19   The visual analysis of bodily motion

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Abstract. Does the visual system process human movement differently from object movement? If so, what are the criteria that the visual system uses to discriminate between human and non-human motions? A series of psychophysical studies was conducted to address these questions by examining the conditions under which the visual perception of human and object motions appears to rely on similar and different mechanisms. To determine whether motion integration across space is similar for human and non-human movements, observers viewed moving stimuli through a set of spatially disconnected apertures. Under these conditions, motion integration across space was found to significantly differ for human and object movements as long as the human movement was upright and consistent with normal locomotion. An apparent-motion paradigm was used to investigate motion integration across time. It was found that human and object movements are similarly perceived at brief temporal intervals. However, important differences arise at slower display rates. Finally, recent PET data indicate motor-system activity during the perception of possible, but not impossible, human movements. When considered together, these results support the hypothesis that the visual analysis of human movement does differ from the visual analysis of a wide variety of non-human movements whenever visual motion signals are consistent with an observer's internal representation of possible human movements.

19.1 Introduction

Over the past thirty years, researchers have repeatedly noted that human observers demonstrate an exquisite visual sensitivity to the movements of other people. Such statements imply that our visual sensitivity to human movement must differ from, or even be superior to, our visual sensitivity to the movements of non-human objects. Does the visual analysis of human movement actually differ from other motion analyses? If so, under what conditions?

The identification of significant differences between the visual analysis of human and non-human movements would be important because it would challenge the commonly held assumption that the visual system is a general-purpose processor that analyzes all visual stimuli in the same manner. An alternative to the general-purpose processor approach is the proposal that the visual analyses may be best understood in relation to the motor outputs they subserve (e.g. Bridgeman 1992, this volume, Chapter 5; Goodale and Milner 1992; Milner and Goodale 1995; Prinz 1997; Rossetti and Pisella, this volume, Chapter 4). It should be fairly obvious that the visual perception of a waving friend and a wind-blown tree are normally associated with different motor responses on the part of the observer. I might wave back to a friend, but I would never wave back to a swaying tree. Thus, the intimate connection between human social behavior and human movement perception may render some separation between human and non-human motion analyses.

Increasingly, neurophysiological evidence supports the existence of neural mechanisms dedicated to the analysis of primate movement. For example, single-cell recordings in the anterior superior temporal polysensory area (area STPa) of the monkey have repeatedly identified cells that are conjointly sensitive to particular primate forms and motions (e.g. Bruce, Desimone, and Gross 1981;

Jellema and Perrett, this volume, Chapter 18; Oram and Perrett 1994; Perrett, Harries, Mistlin, and Chitty 1990). Consistent with this, human brain-imaging studies have revealed that neural responses in this region are tied to the perception of simplified displays of human dance (Bonda, Petrides, Ostry, and Evans 1996). Other single-cell recordings have resulted in the identification of 'mirror neurons' in the premotor cortex that respond selectively when a monkey performs some action and when that monkey watches another monkey or a human perform the same action (Gallese *et al.* this volume, Chapter 17; Rizzolatti, Fadiga, Gallese, and Fogassi 1996). Again, in the human, when subjects passively observe the actions of another human so that they can later imitate those actions, selective PET activity is found in premotor cortex (Decety *et al.* 1997). These findings are particularly intriguing because they suggest that the visual perception of human action may involve a functional linkage between the perception and production of human motor activity that is absent from the perception of object movement (Viviani, this volume, Chapter 21; Viviani, Baud-Bovy, and Redolfi 1997). We shall return to this point later.

Thus far, we have been very careful to draw a simple distinction between human movement and non-human movement. Given the findings from the above single-cell recording experiments in which monkey STPa and mirror neurons respond to both human and monkey movement, this human–non-human dichotomy is probably misleading. Numerous potential dichotomies present themselves as possible alternatives, including primate versus non-primate, animal versus non-animal, animate versus inanimate, living versus non-living, etc. Obviously, much more data are needed before one can confidently posit the optimal dichotomy; assuming that one even exists. Studies currently underway in our laboratory address the theoretical utility of these and other possibilities. However, for the purposes of this paper, we prefer to start at the beginning by comparing human movement with the movement of inanimate, non-living objects. If the visual system treats human motion differently from other motions, this difference should be most easily identified with the human–object comparison. Only after processing differences between these two non-overlapping event categories have been established would it make sense to try to develop more fine-grained definitions. Moreover, to maintain a clean separation between these two categories, we initiate our studies with the use of human movements that do not involve objects—either their physical or implied (pantomimed) presence. Thus, for the purposes of this paper, we use the terms 'human movement' and 'action' interchangeably to refer to non-goal-directed movements of the human limbs about an intact human body.

In sum, the goal of this paper is to determine whether the visual perception of human movement differs from the visual perception of moving objects. Are there conditions under which the visual system treats human and object motions similarly? By addressing these issues, we hope to develop a deeper understanding of the cues that the visual system uses to define a stimulus event as a human movement.

Our investigation is structured as follows. We begin with a very brief review of some of the data that demonstrate that motion processes are necessary for the representation of human displacement. Given that motion appears to be a defining characteristic of human action, we systematically examine various fundamental characteristics of complex motion perception. This begins with a review of the need for the integration of local motion signals across space. We then examine whether motion integration across space is similar during the visual analysis of object and human movement. Motion integration over time is then addressed within the context of apparent motion of human and object movements. Finally, recent neurophysiological data concerning the visual perception of human and object movement are discussed.

19.1.1 Is motion needed for the representation of the human body?

It has been asserted that the visual system constructs different representations for action and recognition (e.g. Milner and Goodale 1995). One of the ways in which these representations are thought to differ is in their generalization across viewpoint changes. Two general classes of representations are used to explain how we recognize objects in novel orientations. In egocentric representations, stimuli are represented in specific orientations relative to the observer. Such representations are therefore known as view-dependent. Perception for action is thought to rely upon these viewpoint-dependent, egocentric representations (Milner and Goodale 1995). Representations can also be object-centered when stimuli are represented as structural descriptions that are independent of the stimulus' orientation relative to the observer. Such viewpoint-independent, object-centered representations are thought to underlie perception for recognition (Milner and Goodale 1995).

