
Dynamic representations of human body movement

Zoe Kourtzi[¶], Maggie Shiffrar

Department of Psychology, Rutgers University, Newark, NJ 07102, USA

Received 19 June 1998, in revised form 19 October 1998

Abstract. Psychophysical and neurophysiological studies suggest that human body motions can be readily recognized. Human bodies are highly articulated and can move in a nonrigid manner. As a result, we perceive highly dissimilar views of the human form in motion. How does the visual system integrate multiple views of a human body in motion so that we can perceive human movement as a continuous event? The results of a set of priming experiments suggest that motion can readily facilitate the linkage of different views of a moving human. Positive priming was found for novel views of a human body that fell within the path of human movement. However, no priming was observed for novel views outside the path of motion. Furthermore, priming was restricted to those views that satisfied the biomechanical constraints of human movement. These results suggest that visual representation of human movement may be based upon the movement limitations of the human body and may reflect a dynamic interaction of motion and object-recognition processes.

1 Introduction

Human observers are particularly sensitive to human body movements. While the human body is highly articulated and moves nonrigidly, observers can readily recognize human movements from the relative motions of a few local elements (Johansson 1973). Such displays can be created by filming the actions of human actors with point lights attached to their major joints and head in an otherwise darkened environment (Johansson 1973; Marey 1895/1972). Observers of these highly simplified point-light displays can identify numerous activities, discriminate the gender of the actor, and even recognize friends (Cutting 1987; Cutting et al 1978; Dittrich 1993; Kozlowski and Cutting 1977).

Given the above considerations, human body motions seem to be an exceptional candidate for investigating how the visual system represents complex objects undergoing nonrigid motion. Traditional theories of object recognition suggest that such highly articulated objects should be particularly difficult to recognize when they move nonrigidly (Biederman 1987). This recognition difficulty is tied to the fact that nonrigid motion yields structurally dissimilar views of an object. Our ability to recognize a novel view of an object is thought to depend upon a visual process in which previously seen or 'known' views of that object are generalized to nearby novel views (Bülthoff and Edelman 1992; Edelman and Weinshall 1991; Logothetis et al 1994, 1995). Contiguous views of an object most likely share similar features and/or part configurations. This structural similarity between 'known' object views may facilitate generalization to novel views. On the other hand, dissimilarity between object views is thought to make this generalization process more difficult (Edelman 1997; Edelman and Weinshall 1991; Lawson et al 1994; Poggio and Edelman 1990). As a result, the visual recognition of novel views of nonrigidly moving objects should be fairly slow and inaccurate. Consistently with this, several psychophysical studies have shown that judgments concerning novel views of a human body are slower and less accurate than judgments of known views

[¶]Current address to which correspondence and requests for reprints should be sent: Department of Brain and Cognitive Science, Massachusetts Institute of Technology, NE20-4043, 3 Cambridge Center, 77 Massachusetts Avenue, Cambridge, MA 02139-4307, USA; e-mail: zoe@psyche.mit.edu

(Bülthoff et al 1998; Daems and Verfaillie, submitted; Oloffson et al 1997; Parsons 1987; Verfaillie 1992, 1993).

Priming paradigms represent a commonly used tool for investigating the visual representation of objects across changes in viewpoint. Priming refers to the facilitated judgment or identification of previously viewed stimuli relative to novel stimuli (Bartram 1974). By examining the conditions under which priming occurs, researchers can draw conclusions regarding the type and quality of object representations created by the visual system. For example, priming studies have been used to determine whether human movement is represented in an orientation-dependent or orientation-independent manner (Daems and Verfaillie, submitted; Oloffson et al 1997; Verfaillie 1992, 1993; Verfaillie et al 1994). More specifically, when subjects are asked to discriminate between human and nonhuman point-light walkers, they respond more quickly in trials containing a human walker when the orientation of that walker matches the orientation of the walker from the previous trial. The finding that judgments concerning a point-light walker are facilitated when the walker's orientation is repeated suggests that the visual representation of human movement is orientation dependent (Verfaillie 1992, 1993; Verfaillie et al 1994). Such viewpoint-dependent priming is also found when observers name previously studied human movements (Daems and Verfaillie, submitted; Oloffson et al 1997) or discriminate between human and nonhuman static poses (Daems and Verfaillie, submitted).

The results of studies using different methodologies further support the hypothesis that visual representations of the human body are viewpoint dependent. For example, mental-rotation studies suggest that human body postures in different depth orientations are represented in a viewer-centered reference frame (Parsons 1987). Furthermore, performance in psychophysical tasks requiring the discrimination between point-light walkers and random-dot patterns is worse when the displays are presented from unfamiliar or novel viewpoints than from familiar viewpoints (Bülthoff et al 1998).

Thus, the results of numerous studies suggest that the visual system represents the human body as static sequences of previously encountered views. As a result, when novel views differ from known views, recognition of the human body is disrupted. However, consider the perceptual experience associated with the observation of a pirouetting dancer. As the dancer rotates, novel body views, which can be quite dissimilar from previously experienced views, are presented to the observer. Yet, observers have the perceptual experience of a continuous event. That is, the presentation of novel views does not disrupt the perception of the dancer's motion. This apparent dichotomy between the existence of viewpoint-dependent representations and the perceptual experience of continuous human movement raises the following question. How does the visual system integrate different views of a moving person so as to yield the perception of continuous human movement?

One approach to this question is based on the proposal that motion processes may play a defining role in the representation of an object, in general, and the integration of different object views, in particular. Specifically, motion processes may be used to link different views of an object rotated in the frontal plane (Kourtzi and Shiffrar 1997) or in depth (Kourtzi and Shiffrar 1998). The interaction between motion processes and object representations may be particularly important in the case of human movement. Apparent-motion studies suggest that the visual perception of human movement is constrained by the structure of the human body (Shiffrar and Freyd 1990, 1993). Moreover, the representation of the human body, unlike any other object, may be governed by a body schema which continuously specifies body position and the spatial relations among body limbs (Reed and Farah 1995). Last, neurophysiological studies suggest that the so-called 'what' and 'where' pathways, responsible for the analysis of form and spatial properties, respectively, converge in an area (Baizer et al 1991) which contains

neurons exhibiting response selectivity for primate movement (Perrett et al 1990). Thus, form and motion processes may be most likely to converge during the visual interpretation of human movement (Shiffrar 1994; Shiffrar et al 1997).

