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Embodied Motion Perception
*Psychophysical Studies of the Factors
Defining Visual Sensitivity to Self-
and Other-Generated Actions*

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Introduction

Traditionally, the visual system has been understood as a general-purpose processor that analyzes all classes of visual images in the same way (e.g., Marr, 1982; Shepard, 1984). According to this perspective, the same visual processes are employed when observers view objects and people. This is not unrelated to the idea that the visual system is a module (Pylyshyn, 1999) that is "encapsulated" unto itself (Fodor, 1983). While such an approach has produced a plethora of scientific discoveries, it is necessarily limited.

The purpose of this chapter is to confront this modular understanding of the visual system in two steps. The first section will challenge the hypothesis that all visual images are analyzed by the same menu of perceptual processes. This challenge will come from psychophysical studies focusing on the visual analysis of human motion. Human action is often the most frequent, the most psychologically

meaningful, and the most potentially life altering motion in normal human environments. As such, studies of action perception provide a means to understand how the human visual system analyzes a fundamentally important category of motion stimuli. To that end, psychophysical studies will be reviewed that indicate the existence of profound differences between the visual perception of human motion and object motion.

The second section will focus on the question of why; that is, why does the visual perception of human motion differ from the visual perception of object motion? Three possible reasons will be considered. First, human motion is the only category of visual motion that observers can both produce and perceive. As a result, motor processes may selectively contribute to the analysis of and thus selectively increase perceptual sensitivity to human motion. Second, as essentially social animals, human observers have a lifetime of experience watching other people move. From this perspective, human observers may exhibit enhanced perceptual sensitivity to human motion simply because they see so much of it. Finally, human motion carries more social-emotional information than any other category of visual motion. Thus, social-emotional processes might contribute to and facilitate the perception of human movement. Psychophysical tests will be used to investigate each of these possibilities in turn. The take-home message from these studies will be that the visual system cannot be understood as an isolated system. Instead, the visual analysis of human movement depends upon a convergence of motor processes, perceptual learning, and social-emotional processes. But first, does the perception of human motion differ from the perception of object motion?

## Comparing the Perception of Human Motion and Object Motion

Motion is an inherently spatial-temporal phenomenon as it involves the simultaneous change of information over space and time. To perceive movement, our visual system must therefore integrate dynamic changes across space and across time. While each of these processes cannot be understood without the other, researchers traditionally use different techniques to examine each subprocess. That approach will be employed here to compare and contrast the visual integration of human and object motions over space and over time.

Motion Integration across Space

Why does the perception of visual motion require the integration of visual information over space? A primary reason comes from the structure of the visual system itself.

The Aperture Problem

Neurons in early stages of the visual system have relatively small receptive fields that measure luminance changes within very small image regions (e.g., Hubel & Wiesel, 1968). Small measurement areas mean that each neuron can only respond to a tiny subregion of an image. These local measurements must be combined to compute the motion of whole objects. A complication to this combinatorial process results from the fact that the local motion measurements obtained by individual neurons provides only ambiguous information. This ambiguity, illustrated in Figure 4.1, is commonly referred to as the aperture problem. To understand this problem from a spatial perspective, first consider that the motion of any luminance edge can be decomposed into the portion of motion that is parallel to the edge's orientation and the portion that is perpendicular to the edge's orientation. Because a neuron cannot track or respond to the ends of that edge if those ends fall outside of its receptive field, the neuron cannot measure any of the motion that is parallel to the edge. Instead, each motion sensitive neuron can only detect the component of motion that is perpendicular to the orientation of an edge. Because only this perpendicular component of motion can be measured, all motions having the same perpendicular component of motion will appear to be identical even when they differ significantly in their parallel
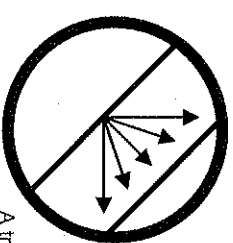
A translating line at time T

The same line at time T + Δt

Figure 4.1   The aperture problem. Whenever a translating line is viewed through a relatively small receptive field, only the component of motion perpendicular to the line's orientation can be measured. As a result, an infinitely large family of different translations that all share the same perpendicular component of motion (illustrated here by the 5 arrows) cannot be distinguished from one another.

components of motion. As a result, a directionally selective neuron will give the same response to many different motions. Because all known visual systems, whether biological or computational, have neurons with receptive fields that are limited in size, this measurement ambiguity has been extensively studied (e.g., Hildreth, 1984; Shiffrar & Pavel, 1991; Wallach, 1976).

How does the visual system compute the motions of whole objects from local measurements that are inherently ambiguous? While local motion measurements are ambiguous, motion measurements from two differently oriented and rigidly connected luminance edges can be unambiguously interpreted (Adelson & Movshon, 1982). When differently oriented edges belong to the same solid object, the integration their motion signals is appropriate. However, when differently oriented edges belong to different objects or to the same nonrigid object, their motion signals should not be integrated but rather segmented or analyzed separately. Indeed, the integration of motion measurements across different objects could have disastrous consequences. Imagine, for example, that you want to cross a street on which two cars are traveling toward each other at equal speeds. If your visual system combined motion measurements across these two cars, then these measurements would cancel each other out (because they are equal and opposite). In this case, your visual motion system would conclude that there is no motion in the street and as a result, you might step out to cross it. Obviously, people having visual systems that work in such a manner are no longer with us. So how does the visual system solve this aperture problem?

The visual system can overcome the ambiguity of local motion measurements by picking image solutions that are local or global in their levels of analysis. At the local level, the visual system can uniquely interpret ambiguous edge motion by relying on visible edge discontinuities. Objects and people have boundary discontinuities such as endpoints (e.g., fingertips and pencil erasers) and regions of high curvature (e.g., elbows and corners) that indicate where one object ends and the next object begins. Motion processes use these local form cues to strike the correct balance between motion integration within individual objects and motion segmentation across different objects. A global solution to the aperture problem involves integrating local motion signals across larger, spatially disconnected image regions. Models of this global integration process include the "intersection of constraints" and vector averaging (e.g., Adelson & Movshon, 1982; H. Wilson, Ferrera, & Yo, 1992).