However, recent perceptual-priming experiments call into question this strict dichotomy between representational formats (Kourtzi and Shiffrar 1997, 1999b). More specifically, when observers view static presentations of a human actor, their visual systems appear to represent these different views of the actor in an egocentric manner. However, when these same views are presented under conditions of apparent motion, object-centered representations of the human body result (Kourtzi and Shiffrar 1999a). These object-centered representations only appear when views of a human actor are consistent with the biomechanical limitations of the human body. Two conclusions can be drawn from these results. First, the visual representation of human movement may depend upon the movement limitations of the human body. We will return to this point repeatedly in subsequent studies. Second, motion processes appear to play a necessary and fundamental role in the perception and representation of the dynamic human body. Do motion processes play the same role in the perception and representation of moving objects? This question is discussed in the following section.

19.1.2 Motion integration and segmentation

While sipping a cup of tea at an outdoor café, I visually scan my environment. In doing so, I observe trees gently bending with the wind, my rotating tea-cup, cars zipping down the street, and people rushing by. To make sense of these different motions, my visual system must simultaneously perform two apparently conflicting tasks. On one hand, it must separate motion signals belonging to different objects. It would be an error for me to confuse the motion of a car with the motion of a pedestrian. On the other hand, my visual system must also combine motion cues belonging to the same object. While a pedestrian's swinging arms usually move in opposing directions, these motion signals must be combined before I can visually interpret the movements of an entire person. These simultaneous processes of integration and segmentation are what allow us to interpret moving stimuli (see Shiffrar 2001, for review).

The accurate integration and segmentation of motion information poses a challenge to the visual system as a result of some of the structural characteristics of the neurons that make early motion measurements (e.g. Hubel and Wiesel 1968; Movshon, Thompson, and Tolhurst 1978). First, neurons in the early stages of the visual system have relatively small receptive fields and as such can only respond to changes within very small regions of an observer's field of view. As a result, in order to interpret the motion of an object or animal, motion information must be combined across much larger regions of retinal space. Second, early motion–sensitive neurons are conjointly sensitive to direction and orientation. This combined sensitivity means that directionally sensitive neurons with
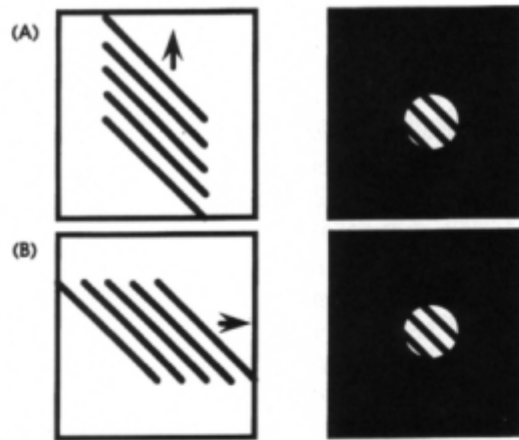
Fig. 19.1 The aperture problem. (A) On the left, a diagonal line translates upward. Each line segment shows the position of the translating line at a different time. On the right, the vertically translating line is viewed through a small window or aperture. Such apertures can be used to represent the receptive field of a neuron. (B) On the left, a diagonal line translates rightward. Again, each line segment illustrates the position of the translating line at a different time. On the right, the rightwardly translating line is viewed through an aperture. Note that the upward (A) and rightward (B) motions appear to be identical when they are viewed through an aperture that hides the end points of the line. This so-called aperture problem refers to the fact that the motion of a translating line or grating is ambiguous. This ambiguity arises from the fact that the component of translation parallel to a line's orientation can not be measured unless the real ends of the lines are visible.

small receptive fields will sometimes give the same response to very different motions. Thus, the activity of any particular neuron provides only ambiguous motion information.

This ambiguity, illustrated in Fig. 19.1 (A and B), is commonly referred to as the aperture problem. The aperture problem can arise whenever the motion of a continuous luminance edge must be estimated from the activity of a receptor having a small receptive field. To understand this problem from a spatial perspective, first consider that the motion of any line can be decomposed into the portion that is parallel to the line and the portion that is perpendicular to the line. Because a neuron cannot track or 'see' the ends of the line if those ends fall outside of its receptive field, the neuron cannot measure any of the motion that is parallel to the line's orientation (that is, along the length of the line). As a result, a neuron can only detect the perpendicular component of the line's motion. Because only this perpendicular component of motion can be measured, all motions having the same perpendicular motion will appear to be identical even if these motions differ significantly in their parallel component. Thus, a 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; Wallach 1935).

How can observers interpret the motions of objects or humans when early motion measures are inherently ambiguous? While the interpretation of a single translating line is ambiguous, the possible interpretations of its motion are limited to a large family of related motions. All of the members
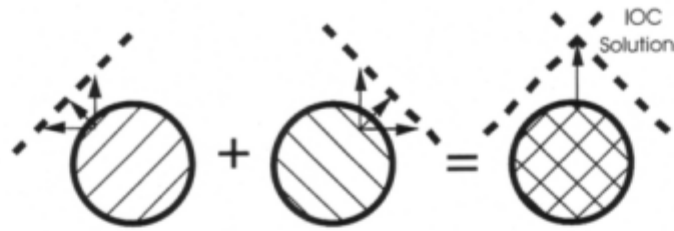
Fig. 19.2 The intersection of constraints solution to the aperture problem. Because of the aperture problem, the true motion of a line or grating viewed within an aperture could be any one of an infinitely large family of different motions defined by its constraint line (shown here as a dashed line). The visual system can overcome this ambiguity by considering the motion measurements from two or more differently oriented lines. That is, while the measured motion of a single translating line is consistent with infinitely many interpretations, measurements of differently oriented lines can be combined to uniquely interpret the line motion. This unique solution is defined by the point of intersection of two different constraint lines (shown on the right) and is known as the intersection of constraints or IOC solution.

of this family differ only in the component of translation that is parallel to the line's orientation. Members of two hypothetical families are illustrated by the groups of three arrows in Fig. 19.2.