The goal of the current set of studies was to investigate further how the visual system represents different views of a human body in motion. How do observers recognize novel views of a human body rotating in depth? Do biomechanical constraints on human movement affect the way in which the human body is represented? A priming paradigm was used to address these questions. More specifically, in experiment 1 we asked whether priming would occur for novel views of a human form rotated in depth when these views were consistent or inconsistent with the biomechanical limitations of human movement. Experiment 2 investigated how the visual system represents the movement of mannequin figures that preserve the global structure of the human body but undergo movements that are not limited by biomechanical constraints.

2 Experiment 1

2.1 *Human-model movements*

In the physical world, highly dissimilar views of human bodies are revealed as people move. Are motion processes used to link these views? If so, then this linkage should be restricted within the path of human movement. Previous research supports the hypothesis that motion can readily link different views of rotating two-dimensional and three-dimensional objects (Kourtzi and Shiffrar 1997, 1998). Specifically, when object views are linked by apparent motion, similarity judgments are primed for novel views falling within the path of motion of the object. This result holds true even for rotations extending up to 150°. While priming is observed for novel views falling within the path of motion, it is not found for object orientations that are outside of the path of motion. On the other hand, all novel views of static objects are primed as long as their orientation is within 45° of a 'known' view. Thus, these results suggest that the visual system integrates multiple object views during the analysis of the motion of an object rather than through spatiotemporal associations between static views. Can motion processes also link different views of a human form even when those views are structurally dissimilar?

Additionally, several studies of the perception of human body motion have suggested that human movement percepts are constrained by the biomechanical properties of the human body (Shiffrar and Freyd 1993). Specifically, under long-range apparent-motion conditions, subjects report the perception of normal human movement even when this motion violates the shortest-path constraint. However, under short-range apparent-motion conditions, subjects report the perception of physically impossible human movements (Shiffrar and Freyd 1990, 1993). How does the visual system represent human movements that violate normal biomechanical constraints?

To address these questions, an immediate-priming paradigm, in which a pair of targets follows a briefly presented prime object, was adapted from Sekuler and Palmer (1992). Subjects were primed with two views of a human movement linked by apparent rotation in depth (apparent-motion condition) or not linked by apparent motion (static condition). The first prime view was the initial posture of a human movement while the second prime view was the final posture of the movement rotated in depth. Priming was indicated by faster reaction times when the two targets were the same as the prime. Any differences in priming between views of a moving and static human body would suggest differences in the representation of human motion.

2.2 *Method*

2.2.1 *Subjects.* Forty undergraduate students, recruited from the Rutgers University subject pool, participated in this experiment. All subjects had normal or corrected-to-normal vision and were naive to the hypothesis under investigation.

2.2.2 Materials. Stimuli were presented on a 21-inch color monitor with a resolution of 1024×768 pixels and 60 Hz refresh rate controlled by a PowerMac 7100. The monitor was positioned 95 cm from a chin rest and the stimuli were drawn within a square area on the screen $4.8 \text{ deg} \times 4.8 \text{ deg}$ of visual angle. Subjects viewed the stimuli through a circular aperture to minimize framing effects from the monitor.

The stimuli consisted of a set of human body postures designed with Fractal Design Poser 2.0 software. The model's height from head to toe was 4.04 deg while the torso width was 0.724 deg and the horizontal extent when both arms of the model were fully extended laterally was 2.9 deg. Each of the five prime stimuli consisted of a two-frame sequence depicting a particular human movement. The five sequences were as follows: (i) in the first frame, the left arm was stretched out to the left and, in the second frame, it was bent downward at the elbow, (ii) the right arm stretched out to the right and then straight up above the head, (iii) the left leg was stretched out to the left and then bent at the knee so that the toes touched the right knee, (iv) the right leg was stretched out in front and then bent at the knee, (v) the right arm was stretched up above the head and then bent back behind the head. Figure 1a illustrates

