man action readily communicates intentions and feelings. In recent
years, remarkable advances have been made in our understanding
of the visual, motoric, and affective influences on perception of hu-
man action, as well as in the elucidation of the neural concomitants
of perception of human action. This article reviews those advances
and, where possible, draws links among those findings.

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Kinematics:
analysis of the
motions of objects
without regard to the
forces producing
them

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light tokens (point
lights) placed on the
major body parts of
an actor

INTRODUCTION

Perceiving the actions, moods, and intentions of other people is one of most important social skills we possess, and vision provides a particularly rich source of information in support of this skill. Although we can discern a person's affective state from static pictures, motion provides even more reliable and compelling information. As Darwin (1872) noted in his seminal work, *The Expression of Emotions in Man and Animals*, actions speak louder than pictures when it comes to understanding what others are doing and feeling.

In recognition of the importance of action in everyday human social discourse, psy-

chologists and cognitive neuroscientists have intensively studied the visual analysis of human action. Some studies have focused on the kinematics specifying different activities and emotional states, others have examined the role of motor involvement in action perception, and still others have sought to uncover the brain mechanisms mediating action perception. In this review, we survey that work, highlighting studies that have employed point-light (PL) animations to isolate human kinematics. Our survey is necessarily selective, for the literature on this topic is quite large. Interested readers can consult other available publications that review material on human action and social perception (Allison et al. 2000, Blakemore & Decety 2001, Knoblich et al. 2006, Puce & Perrett 2003).

The perception of human action depends upon multiple sources of information including sensory, motor, and affective processes. We begin with an overview of the behavioral research supporting the contributions of each of these processes to the analysis of human movement. We give greater weight to the role of visual processes since more research has been conducted in that area. We conclude with an introduction to the neural circuitry underlying action perception.

Perceiving Human Form and Action from Kinematics

Imagine seeing a woman on a golf course, poised over a golf ball with a putter in her hands. You expect to see her smoothly strike the ball, and when she does, you are not surprised. But could you recognize what the person was doing based solely on the dynamics of the body movements in the absence of all other clues? And if you did perceive that the person was a golfer executing a putt, could kinematics alone tell you that it was Annika Sörenstam and not Tiger Woods? The answer to both questions turns out to be "yes." What accounts for this impressive perceptual ability?

Creating Human Motion

First to tackle this technical problem was the French physiologist and physician Etienne-Jules Marey (1884). His lifelong passion to understand movement led him to develop "chronophotography," a high-speed photographic technique that captured multiple successive images on a single photographic plate. To highlight the kinematics of gait, for example, Marey filmed a person walking while wearing a black suit with small markers attached to the joints. The resulting photograph embodied a space/time record of the changing positions of the joints (**Figure 1***A*).

The modern-day instantiation of Marey's technique was realized by Swedish psychologist Guntar Johansson (1973), who devised the technique known as PL animation of biological motion. With this technique, the activity of a human is portrayed by the relative motions of a small number of markers positioned on the head and the joints of the body (**Figure 1***B*). Following Marey's lead, Johansson filmed an actor wearing small lights attached to the joints of his body. The resulting video clips depicted only the patterns of motion of the lights and not the rest of the body. In recent years, more refined PL animation techniques have been developed through the use of computer animation (Cutting 1978) and motion-capture technology paired with animation software (Ma et al. 2006, Vanrie & Verfaillie 2004). With all of these techniques, static frames of the resulting animation typically appear as meaningless assemblages of dots, with little hint of an underlying configuration. But when the successive PL frames are shown in rapid succession, naïve observers experience compelling apparent motion depicting a human form engaged in a specific activity. Several laboratories have created Web-based archives containing examples of human motion, available as movie files and/or 3D coordinate files. See Blake & Shiffrar (2006) for a Website showing demonstration PL animations and listing URL addresses for accessing and downloading sets of stimuli.

To be sure, there are techniques other than PL animation for examining the perception of human motion, and these tend to add form information to the kinematics. For example, one can connect the points in PL animations with visible line segments to create stick figures (Hodgins et al. 1998). Partial occlusion of these line segments provides a measure of motion integration across the limbs of human actors (e.g., Shiffrar et al. 1997, Sinha & Poggio 1996). Motion capture systems also have been used to obtain precise measurements of human action upon which bodily and facial forms can be superimposed to create "embodied" actors (e.g., Hill & Johnston 2001) presented within virtual reality displays (e.g., Morris et al. 2005). Displays depicting the whole bodies (e.g., Knoblich & Flach 2001) and body outlines (Ambady et al. 1999) in motion have been successfully used to measure visual sensitivity to human action, even under conditions where the observer himself is engaged in motor activity (Chartrand & Bargh 1999). Action perception can also be studied by systematically exaggerating the actions from statistically defined action prototypes (Pollick et al. 2001a) or by morphing between PL animations depicting different categories of activity (Giese & Lappe 2002). Finally, human motion perception can be studied with displays that are completely devoid of physical motion. For example, two static frames can be pulled from a movie of a simple human action (**Figure 1***C*). When these static images are sequentially presented at temporal rates consistent with the amount of time normally required to perform the depicted action, observers perceive biomechanically plausible paths of apparent human action (Heptulla-Chatterjee et al. 1996, Shiffrar & Freyd 1990).

VISUAL ANALYSIS OF HUMAN MOTION
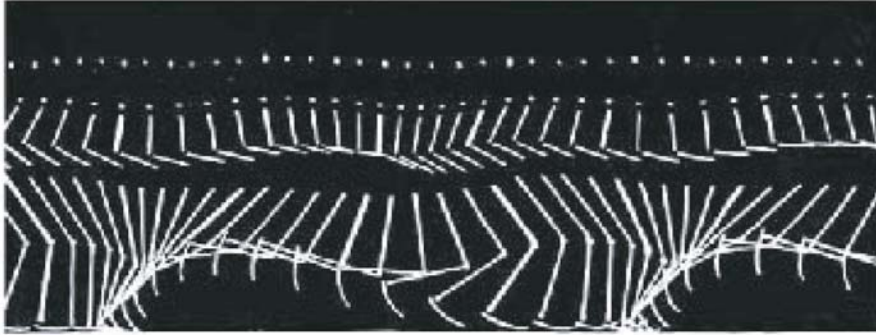
Observers have no trouble identifying what an actor is doing in a given PL display (e.g., Dittrich 1993, Norman et al. 2004),
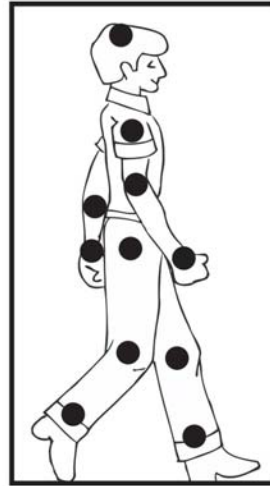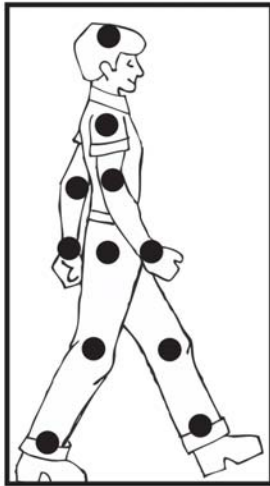
Apparent motion: perception of smooth motion from brief, successive exposures of static images