How does the visual system select the correct level of analysis when dynamic images have different local and global interpretations? In one series of psychophysical studies that examined this question, simple translating and rotating objects were viewed through multiple apertures. Local motion analyses would lead to the interpretation of each visible edge moving independently of the other edges. Global analyses would involve the integration of motion signals across the edges and lead to the interpretation of a coherent moving object instead of the interpretation of multiple edges moving independently (Figure 4.2). The results of these studies demonstrate that the visual system tends to default to local analyses even when local solutions conflict with an observer's prior knowledge of the underlying object's shape (Shiffrar & Lorenceau, 1996; Shiffrar & Pavel, 1991). The same default to local analyses is found when observers view relatively complex nonrigid objects, such as cars and scissors, through apertures (Shiffrar, Lichtey, & Heptulla-Chatterjee, 1997).

(A)

(B) Local Solution
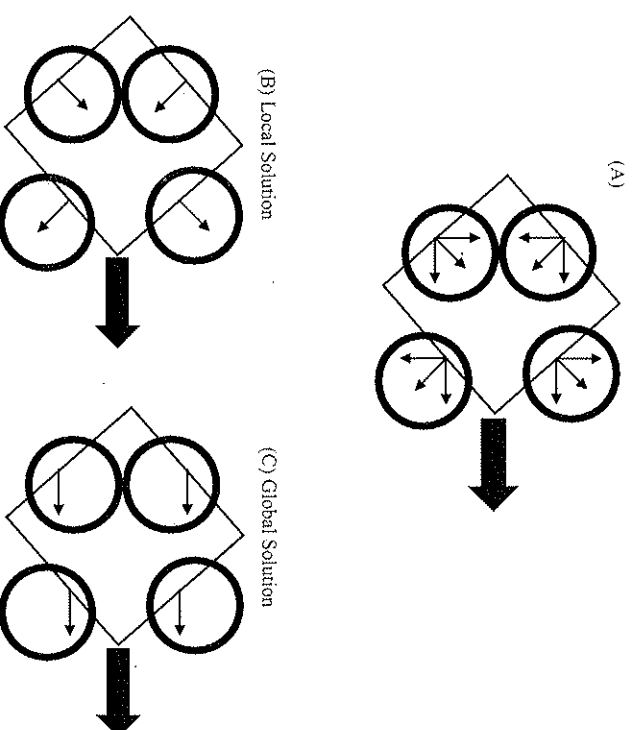
(C) Global Solution

Figure 4.2   Two solutions to the aperture problem. (A) A diamond translates to the right and is viewed through four apertures. The motion measurement within each aperture is ambiguous. (B) In a local interpretation, the motion within each aperture is interpreted independently of the other apertures. As a result, in this case, each line segment appears to translate in the direction perpendicular to its orientation. (C) In a global interpretation, motion signals are integrated across apertures so that all line segments appear to translate in the same, veridical direction.

But something entirely different happens when observers view human motion through multiple apertures. In this case, the visual system defaults to global image interpretations. For example, when a stick figure rendition of a walking person is viewed through apertures, observers readily and accurately interpret the motions of the visible line segments as a coherent, global whole. Typical descriptions of such stimuli include: "a walker," "a man walking," and "someone moving." Conversely, nonrigid object motion, such as a pair of scissors opening and closing, is perceived as globally incoherent when viewed through apertures. Typical descriptions of moving objects seen through apertures include "wormlike things that get longer," "undulating lines," and "a bunch of lines." This pattern of results suggests that the processes underlying the integration of visual motion signals across space differ for human motion and object motion.

Is the integration of human motion signals over space always different from the integration of object motion over space? Psychophysical evidence suggests that only physically possible human actions are more globally integrated. For example, if a person walks impossibly fast or impossibly slow behind a set of apertures, observers default to local interpretations (Shiffrar et al., 1997). If observers view an upside-down person walking behind apertures, they interpret the display locally and hence, do not integrate motion information across the line segments. Thus, only physically possible human movement appears to be integrated over larger spatial extents than object motion. The implications of this finding will become clear during the discussion of the impact of motor experience and visual experience on action perception later in this chapter.

Point-Light Displays

Point-light displays represent another technique that is commonly used to examine motion integration across discontinuous regions of space. This technique was originally developed by Etienne Jules Marey for his studies of human gait in the 1890s (Marey, 1895/1972). In the 1970s, Gunnar Johansson introduced this technique to the vision sciences. In it, small markers or point-lights are attached to the major joints of moving actors, as illustrated in Figure 4.3A. The actors are filmed so that only the point-lights are visible in the resultant displays (see Figure 4.3C). Even though a vast amount of information is removed from the original stimuli, observers of the
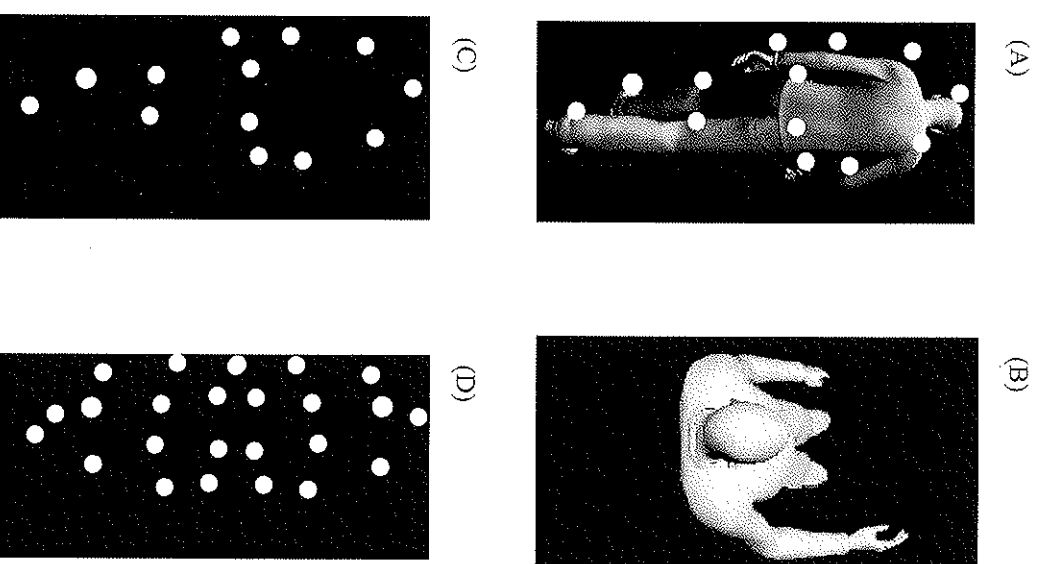
Figure 4.3 Point-light walker displays. (A) Markers are placed on the main joints and head of a walking person viewed from a sagittal perspective (B) An egocentric or allocentric view of a point-light walker (C) In the experimental displays, only the motions of the point-lights are visible. (D) Point-light walkers can be masked with additional points moving with the same trajectories.