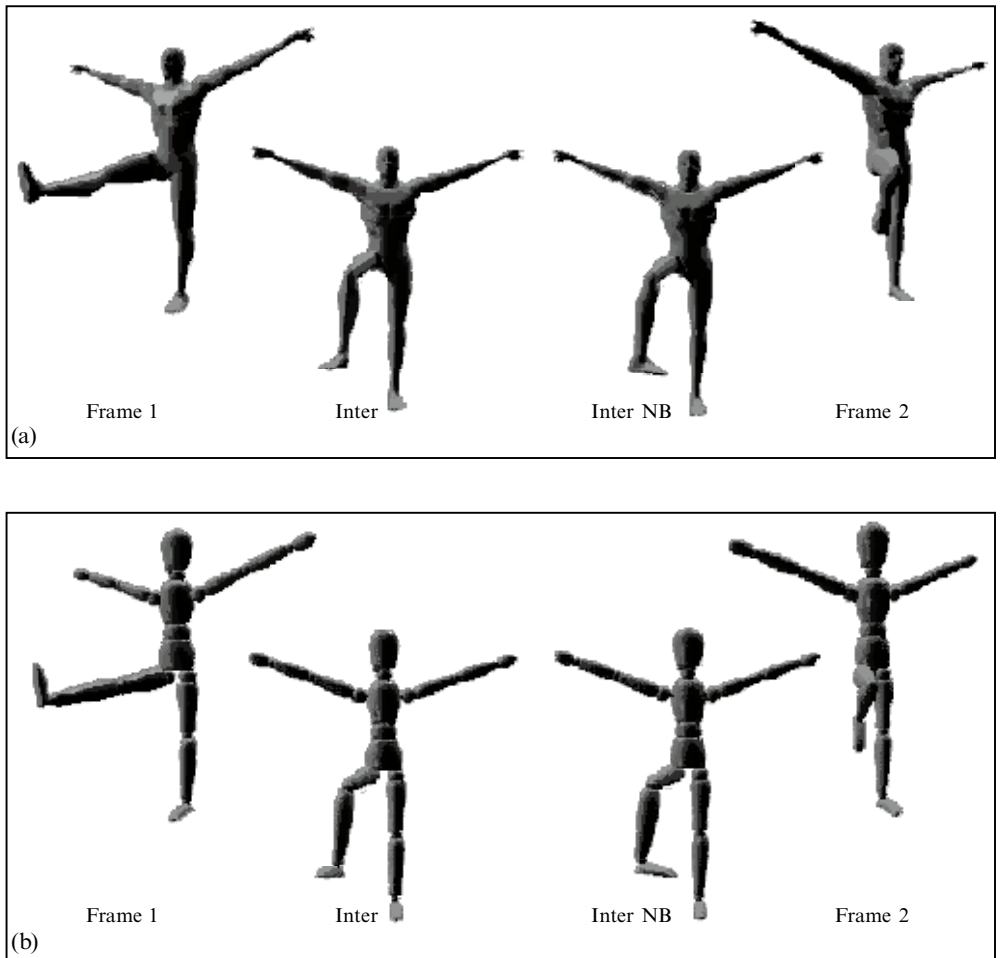


Figure 1. (a) An example of stimuli used in experiment 1: the two prime views (Frame 1, Frame 2) and the novel target views in between the prime views that were either consistent (Inter) or inconsistent (Inter NB) with the biomechanical constraints on the human body. (b) The same four views of a sample stimulus from experiment 2.

an example of the stimuli used: in the first frame (Frame 1) the left leg is stretched out to the left and then bent at the knee in the second frame (Frame 2). Each pair of prime views differed by a rigid, clockwise or counterclockwise rotation of the body in depth. The length of the rotation path connecting the two body positions was held constant. The primes were sequentially presented within the $4.8 \text{ deg} \times 4.8 \text{ deg}$ display area in the center of the screen, while the targets were simultaneously presented 0.6 deg to the left and right of the screen center.

2.2.3 Procedure. The experimental procedure is illustrated in figure 2. Each trial began with a fixation point presented for 1500 ms, followed by the first prime frame shown for a variable duration as described below. Then the second prime frame followed for the same duration as the first. A blank screen was then displayed for 500 ms followed by a pair of targets presented until the subject responded (with a 3 s maximum). Subjects carefully observed the prime displays and then pressed a key if the two subsequent targets matched each other. Time from target presentation to subject response was measured in milliseconds. This ‘go–no-go’ task was used to reduce the variability often observed in priming studies that require subjects to select one of two different motor responses (Biederman and Gerhardstein 1993). Subjects were instructed that both reaction time and accuracy were important. Overall feedback (mean reaction time and percentage of correct responses) was provided at the end of each block of trials.

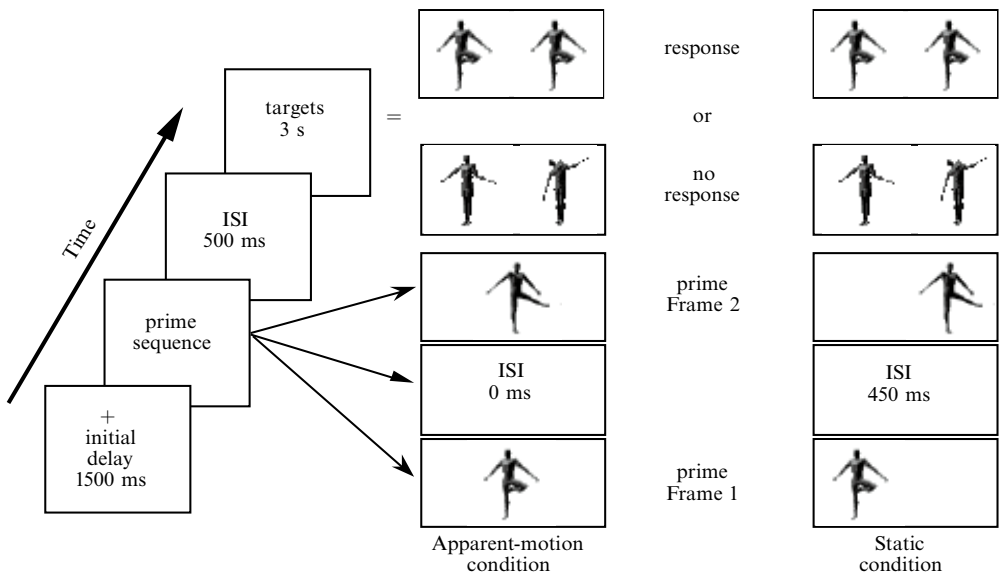


Figure 2. Experimental design for the apparent-motion and static conditions.

The first prime frame was presented at a view arbitrarily defined as the starting view. The second view was always a depth-rotated version of the first view. The two views could differ by a 60° or a 120° rotation around the y -axis. Our previous studies (Kourtzi and Shiffrar 1998) showed that a depth rotation of 60° placed the novel views close enough to the prime views for priming to be observed even when the prime views were presented statically. However, a depth rotation of 120° resulted in priming for novel views only when the prime views were linked by apparent motion. The duration of the two prime frames varied with the rotation angle between them so that the optimal apparent motion in depth was achieved. These durations were selected from pilot studies in which subjects reported the most compelling motion percepts when each

prime frame was presented for the duration used by Shepard and Judd (1976) for the corresponding angle plus a constant of 100 ms. This procedure yielded durations of 251 and 309 ms for the two rotation angles, respectively. The interstimulus interval between the two prime frames was 0 ms in the apparent-motion condition and 450 ms in the static condition. In the apparent-motion condition, the first and second prime frames were presented so that the human model appeared to rotate smoothly in depth while simultaneously moving one limb. In the static condition, the second prime frame was displaced 2.41 deg to the right of the first. This spatiotemporal separation between the two prime frames eliminated the perception of apparent motion in the static condition.