A

B

C

even when the number of possible activities is quite large. Observers also readily perceive the identity (Cutting & Kozlowski 1977, Fani et al. 2005, Troje et al. 2005) and sex (Kozlowski & Cutting 1977, 1978; Mather & Murdoch 1994; Sumi 2000; Troje 2002) of a PL-defined walker, although recognition performance is not perfect (Pollick et al. 2005). People can also easily discern activities (e.g., dancing) involving two or more individuals (Mass et al. 1971), and they can judge the emotional implication of an action when viewing PL animations of the whole body (Clarke et al. 2005, Dittrich et al. 1996, Walk & Homan 1984) or even the movements of individual limbs (Pollick et al. 2001b). Facial expressions, too, can be portrayed using PL animation, and people viewing PL faces can identify the facial expression being executed (Bassili 1978) as well as the sex of the actor (Hill et al. 2003). Viewing a PL animation of a talker's face makes it easier to understand what the talker is saying when the vocalizations are heard in noise (Rosenblum et al. 1996). Also of practical relevance, reflective markers worn on the joints of the body make pedestrians walking at night much more conspicuous to drivers (e.g., Wood et al. 2005).

As expected, sensitivity to human motion increases with the number of illuminated joints as well as with the exposure duration of the animation (Neri et al. 1998, Poom & Olsson 2002, Thornton et al. 1998). But even under impoverished or potentially ambiguous conditions, perception of human motion is remarkably robust. Thus observers can recognize human activity when a PL animation is presented for less than one-tenth of a second (Johansson 1973), when the dots are blurred or randomized in contrast polarity over time (Ahlström et al. 1997; but see Mather et al. 1992), or when stereoscopic depths of the dots marking the joint positions of a PL walker are scrambled such that the 3D locations of the dots are unrelated to their implied depth orderings for the human figure (Ahlström et al. 1997, Bülthoff et al. 1998, Lu et al. 2006). Also testifying to the robustness of human motion, observers can easily recognize a walking person when the PL animation is embedded in an array of dynamic noise dots that far outnumber the dozen or so dots defining the person (Bertenthal & Pinto 1994, Cutting et al. 1988, Ikeda et al. 2005). At least for PL walkers, the points defining the wrists and ankles are crucially important when judging the direction of walking (Mather et al. 1992), while the points defining the mid-limb joints (elbow and knees) and the torso (shoulder and hips) contribute significantly to detection of PL walkers embedded within noise (Pinto & Shiffrar 1999). Human action is most compelling when the PL tokens are placed on the joints of the body, but observers can still detect PL human figures when tokens are placed on positions other than the joints, such as intermediate positions on the limbs (Bertenthal & Pinto 1994). Perception of human motion is seriously disrupted by perturbations in the temporal relations of the PL tokens (Bertenthal & Pinto 1993). Introducing spatiotemporal jitter into the phase relations of the moving dots disturbs the quality of human motion (e.g., Grossman & Blake

Dynamic noise: an array of randomly positioned dots that can camouflage perception of PL animations when the noise dots are sufficiently dense

Spatiotemporal jitter: means of degrading perception of PL animations, where the relative timing and positions of the moving dots are perturbed

Figure 1

Examples of animation techniques used to study perception of human motion. (*A*) Photograph produced by prolonged film exposure while a person outfitted with small metallic markers walked from left to right. The resulting image highlights the kinematics of this action. (*B*) Two frames from an animation of a point-light walker. In the actual animation, only the dots are visible—the outline of the human figure is shown here only to make obvious the fixed positions of the dots on the human body. (*C*) Two frames showing a person moving her arm from one position to another. When the two frames are briefly shown in succession with an adequately long blank interval between the two presentations, one sees the arm move in the only direction mechanically plausible for this event. [Photograph from Marey (1884), now in the public domain.]

Inversion effect:
difficulty of
perceiving PL
animations when
they are shown
upside down

1999) and seriously impairs detection of human motion embedded in noise (e.g., Hiris et al. 2005a). Likewise, PL animations depicting abnormally slow walking movements produce perception of rotation in depth about a vertical axis, not perception of slow human gait (Beintema et al. 2006).

One of the hallmark characteristics of human motion perception is its vulnerability to inversion: Human action is difficult to perceive in inverted PL animations (e.g., Sumi 1984). In this respect, bodily motion perception resembles face perception, which is also highly susceptible to inversion (Valentine 1988). This orientation dependence operates in egocentric, not environmental, coordinates: PL animations shown upright with respect to gravity are nonetheless difficult to perceive when the observer's head is turned so that the retinal image of those animations is no longer upright with respect to head position (Troje 2003). Prior knowledge cannot counteract this inversion effect: Informing observers ahead of time that they'll be seeing upside-down people does not help them identify what they've seen, which implies that they cannot mentally rotate the images (Pavlova & Sokolov 2000). With practice, observers can learn to detect inverted human motion (Hiris et al. 2005b, Shiffrar & Pinto 2002), but in so doing observers are relying on detection of conspicuous clusters of dots, not on global impression of a human figure.

Besides its vulnerability to inversion, visual sensitivity to human motion (indexed by susceptibility to noise dot motion) is also compromised when a PL figure is imaged in the visual periphery, and this impairment is not simply attributable to the periphery's reduced visual resolution—increasing the sizes of the PL dots and the overall size of the human figure cannot compensate for this loss in sensitivity (Ikeda et al. 2005). Perception of human motion is also impaired when PL animations are viewed under dim light conditions (Grossman & Blake 1999).

Observers can use kinematics information to infer properties of objects with which PL actors are interacting. Thus, for example, people can accurately estimate the weight of a lifted object from observing the lifting motion alone (Bingham 1993), and they can judge the elasticity of a support surface by watching a PL person walking on that surface (Stoffregen & Flynn 1994). There is disagreement whether observers are directly perceiving kinetic object properties from human kinematics information (Runeson & Frykholm 1981) or, instead, are deploying heuristics to infer object properties from kinematics (e.g., Gilden & Proffitt 1994). In either event, however, there is no doubt that kinematics can accurately specify the act of lifting and, moreover, the effort required to do so (Shim et al. 2004).

