

**Predictive extrapolation of observed body movements is tuned by knowledge of the
body biomechanics**

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Stimuli, data and SPSS syntax used to run the analyses have been made available on OSF (<https://osf.io/s9txg/>). We have no conflicts of interest to disclose.

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Abstract

After a moving object has disappeared, observers typically mislocate its final position to where that object would have been if it had briefly continued to move. Previous studies have shown that this “forward displacement” (FD) is significantly smaller when observers see an upper-limb movement directed away from the body that would have been biomechanically impossible to continue along the same trajectory after it has disappeared than when the movement is directed toward the body and would have been easy to continue. This finding has been argued to reflect an implicit influence of observers’ biomechanical knowledge on FD. However, this effect could also result from a “landmark attraction”, which has been shown to reduce the size of displacement when an object moves away, rather than toward, from a landmark. To discriminate these possibilities, we measured the FD elicited by arm movements directed away or toward the body, which would have been biomechanically impossible or easy to continue after the stimuli disappeared, and by highly similar movements of geometrical shapes. In two experiments, we found a significantly larger effect of movement direction for the human stimuli. Thus, knowledge of the body biomechanics influences FD for body movements.

Keywords: visual perception, prediction, representational momentum, biological motion, biomechanical knowledge

Public Significance Statement

After a moving object has disappeared, people typically mislocate its final location to where it would have been if it had continued to move for a short period of time. Such error is widely assumed to be a by-product of a highly adaptative function of the visual system that extrapolates the future location of moving objects in order to compensate for the informational lag due to neural transmission. Here, we report that perceptual extrapolation of body movements is influenced by knowledge of the body biomechanics, and that this effect cannot be accounted for by previously uncontrolled confounded factors.

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Suppose that you are watching a tennis game on television. Your favorite player hits the ball but, almost immediately after, the program is interrupted by an advertisement. How accurate do you think you would be at indicating the last location of the ball? Research tells us that you would probably be less accurate than you think. Just a few hundred milliseconds after seeing a moving object suddenly disappear, people typically mislocate its final location to the place where that object would have been if it had continued to move for a short period of time. This bias is often referred to as “representational momentum” (Freyd & Finke, 1984). However, this term also refers to a particular causal mechanism of forward displacement (see Hubbard, 2005 for discussion). Hence, to avoid any misunderstanding, in this paper we will use the term “forward displacement” (FD) to refer to the mislocalization of the final position of a target where it would have been if it has continued to move for a short period of time along its initial trajectory (Hubbard, 2005). Although FD is experimentally revealed by errors in locating the last position of a moving stimulus, it is widely assumed to be a by-product of a highly adaptive function of our visual system that extrapolates the future location of moving objects in order to compensate for the ~100 ms delay in the neural transmission of information from photoreceptors to early visual processing regions (Hubbard, 2015, 2017; Nijhawan, 2008). Although we are not explicitly aware of it, the visual system faces this type of extrapolation problem hundreds of times per day, whenever we encounter moving objects. If the visual system did not solve the problem posed by neural transmission delay so efficiently, we would not be able to track moving objects: our eyes would always look where a moving object has been, not where it is. We would also have severe difficulties to synchronize our actions with others, to intercept moving objects, and to avoid collision with them (Aschersleben, 2002; Repp, 2005; Zago, McIntyre, Senot, & Lacquanti, 2009).

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Despite much progress, how the brain solves this engineering problem remains unclear. Identifying the factors that influence FD provides a window into this issue (see Hubbard, 2017 for review). In the research reported here, we investigated whether FD for body movements is influenced by knowledge of the body biomechanical constraints.

In line with this idea, previous studies have reported that although estimates of the final position of a body movement are typically shifted forward (Verfaillie & Daems, 2002), this bias is smaller, or even inverse, when the movement is unpredictable (Munger, 2015), or when it would have been impossible to continue along the same trajectory due to the biomechanical limits of the human body (Vannuscorps & Caramazza, 2016a; Wilson et al., 2010). In one of these studies, participants saw video clips depicting a computer-generated actor performing either an internal or an external rotation of the right shoulder (like in Figure 1, below) and had to decide whether a subsequent probe picture matched the position of the hand at the end of the video (Vannuscorps & Caramazza, 2016a). The last frame of the video was identical for both the internal and the external rotation conditions and displayed the hand positioned close to the limit of amplitude of external rotation of the shoulder. Thus, the movement of internal rotation would have been easy to continue further along the same trajectory by the actor whereas the external rotation would be very difficult, if not impossible, to continue further along the same trajectory. Three pictures were used as probes: the same as the last frame and two probes displaying the actor's hand slightly displaced backward or forward along its initial trajectory (± 4 degrees of shoulder rotation).