The visual system can solve the aperture problem by taking advantage of this regularity in possible motions. To do so, individually ambiguous motion estimates from two differently oriented lines must be combined. As long as two differently oriented lines are rigidly connected to each other, and actually moving in the same direction, their corresponding constraint lines will intersect at a single point. This point, known as the intersection of constraints or IOC, defines the only possible motion interpretation that is shared by the two rigidly connected translating lines. Thus, when the visual system is correct in assuming that two lines are rigidly connected to each other, then the motion of the stimulus defined by those lines can be uniquely interpreted.

Experimental support for this IOC approach comes from studies examining the visual perception of and neural response to spatially overlapping edges and gratings. In their influential behavioral experiments, Adelson and Movshon (1982) asked subjects to report whether superimposed sinusoidal gratings (illustrated on the right side of Fig. 19.2) appeared to move as a coherent whole. When the luminance contrast and the spatial frequency of the two gratings were similar, subjects perceived a single plaid pattern translating in the direction of the IOC solution. On the other hand, when the two gratings differed significantly in their spatial frequency or contrast, subjects reported the perception of two independently translating gratings that slid over one another. These results suggest that when overlapping stimuli are structurally similar, the visual system assumes that they belong to the same object and, as a result, combines their component motions.

19.2 Motion integration across space: objects

The above results provide just one example of how the visual system might solve the aperture problem for superimposed gratings presented within a single receptive field or region of visual space. How does the visual system link motion signals across space? Previous theories assumed that non-overlapping, moving edges would be analyzed and perceived in the same way as overlapping edges. However,

subsequent behavioral tests have not supported this hypothesis. When subjects view differently oriented edges through disconnected apertures, they experience systematic difficulties in their ability to link motion signals across the disconnected edges (Shiffrar and Pavel 1991; Lorençeau and Shiffrar 1992). For example, when viewing a simple, rigidly rotating polygon through a set of apertures, subjects cannot combine motion measurements accurately across the polygon's edges (Shiffrar and Pavel 1991). Instead, subjects perceive non-rigid movement. Even when they know that they are viewing a square rigidly rotating behind four stationary apertures, they still perceive either disconnected rotating line segments or a pulsating elastic figure. Thus, although theories of motion perception are based on the assumption that the visual system overcomes the ambiguity of individual motion measurements by combining those measurements, observers are often unable to perform this crucial task.

What is the cause of subjects' inability to integrate velocity estimates across the different sides of a rotating object? In classic motion-integration studies (e.g. Adelson and Movshon 1982), edges undergo translation rather than rotation (Shiffrar and Pavel 1991). Therefore, to ensure that the differences in motion integration within and across spatial locations suggested by the above study did not result from differences in the type of motion used, motion integration across translating edges was examined (Lorençeau and Shiffrar 1992). To that end, subjects in another series of experiments viewed a diamond figure rigidly translating behind a set of spatially separated apertures, as shown in Fig. 19.3(A). In a two-alternative forced-choice procedure, subjects performed a direction discrimination task constructed so that the diamond's direction of translation could only be determined from an integration of the motion measurements across the diamond's visible edges. When the translating diamond was centrally presented at high luminance contrast, subjects performed at chance levels in the direction discrimination task. That is, even though subjects knew they were viewing a translating diamond, they could not link motion signals across the diamond's sides and determine its direction of motion. Instead, under these conditions, the visual system interpreted the display as four independently translating object fragments.
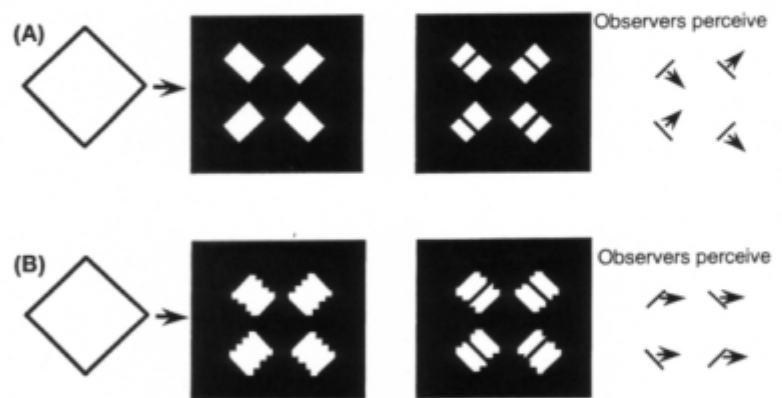

Fig. 19.3 (A) A diamond translates rightward behind four rectangular windows. The four visible line segments appear to move in different directions. (B) However, if the shape of the window edges is changed so that positional noise is added to the visible line endings, the same four edges now appear to move coherently.

When considered together, the results of the above studies clearly suggest that the integration of motion signals within a single region differs from the integration of motion signals across disconnected spatial locations. So how does the visual system control the integration of motion information across different spatial locations? Outside of the laboratory, visual scenes usually contain multiple objects. To identify dynamic actions and objects in natural scenes, the visual system must integrate motion measurements originating from the same physical unit while segmenting motion measurements arising from different units. Because the ends of lines (or terminators) and the ends of surfaces (or corners) are simple form cues that signal object boundaries, such discontinuities may determine when motion measurements are linked across edges. This hypothesis was tested in the following studies.

If contour discontinuities determine whether motion integration or segmentation occurs, then manipulations of discontinuity visibility should significantly alter the visual interpretation of dynamic images. In the previously described translating diamond display, four stationary apertures were positioned so that only one segment of each of the diamond's four sides could be viewed. The apertures were rectangular so that the visible length of each segment remained constant as the diamond moved. This created eight (two per segment) high-contrast terminators that smoothly translated back and forth along the obliquely oriented aperture sides. We manipulated the visibility of these terminators in three very different manners: luminance contrast, positional noise (as indicated in Fig. 19.3(B)), or peripheral presentation. In every case, when terminator visibility was low, because terminators were presented at low luminance contrast, with added noise, or in peripheral vision, performance was high since motion integration across the visible diamond segments was facilitated. Conversely, whenever the terminators became more visible, performance dropped. Since accurate performance requires motion integration, this performance decrease suggests that motion segmentation increased with terminator visibility. This pattern of results strongly suggests that terminators determine whether motion information is integrated or segmented; that is, whether the visual system interprets moving objects as coherent or fragmented (Lorençeau and Shiffrar 1992).