resultant point-light displays readily perceive human motion (e.g., Johansson, 1973, 1976). Indeed, from point-light displays alone, observers can accurately determine an actor's gender (Pollick, Key, Heim, & Stringer, 2005), emotional state (Clarke, Bradshaw, Field, Hampson, & Rose, 2005), and deceptive intent (Runeson & Frykholm, 1983).

The results of studies using point-light displays similarly support the hypothesis that the visual perception of human movement depends upon a mechanism that globally integrates motion signals across space (e.g., Ahlström, Blake, & Ahlström, 1997; Bertenthal & Pinto, 1994; Cutting, Moore, & Morrison, 1988). One approach to this issue involves the presentation of point-light walkers within point-light masks (Figure 4.3D). A point-light mask can be constructed by redistributing the spatial locations of each point from one or more point-light walkers. The size, luminance, and velocity of the points remain unchanged. Thus, the motion of each point in the mask is identical to the motion of one of the points defining the walker. As a result, only the spatially global configuration of the points distinguishes the walker from the mask.

The finding that subjects are able to detect the presence as well as the gait direction of an upright point-light walker hidden within a point-light mask indicates that the mechanism underlying the perception of human movement operates over large spatial scales (Bertenthal & Pinto, 1994). When the same masking technique is used with nonhuman motions, such as arbitrary figures (Hiris, Krebeck, Edmonds, & Stout, 2005), and horses (Pinto & Shiffrar, 2007), significant decrements are found in observers' ability to detect these nonhuman objects. These results add further support for the hypothesis that observers are better able to integrate human motion than nonhuman motion across disconnected regions of space.

Motion Integration across Time

Psychophysical researchers have traditionally used the phenomenon of apparent motion to investigate the temporal nature of visual motion processes. In classic demonstrations of apparent motion, two spatially separated objects are sequentially presented so that they give rise to the perception of a single moving object. Early studies demonstrated that apparent motion percepts depend critically upon the relationship between the temporal and spatial separations of the displays (Korte, 1915; Wertheimer, 1912). Indeed, these early studies triggered the establishment of Gestalt psychology by demonstrating that perception differs from the summation of stimulus attributes (Ash, 1995).

In all apparent motion displays, the figure(s) shown in each frame can be connected by an infinite number of possible paths. Observers typically report seeing only the shortest possible path of apparent motion (e.g., Burt & Sperling, 1981) even when that shortest path is physically impossible. This phenomenon is commonly referred to as the shortest path constraint. An example can be found in old Western movies showing horse drawn wagons in motion. Interestingly, the wagon wheels sometimes appear to rotate rapidly in the wrong direction (Shiffrar, 2001). This perceptual illusion is an example of the shortest path constraint. Because the continuous rotational motion of the wheel spokes is depicted via discontinuous movie frames, the wheel spokes can physically rotate farther between frames than the interspoke distance. When this happens, the shortest distance between spokes can be backwards rather than forwards. As a result, observers perceive backward wagon wheel rotation. Even though such motion is physically impossible, observers nonetheless see it clearly. Thus, observers perceive the shortest possible paths of apparent object motion even when those paths are physically impossible.

An interesting violation of this shortest path constraint is found with human motion. When humans move, their limbs follow curvilinear trajectories. As a result, the shortest, rectilinear path connecting any two limb positions is inconsistent with the biomechanical limitations of human movement. Given the visual system's shortest-path bias, this raises of question of whether observers of human movement perceive paths of apparent human movement that traverse the shortest possible distance or paths that are consistent with the movement limitations of the human body. This question has been tested in studies of apparent motion perception with stimuli consisting of photographs of a human model in different poses. The poses were selected so that biomechanically possible paths of apparent human motion conflicted with the shortest possible paths (Shiffrar & Freyd, 1990, 1993). For example, one stimulus consisted of two photographs of a standing woman with her right arm positioned on either side of her head (Figure 4.4). The shortest path connecting these two arm positions would require the arm to pass through the head while a biomechanically plausible path would require the arm to move around the head. When subjects viewed such stimuli, their perceived paths of motion changed with the stimulus onset asynchrony (SOA) or the amount time between the onset of

one photograph and the onset of the next photograph. At shorter SOAs, subjects perceived the shortest, physically impossible motion path. With increasing SOAs, observers were increasingly likely to see apparent motion paths consistent with the biomechanical constraints on human movement (Shiffrar & Freyd, 1990). Conversely, when viewing photographs of inanimate control objects, subjects consistently perceived the shortest path of apparent object motion at all SOAs. Importantly, when viewing photographs of a human model positioned so that a short path is biomechanically plausible, observers always reported seeing this short path (Shiffrar & Freyd, 1993). Thus, subjects do not simply report the perception of longer paths with longer SOAs. Moreover, observers can perceive apparent motion of nonbiological objects in a manner similar to apparent motion of human bodies. However, these objects must contain a global hierarchy of orientation and position cues resembling the entire human form before subjects perceive humanlike paths (Heptulla-Chatterjee, Freyd, & Shiffrar, 1996). This pattern of results suggests that human movement is analyzed by motion processes that operate over relatively large temporal windows and that take into account the biomechanical limitations of the human body.