The results of this experiment were clear-cut. When the movement would have been easy to continue for the actor, participants judged that the position of the actor's hand depicted on the probe matched the position at the end of the video in approximately 70% of

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the forward probe trials, but in only about 20% of the backward probe trials. This disproportionate difficulty to discriminate the final position of a moving stimulus from that depicted on a forward probe vs. on a backward probe is a typical index of FD. Interestingly, when the inducing movement would have been hard or impossible to continue along the same trajectory, proportions of errors dropped to 50% and 40% on the forward and backward probes respectively.

This apparent tuning of FD by the biomechanical plausibility of movements has been observed in experiments using both implied and continuous motion, different types of upper limbs movements, executed by both real and computerized 3D actor models, and in both typically developed participants and in people born without upper limbs (Vannuscorps & Caramazza, 2016a; Wilson et al., 2010). To date, this effect has been interpreted as a result of the implicit influence of knowledge of the body biomechanical constraints on FD. If this interpretation were correct, these findings would contribute unique evidence that FD is influenced by knowledge of objects' typical range of motion. Indeed, the results of previous studies addressing this issue were either unclear (Reed & Vinson, 1996; Vinson & Reed, 2002) or at odds with this conclusion (Nagai and Yagi, 2001). Among the seven experiments reported by Reed and Vinson (Reed & Vinson, 1996; Vinson & Reed, 2002), the authors compared the displacement elicited by different objects of identical or similar shape moving in different directions in two experiments (Experiments 1 and 4 from Reed & Vinson, 1996). In these two experiments, they compared the FD elicited by implied motion of a "rocket" and a "steeple" (Experiment 1) or a "church" (Experiment 4). Based on the premise that rockets typically tend to go up while steeples/churches do not move at all, the authors reasoned that if knowledge of the typical motion of objects influences FD, then the FD elicited by upward

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implied motion should be larger for the rocket than for the church/steeple. This prediction was verified, leading the authors to suggest that FD is influenced by typical, real-world motion of objects. However, the larger FD for the rocket did not interact significantly with the direction of motion (up or down). Therefore, an alternative interpretation is that FD is influenced by whether a depicted object may move or not, independently from their typical way of moving. In line with this alternate interpretation, the FD elicited by implied motion of the rocket was of a very similar size when participants saw the rocket moving up and when it was moving horizontally towards the left or right (Experiment 1). As rockets depicted upright never move horizontally, this finding seems very difficult to reconcile with the conclusion that FD is influenced by knowledge of the typical motion of objects.

However, a close look at the stimuli used in previous studies claiming to report an implicit influence of knowledge of the body biomechanical constraints on FD suggests an alternative explanation. In all previous experiments, the upper-limb movements that were easy to continue along the same trajectory were directed toward the (static) body while those that were hard to continue were directed away from the body (Vannuscorps & Caramazza, 2016a; Wilson et al., 2010). This reflects a general property of the biomechanical constraints of the upper limbs, which makes it easier to move one's hand towards than away from the body (e.g., the medial-over-lateral advantage; Vannuscorps, Pillon & Andres, 2012). However, this introduces a confound between a putative effect of the biomechanical constraints on FD and the fact that FD is typically larger when an object moves towards, rather than away from, a static object that provides a point of reference (Hubbard & Ruppel, 1999) – an effect assumed to result from the influence of the so-called “landmark attraction

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effect” on displacement, which is a tendency to judge the distance from a target to a landmark as being smaller than the distance from the landmark to that target (Bryant & Subbiah, 1994).