19.2.1 Motion integration across space: action

The previous studies indexed some of the information that the visual system uses to interpret the motion of simple shapes. Are the cortical mechanisms that were tapped during these studies also involved in the analysis of human movement? If the perception of human action truly differs from the perception of moving objects, then these two perceptual analyses may differ in their spatial constraints. Is the integration of human movement across space different from the spatial integration of object movements? This question was addressed with an adaptation of the polygon-moving-behind-apertures display described above. In this experiment, the moving polygon was replaced with a translating car, opening and closing scissors, or a walking human, as indicated in Fig. 19.4(A). Subjects simply viewed one of these three items moving behind a set of specially constructed apertures (see Fig. 19.4(B)) for six seconds and reported what they observed (Shiffrar, Lichtey, and Heptulla-Chatterjee 1997). The apertures were constructed so that only straight edges; that is, no corners or end points, were visible. The subjects verbally reported what they saw. An audiotape of their descriptions was given to a naïve scorer who categorized the subjects' descriptions as either reflecting local segmentation (independently moving line segments) or global integration (a whole object or being). If human movement is analyzed over a greater spatial extent than object motion, then observers should be more likely to identify the walking human figures than the inanimate objects moving behind apertures. In a control condition, subjects viewed static versions of each of the three displays.
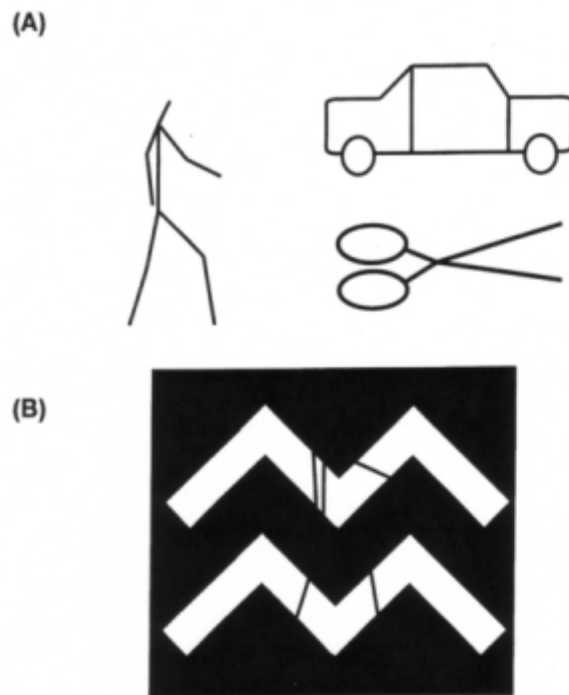
(A)

(B)

Fig. 19.4 (A) Examples of the walking figure, car, and scissors stimuli used in the multiple aperture studies. (B) The aperture through which each of the stimuli were viewed. Here the apertures are visible, as in the control condition. In the experimental condition, the apertures were statically invisible. This example depicts one static frame of the walker viewed through the apertures.

The results of a series of experiments clearly suggest a fundamental difference between the visual integration of object and human motion across space. First, no subjects in the control conditions were able to recognize the partially occluded car, scissors, or human when they were presented statically. This result adds further support for the hypothesis that stimulus motion is necessary for the visual perception of human action.

In the motion condition, a large split was found in subjects' ability to identify the human and objects. When a walking human figure was viewed through apertures, all subjects readily and accurately identified the walker. Typical responses to the walker stimulus included: 'a walker,' 'a man walking,' and 'someone moving.' On the other hand, when observers viewed moving objects (the scissors or cars) through the same apertures under the same conditions, they were unable to recognize these objects. Instead, subjects described these object displays as sets of line segments moving incoherently. Typical descriptions of the moving car and scissors stimuli included: 'lines moving,' 'birds,' 'worm-like things that got longer,' 'undulating lines,' and 'a bunch of lines.' Such descriptions suggest that subjects could not group motion information across the apertures—just as with the rotating square and translating diamond displays described in the previous section. Yet subjects were readily able to group and interpret motion signals when those signals were consistent with the interpretation of a walking human. This pattern of results suggests that action perception and object

perception may depend upon different motion integration mechanisms. This appears to hold true even when both are performed for the purpose of recognition.

However, an alternative explanation of subjects' inability to recognize the partially occluded car and scissors is simply that these figures were not recognizable. The walker, car, and scissors represent different classes of stimuli that vary significantly along several dimensions. Did subjects recognize the walker because it was sufficiently complex and descriptive while the car and scissors stimuli were not? To address this concern, we modified the displays so as to facilitate motion integration.

Occluded objects have two different types of surface boundaries: real boundaries and temporary boundaries created by the occluding surface. Accurate object recognition requires that the visual system rely on real boundaries and discount temporary boundaries (Kanizsa 1979). One of the ways that the visual system distinguishes real from temporary boundaries involves the use of occlusion cues. When depth cues suggest that contour terminators are the temporary result of another occluding surface, those terminators do not influence image interpretation (Shimojo, Silverman, and Nakayama 1989). On the other hand, in the absence of compelling occlusion cues, terminators play a defining role in image interpretation. In the previous experiment, no depth cues were present since the apertures were invisible. In the present experiment, we added occlusion cues to the multiple aperture display so that the terminators would be correctly classified as temporary and subsequently discounted from the motion analysis. To this end, we simply increased the luminance of the area surrounding each aperture so that T-junctions would be created where the lines intersected the now visible apertures. This manipulation should eliminate terminator-based interpretations of the moving lines and thereby facilitate motion integration across space. When subjects viewed the walker, car, and scissors through these new visible apertures, they correctly recognized all three objects. Thus, the car and scissors displays were recognizable and therefore could have been interpreted in the same global manner as the walker.