Accurate perception of PL figures is not limited to human activity. Mather & West (1993) demonstrated that people could identify animals, such as a camel, goat, baboon, horse, and elephant, whose movements were represented by PL animations. People found this task impossible, however, when viewing a single, static frame from the PL sequence. Bellefeuille & Faubert (1998) showed that observers could identify the shape of an animal as accurately when using PL animations as they could when viewing animal shapes defined by luminance contrast. Jokisch & Troje (2003) showed that human observers viewing PL animations of striding dogs could accurately recover the size of the dog using just the stride frequency depicted by the moving dots. For that matter, humans are not the only biological creatures that can perceive animal motion with PL stimuli. Successful discrimination has also been demonstrated in cats (Blake 1993), pigeons (Dittrich et al. 1998, Omori & Watanabe 1996), and newly hatched chicks (Regolin et al. 2000).

The ability to perceive PL depictions of human motion arises early in life, as evidenced by preferential looking studies: Infants four months old will stare at human motion sequences for longer durations than they will at the same number of dots undergoing random motions, a preference not exhibited when infants view an inverted PL person

(Bertenthal 1993, Fox & McDaniel 1982). Sensitivity to human motion is also evidenced in eight-month-old infants by differences in amplitude of event-related potentials (ERPs) to upright versus scrambled PL animations (Hirai & Hiraki 2005) and to upright versus inverted PL animations (Reid et al. 2006). At these young ages, however, children are not yet completely adult-like in their sensitivity to human motion (Bertenthal & Pinto 1993, Pinto 2006). Using behavioral testing, Pavlova et al. (2001) have shown that young children between the ages of three and five steadily improve in their ability to identify human and nonhuman forms portrayed by PL animations, with adult levels of performance achieved by age five. At the other end of the development time scale, observers older than 60 years are quite good at discriminating among various forms of human motion even when the PL sequences are brief in duration or the dots are partially occluded (Norman et al. 2004). This preservation of the ability to perceive human motion stands in contrast to age-related deficits in speed discrimination (Norman et al. 2003), coherent motion detection (Gilmore et al. 1992), detection of low-contrast moving contours (Sekuler et al. 1980), and perception of self-motion from optic flow (Warren et al. 1989). In sum, the human visual system appears to be especially well adapted for the perception of other people's actions.

Top-down and Bottom-up Influences on Human Motion Perception

The decreased sensitivity to inverted displays of human movement described above suggests that low-level visual mechanisms may not be sufficient to account for action perception. There is debate in the literature about the involvement of top-down influences in perception of human motion, where top-down means conceptually driven processing. As with so many of these kinds of debates, the emerging resolution entails a synthesis of bottom-up and top-down determinants

(Kroustallis 2004, Thornton et al. 1998). Still, it is useful to consider the kinds of evidence that favor one view or the other, which we do here.

Evidence for the role of low-level visual processes in the perception of human movement comes from several lines of research. Johansson (1973), the inventor of the PL technique, thought that perceptual process underlying human motion sequences involved vector analysis of the component body parts (defined by pairs of dots), with those vectors then incorporated into a single structured percept. Similar theories built around different assumptions were subsequently advanced by Webb & Aggarwal (1982) and by Hoffman & Flinchbaugh (1982). Construed in this way, the problem boils down to a variant of the structure from motion problem encountered in other aspects of motion perception and solved using bottom-up, data-driven information supplemented by assumptions about the nature of objects (Ullman 1979).

To determine whether low-level motion analyses underlie the perception of human movement, Mather et al. (1992) inserted blank intervals between successive frames of a PL animation, reasoning that low-level motion analysis is restricted to very brief interstimulus intervals (ISIs), whereas high-level motion favors longer ISIs. On direction discrimination tasks involving a PL walker, Mather et al. found that perception of human gait was best at the shortest ISIs and deteriorated with longer ISIs. Mather et al. concluded that the perception of human motion relies on signals arising within low-level visual mechanisms whose response properties are constrained to operate over short spatial and temporal intervals.

Subsequent work showed, however, that higher-level visual processes also support perception of human motion. Thornton and colleagues (1998) found that human gait can be perceived with PL animations over a range of temporal display rates that exceed the value typically associated with low-level, local motion analysis (e.g., Baker & Braddick 1985).

Event-related potential: electrical brain activity registered from the scalp

ERP: event-related potential

More recently, several studies have shown that perception of human motion, under some circumstances, requires focused visual attention. Cavanagh et al. (2001) used a visual search paradigm to show that imposition of an attentional load made it more time consuming for observers to pick out an "oddball" PL walker among an array of PL figures. Similarly, Thornton et al. (2002) found that when a PL sequence is embedded among dynamic noise dots, attention is crucial for perceiving the human figure at long ISIs but not at short ISIs. The same pattern of results was found when Thornton et al. used a very brief ISI but varied the type of masking noise. To perceive a human figure in a mask of scrambled dots (i.e., dot motions with vectors identical to the PL dots), observers had to attend to the animation. Conversely, in random noise mask (i.e., dots randomly replaced each frame), distracted attention had no effect on walker detection. Still, when PL stimuli are designed to render such top-down processes ineffective, bottom-up processes guide the perception of PL animations. For example, ignored PL walkers are processed at a level sufficient to impact the perception of attended PL walkers (Thornton & Vuong 2004). Thus, both bottom-up and top-down processes are employed during the perceptual analysis of PL animations of human motion.

Human motion itself can also exert a top-down influence on other aspects of perception. For example, Watson et al. (2004) found that dichoptically viewed PL walkers differing in color and in heading direction produced binocular rivalry, meaning that observers saw one PL walker or the other over time. Based on this and related results, Watson and colleagues concluded that dominance during rivalry resulted from the integration of high-level perceptual organization (responsible for perception of human motion) with lower-level inhibition between cortical representations of input from the two eyes. Human motion can also influence the perceived direction of translational motion. Thus, when a coherent PL person walks in front of a counterphase flickering grating with no net directional energy, the grating appears to translate in the direction opposite the walker's heading, just as the physical environment flows past us when we walk (Fujimoto 2003). In a similar vein, the global motion engendered by a PL walker provides an effective reference frame for judging whether or not local dot motions are coherent (Tadin et al. 2002). All of these studies imply that human motion exerts a significant influence on putatively low-level motion processing.

Visual Form Influences Perception of Human Motion

PL animations of human activity seemingly contain little form information about the human body, yet people can easily detect PL figures appearing within a cloud of moving "noise" dots whose local motions are identical to those defining the PL figures. Based on motion alone, detection of a PL figure should be extraordinarily difficult under these conditions. Evidently, the visual analysis of human motion is constrained by the hierarchical structure of the human body, for otherwise it would be hopelessly difficult to segregate moving "body" dots from moving "noise" dots and, therefore, to track given body dots over time. Indeed, when PL animations contain motion vectors that violate the hierarchical structure of the human body, observers experience great difficulty detecting the presence of a PL body part (Pinto & Shiffrar 1999).