The goal of the study reported here was to test whether FD for body movement is influenced by knowledge of the body biomechanical constraints in addition to the more general effect of landmark attraction. To do so, we asked participants to discriminate the final position of a human actor’s arm movement directed either towards or away from the body and that would have been either biomechanically easy or impossible to continue along the same trajectory after it disappeared, or of highly similar movements made by an articulated abstract shape, from that depicted on a forward or a backward probe. This allowed testing for three predictions. First, in line with the idea that the visual system extrapolates the future location of moving objects, we predicted a disproportionate difficulty (i.e., a larger number of errors) to discriminate the final position of a moving stimulus from that depicted on a forward probe compared to that depicted on a backward probe. We used the size of this difference as an index of the relative size of FD in different experimental conditions: provided that the task is sensitive, a larger FD in one condition is expected to decrease the number of errors on the backward probes, to increase the number of errors for forward probes and, therefore, to increase the difference between the number of errors for forward minus backward probes. Second, in line with the influence of landmark attraction on displacement, we predicted a larger FD when a stimulus moves towards than away from the body/shape (Hubbard & Ruppel, 1999). Third, we predicted that if there is an additional influence of knowledge of the body biomechanical constraints on FD for body movements, the difference between the two movement directions should be significantly larger for the human body stimulus than for the abstract shape stimulus.

Experiment 1

Method

Participants

Prior studies examining factors involved in FD often produce medium effect sizes (i.e. $d = .6$ in Vannuscorps & Caramazza, 2016a, and Wilson et al., 2010). Given that such effect size requires around 20 participants to reach 80% power (one-tailed, alpha level = .05), and based on a pilot study on 32 participants, we defined a sample size of 30 participants before the start of the experiment to reach sufficient power. To meet this number, a total of 48 students took part in the experiment and received course credit for their participation. Eighteen participants were excluded based on predefined exclusion criteria (cf. procedure section) before any data analysis. The final sample included 29 females and one male with normal or corrected-to-normal vision ($M = 20.1$; $SD = 3.2$). Data collection was carried out from September to October 2020 in sessions lasting approximately 60 minutes. The study was approved by the biomedical ethics committee of the Cliniques Universitaires Saint-Luc, Brussels, Belgium, and all participants gave their informed consent.

Stimuli and apparatus

Stimuli consisted of four video-clips, illustrated on Figure 1, panel A, and six pictures. They were divided in two sets. The “HUMAN” set included two video-clips obtained from Vannuscorps and Caramazza (2016a; Experiment 7). They depicted a computer-generated actor (approximately $17.7^\circ \times 12.2^\circ$ of visual angle) facing the participant, with the right arm raised so as to form a 60° angle with the body and flexed so as to form a 90° angle between the arm and the forearm. In the first video (“TOWARD” condition on Figure 1, panel

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A), a first frame depicting the actor's right forearm tilted 80° counterclockwise from the mid-sagittal line was followed by a 60° internal rotation of the right shoulder (i.e., toward the body midline). In the second video ("AWAY" condition on Figure 1, panel A), a first frame depicting the actors' forearm tilted 40° clockwise from the mid-sagittal line was followed by a 60° external rotation of the right shoulder (i.e., away from the body midline). The actor's body, left arm and face remained still. The last frame of the two video-clips was identical and depicted the hand positioned close to the typical limit of amplitude of the external rotation of the shoulder (Gill et al., 2020; Hill et al., 2010). In both video-clips, the first frame was presented for 1000 ms. This ascertained that participants had enough time to recognize the object depicted on the screen before that object started to move. After that first frame, the movement was induced by presenting 12 frames on which the rotation of the forearm was increased by steps of 5° for 16 ms each (200 ms in total). This way, the TOWARD video-clip depicted a rotating movement of the arm of constant velocity that would be easy to continue along the same trajectory after the position of the hand on the last frame and the AWAY video-clip depicted a rotating movement of the arm of constant velocity that would be biomechanically difficult to continue along the same trajectory after the position that the hand reached on the last frame.

The "SHAPE" set included two video-clips illustrating movements very similar to those depicted in the two video-clips of the "HUMAN" set. The only difference was that the body of the human actor was replaced by a large red rectangle, his arm by a narrow red rectangle and his forearm arm by a narrow grey rectangle (see Figure 1, panel A).

Both sets of stimuli also included three pictures, used as probes in the experiment. A first picture was the last frame of the video-clips. This picture will be referred to hereafter as

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the “target” probe. The two other pictures depicted the hand of the actor (in the HUMAN condition), or the narrow grey rectangle (in the SHAPE condition) slightly (4°) tilted further away or toward the actor (in the HUMAN condition) or the large red rectangle (in the SHAPE condition). This tilt shifts (4°) was selected after pilot experiments because it maximized the number of errors for the forward probes while minimizing the number of errors for the backward probes (i.e., it maximized the task sensitivity). Larger tilt shifts led to a sharp decrease of errors.