Before beginning the experimental trials, each subject completed a block of ten practice trials with objects that differed from those of the experimental trials. Most subjects obtained reaction times of less than 1000 ms by the end of the practice block. Subjects having longer reaction times completed a second practice block.

The experimental session consisted of six blocks each containing twenty trials. The targets in each block were presented in one of five orientations around the y -axis: the first orientation of the prime at the starting position of the movement (Frame 1), the second orientation of the prime (Frame 2) at the final position of the movement, the orientation halfway between the two prime orientations (Inter) and midway through the movement, an orientation before the first prime orientation (Extra 1) before the starting position of the movement, or an orientation beyond the second prime orientation (Extra 2) after the final position of the movement. The orientation of the Inter target equaled the first orientation of the prime plus half the rotation angle. The Extra 1 orientation equaled the first orientation of the prime minus half of the rotation angle. The Extra 2 orientation equaled the second orientation of the prime plus half of the rotation angle. Thus, the orientation of the Inter, Extra 1, and Extra 2 targets all deviated equally from the prime orientations. Table 1 shows all of the target orientations in such a way that zero refers to the starting orientation. Targets were also presented at an additional orientation that was the same as Inter except that the body posture violated the biological constraints of human movement (figure 1a). Thus, the human model was presented at an orientation halfway between the two prime orientations and midway through the movement, but the moving limb was twisted in a biomechanically impossible way. For example, the arm and the wrist, the leg and the ankle, or the elbow was twisted beyond the point of flexibility normally allowed by human joints. We refer to this test frame as Inter nonbiological (or Inter NB).

Table 1. Orientations ($^{\circ}$) of the two target objects (same as prime or different from prime) as a function of the prime rotation angle.

Prime rotation angle/ $^{\circ}$	Same as prime		Different from prime		
	Frame 1	Frame 2	Inter, Inter NB	Extra 1	Extra 2
60	0	60	30	-30	90
120	0	120	60	-60	180

Each target orientation was run in a separate block. Block order was counterbalanced across subjects. Stimulus order was randomized within each block. Each block contained five trials in which the targets matched each other as well as the prime, five trials in which the targets matched each other but differed from the prime, and ten trials in which the targets differed from each other and the prime. The targets that matched each other but differed from the prime consisted of body postures that involved a different motion of the same limb that was presented in the prime. Thus, any priming observed

would be specific to a movement rather than to a category of movements, such as all left-arm movements. The targets that differed from each other and the prime were body postures involving different limb motions.

In a between-subjects design, two groups of ten subjects completed the apparent-motion condition and two groups of ten subjects completed the static condition. Each group of subjects observed stimuli at only one rotation angle so that every subject only viewed the movements in novel orientations.

2.3 Results

In all experiments, only reaction times to correct responses are reported because all subjects exhibited ceiling levels of performance accuracy. Errors were infrequent and were not systematically associated with any of the experimental conditions. The average reaction time across subjects was 520 ms with a standard deviation of 104 ms. Priming is reported as a repeated measurement, or as the reaction-time difference between trials in which the prime and targets were identical and trials in which the prime and targets differed. The results are reported on the basis of subjects and collapsed over items and direction of rotation (clockwise or counterclockwise), because no systematic patterns of differences were observed for these variables.

Repeated ANOVAs with Priming as the within-measure variable indicated significant priming for Frame 1 ($F_{1,39} = 83.5$, $p < 0.001$), Frame 2 ($F_{1,39} = 51.2$, $p < 0.001$), Inter ($F_{1,39} = 11.1$, $p < 0.01$), but not for Extra 1 ($F_{1,39} = 2.4$, $p = 0.132$) or Extra 2 ($F_{1,39} = 0.332$, $p = 0.567$). Significant negative priming was observed for Inter NB ($F_{1,39} = 4.5$, $p < 0.05$); that is, reaction times were faster when the targets were different from the prime than when the targets were the same as the prime. Table 2 reports priming in both the apparent-motion and the static condition across rotation angles. The reported p -values were derived from one-tail paired t -tests used to test the unidirectional hypothesis that faster reaction times are observed when the targets match the prime than when the targets differ from the prime.

Table 2. Amount of priming (expressed in milliseconds) across rotation angles for all possible orientations in (a) experiment 1, apparent-motion condition; (b) experiment 1, static condition; (c) experiment 2.

Rotation angle/°	Frame 1		Frame 2		Inter	
	priming	p	priming	p	priming	p
(a) 60	36.9	0.000	31.8	0.025	43.1	0.024
120	51.9	0.003	42.1	0.001	45.5	0.005
(b) 60	44.4	0.000	42.5	0.000	48.7	0.000
120	68.7	0.000	45.3	0.002	-26.5	0.023
(c) 60	48.6	0.001	48.2	0.000	46.6	0.001
120	52.8	0.000	50.4	0.000	48.9	0.000
	Inter NB		Extra 1		Extra 2	
	priming	p	priming	p	priming	p
(a) 60	-18.4	0.108	-27.5	0.023	2.3	0.408
120	-18.1	0.108	-7.1	0.304	1.1	0.464
(b) 60	-0.720	0.481	20.3	0.018	21.7	0.006
120	-23.2	0.076	-25.4	0.041	-44.2	0.058
(c) 60	27.2	0.024	1.4	0.474	-19.5	0.092
120	42.8	0.005	-16.8	0.165	-1.7	0.408

A repeated ANOVA with Priming as the within-measure variable and Condition (apparent motion or static), Rotation angle (orientation difference between the first and second prime), and Test frame (Frame 1, Frame 2, Inter, Inter NB, Extra 1, or Extra 2) as the independent variables indicated significant main effects of Priming ($F_{1,216} = 30.9$, $p < 0.001$), Rotation angle ($F_{1,216} = 4.5$, $p < 0.05$), and Test frame ($F_{5,216} = 18.7$, $p < 0.001$), but no main effect of Condition ($F_{1,216} = 0.035$, $p = 0.851$). Significant interactions were observed between Condition and Rotation angle ($F_{1,216} = 12.8$, $p < 0.01$) and Test frame and Rotation angle ($F_{5,216} = 2.8$, $p < 0.05$).