Several lines of evidence underscore the importance of bodily form. For one thing, sequential presentation of two static pictures of a person performing some action is sufficient for the perception of human action, even though such displays contain minimal motion information (e.g., Heptulla-Chatterjee et al. 1996). For another, there is evidence that the changing positions of the moving points in a PL animation convey sufficient form cues for the detection of a PL walker. To dissociate position and motion, Beintema & Lappe (2002) designed a variant of the point-light

animation in which the positions of the dots are not confined to the joint but instead can appear anywhere along the limbs. Moreover, the dots change their positions along the limbs unpredictably from frame to frame. While these two manipulations should not disrupt specification of body shape, they make it virtually impossible to perceive coherent motion of the dots defining an activity. Nonetheless, observers viewing these displays can judge with reasonable accuracy the direction (left versus right) in which a PL figure is walking. In fact, detection performance measured using these special PL animations is well predicted by the total number of points seen in a trial, irrespective of the distribution of these points over time (Beintema et al. 2006). This result is consistent with a simple template-matching model in which the positions of the stimulus dots in each single frame are matched to the posture of a human body template (Lange & Lappe 2006). This model suggests that human movements can be discriminated by an accumulation of evidence for the body postures indicated by the positions of stimulus dots.

Additional evidence for the importance of bodily form in the perception of human motion comes from Hiris and colleagues (2005a). They created "arbitrary" motion sequences by relocating the dots from a PL walker. Thus, for example, a wrist dot might be placed at the location of the shoulder dot and the shoulder dot relocated to the position of the knee, and so on. The resulting arbitrary figure comprised the same dot motions as the walker in the absence of a human form. Following the design of studies with masked PL walkers, the arbitrary figures were presented within a mask of dynamic dots. With practice, observers learned to discriminate whether or not the arbitrary figure was presented in a mask, with performance eventually approaching that achieved with an ordinary PL walker. However, observers described performing this task by looking for a characteristic cluster of dots at a given location, a strategy very dissimilar from that used with upright PL walkers in noise. Moreover, inverting the ar-

bitrary figure had no effect on detection performance, in stark contrast to the effect of inversion on detection of PL walkers. When a display change forced observers to detect the global pattern of motion in the arbitrary figures, performance hovered near chance levels regardless of practice (Hiris et al. 2005a). Thus, the human form is important for the perception of human motion, especially when it is impossible to rely on local motion regularities. Such results further suggest that different processes are employed during the analyses of human motion and object motion (Shiffrar & Pinto 2002).

Taken together, then, current research indicates that both form and motion play critical roles in the perception of human action. This interplay between form and motion information in the visual specification of human action has been formalized in a computational model developed by Giese & Poggio (2003). Their model is based on bottom-up visual signals analyzed in parallel in a form pathway and a motion pathway, which they identify with the ventral stream and dorsal stream pathways, respectively. The core principle of their model is that human motion is represented as learned sequences or "snapshots" of human shapes and optic flow patterns. Inhibition insures that the neural instantiations of these snapshots are activated only in the correct temporal sequence as incorrect sequences are inhibited. This renders the model highly sensitive to disturbances in the normal temporal relationships among the motions of PL tokens (recall Bertenthal & Pinto 1993, Hiris et al. 2005a). Through successive transformations within the model, more global aspects of the human form and its resulting kinematics are extracted, with size and position invariance embodied at higher levels. In both pathways, representations are stored as 2D, view-dependent patterns; this aspect of the model dovetails with the known view dependence of perception of human motion (e.g., Bülthoff et al. 1998, Sumi 1984). As Giese and Poggio acknowledge, their model remains incomplete in that it does not incorporate top-down

Template-matching model: theory that perception of biological motion results from concatenation of static views of the body

influences such as attention (e.g., Thornton et al. 2002). Still, this ambitious model makes a number of testable predictions, some of which have since been confirmed (Peuskens et al. 2005).

MOTORIC CONTRIBUTIONS TO PERCEPTION OF HUMAN MOTION

So far, we have focused on visual sensitivity to human motion. But what are the origins of that sensitivity? Converging lines of evidence strongly suggest that our keen ability to perceive the actions of other people results, in part, from the massive experience we have accumulated over the years in planning and executing self-produced activities. Prinz (1997) and Hommel et al. (2001) have formalized this idea as the common coding principle and the theory of event coding, respectively. According to both of these accounts, sensory representations used during action perception overlap with the motor representations used during action planning. This section summarizes converging lines of evidence supporting this view as it applies to perception of human motion (but see Decety & Grèze 1999).

First, if action perception and action production share common representations, then an observer's own activities should influence that observer's perception of the activities of other people. This, in fact, happens. For example, an observer is better able to notice a change in the limb position of an actor when the observer, too, is moving the corresponding limb (Reed & Farah 1995). Similarly, an observer's ability to discriminate the gait speeds of a PL walker depends upon whether the observer is standing or walking (Jacobs & Shiffrar 2005), and the ability to judge the size of a box being lifted by an actor depends on the weight of a box being lifted by the observer (Hamilton et al. 2004).

Second, if motor experience does indeed affect visual sensitivity to human action, then observers should demonstrate maximum sensitivity to actions most familiar to them and reduced sensitivity to actions unfamiliar to them. These predictions, too, have been confirmed. Consider, for example, a study by Knoblich & Flach (2001) in which movies were made of individuals throwing darts at a board. Returning to the laboratory one week later, these individuals viewed short video sequences showing an arm throwing a dart that always stopped at the moment the dart was released. Participants then predicted where the dart would hit the board. Prediction accuracy was highest when participants viewed sequences of their own dart throws. In a similar vein, an observer is especially good at judging whether a pair of PL animations portrays the same actor when those animations were produced by filming the observer himself several months earlier (Loula et al. 2005). In contrast, observers are relatively poor at discriminating the gait speed of a PL walker when the spatiotemporal characteristics of the gait fall outside the range of physically possible human gaits or when the gait was produced by someone other than the observer (Jacobs et al. 2004). Interestingly, people can improve their ability to discriminate unusual action styles simply by repeatedly executing that action style themselves, and this improvement occurs even when people practice while blindfolded (Casile & Giese 2006). Motor learning, in other words, influences visual perception of the learned motor behavior.

A third category of evidence bearing on the action perception/production linkage comes from studies of patients with congenital or disease-related disorders that affect proprioceptive mechanisms and/or motor behavior. Here, too, the results are revealing. One study (Bosbach et al. 2005) assessed action perception in two individuals with no sense of cutaneous touch or proprioception, a condition arising from sensory neuropathy. Unlike normal, control volunteers, both of these individuals had difficulty deducing whether or not another person was surprised at the weight of a lifted object, based on viewing the kinematics of that person's lifting activity. In another study (Funk et al. 2005), an individual born

Common coding principle: theory that perceiving and acting share common mental representations

without hands perceived biomechanically impossible hand rotations under stimulus conditions where normally limbed individuals see hand rotations that conform to natural limb trajectories. Importantly, this individual with hand aplasia also experienced no phantom sensation of the congenitally missing hands. Evidently, the ability to represent executable actions constrains the ability to perceptually interpret similar actions performed by other people (Shiffrar 2006). In another patient study (Pavlova et al. 2003), human motion perception was assessed in teenage adolescents who varied in terms of their locomotion ability—the subject population ranged from normal to those with congenital walking disability resulting from spastic cerebral palsy. Sensitivity to human motion was unrelated to severity of motor disorder, implying that the ability to plan a body movement is sufficient for the development of human motion perception. This does not mean that perception and production arise from different brain areas, but rather that a common coding network does not require fine motor execution for utilization in perception.