Hereafter, these pictures will be referred to as the probes. Each probe will be named alternatively “FORWARD probe” or “BACKWARD probe” depending on whether it depicts the hand of the actor (in the HUMAN condition), or the narrow grey rectangle (in the SHAPE condition) slightly forward along their initial trajectory (i.e., in the future) or in the reverse direction (i.e., in the past).

All stimuli were displayed on a light grey background (hex code: #CCCCCC). The experiment was controlled by Psychopy 1.90.3 (Peirce, 2007) and presented on a 60 hz monitor.

Procedure

During the experiment, participants sat at approximately 60 cm from the computer screen. The experimental session comprised four tasks, all performed by all participants in a within-subject design.

Participants first performed a task testing their perception of the movements induced by the video-clips of the SHAPE condition. Their head and eye movements were not constrained. As illustrated in Figure 1, panel B, in each trial of this task the participants viewed one of the two SHAPE video-clips (in a randomized order) followed by a blank screen

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for 250 ms, one of the three probe pictures for 250 ms, a second blank screen for 250 ms and then, a screen displayed until a response was recorded and on which was written the phrase “same position or not?”. The task of the participants was to decide whether the grey rectangle/the hand of the actor on the probe picture was exactly at the same place as it was at the end of the video-clips. Participants responded by pressing the keys “o” for yes or “n” for no (corresponding to the first letter of the equivalent words “oui” and “non” in French) on a computer keyboard. There was no time pressure or constraint. After a response was recorded, there was a 1000 ms interval before the next trial. Participants performed three blocks of 60 trials each, interspersed with short breaks. In each block, the two movement directions (TOWARD/AWAY) and three types of probes (BACKWARD/ TARGET/ FORWARD) were in equal proportion and randomized. Thus, there were 30 trials per each combination of movement direction and type of probe, for a total of 180 trials. The first block started with 18 additional practice trials to familiarize participants with the task.

In the second task, participants were interviewed and asked to indicate whether the stimuli they saw during the first task reminded them anything familiar, and if so, what. Participants’ verbal responses were encoded by the experimenter and were later used to exclude participants who had associated these stimuli to a human body from the analyses (exclusion criteria 1). This allowed making sure that the data from the shape condition were not contaminated by some participants who had assimilated these movements to human movements.

In the third task, we tested participants’ perception of the HUMAN video-clips. This task had the same design as the SHAPE task described above (see Figure 1, panel B), except that there were no practice trials given that participants were already familiar with the task.

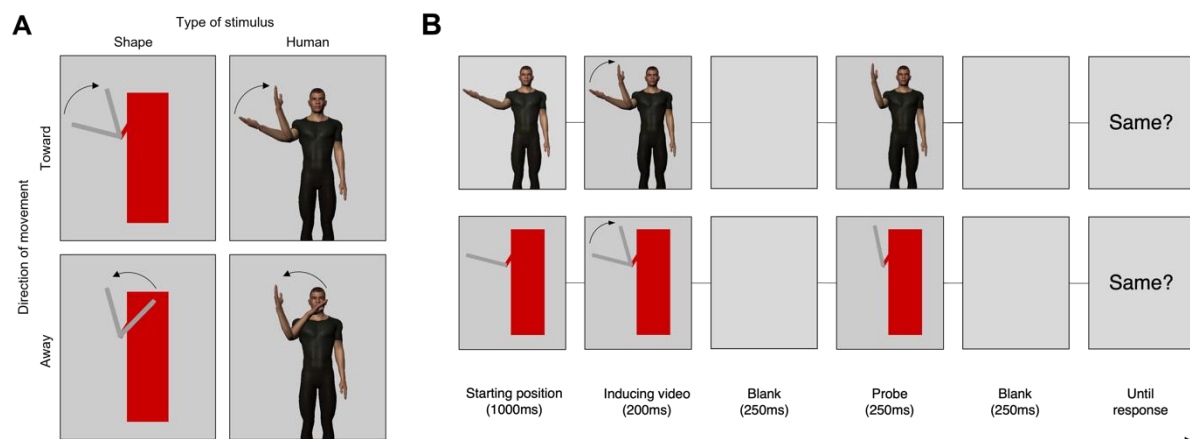
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Finally, participants were questioned regarding the purpose of the experiment. We asked the following question: “Have you thought about the purpose of the experiment during the task? If so, what do you think the experiment is about, and what do you think we expect to observe?” Participants’ responses were encoded by the experimenter and were later used to exclude any participants who had correctly guessed the purpose of the experiment (exclusion criteria 2).