Priming differences between the apparent-motion and static conditions are summarized in figure 3. A repeated ANOVA with Priming as the within-measure variable and Rotation angle and Test frame as the independent variables showed significant main effects of Priming ($F_{1,108} = 16.3$, $p < 0.001$) and Test frame ($F_{5,108} = 10.6$, $p < 0.001$) in the apparent-motion condition. No significant effect of Rotation angle ($F_{1,108} = 1.07$, $p = 0.302$) was observed. Fisher's a posteriori comparisons showed that Frame 1, Frame 2, and Inter were significantly more primed than Extra 1 ($p < 0.001$), Extra 2 ($p < 0.001$), and Inter NB ($p < 0.001$). The same analysis in the static condition showed significant main effects of Priming ($F_{1,108} = 14.5$, $p < 0.001$), Rotation angle ($F_{1,108} = 16.4$, $p < 0.001$), and Test frame ($F_{5,108} = 10.2$, $p < 0.001$). A significant interaction was observed between Rotation angle and Test frame ($F_{5,108} = 4.5$, $p < 0.001$). Fisher's a posteriori comparisons showed that Frame 1 and Frame 2 were significantly more primed than Inter ($p < 0.001$), Extra 1 ($p < 0.001$), Extra 2 ($p < 0.001$), and Inter NB ($p < 0.001$).

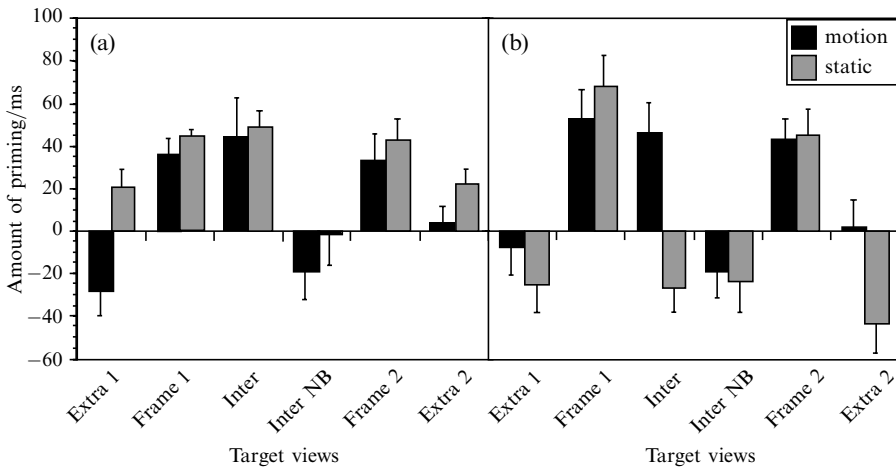


Figure 3. Results from experiment 1: Amount of priming (expressed in milliseconds) for the human-model targets in the apparent-motion and the static conditions for (a) the small (60°) and (b) the large (120°) rotation angles in all the possible target orientations.

For the small rotation angle (60°), a one-way ANOVA with Priming as the dependent variable and Test frame as the independent variable showed a main effect of Test frame ($F_{5,54} = 5.3$, $p < 0.001$) in the apparent-motion condition and in the static condition ($F_{5,54} = 4.3$, $p < 0.001$). Fisher's a posteriori comparisons showed that Frame 1 and Frame 2 were significantly more primed than Extra 1 ($p < 0.01$) and Inter NB ($p < 0.01$) in the apparent-motion condition. Also, Inter was significantly more primed than Extra 1 ($p < 0.001$), Extra 2 ($p < 0.05$), and Inter NB ($p < 0.01$). In the static condition Frame 1 and Frame 2 were significantly more primed than Inter NB ($p < 0.001$). Also, Inter was significantly more primed than Extra 1 ($p < 0.05$), Extra 2 ($p < 0.05$), and Inter NB ($p < 0.001$).

For the large rotation angle (120°), a main effect of Test frame was found in both the apparent-motion condition ($F_{5,54} = 5.4$, $p < 0.001$) and the static condition ($F_{5,54} = 8.4$, $p < 0.001$). Fisher's a posteriori comparisons showed that Frame 1, Frame 2, and Inter were significantly more primed than Extra 1 ($p < 0.01$), Extra 2 ($p < 0.01$), and Inter NB ($p < 0.001$) in the apparent-motion condition. In the static condition, Frame 1 ($p < 0.01$) and Frame 2 ($p < 0.001$) were significantly more primed than Inter, Extra 1, Extra 2, and Inter NB.

2.4 Discussion

Motion appears to link views of human body movement readily and to facilitate the representation of novel views within the path of normal human motion. Consistent with previous studies (Kourtzi and Shiffrar 1997, 1998), the current results showed that target views at the same orientation as the primes were primed in both the apparent-motion and the static condition for both the 60° and the 120° rotation angle. Novel target views respecting the biomechanical constraints of human motion were primed in the static condition but only for the 60° rotation angle. On the other hand, in the apparent-motion condition, the same novel target views were primed when they fell in between the two prime views for both rotation angles. Target views falling outside either end of the rotation path were primed in the static condition but not in the motion condition. Novel target views falling in between the prime views that violated the biomechanical constraints of human motion were not primed either in the apparent-motion or in the static condition.