This conclusion is further supported by studies of point-light walkers. When observers are asked to detect point-light walkers in a mask, walker detection performance is above chance even when significant temporal gaps are inserted between the frames (Thornton, Pinto, & Shiffrar, 1998). Since the perceptual interpretation of point-light displays requires spatially extended motion processes, and since apparent motion displays require temporally extended motion integration, this result suggests that observers can integrate human motion, but not object motion, over unusually large spatio-temporal extents.

Figure 4.4 Apparent human motion displays. Two frames depict a woman positioning her hand in front of and behind her head. At shorter SOAs, her hand appears to translate through her head. As SOAs increase, her hand increasingly appears to move around her head.

The studies described above depended upon different methodologies. Nonetheless, the results of these behavioral studies converge with imaging brain data (e.g., Virji-Babul, Cheung, Weeks, Kerns, & Shiffrar, 2007) to suggest the same conclusion; namely, that the visual analysis of human movement differs from the visual analysis of object movement. This difference appears to be profound since it affects early visual processes such as the integration of motion information over discontinuous spatial and temporal extents. One implication of this difference is that the visual perception of human motion can tolerate more noise than the visual perception of object motion. Such robust perceptual analyses of human action allow observers to extract copious information from highly degraded depictions of human action. The goal of the next section of this chapter is to examine some possible factors that might give rise to this impressive perceptual ability.

Why Do Action Perception and Object Perception Differ?

The previous section outlined some of the evidence suggesting that the visual analysis of human motion differs fundamentally from the visual analysis of object motion. This section will address three possible reasons for this difference. First, human motion is the only category of visual motion that human observers can both produce and perceive. Human observers have an action control system that can reproduce the movements of other people, but not the movements of crashing waves or wind blown trees. As a result, input from an observer's own motor system might selectively enhance the perceptual analysis of human action (see Knoblich chapter for more discussion on this topic). Second, as inherently social animals, human observers have a lifetime of experience watching other people move. Thus, extensive visual experience with human action might account for differences between the visual analysis of object and human motion. Finally, human movement carries more socially relevant information than object motion. This raises the question of whether social-emotional processes might contribute to the visual analysis of human motion and thereby differentiate human motion perception from object motion perception. Each of these factors is considered below.

Motor Expertise

Does the human visual system take advantage of the wealth of information available in the observer's own motor system during the perceptual analysis of other people's actions? If motor processes contribute to the visual analysis of human movement, then motor activity should be found during the perceptual analysis of human movement but not object movement. Research on mirror neurons in macaques (e.g., Rizzolatti, Fogassi, & Gallese, 2001) and humans (e.g., Iacoboni, Woods et al., 1999) supports this prediction. Mirror neurons, first discovered in the ventral premotor cortex of the macaque, respond both when an observer performs an action and when that observer watches someone else perform the same action (Rizzolatti et al., 2001). That is, watching another individual perform some action triggers activation of the observer's motor representation of that action. Increasing evidence suggests that the perception, interpretation, and identification of other people's actions depend upon activation of the observer's motor planning system (e.g., Blake & Shiffrar, 2007; Prinz, 1997; Wilson, 2001).

Other imaging work has directly compared the perception of human motion and object motion. In one such study, PET activity was recorded while subjects viewed apparent motion sequences of human and object movement (Stevens, Fonlupt, Shiffrar, & Decety, 2000). As before (Shiffrar & Freyd, 1990, 1993), this study used two types of apparent motion stimuli. Human action picture pairs showed a human model in different positions in which the biomechanically possible paths of movement conflicted with the shortest, physically impossible paths (see Figure 4.4). The second set of picture pairs consisted of nonliving objects positioned so that the perception of the shortest path of apparent motion would require one solid object to pass through another solid object. When the human picture pairs were presented slowly (with SOAs of 400 ms or more), subjects perceived biomechanically possible paths of apparent human motion. Under these conditions, PET scans indicated significant bilateral activity in observers' primary motor cortex and cerebellum. However, when these same picture pairs were presented more rapidly (with SOAs less than 300 ms), subjects then perceived the shortest and physically impossible paths of human movement, and selective motor system activity was no longer found (Stevens et al., 2000). Conversely, when the pictures of objects were presented

at either fast or slow SOAs, no motor system activation was indicated. Thus, the observation of physically possible actions triggers activation of the observer's action control system. This conclusion is consistent with common coding theory (Prinz, 1997) in suggesting that perceptual and motor systems share representations for the same actions. Indeed, much evidence indicates that common motor areas are active during the observation and the planning of movement (e.g., Decety & Grezes, 1999). Since motor system activation does not occur during the observation of biomechanically impossible actions (Stevens et al., 2000), it appears that the ability to plan an observed action is critical (Wilson, 2001).

The above neurophysiological findings are not immune to an alternative interpretation. That is, does motor system activation during action perception actually alter perceptual processes? Or, does it reflect some automatic planning of motor responses to the observed actions? Psychophysical studies indicate that motor processes significantly impact perceptual processes and that this perceptual-motor interaction differentiates human motion perception from other categories of visual motion perception. Studies of the two-thirds power law provide a clear example (e.g., Viviani & Stucchi, 1992). This law describes the algebraic relationship between the instantaneous velocity and radius of curvature for trajectories produced by unconstrained human movements. An extensive series of psychophysical studies has indicated that visual perception is optimal for movements that are consistent with the two-thirds power law. Movements that violate this fundamental principle of human movement are not accurately perceived (Viviani, 2002). Thus, it can be argued that the human visual system is optimized for the analysis of human generated movements. This optimization suggests that motor system activation during action perception reflects the impact of motor processes on perceptual processes.