In summary, converging lines of evidence indicate that one's own actions can affect one's perception of the actions of others. Indeed, some have argued that observers' motor constraints influence their percepts of all moving stimuli (Viviani 2002, Viviani & Stucchi 1992). For that matter, the causal arrow can point in the opposite direction: action perception can influence action execution. Thus, for example, participants in one study were asked to make arm movements while viewing another person (biological) or a robot (nonbiological) execute arm movements (Kilner et al. 2003). Participants' own arm movements exhibited significantly more variability when they viewed human arm movements than when they viewed robot arm movements. This and other results implicate a tight coupling between observation and performance of action. All of these results are consistent with the idea that observers spontaneously simulate, in their motor planning system, the ac-

tions that they observe (Blakemore & Decety 2001, Jeannerod 2004). Moreover, there is reason to believe that this spontaneous simulation occurs at an unconscious level. For example, when a seated observer views another person running on a treadmill, the observer's own respiration rate increases with treadmill speed and hence runner exertion (Paccalin & Jeannerod 2000). When observers view different poses of a moving person, perceptual priming, as assessed by reaction time in a body-pose discrimination task, is restricted to body views that satisfy the biomechanical limitations on human movement (Kourtzi & Shiffrar 1999), a finding that indicates the existence of implicit visual representations of human movement. Likewise, judgments of gait direction are facilitated whenever the previously viewed PL person walks in the same direction, a finding that implies that implicit knowledge of gait dynamics influences visual sensitivity to human motion (Verfaillie 2000). Finally, people tend to mimic the actions of other people without even realizing it, a tendency dubbed the chameleon effect (Chartrand & Bargh 1999). Here, too, we see evidence for tight perception-action coupling operating at an unconscious level.

SOCIAL DETERMINANTS OF PERCEPTION OF HUMAN MOTION

Visual comprehension of human actions promotes effective social interaction. It is natural to assume, therefore, that the sensori-motor analyses underlying perception of human action should incorporate our social needs, and this assumption is supported by evidence. Observers can perceive a wide range of socially relevant characteristics from highly degraded depictions of human action including an actor's identity (Loula et al. 2005), sex (Barclay et al. 1978), sexual orientation (Ambady et al. 1999), dancing ability (Brown et al. 2005), openness (Brownlow et al. 1997), social dominance (Montepare & Zebrowitz-McArthur 1988), vulnerability to attack (Gunns et al.

2002), and intent to deceive (Runeson & Frykholm 1983). Face perception, too, is facilitated by dynamic information such as shifts in eye gaze, lip movements and changes in expression (Haxby et al. 2000, O'Toole et al. 2002). These diverse findings imply that the human visual system is tuned for the pickup of socially relevant information.

One particularly salient characteristic conveyed by human activity is the emotional states of observed individuals. It is well established, for example, that observers can readily identify the emotion being portrayed by a PL actor (e.g., Atkinson et al. 2004). Pollick and colleagues (2001b) have shown that an action as simple as the movements of a PL arm knocking against a door are sufficient for observers to discriminate the emotion of the individual executing the arm movements.

Given this keen sensitivity to socially relevant kinematics, it is reasonable to expect that social processes, per se, should influence action perception. Recent evidence implies that this is so. For example, when observers are asked to detect the presence of a PL walker in a complex PL mask, their performance depends upon the emotion conveyed by the PL walker: Observers detect the presence of angry PL walkers more accurately than they detect neutral, happy, sad, or fearful PL walkers (Chouchourelou et al. 2006). In another study (Clarke et al. 2005), PL animations were created depicting two people engaged in an emotional interaction (i.e., the emotions conveyed included sadness, anger, and disgust). Observers viewing these animations were better able to judge the emotion being expressed when they could see both PL actors, not just one or the other. Social context, in other words, aided perception of emotion. Evidence for the importance of social processes in action perception also comes from the chameleon effect, wherein individuals unconsciously mimic the actions of other people. Social mimicry may serve to increase rapport between individuals, since mimicked individuals express greater liking for those who mimic their actions (Chartrand & Bargh

1999) and since individuals who bring feelings of social exclusion into an interaction are more likely to mimic the other person (Lakin & Chartrand 2003). Such evidence suggests that social processes constrain and are constrained by connections between action perception and action production.

NEURAL BASES OF PERCEPTION OF HUMAN MOTION

The visual and functional importance of human motion perception is instantiated in a specialized neural network. In this final section, we review some of the evidence for the existence of these neural mechanisms for the analysis and interpretation of human motion, including mechanisms responsible for the influences of emotion and motor programming. This section is necessarily brief; for more thorough coverage, see Decety & Grèzes (1999), Puce & Perrett (2003), and Grossman (2006).

Single-Cell Recording Studies

The first neurophysiological evidence for the existence of a brain area visually coding human movement came from the work of Perrett et al. (1982, 1985). Recording from single cells in macaque cortex, these researchers discovered neurons in the superior temporal sulcus (STS) selectively responsive to human forms and motions within an observer-centered coordinate system (Oram & Perrett 1994). The STS represents a point of convergence for the dorsal and ventral visual streams (Felleman & Van Essen 1991), befitting STS's ability to integrate form and motion information arising from the same person (Oram & Perrett 1996, Shiffrar 1994). Although STS neurons are largely visual, their activity can be modulated by the motor system (Hietanen & Perrett 1996) and by the amygdala (Aggleton et al. 1980).

More recently, another remarkable category of visually activated neurons was

identified in both the ventral premotor cortex and in the inferior parietal cortex of the alert, behaving monkey (Rizzolatti et al. 2001, Rizzolatti & Craighero 2004). Called mirror neurons, these brain cells respond when an animal performs a visually guided activity (e.g., grasping) and, significantly, when the animal observes another individual executing that activity. These unique neurons respond only when an activity involves primate motion, not motion of, say, a mechanical device that simulates the action. Moreover, these neurons also respond to sounds associated with a given action. Significantly, they only respond when the action is goal-directed, as specified by the context in which the action occurs (Fogassi et al. 2005).

These groundbreaking neurophysiological studies paved the way for investigations of human brain mechanisms involved in the perception of human action, investigations to which we now turn.

Neuropsychological Studies

The first clues implicating specialized neural machinery for the analysis of human action in the human brain came from neuropsychological studies revealing selective visual deficits in individuals with focal brain lesions. Schenk & Zihl (1997) identified two patients with parietal lobe lesions who experienced difficulty perceiving a PL walker in noise but had no problem discriminating direction of coherent motion of dots. In a similar vein, patient AF (Vaina et al. 1990), who had bilateral lesions within the posterior visual pathway, had great difficulty perceiving coherent motion in random-dot cinematograms but could easily recognize human activities presented in point-light animations. Conversely, patient AL (Cowey & Vaina 2000) could not recognize PL depictions of human motion even though she could detect movement of the dots and could see that not all were moving in the same direction. These case studies and others (e.g., Battelli et al. 2003) point to the occipito-parietal region for the analysis of the complex kinematics characteristic of human motion.