These results seem consistent with studies suggesting that human body movements are represented in a viewpoint-dependent manner and that the recognition of static novel views can occur via a generalization from known views (Bülthoff et al 1998; Bülthoff and Edelman 1992; Edelman and Weinsall 1991; Logothetis et al 1994, 1995; Perrett et al 1996). However, this generalization process seems to be restricted to small rotation changes that are equal to or less than approximately 45° . The current results suggest that motion can expand these restricted generalization fields to large rotational changes but only within the path of the human motion. These results suggest that movements, which produce changes in human body form, can be represented in an orientation-invariant manner within the path of human movement. This conclusion differs from previous proposals that the representation of human movement is orientation specific (Bülthoff et al 1998; Oloffson et al 1997; Parsons 1987; Verfaillie 1992, 1993). However, in previous studies, as in the static condition of the current study, different views of a human body were not linked by motion. The results of the apparent-motion condition in this experiment suggest that motion processes may facilitate generalization across structurally dissimilar views of a human body so that observers perceive human movement as a continuous event.

Moreover, the visual system seems to take into account complex structural information, such as the biomechanical constraints on human movement, when representing objects in motion. Novel human body views falling between 'known' views were primed only when they respected the laws of normal human movement. This finding is consistent with the proposal that objects are represented dynamically; that is, as entities that change over time in a specific spatial direction (Freyd 1987). These dynamic object representations may be constrained by fundamental ecological principles such as gravity and elasticity (Freyd 1987; Shepard 1984, 1994; Shiffrar and Shepard 1991). The following experiment investigated further how biomechanical motion constraints affect human body representations.

3 Experiment 2

3.1 *Mannequin-model movements*

The results of experiment 1 suggest that visual representations of the human body are influenced by human biomechanics. However, the existence of an experimental confound permits an alternative explanation. That is, the nonbiological views of the human model were created by adding an extra motion, such as an impossible twist of the arm, to the motions of the biological views. Thus, the novel and known views of the nonbiological stimuli were less similar than the corresponding views of the biological stimuli. As a result, the generalization between the novel and known views may have been more difficult for the nonbiological stimuli.

The current experiment was designed to discriminate between these two explanations. To that end, mannequin figures, created from hierarchically joined cylinders, were used in the same paradigm as in experiment 1, as illustrated in figure 1b. It has been suggested that these figures have the same global structure as the human body and that their motions can be perceived similarly to the motions of the human body (Heptulla-Chatterjee et al 1996). However, these figures are not subject to the same biomechanical joint constraints as the human body. For example, the arm of a mannequin figure has more degrees of freedom than a human arm. Thus, a novel view of a mannequin, created by adding an extra nonbiological movement, could be consistent with the physical constraints of the motion of the mannequin while violating human biomechanical constraints. Will novel views of mannequin movements show priming even when they violate the biomechanical constraints of human movement? If so, then one could conclude that the nonbiological views used in experiment 1 were unprimed because they violated human biomechanical constraints and not because they introduced an additional movement.

3.2 *Method*

3.2.1 *Subjects.* Twenty undergraduate students, recruited from the Rutgers University subject pool, participated in this experiment. All subjects had normal or corrected-to-normal vision.

3.2.2 *Materials and procedure.* The human stimuli used in experiment 1 were replaced with mannequin stimuli (again constructed with Fractal Design Poser 2.0) of the same overall shape and size. Figure 1b illustrates an example of the mannequin figures used in this experiment. The mannequin displays were presented within the same display subregion of the monitor, $4.8 \text{ deg} \times 4.8 \text{ deg}$, and underwent the same displacements as the human-model displays used in experiment 1. The procedure was identical to the apparent-motion condition of experiment 1. In a between-subjects design, two groups of ten subjects observed stimuli at either the 60° or 120° rotation angle.

3.3 *Results*

Repeated ANOVAs with Priming as the within-measure variable indicated significant priming for Frame 1 ($F_{1,19} = 59.6, p < 0.001$), Frame 2 ($F_{1,19} = 80.4, p < 0.001$), Inter ($F_{1,19} = 43.2, p < 0.001$), and Inter NB ($F_{1,19} = 15.7, p < 0.001$). No priming was observed for Extra 1 ($F_{1,19} = 0.349, p = 0.561$) or Extra 2 ($F_{1,19} = 1.8, p = 0.189$). Table 2 reports priming and p -values from one-tail paired t -tests across rotation angles.

A repeated ANOVA with Priming as the within-measure variable and Rotation angle (orientation difference between the first and second prime) and Test frame (Frame 1, Frame 2, Inter, Inter NB, Extra 1, or Extra 2) as the independent variables indicated significant main effects of Priming ($F_{1,108} = 60.3, p < 0.001$) and Test frame ($F_{5,108} = 11.2, p < 0.001$), but no main effect of Rotation angle ($F_{1,108} = 0.316, p = 0.575$). Fisher's a posteriori comparisons showed that Frame 1, Frame 2, Inter, and Inter NB were significantly more primed than Extra 1 ($p < 0.001$) and Extra 2 ($p < 0.001$).

As shown in figure 4, for the small rotation angle (60°), a one-way ANOVA with Priming as the dependent variable and Test frame as the independent variable showed a main effect of Test frame ($F_{5,54} = 4.7$, $p < 0.001$). Fisher's a posteriori comparisons showed that Frame 1, Frame 2, and Inter were significantly more primed than Extra 1 ($p < 0.01$) and Extra 2 ($p < 0.001$). Also, Inter NB were significantly more primed than Extra 2 ($p < 0.01$).

For the large rotation angle (120°) a main effect of Test frame was found ($F_{5,54} = 7.5$, $p < 0.001$). Fisher's a posteriori comparisons showed that Frame 1, Frame 2, Inter, and Inter NB were significantly more primed than Extra 1 ($p < 0.001$) and Extra 2 ($p < 0.001$).