Additional support for the hypothesis that motor processes impact perceptual processes during action perception comes from studies of perception by acting, rather than passive, observers. These studies show than the perception of other people's actions depends upon the actions being performed by the observer. For example, when observers perform a speed discrimination task that requires them to compare the gait speeds of two point-light walkers, their perceptual sensitivity to gait speed depends upon whether they themselves stand, walk, or ride a bicycle during task performance (Jacobs & Shif-

frar, 2005). Walking observers demonstrated the poorest perceptual sensitivity to the speeds of other people's gaits. This performance decrease likely reflects competing demands for access to shared representations (e.g., Prinz, 1997) that code for both the execution and perception of the same action. Other studies have shown that the perceptual ability to interpret the weight of a box being lifted by another person depends on the weight of the box being lifted by the observer (Hamilton, Wolpert, & Frith, 2004). Thus, moving and stationary observers can perceive human movement very differently. This difference provides further support for the hypothesis that motor processes impact the visual analysis of human action.

Under real world conditions, observers frequently analyze the movements of other people for the purpose of action coordination. This process requires moving observers to compare their own actions with the actions of other people. Psychophysical research indicates that when observers move, their ability to compare their own actions with the actions of another person depends upon the potential for action coordination. When action coordination is possible, visual analyses of gait speed depend upon the observer's own gait speed, exertion level, and prior walking experience (Jacobs & Shiffrar, 2005). Conversely, when the same gait speed discriminations are performed under conditions in which action coordination is impossible, gait speed perception is independent of the observer's gait speed, effort, and prior walking experience. Thus, moving observers perform visual analyses of human movement that are distinct from the visual analyses performed by stationary, noninteractive observers.

Finally, recent research shows that motor learning significantly influences action perception. For example, observers can improve their perceptual sensitivity to unusual actions by repeatedly executing those actions while blindfolded (Casile & Giese, 2006). Thus, motor learning enhances visual sensitivity to the motor behaviors of other people. Consistent with this, motor system activation is found when ballet and capoeira dancers watch movies of other people performing the dance style that they themselves perform (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005). Furthermore, studies of patients with disorders of motor behavior support the impact of motor processes on action perception. One such study assessed the visual analysis of human action by children with motor impairments resulting from Down's syndrome (Virji-Babul, Kerns, Zhou, Kapur, & Shiffrar, 2006). In these studies, children with Down's syndrome

and matched controls made perceptual judgments of point-light displays of moving people and objects. Children with Down's syndrome demonstrated significant decrements in their perceptual analyses of point-light actions.

Does perception-action coupling require action performance or simply action representation? Since common motor areas are active during action observation and planning, the ability to plan an action may be sufficient to differentiate action perception and object perception. This issue was addressed when observers born without hands were asked to interpret apparent motion displays of hand rotations (Funk, Shiffrar, & Brugger, 2005). The perception of apparent hand rotation depended upon whether observers had a mental representation or "body schema" of their own hands. An individual who was born without hands, and apparently lacking a hand schema, consistently perceived biomechanically impossible paths of apparent hand rotation at all SOAs. Conversely, another individual who was born without hands but nonetheless having hand schema (as assessed by the presence of phantom sensations of congenitally missing limbs, among other measures) did not differ from "handed" control observers in her perception of paths of apparent hand rotation. That is, at short SOAs, she and control observers reported the perception of physically impossible paths of apparent hand rotation. At long SOAs, she and control observers reported the perception of biomechanically possible paths of apparent hand rotation. Evidently, the ability to represent executable actions constrains the ability to perceptually interpret similar actions performed by other people (Shiffrar, 2006). Thus, one need not physically execute an action to alter one's perception of that same action in others. Instead, the ability to represent an action appears to be sufficient.

Visual Expertise

According to Johansson (1973), observers form vivid percepts of human movement from point-light displays because they have extensive prior experience watching or perceptually "overlearning" human movements. While Johansson's theory proposed that the same grouping principles apply to both human and object motion, he nonetheless argued that the vividness with which point-light displays of human action are perceived results from observers' greater visual experience with human motion.

A more recent study supports the visual experience hypothesis of human motion perception (Bülthoff, Bülthoff, & Sinha, 1998). In this experiment, observers viewed point-light displays of human walkers and rated the degree to which each figure looked human. Displays that retained their normal 2D projection, even when scrambled in depth, were rated as highly human. That is, despite considerable anomalies in three-dimensional structure, observers still perceived the point-light human walkers as human. Such data suggest that visual experience with the human form significantly impacts the perceptual organization of human movement. Indeed, visual experience was strong enough to override substantial depth distortions.

Eleanor Gibson argued that only behaviorally relevant experience influences perceptual sensitivity (Gibson, 1969). Consistent with this, visual experience influences action perception under behaviorally relevant experimental conditions. For example, in one study, observers viewed point-light displays of walking friends (Jacobs, Pinto, & Shiffrar, 2004). Gait type was manipulated such that point-light friends performed commonly occurring gaits and rare gaits. Observers' ability to report the identity of each point-light walker depended upon the frequency of gait occurrence. Walker identification was significantly better with common gaits than with rare gaits. Since observers presumably have more real world experience watching their friends walk with common gaits, such data support the hypothesis that visual sensitivity to human movement depends upon visual experience. Since observers have a lifetime of experience watching other people move, such extensive visual experience with human movement might help to differentiate it from the visual perception of object movement. Consistent with this, imaging data indicate that neural activity in an area known to process human motion, the posterior region of the superior temporal sulcus (e.g., Bonda et al., 1996; Oram & Perrett, 1994), is modulated by visual experience (Grossman & Blake, 2001). Furthermore, computational models have shown that numerous aspects of human motion perception can be explained by visual experience alone (e.g., Giese & Poggio, 2003).

Motor Experience vs. Visual Experience

The above studies suggest that the visual analysis of human movement depends on both visual experience and motor experience.