Does the type of displayed locomotion influence an observer's ability to integrate motion cues across space? Or, are all human movements analyzed in the same manner? To answer these questions, we modified the walker-behind-apertures stimulus described above so that the walker's locomotion fell either within or outside the spatial and temporal parameters corresponding to realistic walking speeds (Barclay, Cutting, and Kozlowski 1978). Subjects were individually presented with the walking stick-figure behind invisible apertures at one of six possible walking speeds. As before, they were simply requested to describe the display to a tape recorder. Subjects' responses were categorized by a naïve scorer as either correct, global interpretations or local, disconnected descriptions. The results showed ceiling levels of recognition performance at those walking speeds falling within the range of normal walking. Performance dropped significantly at display rates above and below this spatial–temporal range. Thus, non-normative actions may not be analyzed in the same manner as commonly performed actions. This possibility will be addressed again in subsequent sections.

Is the integration of human motion signals over space always different from motion integration with non-human objects? Previous research suggests that spatial orientation may be an important factor in the perception of human action (e.g. Bertenthal and Pinto 1994; Dittrich 1993). To test whether stimulus orientation influences motion integration, we presented the same displays as either upright, upside down, or rotated by 90 degrees. All figures were viewed through the original set of invisible apertures. Once again, subjects were simply asked to verbally describe one of the nine stimulus displays (car, scissors, or car at 0, 90, or 180 degree orientations). The results indicate that recognition of the walker was strongly influenced by stimulus orientation. While all subjects correctly identified the upright walker, only 30% recognized the horizontally oriented walker and only

10% recognized the inverted walker. Incorrect responses in the 90 and 180 degree walker conditions included such descriptions as: 'intersecting lines,' 'birds flying,' 'two sets of lines making circular motion,' and 'little dotted lines.' Correct responses included, 'someone walking,' 'a person,' 'a guy walking,' and 'RuPaul.' None of the subjects in the scissors conditions correctly identified that figure in any orientation. The car stimulus was only correctly identified once in its canonical orientation. As before, incorrect responses to the car and scissors stimuli involved various descriptions of independently moving line segments. These results are consistent with the orientation specificity of human motion analyses. That is, only upright human movement appears to be analyzed differently from the motion of inanimate objects. Impossible human movements, such as those shown in our 90 and 180 degree orientation conditions or at improbable walking speeds, appear to be analyzed in the same spatially local manner as objects. These results suggest that the mere presence of the human form in motion is not sufficient to trigger those neural mechanisms that may be dedicated to the analysis of human movement.

19.3 Motion integration across time: actions and objects

Psychophysical researchers commonly use the phenomenon of apparent motion to investigate the temporal nature of motion processes. In classic demonstrations of apparent motion, two stationary dots are presented sequentially. Under appropriate spatio-temporal conditions, the two stationary dots are perceived as a single moving dot. While there are an infinite number of possible paths connecting the two dots, observers almost always perceive motion along the shortest path (e.g. Burt and Sperling 1981). Researchers have concluded that an object's identity does not influence the perception of its movement since observers perceive the shortest path of apparent motion even when that path requires a significant shape deformation (e.g. Shepard 1984).

If the perception of human movement differs from the perception of object movement, will the presentation of human movement influence the visual perception of apparent motion? When humans move, their limbs tend to follow curved rather than straight trajectories. Given the visual system's shortest-path bias, will observers of human movement be more likely to perceive apparent motion paths that are consistent with the movement limitations of the human body or paths that traverse the shortest possible distance? This hypothesis was tested with stimuli consisting of
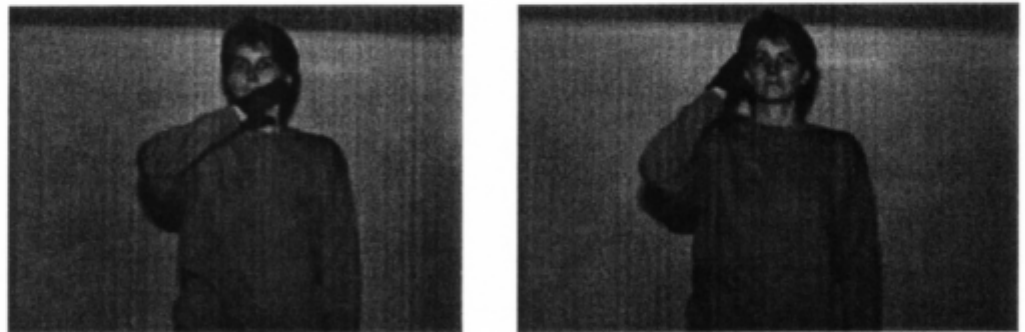

Fig. 19.5 A sample apparent-motion stimulus from Shiffrar and Freyd (1990). When these two photographs are shown sequentially, subjects perceive the hand moving through the woman's head at short SOAs. As SOA increases, subjects increasingly report the perception of the woman's hand moving around her head.

photographs of a human model in different positions created so that the biomechanically possible paths of motion conflicted with the shortest paths.

For example, one stimulus, shown in Fig. 19.5, consisted of two photographs in which the first displayed a standing woman with her right hand positioned on one side of her head while the second photograph showed this same hand positioned on the other side of her head. The shortest path connecting these two hand positions would require the hand to move straight through the head while a biomechanically plausible path would entail the hand moving around the head. Which path of motion do people see? To answer this question, we created many different picture pairs of a human model who oriented one of her limbs in two different positions. For each set of poses, the shortest path of human movement connecting the two limb positions required one of two possible violations of normal human movement. In one case, which we refer to as a violation of body solidity, a limb would have to pass through some other physically solid part of the model's body. In the second case, involving a violation of the joint constraint, the shortest path of motion would require the breakage of one of the model's joints. These two types of stimuli were randomly organized and presented to subjects in a tachistoscope. On every trial, participants simply viewed an alternating picture pair for as many presentation cycles as they liked and then described the path or paths of apparent motion that they perceived. Across trials, we varied the SOA or the amount time between the onset of one photograph and the onset of the next photograph.

When participants viewed these alternating picture pairs, their perceived paths of apparent motion changed with the SOA. At short SOAs (less than approximately 200 ms), subjects consistently reported seeing the shortest, physically impossible paths of human movement. For example, under these conditions of rapid picture alternation, subjects viewing the picture pair shown in Fig. 19.5 reported clearly seeing the woman's hand move straight through her head. Yet, with increasing SOAs, perceived motion paths changed and observers increasingly saw apparent-motion paths that are consistent with normal human movement (Shiffrar and Freyd 1990). So, in the case of Fig. 19.5, as the rate of alternation slowed, subjects increasingly reported that they saw the woman's hand move around her head.