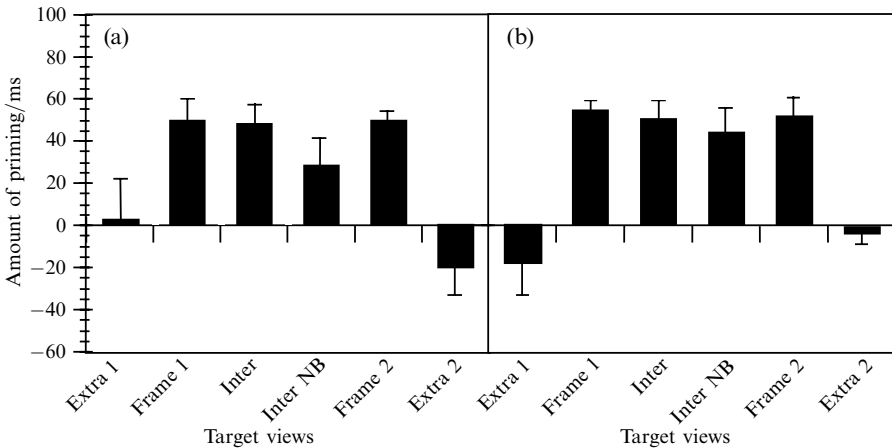


Figure 4. Results from experiment 2: Amount of priming (expressed in milliseconds) for the mannequin targets in all possible orientations across (a) the small (60°) and (b) the large (120°) rotation angles.

3.4 Discussion

The results of experiment 2 suggest that the visual system takes into account biological motion constraints when representing human body movements. Specifically, apparent motion facilitated the representation of novel views within the path of the motion of the mannequin. Consistently with the results of experiment 1, target views at the same orientation as the primes were primed in the apparent-motion condition for both the 60° and the 120° rotation angle. Novel views falling outside the path of motion were not primed. However, novel views falling within the path of motion were primed even when these views violated the biomechanical constraints of the human body motion.

These results seem inconsistent with the recent suggestion that motions of mannequin figures can be perceived similarly to motions of the human body (Heptulla-Chatterjee et al 1996). However, these earlier studies investigated how structural solidity rather than joint flexibility may affect the perception of human body movements. While mannequin figures and human bodies are both solid, their motions are not subject to the same limits on joint flexibility. As a result, mannequin movements can be dynamically represented even when humans cannot perform these movements.

Taken together, these results suggest that the visual system takes into account information specific to the structure of an object when representing object motion. Failure to find priming for views violating the biomechanical constraints of human body motion with human models (experiment 1) was not due to the introduction of an additional motion. That is, rapid recognition of novel views of a moving human requires that these views must respect the biomechanical constraints of human motion. These results are consistent with recent studies showing priming for previously seen views of possible but not impossible human poses (Daems and Verfaillie, submitted).

4 General discussion

The visual system seems to represent human body movements dynamically in a manner that respects the biomechanical constraints imposed by the structure of the human body (Shiffrar and Freyd 1990, 1993). Specifically, novel views of a human body in motion seem to be represented only when they are consistent with the range of normal human movements. These results suggest important interactions between object form and motion processes.

Object identity and motion are assumed to be processed separately by the ventral ‘what’ system and the dorsal ‘where’ system (DeYoe and van Essen 1988; Ungerleider and Mishkin 1982). However, several neurophysiological studies suggest that form and motion analyses may be integrated during the processing of biological motion. Anatomical evidence demonstrates that the ‘what’ and ‘where’ pathways converge in the superior temporal sulcus (Baizer et al 1991; Goodale and Milner 1992). Numerous cells have been found in the macaque superior temporal sulcus (Perrett et al 1990) and inferotemporal cortex (Wachsmuth et al 1994) that respond selectively to an entire human body or body parts but not to inanimate objects. About 90% of these cells respond to the human body in a viewer-centered manner, whereas the remaining cells respond equally well to any view of the body. These findings suggest that, most of the time, views of a primate body are represented in an orientation-specific manner. If so, then the results of the current experiments suggest that these views can be linked together, on the fly, by motion processes.

Taken together, these neurophysiological studies and the current priming results provide further evidence that human body movements can be represented as collections of viewpoint-specific images (Bülthoff and Edelman 1992; Bülthoff et al 1998; Edelman and Weinsall 1991; Logothetis et al 1994, 1995; Perrett et al 1996). Traditional models of object recognition predict that human body movements resulting in structurally dissimilar views should be particularly difficult to recognize (Biederman 1987). However, the results of the current experiments indicate that such views can be readily recognized when they are linked by apparent motion. It is possible that the visual system constructs representations of novel views in a path-specific manner during the analysis of the human motion rather than through spatiotemporal associations between static snapshots. If so, then representations of the human body may be continuously updated and remapped relative to the observer during the perception of human movement. This ‘dynamic remapping’ of human movement appears to be constrained by the structure and kinematics of the human body and may play an important role in an observer’s successful interactions with other humans.

Acknowledgements. This research was supported by a grant from the Sigma Xi Foundation to Zoe Kourtzi and a grant from the National Eye Institute (EY099310) to Maggie Shiffrar. Some of the results discussed in this article were first presented at the 1998 meeting of the Cognitive Neuroscience Society in San Francisco, CA. We thank two anonymous reviewers for their helpful comments.

References

- Baizer J S, Ungerleider L G, Desimone R, 1991 “Organization of visual inputs to inferior temporal and posterior parietal cortex in macaques” *Journal of Neuroscience* **11** 168–190
- Bartram D J, 1974 “The role of visual and semantic codes in object naming” *Cognitive Psychology* **6** 325–356
- Biederman I, 1987 “Recognition-by-components: A theory of human image understanding” *Psychological Review* **94** 115–117
- Biederman I, Gerhardstein P C, 1993 “Recognizing depth-rotated objects: Evidence and conditions for three-dimensional viewpoint invariance” *Journal of Experimental Psychology: Human Perception and Performance* **19** 1162–1182
- Bülthoff I, Bülthoff H H, Sinha P, 1998 “Top–down influences on stereoscopic depth-perception” *Nature Neuroscience* **1** 254–257