Which type of experience has the larger impact on action perception? One study examined this question by presenting observers with point-light movies of their own movements, the movements of their friends, and the movements of strangers (Loula, Prasad, Harber, & Shiffrar, 2005). Every observer has the greatest motor experience with his or her own actions. Observers have the greatest visual experience with saggital views of the actions of frequently observed friends. Since observers have neither specific motor nor visual experience with the actions of strangers, stranger motion can serve as a baseline control stimulus. To the extent that motor experience defines the visual analysis of action, observers should be best able to recognize their own movements. If view dependent visual experience is the primary determinate of visual sensitivity to human movement, then observers should be most sensitive to the movements of their friends. Finally, the relative impact of motor experience and visual experience on the visual analysis of human motion can be assessed by the relative magnitude of these two effects.

To test these predictions, point-light displays were created of participants, their friends, and strangers performing a variety of actions. Participants were recruited so that everyone in each triplet had the same gender and body type to ensure that neither gender (Pollick et al., 2005) nor weight (Runeson & Frykholm, 1983) could serve as the basis for discrimination. During stimulus construction, participants were told that they were assisting in the creation of stimuli for a study of action, rather than actor, perception. As a result, participants naturally mimicked the action styles modeled by the same experimenter.

Two to three months after the point-light displays were created, participants returned to the lab to perform a two alternative forced choice identity discrimination task. Each trial consisted of two short movies depicting two different point-light defined actions (e.g., someone walking in movie 1 and someone jumping in movie 2). On half of the trials, the two movies depicted the same person. This person could have been the observer, the observer's friend, or the observer's matched stranger. On the other half of the trials, the two movies depicted two different people. After viewing both movies, observers reported with a button press whether the two movies depicted the same person or two different people. Observers demonstrated the greatest perceptual sensitivity to point-light displays of their own actions. Since observers have the greatest motor experience with their own movements, this result supports the hypothesis that motor

processes contribute to the visual analysis of human movement (e.g., Prinz, 1997; Shiffrar & Pinto, 2002; Viviani & Stucchi, 1992). Importantly, task performance with the friend stimuli was superior to performance with the stranger stimuli. This result supports the hypothesis that visual sensitivity to human movement depends upon visual experience (e.g., Bulthoff et al., 1998; Giese & Poggio, 2003; Johansson, 1973). Lastly, the relative sizes of the effects indicated that motor experience is a significantly larger contributor to the visual analysis of human movement, at least in the case of identity perception. The results of a subsequent series of control studies suggested that this pattern of results depends upon motion processes, stimulus orientation, and action type (Loula et al., 2005).

The ability to differentiate self from other generated actions may depend upon an observer's ability to predict the outcome of an observed action. Indeed, observers are better able to predict the outcomes of their own actions. For example, when participants viewed videos of themselves and strangers throwing darts at a target, they were better able to predict the results of their own dart throws than the dart throws of strangers (Knoblich & Flach, 2001). Taken together, these results suggest that motor processes are a major contributor to the visual analysis of human movement.

Controlling for Viewpoint Dependent Visual Experience
While the above findings paint a compelling picture of the importance of motor experience in the perceptual analysis of human action, a potentially important factor muddles this picture. Simply put, motor experience is inherently confounded with visual experience. Every time you gesture or walk down the stairs, you see your own actions. This raises the question of whether enhanced perceptual sensitivity to one's own actions might result, fully or in part, from the massive observational experience that people have with their own actions.

The frequencies with which one produces and perceives one's own actions are naturally confounded. Viewpoint manipulations offer a means of decoupling them. Observers have a lifetime of experience perceiving their own actions from an egocentric or first-person viewpoint (Figure 4.3B). Conversely, aside from watching oneself in a mirror, observers have little experience perceiving their own actions from an allocentric or third-person viewpoint. Obviously, the reverse pattern holds for the perception of other people's actions

since observers view others, by definition, from a third-person perspective (Figure 4.3A). To the extent that viewpoint dependent visual experience defines performance in identity perception tasks, observers should show the greatest perceptual sensitivity to first-person views of their own actions. Conversely, to the extent that observers construct representations of themselves with the same neural processes with which they represent other people, observers should show the greatest perceptual sensitivity to third-person views of their own actions and the actions of other people (Jeannerod, 2003).

To test these predictions, participants viewed point-light movies of themselves, friends, and strangers performing various actions from first-person and third-person viewpoints. Performance on the same identity discrimination task described above suggests that, at least for the purpose of identity perception, observers demonstrate significantly greater perceptual sensitivity to their own actions from the third-person view than from the first person view. Thus even though observers have the most visual experience with egocentric views of their own actions, self-recognition from those views is very poor (Prasad & Shiffrar, 2008). This result indicates that enhanced self-recognition cannot be attributed to visual experience.

What about Bodily Form?
The proposal that observers use their own motor system to analyze the actions of other people implicitly assumes that observers somehow overlook significant differences between their own bodies and other people's bodies. That is, the ability to map one's own motor experience onto someone else's actions necessitates a matching or alignment of executable and perceived actions. Developmental research suggests that people may come into the world primed for such egocentric body matching (Meltzoff & Moore, 2002). Patient research suggests that the detection of a correspondence between observed motion patterns and the observer's own body representation triggers motor-based analyses of human motion (e.g., Funk et al., 2005). When no correspondence can be found between an observer's representation of his or her own body and that observer's perception of other people's bodily actions, those actions appear to be analyzed as objects; that is, without the benefit of motor processes (Funk et al., 2005). Similarly, when observers view point-light depictions of a moving actor in which the actor's limbs are re-positioned so that they are inconsistent with the normal hierarchical structure

of human bodies, perceptual sensitivity to that motion drops significantly (Pinto & Shiffrar, 1999). Similar results are found with the perception and representation of static body postures (Reed & Farah, 1995; see also the chapter by Reed and colleagues in this volume).