Stimuli, data and SPSS syntax used to run the analyses have been made available on OSF (<https://osf.io/s9txg/>).

Figure 1

Material and trial sequence



Note. **A.** Illustration of the four video-clip stimuli. **B.** Trial sequence and illustration of a forward probe picture used in the HUMAN and SHAPE conditions.

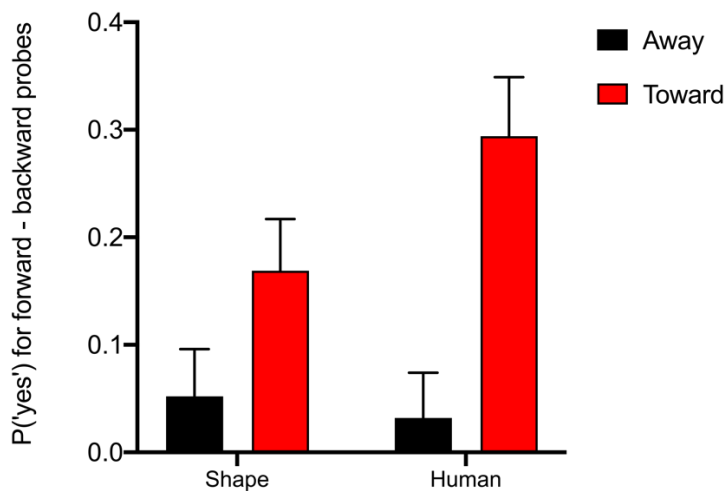
Results and discussion

Among the 48 students that took part in the experiment, 18 were excluded before any data analysis because they associated the shape movements to human body movements (exclusion criteria 1). No participant was able to guess the purpose of the experiment (exclusion criteria 2). The results of the 30 other participants are displayed on Figure 2. First, we conducted a series of paired t-tests (Bonferroni corrected) to test for the presence of FD in participants' responses (i.e., a significantly larger probability of "yes" responses for the forward than for the backward probes) in the four separate conditions (SHAPE-TOWARD, SHAPE-AWAY, HUMAN-TOWARD, HUMAN-AWAY). The result of these analyses indicated a significantly larger probability of "yes" response for forward than backward probes in the SHAPE-TOWARD, $t(7192) = 6.92, p < .001$, SHAPE-AWAY, $t(7192) = 2.29, p = .01$ and HUMAN-TOWARD, $t(7192) = 11.07, p < .001$ conditions, but not in the HUMAN-AWAY condition, $t(7192) = 1.49, p = .07$.

Second, we tested whether FD for body movements was influenced by knowledge of the body biomechanical constraints, over and above the expected influence of landmark attraction. Landmark attraction should lead to a generally larger FD for the movements directed towards than away from the HUMAN/SHAPE. An additional influence of knowledge of the body biomechanical constraints on RM should lead to a larger difference between the two movements direction for the human body than for the abstract shape stimuli. To test these hypotheses, we entered participants responses (yes/no) as a dependent variable in a generalized linear mixed model (GLMM) and Probe (FORWARD/BACKWARD), Direction of movement (TOWARD/AWAY) and Type of stimulus (SHAPE/HUMAN) as fixed within-subject factors, and Participant as a random factor. In line with the tested hypothesis, the result of the

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main analysis indicated (1) a larger FD for movements performed toward the abstract shape ($M = .17, SE = .02$) than away from it ($M = .05, SE = .02$), $F(1,3596) = 9.75, p = .002, OR = 1.58$; (2) a larger FD for movements performed toward ($M = .29, SE = .02$) than away from the body ($M = .03, SE = .02$), $F(1,3596) = 58.86, p < .001, OR = 3.27$; and more importantly, (3) a larger difference of FD between toward and away movements in the human condition ($M = .26, SE = .03$) than in the shape condition ($M = .12, SE = .03$), $F(1,7192) = 10.58, p = .001, OR = 2$).

Figure 2*Results of experiment 1*

Note. Probability of “yes” responses for forward minus the probability of “yes” responses for backward probes as a function of Direction of movement and Type of stimulus. Error bars depict 2 standard errors above the mean.