- Bülthoff H H, Edelman S, 1992 "Psychophysical support for a 2-D view interpolation theory of object recognition" *Proceedings of the National Academy of Sciences of the USA* **89** 60–64
- Cutting J E, 1987 "Perception and information" *Annual Review of Psychology* **38** 61–90
- Cutting J E, Proffitt D R, Kozlowski L T, 1978 "A biomechanical invariant of gait perception" *Journal of Experimental Psychology: Human Perception and Performance* **3** 357–372
- Daems A, Verfaillie K, submitted "Viewpoint-dependent priming effects in the perception of human actions and body postures" *Visual Cognition*
- DeYoe E A, Essen D C van, 1988 "Concurrent processing streams in monkey visual cortex" *Trends in Neurosciences* **11** 219–226
- Dittrich W H, 1993 "Action categories and the perception of biological motion" *Perception* **22** 15–22
- Edelman S, 1997 "Computational theories of object recognition" *Trends in Cognitive Sciences* **1** 296–304
- Edelman S, Weinshall D, 1991 "A self-organizing multiple view representation of 3-D objects" *Biological Cybernetics* **64** 209–219
- Freyd J J, 1987 "Dynamic mental representations" *Psychological Review* **94** 427–438
- Goodale M A, Milner A D, 1992 "Separate visual pathways for perception and action" *Trends in Neurosciences* **15** 20–25
- Heptulla-Chatterjee S, Freyd J J, Shiffrar M, 1996 "Configural processing in the perception of apparent biological motion" *Journal of Experimental Psychology: Human Perception and Performance* **22** 916–929
- Johansson G, 1973 "Visual perception of biological motion and a model for its analysis" *Perception & Psychophysics* **14** 201–211
- Kourtzi Z, Shiffrar M, 1997 "One-shot view-invariance in a moving world" *Psychological Science* **8** 461–466
- Kourtzi Z, Shiffrar M, 1998 "The representation of three-dimensional, rotating objects" *Acta Psychologica: A Special Issue on Object Perception & Memory* (in press)
- Kozlowski L T, Cutting J E, 1977 "Recognizing the sex of a walker from a dynamic point-light display" *Perception & Psychophysics* **21** 575–580
- Lawson R, Humphreys G W, Watson D G, 1994 "Object recognition under sequential viewing conditions: evidence for viewpoint-specific recognition procedures" *Perception* **23** 595–614
- Logothetis N, Pauls J, Bülthoff H H, Poggio T, 1994 "View-dependent object recognition by monkeys" *Current Biology* **4** 401–414
- Logothetis N, Pauls J, Poggio T, 1995 "Shape representation in the inferior temporal cortex of monkeys" *Current Biology* **5** 552–563
- Marey E J, 1895/1972 *Movement* (New York: Arno Press and New York Times) (originally published in 1895)
- Oloffson U, Nyberg L, Nilsson L-G, 1997 "Priming and recognition of human motion patterns" *Visual Cognition* **4** 373–382
- Parsons L M, 1987 "Imagined spatial transformations of one's hands and feet" *Cognitive Psychology* **19** 178–241
- Perrett D I, Harries M, Mistlin A J, Chitty A J, 1990 "Three stages in the classification of body movements by visual neurons", in *Images and Understanding* Eds H B Barlow, M Weston-Smith (Cambridge: Cambridge University Press) pp 94–107
- Perrett D I, Oram M W, Wachsmuth E, 1996 *Evidence Accumulation in Cell Populations Responsive to Faces: An Account of Generalisation of Recognition without Mental Transformations* unpublished manuscript, St Andrews University, Scotland
- Poggio T, Edelman S, 1990 "A network that learns to recognize three-dimensional objects" *Nature (London)* **343** 263–266
- Reed C L, Farah M J, 1995 "The psychological reality of the body schema: A test with normal participants" *Journal of Experimental Psychology: Human Perception and Performance* **21** 334–343
- Sekuler A B, Palmer S E, 1992 "Perception of partly occluded objects: A microgenetic analysis" *Journal of Experimental Psychology: General* **121** 95–111
- Shepard R N, 1984 "Ecological constraints on internal representation: Resonant kinematics of perceiving, imagining, thinking, and dreaming" *Psychological Review* **91** 417–447
- Shepard R, 1994 "Perceptual–cognitive universals as reflections of the world" *Psychonomic Bulletin and Review* **1** 2–28
- Shepard R N, Judd S A, 1976 "Perceptual illusions of rotation of three-dimensional objects" *Science* **191** 952–954
- Shiffrar M, 1994 "When what meets where" *Current Directions in Psychological Science* **3** 96–100
- Shiffrar M, Freyd J J, 1990 "Apparent motion of the human body" *Psychological Science* **1** 257–264

-
- Shiffrar M, Freyd J J, 1993 "Timing and apparent motion path choice with human body photographs" *Psychological Science* **4** 379–384
- Shiffrar M, Lichtey L, Heptulla-Chatterjee S, 1997 "The perception of biological motion across apertures" *Perception & Psychophysics* **59** 51–59
- Shiffrar M, Shepard R N, 1991 "Comparison of cube rotations around axes inclined relative to the environment or to the cube" *Journal of Experimental Psychology: Human Perception and Performance* **17** 44–54
- Ungerleider L G, Mishkin M, 1982 "Two cortical visual systems", in *Analysis of Visual Behaviour* Eds D G Ingle, M A Goodale, R J W Mansfield (Cambridge, MA: MIT Press) pp 549–586
- Verfaillie K, 1992 "Variant points of view on viewpoint invariance" *Canadian Journal of Psychology* **46** 215–235
- Verfaillie K, 1993 "Orientation-dependent priming effects in the perception of biological motion" *Journal of Experimental Psychology: Human Perception and Performance* **19** 992–1013
- Verfaillie K, De Troy A, Van Rensbergen J, 1994 "Transsaccadic integration of biological motion" *Journal of Experimental Psychology: Learning, Memory, and Cognition* **20** 649–670
- Wachsmuth E, Oram M W, Perrett D I, 1994 "Recognition of objects and their component parts: Responses of single units in the temporal cortex of the macaque" *Cerebral Cortex* **4** 509–522