In a second study, we found that when subjects viewed a different set of human model photographs created so that the shortest movement path was a biomechanically plausible path and longer movement paths were physically impossible (i.e. the reverse of that described above), observers always reported seeing the shortest path (Shiffrar and Freyd 1993). Thus, subjects do not simply report the perception of longer paths with longer presentation times. Instead, the perception of normal human movement, *per se*, becomes increasingly likely over extended temporal intervals.

Does the perception of non-human objects in apparent motion also change with temporal display rates? To answer this important question, we designed apparent-motion displays consisting of pairs of photographs of inanimate control objects, such as clocks and erasers, positioned so that their locations and orientations replicated the positions and orientations of the limbs and torso of the human model used in the previously described human apparent-motion studies. Thus, these objects were positioned so that the shortest paths of apparent motion required the perception of some physically impossible motion such as a stapler passing through an eraser. As before, naïve subjects viewed these picture pairs in a tachistoscope and reported their perceived paths of apparent motion across variations in SOA. When viewing these photographs of inanimate objects, subjects consistently reported perceiving the shortest possible path of apparent motion across all SOAs (Shiffrar and Freyd 1990). That is, they perceived objects passing through one another at all display rates. There was no tendency to report the perception of physically possible events, such as one object moving

around another object, at slower rates of picture alternation. This pattern of results suggests two conclusions. First, during short temporal intervals, both objects and actions are interpreted as following the shortest path of apparent motion even when that path is physically impossible. This finding suggests that under some temporal conditions, human actions and moving objects may be similarly analyzed. On the other hand, when temporal display rates are extended, the perception of human action and moving objects differ, since observers perceive physically possible human movements but physically impossible object movements. These results support the hypothesis that human movement may be analyzed by processes that differ from those underlying the analysis of object movement.

In the above experiments, contextually isolated human movements were examined. In the outside world, humans frequently move about objects. Does motion integration over time proceed in the same manner for human movements about the human body as it does for human movements about inanimate objects? If sensitivity to human movements extends to the perception of human movement relative to an object-filled outside world, then observers might perceive paths of apparent motion that are consistent with normal human movements about inanimate objects. On the other hand, if our sensitivity to human motion reflects the activity of an isolated, actor-centered system, then observers might only perceive paths of apparent motion consistent with the ways in which humans move relative to themselves.

The above question was addressed with a near replication of the previously described apparent-motion experiments, again involving paired still photographs of a human model in different poses. In the control condition, the poses always depicted the model moving one limb about either side of some part of her body. In the experimental condition, each picture pair from the control condition was modified by a replacement of the part of the body about which the limb moved with a similarly positioned, inanimate object having roughly the same size and orientation. In both experimental and control conditions, subjects simply reported the perceived path of apparent motion as the SOA varied. The results showed that nearly identical patterns of apparent motion were reported in both conditions. Specifically, at short SOAs, subjects perceived the human model's displaced limb to pass through another body part as well as through an inanimate object. At long SOAs, the model's limb now appeared to move around both objects and body parts. This pattern of results indicates that the tendency to see biomechanically consistent paths of apparent motion with increasing temporal duration is not limited to the movement of human limbs about the human body. Instead, our visual sensitivity to human movement appears to be general and incorporates how human bodies move with respect to inanimate objects (Heptulla-Chatterjee, Freyd, and Shiffrar 1996).

Is the presentation of realistic images of the human body necessary for the perception of apparent human motion? In other words, do any particular physical cues to the human body, such as skin, eyes, hair, or body shape, trigger the processes underlying the visual analysis of human movement? To answer this question, we created a new set of stimuli depicting the global structure of the human body out of a non-human material. Stimuli were created by videotaping a wooden mannequin posed in approximately the same positions as the human model in our previous work (Shiffrar and Freyd 1990, 1993). In each picture pair, one of the mannequin's limbs was positioned on either side of some part of its body. Thus, while the human body, *per se*, was absent from these stimuli, the global form of the human body was preserved. If the perception of human movement requires the presentation of stimuli with textural or facial cues to the human body, then this mannequin should appear to move in a manner that violates human movement constraints at slow display rates.

When subjects viewed these simplified, wooden renditions of the human body in apparent motion, their perceived paths of apparent motion changed with the temporal display rate. At long

SOAs, subjects still reported paths of apparent motion consistent with the human body even though a human body was not actually present. At short SOAs, they reported the perception of the shortest, physically impossible paths of apparent motion. Thus, under the conditions in which we tested, apparent-motion perception with images of wooden mannequins is indistinguishable from apparent-motion perception with realistic images of a human body. These results indicate that sensitivity to human motion can be evoked by form cues that are not inherently 'animate' or 'biological' in nature. In other words, as demonstrated by Graziano and Botvinick (this volume, Chapter 6), the cortical mechanisms responsible for body schema can be 'fooled' by volumetric shapes having roughly the same size and location as possible body limbs.

What form cues are needed for the perception of human movement? Structure from motion studies using point-light walker displays suggest that pairs of corresponding limbs (i.e. two arms or two legs) are sufficient for the detection of human locomotion within a mask (Pinto and Shiffrar 1999). Given such results, we wondered whether the presentation of a pair of body parts in isolation would be sufficient for the perception of biomechanically plausible paths of apparent human movement. To that end, we presented subjects with partial body stimuli that depicted only one displaced limb and the occluding body part about which the limb was displaced. This manipulation maintained the curvature of the occluding surface as well as the position, orientation, and apparent solidity of the occluding and displaced body parts. However, these subsections eliminated the global hierarchy of limb orientations and positions of the human body. The purpose of this experiment was to determine whether a main effect of SOA would prevail in the absence of a whole human body. Once again the stimuli consisted of picture pairs displayed in an apparent-motion paradigm. As before, subjects were asked to describe their perceived paths of apparent motion across variations in SOA. Interestingly, the results of this experiment differed from those of the previous experiments in which subjects viewed whole human bodies. In the current experiment, subjects consistently reported the perception of the shortest, physically impossible paths of apparent motion. That is, they reported the perception of a limb passing through another limb or a torso at all SOAs. When considered together with the results of the previous apparent-motion studies, these results suggest that a hierarchy of limb position and orientation cues consistent with a complete human form, or possibly the upper or lower half of the human body, may be necessary for the integrated analysis of human movement (Heptulla-Chatterjee *et al.* 1996).