Recently, Heberlein and colleagues (2004) studied the abilities of brain-damaged patients to judge the emotionality and personality characteristics of actors portrayed by PL animations. Some patients were impaired on one task but not the other, which implied the existence of distinct neural mechanisms for perception of emotion and perception of personality. By analyzing regions of lesion overlap in these patients, Heberlein et al. (2004) concluded that damage to the somatosensory cortex in the right hemisphere was associated with deficits in judging emotion, and damage to the left frontal opercular cortex was associated with deficits in judging personality traits. The cerebellum, a structure traditionally associated with skilled motor behavior, seems to be uninvolved in perception of PL animations of human motion: Patients with cerebellar damage can readily detect a PL walker in masking noise, but have difficulty judging the direction of coherent dot motion in masking noise (Jokisch et al. 2005a).

Deficits in perception of human motion have been described in several other patient populations. In one study, young autistic children, unlike their age-matched cohorts, made more errors on a visual task requiring discrimination of normal PL actors from scrambled PL sequences; these same autistic children performed normally on a comparably difficult visual grouping task involving discrimination of nonbiological shapes (Blake et al. 2003). This is consistent with the association between autism and STS abnormalities (Waiter et al. 2004). Adult schizophrenic individuals also experience difficulties discriminating normal from scrambled point-light animations (Kim et al. 2005). Children with Down syndrome have difficulties differentiating PL displays of moving objects and people (Virji-Babul et al. 2006). Also exhibiting deficits in perception of PL animations are adolescents suffering periventricular leukomalacia, a form of brain damage associated with premature birth (Pavlova et al. 2006).

Mirror neurons: brain cells responsive when an animal engages in an activity or when it watches another animal engaged in that activity

TMS: transcranial magnetic stimulation

Transcranial magnetic stimulation: technique producing a brief disruption of neural processing

Positron emission tomography: brain imaging technique that uses radioactively labeled tracers to allow visualization of active brain areas

Functional magnetic resonance imaging: the widely used technique that reveals brain activation patterns based on hemodynamic responses to neural activity

fMRI: functional magnetic resonance imaging

PET: positron emission tomography

Individuals in several of these patient populations, including those with autism, schizophrenia, and periventricular leukomalacia, can exhibit social and emotional deficits. It is tempting to wonder whether their deficits in perception of human motion might contribute to their stunted social skills and their inability to perceive and respond appropriately to emotional signals expressed by other people (e.g., Hobson et al. 1988).

Human motion perception is also disrupted by formation of temporary "lesions" in normal individuals, with the "lesion" being induced by transcranial magnetic stimulation (TMS). Grossman et al. (2005) applied repetitive TMS to a region of the scalp overlying posterior brain regions including the superior temporal sulcus. (As mentioned above, the STS is involved in the analysis of human motion in the macaque monkey brain.) For a short time following TMS, observers had more difficulty recognizing PL sequences in noise, but only when sequences were shown in their upright orientation; sensitivity to inverted sequences, although generally poorer, was unaffected by TMS. Nor did TMS applied over motion-sensitive area MT+ have any effect on perception of PL actors, a finding that underscores the unique involvement of the STS in perception of human motion.

Brain Imaging: Visual Processes

In recent years, brain imaging studies have revealed an array of brain areas selectively responsive to human action. In the following sections we focus on brain activations measured using either positron emission tomography (PET) or functional magnetic resonance imaging (fMRI). Action perception studies using magnetic encephalography and event-related potentials can be found in Pavlova et al. (2004, 2006), Hirai et al. (2003), Jokisch et al. (2005b), and Wheaton et al. (2001).

In many of the imaging studies summarized here, investigators contrasted brain activation produced when observers viewed animations of point-light-defined people with

activations produced when viewing scrambled versions of the same animations. Both kinds of sequences comprise identical individual dot trajectories and, therefore, differ only in the global, spatiotemporal coherence of the dots portraying human action. Differences in activation to the two kinds of animations, therefore, would constitute evidence for specific processing of the kinematics defining human motion (with the stipulation that a perceptually demanding task was used to insure that sustained attention was maintained for both categories of animations). What is found in brain imaging studies?

Using PET, Bonda et al. (1996) identified regions along the posterior portions of the superior temporal sulcus (STSp) that were activated when people viewed coherent, but not scrambled, point-light actions. Subsequently, Grossman et al. (2000) pinpointed activation sites in this same STSp area using fMRI (**Figure 2**, see color insert). These investigators also found that point-light actions activated the human MT/V5+ complex, but no more so than did scrambled point-light sequences (see also Howard et al. 1996 and Peuskens et al. 2005). In a follow-up study, Grossman & Blake (2001) found that STSp activation was stronger to upright human motion than to inverted sequences that, as pointed out above, are more difficult to discern as biological. Using a perceptual learning paradigm paired with brain scanning, Grossman et al. (2004) found that STSp activation varied depending on whether observers were able to recognize a given PL sequence as human. In this study, PL human figures were embedded in enough noise to mask recognition to near-chance levels. When viewed prior to training, these masked sequences yielded no selective responses within STSp. But following extensive practice with these masked sequences, observers' recognition performance improved substantially and, moreover, the previously unrecognizable sequences also readily evoked selective responses to human PL sequences in noise. Significantly, the improvements

in recognition performance and in STSp responsiveness generalized to novel PL sequences embedded in noise, which implies neural plasticity within STSp.

In a recent study, Peuskens et al. (2005) found that it was primarily the STSp in the right hemisphere that responds strongly to human motion, a trend evident in the results of others as well (Beauchamp et al. 2003, Grossman et al. 2000, Santi et al. 2003). There is also relatively crude retinotopy within STSp in that a given cluster of voxels can be activated by human action sequences appearing anywhere within five degrees or so of visual angle on either side of central fixation (Grossman et al. 2000). This observation befits the relatively large receptive fields of individual neurons in the homologue of STSp in monkey visual cortex.

STSp is also robustly activated when one views whole-body motions rather than PL sequences (Pelphrey et al. 2003), as well as when one views motion confined to specific limbs or to the eyes, hand, and mouth (Calvert et al. 1997, Grèzes et al. 1998, Puce et al. 1998). Interestingly, brain areas including STSp in the right hemisphere also respond robustly when people view humanly impossible movements (Costantini et al. 2005). Complex motion sequences portraying rigid rotation produce little, if any, activation of STSp (Beauchamp et al. 2002, Grossman & Blake 2002, Pelphrey et al. 2003), and a single static human figure is similarly insufficient to produce STSp activation (Peuskens et al. 2005).