Obviously, different people have differently shaped bodies. If a mechanism exists to find correspondences between an observer's own body schema and percepts of other people's actions, then this mechanism must be able to tolerate commonly occurring variations in people's bodies. While body motion depends upon body shape, it remains to be seen how observers perceive human actions across commonly occurring variations in body shape.

The existence of mirror neurons in macaque monkeys that respond during the monkey's production of an action and during the perception of a human performing that same action (Rizzolatti et al., 2001) suggests bodily form differences can be dismissed. Macaques and humans differ significantly in body height, body weight, and limb proportions. Yet, mirror neurons appear capable of coding action similarities across these body differences. It may be that the system that matches an observer's own body representation with observed actions relies on low spatial frequency cues to global body structure (Heptulla-Chatterjee et al., 1996). If so, this might explain why mirror neurons respond as they do and why, for example, observers can be "fooled" by appropriately positioned rubber hands (Botvinick & Cohen, 1998). This body matching process should fail, in a graded fashion, whenever the low spatial frequency content of an observed body differs substantially from the observer's internal representations of his or her own body (Cohen, 2002; Funk et al., 2005; Pinto & Shiffrar, 1999). If the matching process outlined above actually exists, then observers should be able to overlook bodily differences during the perceptual analysis of human actions.

Previous research findings suggest that observers can recognize their own actions in the absence of bodily form cues (e.g., Knoblich & Prinz, 2001) because velocity changes alone may be sufficient for identity perception (e.g., Knoblich & Flach, 2001). If action recognition depends upon an observer's ability to plan the actions that they observe, then observers should be able to identify their own actions even when those actions are presented on someone else's body. Sapna Prasad and her colleagues tested this hypothesis with the identity discrimination task described above, but modified such that a set of different bodies were superimposed on the actions of

the observers, their friends, and matched strangers. On each trial of this task, observers viewed a short movie of their own actions, the actions of their friends, or the actions of their assigned strangers. These actions appeared on either skeletal bodies (containing no form cues to gender or a specific identity), humanoid bodies (containing form cues to gender but not identity), and character bodies (containing form cues to both gender and identity). After watching each movie, observers reported who they thought had originally produced the action depicted in that movie. Identification performance in this task was found to be independent of body form cues to gender or identity. That is, with all three body types, observers demonstrated the greatest sensitivity to their own actions. Thus, observers can overlook commonly occurring differences in body form as they map representations of their own executable actions onto their perceptions of the actions performed by other people.

Social-Emotional Processes

Do social processes contribute to the visual analysis of human movement? Since human action contains more socially relevant information than any other category of motion stimuli, contributions from social processes to the perception of human action might help to differentiate action perception from object perception.

While the question of whether social processes contribute to action perception has been largely ignored in behavioral studies of visual perception, it is increasingly studied in the rapidly emerging field of social neuroscience. For example, activity in the superior temporal sulcus (STS) is associated with the visual analysis of human movement (e.g., Grossman & Blake, 2002; Hasson, Nir, Levy, Fuhrmann, & Malach, 2004). The STS also plays an important role in social processes (Iacoboni et al., 2004) such as the inference of other people's mental states (Frith & Frith, 1999; Morris, Pelphrey, & McCarthy, 2005). Furthermore, STS activity has been found during social judgments in the absence of bodily motion (Winston, Strange, O'Doherty, & Dolan, 2002). Thus, the STS is increasingly understood as an area involved in the perceptual analysis of social information (e.g., Allison, Puce, & McCarthy, 2000). Human observers readily extract extensive social information such as intent (Runeson & Frykolm, 1983), social dominance (Montepare & Zebrowitz-

McArthur, 1988), emotional state (Clarke et al., 2005; Dittrich, Troscianko, Lea, & Morgan, 1996), gender (Kozlowski & Cutting, 1977; Pollick et al., 2005), and sexual orientation (Ambady, Hallahan, & Conner, 1999) from human motion. When considered together, such findings suggest that social-emotional processes may contribute to the visual analysis of human movement. The two series of psychophysical studies described below tested this hypothesis.

Social Context and Apparent Human Motion

To investigate whether social processes impact the visual analysis of human motion, observers viewed two-frame apparent motion sequences in which the same human actions were presented in social and nonsocial contexts (Chouchourelou & Shiffrar, 2008). This approach is based on the assumption that any differences in motion perception across context variations must be attributable to the contexts since the action is unchanged. The interactions of two people were filmed and two frame apparent motion sequences were created from resulting movies. These picture pairs were further edited so that the displaced images of one actor were removed from both pictures, as shown in Figure 4.5. From this, four conditions were rendered. In the no-context condition, the only the moving actor was displayed. In the human context condition, a single stationary picture of a social human partner was added. For the single-object condition, a refrigerator appeared in the stationary actor's positions. Finally, in the object-specific condition, an object closely related to each specific action was added. Thus, each participant viewed identical human displacements against one of four different contexts. This also provided a test of the hypothesis that the visual analysis of person directed actions differs from the visual analysis of object directed actions (Jacobs & Jeannerod, 2003). If social processes contribute to the visual analysis of human movement, then assessments of apparent motion strength should be context dependent.