Finally, we conducted an exploratory analysis of the responses of the 18 participants originally excluded because they associated the shape movements to human movements. The

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goal of this analysis was to explore whether the influence of knowledge of the body biomechanics on FD is specific to the perception of moving human bodies or whether it can be extended to other stimuli provided they are assimilated to human bodies. The results of these 18 participants were virtually identical to those of the 30 participants who did not associate the shapes to human bodies and were characterized by (1) a larger FD for movements performed toward the abstract shape ($M = .13$, $SE = .03$) than away from it ($M = .02$, $SE = .03$), $F(1,2156) = 12.8$, $p < .001$, $OR = 1.98$; (2) a larger FD for movements performed toward ($M = .26$, $SE = .03$) than away from the body ($M = .02$, $SE = .03$), $F(1,2156) = 42.71$, $p < .001$, $OR = 3.6$; and (3) an interaction characterized by a larger difference of FD between toward and away movements in the human condition ($M = .28$, $SE = .04$) than in the shape condition ($M = .15$, $SE = .04$), $F(1,4312) = 10.58$, $p = .01$, $OR = 1.8$). In sum, the results of this post-hoc analysis suggested that the influence of knowledge of the body biomechanics on perceptual extrapolation is specific to the perception of moving human bodies.

The results of Experiment 1 were in line with the hypothesis that knowledge of the body biomechanical constraints influences FD for body movement perception. Nevertheless, as participants performed the experiment with the two types of stimuli in a fixed order, starting with the shapes, the difference between the two types of stimuli may also be due to a mere order effect. We conducted Experiment 2 to overcome this issue.

Experiment 2

The goal of Experiment 2 was to ensure that the results reported in Experiment 1 could be replicated with slightly different stimuli (i.e. slower video-clips), and when the human and shape stimuli do not differ in their order of presentation. Two groups of participants took part

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in Experiment 2. The first group performed the same four tasks as in Experiment 1. The second group, however, performed only the third (with human stimuli) and the fourth (interview on the purpose of the experiment) tasks. This allowed measuring FD evoked by the upper-limb movements when they are not preceded by a similar task with geometrical shapes (in Group 2) and, ultimately, comparing the FD for the shape (in Group 1) and the human stimuli (in Group 2) unconfounded by a possible order effect.

Method

Participants

As in Experiment 1, a sample size of 30 participants per group was defined a priori. In total, 85 students were tested in the experiment and received course credit for their participation. 54 participants were tested in Group 1, from which 24 were excluded before analyses based on exclusion criteria (cf. procedure section). The final sample was composed of 30 participants (24 females, 6 males, $M = 21.4$, $SD = 2$). Thirty-one participants were tested in Group 2, from which one was excluded. The final sample was composed of 30 participants (24 females, 6 males, $M = 20.7$, $SD = 1.8$). Data collection was carried out from November 2020 to January 2021 in sessions lasting approximately 40 minutes (Group1) or 20 minutes (Group2). The study was approved by the biomedical ethics committee of the Cliniques Universitaires Saint-Luc, Brussels, Belgium, and all participants gave their informed consent. All participants had normal/corrected-to-normal vision.

Stimuli and apparatus

Only two changes were made to stimuli from Experiment 1. First, we reduced the speed of the videos by doubling the duration of all the frames of the video-clips (33 ms instead of 16 ms). This change was introduced to increase our confidence that the effect

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could be replicated with slightly different stimuli. The second difference was that stimuli also included probe pictures depicting a very large displacement (20°) of the actor's hand or of the abstract shape in comparison to their last position in the video. These stimuli were used as catch trials, on the basis of which a new exclusion criterium was established (exclusion criteria 3, see results section). This new exclusion criterium (two errors or more on catch trials) was introduced to allow detecting and excluding participants that were insufficiently paying attention to the task. The apparatus was identical to that of Experiment 1.

Procedure

The procedure was very similar to that of Experiment 1. There were only two differences. First, Group 2 performed only the third (with human stimuli) and the fourth (interview on the purpose of the experiment) tasks. This allowed measuring FD for body movements away and towards the body when these stimuli are not preceded by a similar task with abstract shapes. Second, the number of trials per condition was divided by two, resulting in a total of 15 trials per each combination of movement direction and probe. This resulted in three blocks of 35 trials (5 for each condition of interest plus 5 catch trials), for a total of 105 trials per type of stimulus. This change was introduced after exploratory analyses of the results of Experiment 1, which suggested that reducing the duration of the task would not impact significantly its statistical power.