This result is consistent with the findings of Rizzolatti and his colleagues (1996; see also Gallese *et al.*, this volume, Chapter 17) and Perrett and his colleagues (Jellema and Perrett, this volume, Chapter 18; Perrett *et al.* 1990) that mirror and STPa neurons in the monkey fire when a monkey observes the movements of another monkey or a human. Both the monkey and human share the same hierarchy of limb positions and orientations. As such, both forms are sufficient to drive these cells.

In summary, the above experiments suggest several advances in our understanding of the visual analysis of human movement. First, the visual perception of human movement does differ in some fundamental ways from the visual perception of moving objects. The results of a series of multiple-aperture studies indicated that motion integration over space differs for human and object-based stimuli. Under identical psychophysical conditions, the human visual system selects spatially global interpretations of human movement and spatially local interpretations of object movement. Apparent-motion studies were used to assay the processes underlying motion integration over time. The results of these studies demonstrated important differences between the integration of human movement and object movement over time. Specifically, perceived paths of apparent motion respect the physical limitations of human movement but not of object movement under those conditions

requiring integration over extended temporal intervals. When considered together, these results strongly support the hypothesis that the processes underlying human-movement perception differ from those underlying object-motion perception.

The results of these studies also shed light on some of the cues that the visual system uses to discriminate between object and human movement. First, display orientation may determine whether human motion is interpreted as an action or an object. When human locomotion is presented upside-down or sideways, object-like motion-integration processes appear to dominate perception. Thus far, it appears that the perception of human movement only differs from the perception of object movement when the gravitational constraints on human movement are respected. Second, the presence of textual cues, such as skin or hair, and facial cues, such as eyes or a mouth, to the human body are not necessary for the perception of human movement. A wooden mannequin and a point-light walker (Thornton, Pinto, and Shiffrar 1999), both of which lack such information, can be seen to move in the same manner as a naturalistic human form. However, the presentation of a single limb moving relative to a stationary body part does not lead to the same visual movement analyses as those triggered by a whole body. In other words, at least under some conditions, the visual system treats an isolated limb as an object. Thus, the presence of some portion of the human form, in and of itself, does not appear to be sufficient for human movement processing. Finally, timing appears to play a critical role in the visual system's categorization of human and object movements. In multiple-aperture experiments, recognition performance plummeted when participants observed locomotor displays in which the temporal parameters fell outside of the range of normal human walking. In apparent-motion experiments, participants reported the perception of physically impossible paths of human movement at speeded temporal intervals. Thus, when display timing is incompatible with normal human movement, the visual system appears to interpret the display as a non-human object rather than as a human action even when the display consists of realistic photographs of a human actor.

19.4 What defines an action?

Why might the visual system use spatial orientation and movement timing to determine whether a stimulus should be analyzed as a human action or as a non-human object? To answer this question, it may be important to recall that human movement is the only movement that we can both produce and perceive. Might not the human visual system take advantage of the pool of human movement information available in the motor system to assist it in its analysis of the movements of other humans? If the motor system provides assistance during the visual analysis of human movement, then one might expect that motor system activity should be triggered during the visual perception of those human actions with which an observer has some motor experience (e.g. Decety *et al.* 1997; Prinz 1997; Viviani and Stucchi 1992). That is, motor-system activity during the perception of human movement may depend upon whether the observer is physically able to perform the observed action.

To test this hypothesis, we conducted a brain-imaging study in which PET activity was recorded while subjects viewed two-frame apparent-motion sequences of human and object movement (Stevens, Fonlupt, Shiffrar, and Decety 2000). These displays replicated those used by Shiffrar and Freyd (1990, 1993). As before, there were two types of picture pairs. The human body picture pairs showed a human model in different positions such that the biomechanically possible paths of her movement conflicted with the shortest, physically impossible paths. The second set of picture pairs consisted of non-living 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 the primary motor cortex and cerebellum. However, when these same picture pairs were presented more rapidly (with SOAs less than 300 ms), subjects then perceived impossible paths of human movement, and selective activity in the motor system was no longer found (Stevens *et al.* 2000). On the other hand, when the pictures of non-living objects were presented at either fast or slow SOAs, no selective motor system activation was indicated. Importantly, subjects in this experiment were never given instructions to imitate the observed actions, either during or after the experiment. Instead, subjects remained stationary and simply viewed two-frame apparent-motion sequences. Thus, selective motor-system activity was not associated with an overt or instructed pre-paration to act. When considered together, these results suggest that the visual perception of human movement may benefit from disambiguating motor-system input as long as one is physically cap-able of performing the observed actions. Thus, we may understand the actions of others in terms of our own motor system (Viviani, this volume, Chapter 21).

19.4.1 *Motor experience per se?*

What type of motor experience might be required for the visual perception of human movement? The above studies can not be used to answer this question since the impossible actions, which included movements such as a hand passing through a torso and a foot passing through a leg, could not have been performed by the observers for two different reasons. First, the observers had no per-sonal experience performing these actions. Second, and obviously relatedly, the actions were phys-ically impossible for any human to perform. This distinction is important because if the actions were physically possible human movements, then an observer might have some basic internal schema for those actions even if he or she had never actually performed them (Castiello *et al.*, this volume, Chapter 16; Graziano and Botvinick, this volume, Chapter 6). For example, while I have never performed a back flip, I may have developed some internal representation of that action either from visual experience (such as watching gymnasts in competition) or from some innate body schema that includes information about the range of possible human movements (Berlucchi and Aglioti 1997). Does visual experience, motor experience, or some innate schema of possible bodily movements define which movements the visual system analyzes as actions?