Naïve observers in this experiment were told that they were participating in a study of computer monitor quality. Participants were informed of the phenomenon of apparent motion. They then viewed pairs of sequentially presented images of human movements across interstimulus intervals ranging from 10 to 600 ms and rated the strength of apparent motion on each trial. The results indicated that the same displacements of apparent human motion are experienced
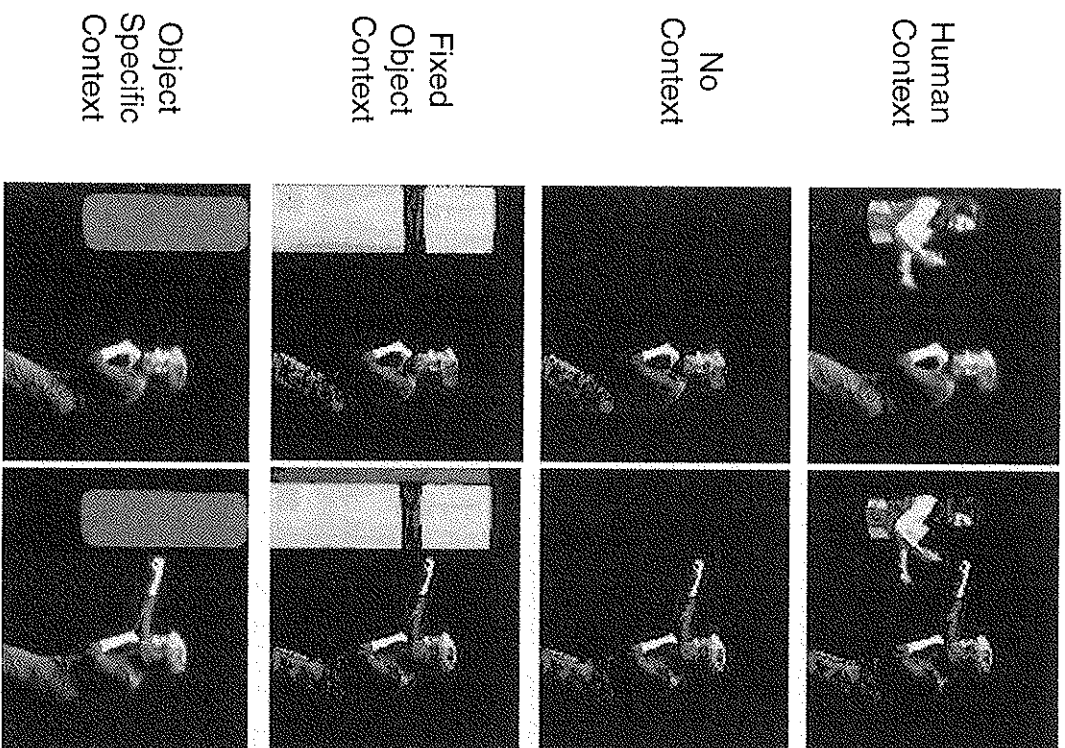
Human
Context

No
Context

Fixed
Object
Context

Object
Specific
Context

Figure 4.5 The two images of the actors were taken from movies of natural social interactions. Across the 4 picture pairs, only the image of the actor on the right changes. All other images are stationary. The moving actor appears in a human context in the top row, devoid of context in the second row, in the context of a refrigerator in the third row, and in the context of an action appropriate punching bag in the bottom row.

very differently as a function of the context. Participants rated human actions directed toward another person as providing more motion than the identical actions directed towards objects or nothing. Since physically identical displacements were perceived differently as a

function of their social context, these results support the hypothesis that social processes significantly impact human action perception (Chouchourelou & Shiffrar, 2008).

In a follow-up control study, apparent motion was assessed with two different sets of actions: person-directed and object-directed. These two sets of actions produced equivalent ratings of apparent motion when shown in isolation. However, when a stationary context was added to each, such that the depicted actions were directed toward people or objects, apparent motion ratings diverged. Person-directed actions received significantly stronger ratings of apparent motion than object-directed actions. These results further support the hypothesis that social processes, per se, facilitate the visual perception of human action.

Perceptual Sensitivity to Emotional Actions

Extensive neurophysiological data point to substantial interconnections between the neural areas involved in the visual analysis of point-light displays of human movement (e.g., STS) and the limbic areas (e.g., amygdala) underlying the analysis of emotion (Brothers, 1997; Puce & Perrett, 2003). These interconnections could serve at least two information processing circuits. First, visual analyses of human action in the STS could be passed on after they are completed to the amygdala for subsequent emotional analysis. According to this model, action detection should be independent of emotional processes since visual processes are completed before emotional processes are initiated. A second possibility is that action analyses in the STS are conducted in interactive collaboration with emotional processes in the amygdala. From this perspective, action detection should be emotion dependent. Given the role of the amygdala in threat detection (e.g., Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003), any interdependence of action detection and emotion should be most evident during the perception of threatening actions.

A series of psychophysical studies compared these two hypotheses through an examination of the visual detection of emotional actions (Chouchourelou, Matsuka, Harber, & Shiffrar, 2006). Point-light movies of walking actors portraying different emotions were constructed so that each point-light walker's emotional state was equally recognizable. These stimuli were placed in specially constructed

masks for a walker detection task. On each trial, a point-light walker either was or was not presented within a mask of identically moving points. Participants simply reported whether or not they saw a walker. Emotion was never discussed or judged. Nonetheless, the results of this study indicated that walker detection was significantly modulated by walker emotion as participants demonstrated the greatest visual sensitivity to the presence of angry walkers. Thus, emotional body expressions can affect the perceptual detection of human action. Such a dependence of emotion on action detection may reflect the existence of an integrated processing circuit between the STS and amygdala. Enhanced detection of threatening actions may represent an important condition under which emotional processes impact perceptual analyses. In sum, emotional processes can define when and how we perceive the actions of other people.

Conclusions

Taken together, the experimental results described above indicate that the visual perception of human movement is a complex phenomenon that depends upon multiple factors including motor planning, visual experience, and emotional processes. Such a conclusion directly challenges modular views of the visual system which assume that vision is unaffected by nonvisual processes. Instead, the current results suggest that what we see depends upon what we have seen in the past, how we move, and how people behave socially. These three processes are likely interdependent. For example, visual experience and motor experience naturally covary as observers most frequently see the same actions that they most commonly perform. Furthermore, the ability to map motor information from our own bodies onto the perceived world likely enables us to become socially attuned beings (see Knoblich chapter). Indeed, we may come into this world ready and able to search for similarities between our actions and those of other people (Meltzoff & Moore, 2002). If so, then the current results can be understood as suggesting that the human visual system is optimized for the organization and analysis of information that matches the observer's own body. The ultimate result of such a perceptual-motor system is a body-based view of the world (Shiffrar, 2006).

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