Stimuli, data, and SPSS syntax used to run the analyses have been made available on OSF (<https://osf.io/s9txg/>).

Results and discussion

Among the 85 students that took part in the experiment, 25 were excluded before data analysis because (1) they associated the shape movements to human body movements

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(exclusion criteria 1, $n = 23$) or (2) they made two errors or more on catch trials (exclusion criteria 3, $n = 2$). No participant was able to guess the purpose of the experiment (exclusion criteria 2). The results of the other participants are displayed on Figure 3. We conducted two series of analyses.

The objective of the first series of analyses was to test whether we could replicate the results of Experiment 1. To do so, we performed the same three analyses on the responses of participants of the Group 1 (Figure 3, panel A). First, we conducted a series of paired t-tests (Bonferroni corrected) on the number of “yes” response for forward and backward probes in all four conditions (SHAPE-TOWARD, SHAPE-AWAY, HUMAN-TOWARD, HUMAN-AWAY) to test for the presence of a FD effect. The results of these analyses indicated that this was the case: there was a significantly larger number of “yes” responses for forward than backward probes in all the conditions, all $t_{s(3592)} > 5.65$, all $p_s < .001$.

Then, we conducted the same GLMM analysis as in Experiment 1. The results of this analysis indicated (1) a larger FD for movements performed toward the abstract shape ($M = .44$, $SE = .03$) than away from it ($M = .33$, $SE = .03$), $F(1, 1796) = 4.78$, $p = .03$, $OR = 1.61$; (2) a larger FD for movements performed toward ($M = .50$, $SE = .03$) than away from the body ($M = .19$, $SE = .03$), $F(1, 1796) = 38.02$, $p < .001$, $OR = 3.98$; and more importantly, (3) a larger difference of FD between toward and away movements in the human condition ($M = .31$, $SE = .05$) than in the shape condition ($M = .11$, $SE = .05$), $F(1, 3592) = 8.42$, $p = .002$, $OR = 2.46$.

Finally, we ran an exploratory analysis of the responses of the 23 participants that were originally excluded because they associated shape to body movements. The results of this analysis indicated (1) no FD difference between movements performed toward the

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abstract shape ($M = .55$, $SE = .04$) and away from it ($M = .53$, $SE = .03$), $F(1,1376) < 0.01$, $p = .97$, $OR = 1$; (2) a larger FD for movements performed toward ($M = .62$, $SE = .03$) than away from the body ($M = .18$, $SE = .04$), $F(1,1376) = 66.67$, $p < .001$, $OR = 8.4$; and (3) an interaction characterized by a larger difference of FD between toward and away movements in the human condition ($M = .43$, $SE = .05$) than in the shape condition ($M = .01$, $SE = .05$), $F(1,2752) = 32.54$, $p < .001$, $OR = 8.1$).

In sum, the results of these three analyses largely replicated those from Experiment 1. There were two differences. The first was the finding of a statistically significant FD for the body movements directed away from the body in the responses of Group 1, while this effect did not reach the significance threshold ($p = 0.07$) in the responses of participants from Experiment 1. The second was the absence of FD difference between movements performed toward and away from the abstract shape in the exploratory analysis of the sample of 23 participants who had associated shapes to human bodies in the responses of Group 1, while this effect was significant in the exploratory analysis of the participants who had originally been excluded from Experiment 1. Importantly, however, these two statistically inconsistent results were in line with the hypothesis (and our finding) that FD is largely reduced (and thus statistical power decreased) when observers view body movements that would have been difficult to continue along the same trajectory.