Santi et al. (2003) used fMRI to dissociate brain areas responsive to whole-body actions portrayed in PL animations from brain areas responsive to visible speech rendered using PL animations. While there were a few overlapping activation areas, the speech animations selectively activated the left hemisphere STSp, portions of auditory cortex, and a network of motor regions including Broca's area; the whole-body PL animations, besides activating STSp in the right hemisphere, selectively activated the fusiform gyrus bilaterally and a network of more rostrally lo-cated cortical areas that Santi et al. (2003) believe are involved in the mirror-neuron system discussed above. It is noteworthy that in STSp, speech, PL human motion, and whole-body human motion activations do not overlap (Beauchamp 2005).

Several studies have identified robust STSp activation associated with viewing complex, natural events involving human activity. To give a few examples, Schürmann et al. (2005) measured increased BOLD signals in STSp while people viewed videotapes of another person yawning, a notoriously contagious activity. Activations in STSp were found regardless of whether observers themselves felt compelled to yawn. In a particularly clever study, Hasson et al. (2004) measured whole-brain fMRI activations in observers while they viewed a continuous audiovisual movie segment containing diverse subject matter and a complex, exciting storyline (*The Good, The Bad, and The Ugly*). Hasson and colleagues used intersubject correlation analysis to find brain regions that responded in a reliable fashion across all observers during the movie. Relevant for our purposes, consistent activations in STSp were associated with movie sequences depicting human activity, relative to sequences devoid of human activity, and these activations were reliably seen in all observers.

Area STSp is also activated when one hears footstep sounds produced by people walking, but not when one hears unstructured noise (Bidet-Caulet et al. 2005). In the monkey, STSp neurons respond strongly to species-specific, emotionally charged vocalizations (Gil-da-Costa et al. 2004). Such auditory sensitivity indicates that portions of this specialized brain area receive multimodal input, and further substantiates the idea that STSp is importantly involved in recognition of human activity (Wheaton et al. 2004).

Over the past few years, the chart of brain territories activated by human motion has enlarged significantly. PL animations have been shown to selectively activate regions on the

EBA: extrastriate
body area

**Extrastriate body
area:** brain region
activated when a
person views a
human body or body
parts

ventral surface of the temporal lobe (Vaina et al. 2001), on the lateral fusiform gyrus (Beauchamp et al. 2002), and in functionally identified areas including the fusiform face area and the occipital face area (Grossman & Blake 2002) Some of those activation regions, however, may be responsive to the implied presence of a human body and not to the dynamics of the PL sequences per se (Peelen & Downing 2005, Peelen et al. 2006). Michels et al. (2005) showed that ventral stream activations could also be evoked using the modified PL animations designed by Beintema and Lappe, animations in which the dots provide position, but not local motion, information.

In an fMRI study using whole-body motion, Bartels & Zeki (2004) found robust activations in the fusiform gyrus of observers while they were viewing action segments of a James Bond movie. The fusiform gyrus is a brain region often associated with face perception (e.g., Kanwisher 2000, Kanwisher et al. 1997), so it is not clear whether results of Bartels and Zeki reflect face perception, body perception, or both. A related fMRI study that overcomes this limitation was performed by Peelen & Downing (2005). They found areas within the fusiform gyrus that were indeed activated when people viewed human bodies without faces or viewed stick figures depicting stylized human bodies without facial features. Careful, individual analyses of these activated areas revealed that they are contiguous with, but not overlapping, foci of activation produced when viewing faces (the conventional "fusiform face area").

We also should mention the existence of the extrastriate body area (EBA). Situated at the junction of the occipital and temporal lobes, the EBA is activated when one views human bodies or isolated body parts; unlike the STSp, EBA activation does not require bodily activity, although body movements can produce strong responses in the EBA (Downing et al. 2001). A recent fMRI study found that the EBA also responds to self-produced body movements, even if the actor cannot see the movements of his/her limbs (Astafiev et al.

2004). This finding implies that the EBA receives inputs from motor areas responsible for the generation of actions; these endogenous signals could contribute to the specification of agency in actions, i.e., identification of whether an action is self-produced or attributable to another. Such a signaling capacity would implicate the EBA as a critical component in the social interpretations of self and others (Jeannerod 2004), likely in conjunction with the STS, since it responds to the motion of others and not the self (Hietanen & Perrett 1996), and the premotor cortex, since it responds differentially to self and other generated movements (Calvo-Merino et al. 2005, Grèzes et al. 2004).

Considered together, these brain imaging studies imply that cortical regions within the so-called ventral stream pathway are importantly involved in perception of the human body and its activities. Such an involvement is broadly consistent with theories that attribute perception of human motion to a confluence of activity from dorsal and ventral stream brain areas, with the STSp representing a lynchpin within this distributed network (Giese & Poggio 2003, Shiffrar 1994).

Brain Imaging: Social-Emotional Processes

The STS constitutes part of a large neural circuit including the amygdala, the orbitofrontal cortex, and the motor system via the parietal system. These areas are key for the perception of and response to objects and events of social and emotional relevance. Indeed, several recent fMRI studies suggest that STSp is involved in the perception of intention from action. For example, Zacks et al. (2001) found that STSp activation was stronger when an observer viewed an actor switching from one activity to another, as if the goal structure of the action were relevant. Even more compelling are the results of Saxe et al. (2004), in which the same visible action was seen in different contexts that changed the implied intentions of the actor. The associated

hemodynamic responses differed depending on the inferred, not directly visualized, intentions of the actor. Saxe et al. (2004) speculate that previous fMRI studies contrasting full-body point-light sequences with scrambled sequences may have unwittingly been localizing neural areas registering perception of intentional action, not just perception of articulate body motions.

Evidence suggests that STS also is activated when an individual attempts to infer the mental states of another behaving agent (Frith & Frith 1999, Morris et al. 2005). For example, STS activation is found when participants make social judgments about other people (e.g., trustworthiness) in the absence of bodily motion (Winston et al. 2002). Furthermore, STS activation is more strongly coupled to the analysis of expressive gestures than to instrumental gestures (Gallagher & Frith 2004). In any case, it is clear that the STS plays a fundamental role in the perceptual analysis of social cues (e.g., Allison et al. 2000), of which body postures and actions are particularly powerful examples. Indeed, it has been proposed that the STS serves to determine the social significance of actions (Iacoboni et al. 2004).

Given the extensive interconnections between the limbic system, particularly the amygdala, and the STS (Adolphs 1999), one could predict that STS modulation should vary as a function of the emotional content of an action. Consistent with this prediction, STS activity increases during the perception of potentially threatening fear-inducing actions (Wheaton et al. 2001). Converging psychophysical measures indicate that observers are best able to detect the presence of angry people (Chouchourelou et al. 2006). Furthermore, STS activity is strongly modulated by dynamic expressions of emotion (LaBar et al. 2003).