A recent study by Brugger and his colleagues (Brugger *et al.* 2000a) suggests that the neural mechanisms underlying action perception may not require limb-specific motor experience. These studies consisted of a series of behavioral, imaging, and neurophysiological investigations of a woman born without legs or forearms. The results beautifully converged to convincingly suggest that body parts can be represented in sensory and motor cortical areas even when they have never been physically present. Furthermore, when presented with the same two-frame apparent-motion displays described above, this woman perceives SOA-dependent paths of apparent human limb movement that follow the same pattern found with observers born with arms and legs (Brugger *et al.* 2000b). Thus, this individual has functional neural representations of the movements of limbs that she has never had. Thus, motor experience, *per se*, does not appear to be necessary for the visual analysis of human movement.

Consistent with this, studies of early development suggest that motor actions may be represented even though they have never been executed. Infants show a selective sensitivity to biomechanically

correct human gait before they can walk (Bertenthal 1993, 1996; Fox and McDaniel 1982). Interpretation of such findings is as complex as it is intriguing. Very young infants exhibit a rhythmic alternation of their legs when they are supported upright (Thelen, Fisher, and Ridley-Johnson 1984). This spontaneous movement pattern suggests that some actions, such as walking, may be subserved by innate mechanisms or representations. These representations may also underlie infants' visual sensitivity to human movement. Additional evidence for such a hypothesis can be derived from studies of imitation in neonates (Bekkering and Wohlschläger, this volume, Chapter 15). Meltzoff and Moore (1983) have demonstrated that newborn infants are capable of imitating the facial gestures of adult models. Imitation requires that infants map the seen adult gesture to their own (unseen) facial musculature. The presence of this capacity in neonates suggests that an innate body representation is accessible to visual processes. Thus, visual observation of human movement and innate body representations may be sufficient for the visual analysis and perception of human movement. If so, this might serve as a critical connection in a bi-directional perception–action linkage.

19.5 Neural bases of the visual perception of human movement

The brain-imaging results described above most likely reflect only one component of the neural circuit responsible for the visual analysis of human movement. The above PET data suggest that the human primary motor cortex probably plays an important role in the visual interpretation of another person's movements. This conclusion extends that provided by earlier magnetoencephalographic or MEG data (Hari et al. 1998). The primary motor cortex is reciprocally connected with the premotor cortex (Rizzolatti, Luppino, and Matelli 1998; Wise, Boussaoud, Johnson, and Caminiti 1997). An extensive series of single-cell recording studies suggests that mirror neurons in the ventral premotor cortex also make important contributions to the visual perception of primate movement (Gallese et al., this volume, Chapter 17). Like neurons in the primary motor cortex, mirror neurons respond both when a monkey performs a particular action and when that monkey observers another primate performing the same action. Since neurons in the ventral premotor cortex only contain representations of hands, arms, and faces, mirror neurons may be dedicated to the interpretation of manual and facial gestures (Gallese et al., this volume, Chapter 17). As such, they may play a pivotal role in the visual interpretation of arm and facial movements subserving communication. This conjecture is strongly supported by brain imaging data which demonstrate that Broca's area, the human equivalent of the premotor cortex and normally considered to be a critical language area, is selectively activated during the observation of finger tapping (Iacoboni et al. 1999). The premotor cortex is indirectly connected with the anterior superior temporal polysensory area (Gallese et al., this volume, Chapter 17). Single-cell recordings in this area have repeatedly identified cells that are selective for monkey and human bodies in motion (e.g. Bruce et al. 1981; Oram and Perrett 1994; Perrett et al. 1990). Importantly, these neurons appear to differ from premotor mirror neurons (Rizzolatti et al. 1996) because while STPa neurons selectively respond to the actions of others, they remain unresponsive to the monkey's own actions (Hietanen and Perrett 1993). Thus, STPa neurons may play a role in helping us to avoid confusing our actions with the actions of others (Carey, Perrett, and Oram 1997) or may be dedicated to the interpretation of complex social behavior (Jellema and Perrett, this volume, Chapter 18) and even empathy (Brothers 1989).

It is important to note, however, that we can not yet postulate with any degree of certainty how these different areas actually contribute to the visual analysis of human movement. The fundamental

stumbling block is that each laboratory uses a different set of tasks and a different class of stimuli to study a different area. Obviously, the next necessary step is to examine the selectivity of each of the above cortical areas to the stimuli and tasks used in the examination of the other areas in this circuit.

19.6 Conclusions

In conclusion, human movement differs from all other movements since it is the only movement that human observers both produce and perceive. In a series of experiments, we found that the visual analysis of human movement can be fundamentally different from the visual analysis of moving, non-living objects. Behavioral and brain-imaging studies suggest that this difference may reflect innate body schemas of and/or visual–motor experience with normal human movement. Thus, the perception of human movement appears to constrained by 'knowledge' of human motor limitations (e.g. Prinz 1997; Rizzolatti *et al.* 1996; Shiffrar 1994; Viviani, this volume, Chapter 21). The visual system appears to take advantage of this perception–action linkage to define which visual movement signals result from human action and which result from moving objects. Possibly as a consequence of this linkage, action perception may not be as straightforward as initially thought. Some of these complexities are discussed below.

The presentation of human movement, in and of itself, may not be sufficient to trigger the mechanisms underlying the visual perception of human movement. Instead, as indicated by the studies discussed here, a human action must be consistent with an observer's internal body schema of possible actions before action-specific perception is demonstrated. Requirements for such a model match include, but are certainly not limited to, the following factors. First, display orientation is critical. If an action is presented upside-down, the action's motion signals appear to be interpreted by the 'object perception' system. Second, if the temporal characteristics of a human action are incompatible with human movement dynamics, the action is interpreted as an object. This holds true for motion integration across both space and time. Moreover, in an apparent-motion paradigm, displays containing only two portions of a human body are not sufficient for the perception of normative human movement. Thus, the presentation of an action outside of the context of a human body may not always be defined as an action by the visual system. Finally, imaging data suggest that the motor system may be involved in the visual analysis of possible, but not impossible, human movements. Taken together, these results suggest that only those movements that are consistent with an observer's internal model of possible human body movements are analyzed by the mechanisms that underlie action perception. Thus, in the visual perception of human action, all actions are not treated equally.

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