Brain Imaging: Motor Processes

Visual perception of human action is also accompanied by activation in the constellation of brain areas involved in motor planning, including both premotor and primary motor cortex (Grèzes et al. 1998, Hamilton et al. 2006, Raos et al. 2004, Santi et al. 2003). Thus, for example, primary motor cortex, M1, is activated when one person observes another person's hand and arm movements (Decety et al. 1997, Hari et al. 1998), but only when those bodily movements are biomechanically possible (Stevens et al. 2000). This association between sensory and motor activation dovetails nicely with the work in nonhuman primates on mirror neurons described above. Indeed, a correlate of this mirror system has been investigated in human observers (see review by Blakemore et al. 2005), including observers viewing PL animations (Tai et al. 2004), and there is some debate over the extent to which such a system could serve as a basis for social cognition (Jacob & Jeannerod 2005). Regardless how this debate plays out, there is little doubt that the perception of another person's actions involves activation of human brain circuits involved in the generation of such actions by the observer (see reviews by Buccino et al. 2004 and Wilson & Knoblich 2005). For example, premotor cortex is activated by PL animations of human action (Saygin et al. 2004). Furthermore, when ballet and Capoeira dancers watch movies of other people performing these two types of dances, premotor (and left STSp) activation is found when they watch their own dance style (Calvo-Merino et al. 2005). Such evidence substantiates the idea that what we see depends, in part, on what we can do.

CONCLUSION

Humans are highly social creatures, and for that reason it is crucial that we be able to perceive what others are doing and to infer from their gestures and expressions what they may be intending to do. Fortunately, perception of these characteristics is easy because human action readily communicates intentions and feelings. So compelling is the information

conveyed by activity that we even perceive human-like characteristics in nonhuman animals whose behaviors resemble our own.[1] The overarching message of this review—human actions visually radiate social cues to which we are exquisitely sensitive—is not new and can be traced to Darwin's writings (1882). As documented in this article, remarkable advances have been made in our understanding of the perceptual, motoric, affective, and neural concomitants of the perception of human action. These advances, in turn, may offer deeper insights into the etiology of disorders such as autism and schizophrenia, in which core symptoms include deficits in social interactions.

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[1]This strong tendency to anthropomorphize is vividly demonstrated by the visually conspicuous mood states—joyful, sorrowful, fearful, and amorous—we perceive in the emperor penguins in the movie *The March of the Penguins*.

FUTURE ISSUES

1. How does the analysis of human movement diverge from the analysis of nonhuman, animal movement?

2. How do the various neural areas associated with the analysis of human movement interact?

3. Faces and bodies are necessarily connected. How does the perception of one affect the perception of the other?

4. How does motor and social learning modify the perceptual analysis of human action?

5. To what extent can the visual system be understood as an inherently communal mechanism that evolved for the analysis of socially relevant information?

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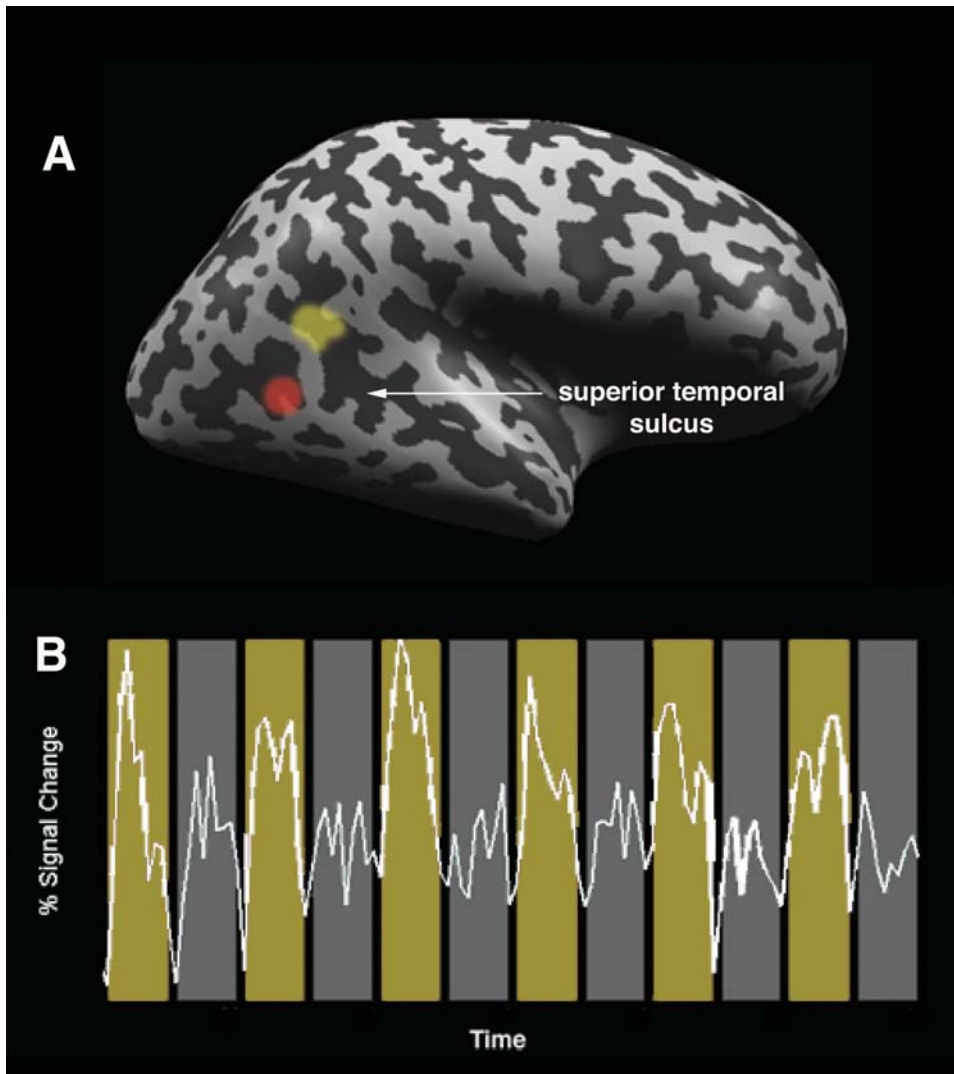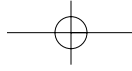
Figure 2

fMRI activation of the posterior portion of the superior temporal sulcus (STSp) upon viewing PL animations. (*A*) Lateral view of the inflated surface of the right hemisphere of the human brain; inflation reveals gyri (*light areas*) and sulci (*dark areas*). The region shown in *yellow* toward the posterior end of the superior temporal sulcus is strongly activated when an observer views PL animations relative to viewing scrambled PL animations. For purposes of reference, motion-sensitive, visual area MT+ is shown in *red*; MT+ responds strongly to both PL and scrambled PL animations. (*B*) Variations over time in fMRI BOLD signal associated with viewing PL animations (*olive-colored bars*) and with viewing scrambled PL animations (*gray bars*). (Redrawn from data collected by Emily Grossman and Chai-Youn Kim.)