The objective of the second series of analyses was to verify that the differences between the human and shape stimuli detected in Experiment 1, and in the analysis of the performance of Group 1 for the two types of stimuli, were not reducible to a mere order effect. To address this issue, we conducted two analyses on the responses of the participants from Group 2, who had performed the task with the human stimuli only (not preceded by the

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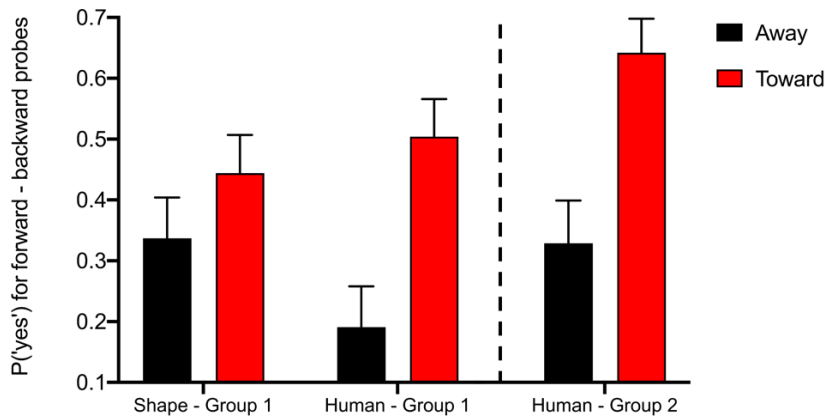
same task with the shape stimuli). First, we conducted two paired t-tests (Bonferroni corrected) to test for the presence of a FD in the two movement directions. The results of these analyses indicated a significant FD for both conditions, both $t_s(1796) > 9.31$, $ps < .001$.

Then, we performed a between-group GLMM analysis of the responses of the participants from Group 2 and of the participants from Group 1 for the abstract shape stimuli with participants responses (yes/no) as a dependent variable, Type of stimulus (SHAPE/HUMAN) as a between-group factor, Probe (FORWARD/BACKWARD) and Direction of movement (TOWARD/AWAY) and as fixed within-subject factors, and Participant as a random factor. Again, the results of this analysis indicated: (1) a larger FD for movements performed toward the abstract shape ($M = .44$, $SE = .03$) than away from it ($M = .33$, $SE = .03$), $F(1, 1796) = 4.78$, $p = .03$, $OR = 1.61$; (2) a larger FD for movements performed toward ($M = .64$, $SE = .03$) than away from the body ($M = .33$, $SE = .03$), $F(1, 1796) = 44.34$, $p < .001$, $OR = 4.92$; and more importantly, (3) a larger difference of FD between toward and away movements in the human condition ($M = .31$, $SE = .04$) than in the shape condition ($M = .11$, $SE = .05$), $F(1, 3592) = 11.66$, $p < .001$, $OR = 2.97$. Hence, the results of this analysis indicated that difference between the two types of stimuli is not reducible to a mere order effect.

Figure 3

Results of Experiment 2

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Note. The probability of “yes” responses for forward minus the probability of “yes” responses for backward probes as a function of Direction of movement and Type of Stimulus for participants from Group 1 and 2. Error bars depict 2 standard errors above the mean.

Discussion

Accurate real-time localization of moving stimuli is a crucial component of motor control and is critical in many daily life activities. The neural transmission and processing delays imply that by the time one sees a moving object in one position, that object is likely to be significantly farther away from that position. This discrepancy between the actual and perceived position of moving stimuli presents a serious engineering problem for one’s mind/brain. If one were to locate objects only based on their perceived location, one would probably have much difficulty to catch a ball on the fly or, more importantly, to track any moving object with our eyes. Despite much progress, how the brain solves this engineering problem is still unclear. The study of the factors influencing FD provides a window into this issue. Indeed, FD is widely assumed to reflect the inner working of the predictive mechanisms used by the brain to extrapolate the future location of moving objects. In this study, we demonstrate that FD for body movement perception is influenced by knowledge

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about how human bodies move, an effect that we refer to as the “biomechanical bias” in body movement perception.

Two previous studies had documented this effect but, in these studies, the effect of the biomechanical constraints was confounded with a landmark attraction effect (Vannuscorps & Caramazza, 2016a; Wilson et al., 2010). The results reported here overcome this limitation. Across two experiments, we show that the larger FD for body movements directed towards or away from the body cannot be accounted for by a landmark effect. If this were the case, this differential effect would have been comparable when participants observe body movements and when they observe very similar movements of an abstract shape. These findings indicate that perceptual anticipation of human body movements is based on an internal model of the typical body biomechanical constraints. As such, our findings extend the work of Verfaillie and Daems (2002), suggesting that observers anticipate the future position of observed body movements, and of Munger (2015), who had reported that this effect is larger for predictable than unpredictable body movements.

This finding corroborates those obtained in two other types of tasks. One early example revealing the influence of biomechanical knowledge on perceptual judgments is the hand laterality judgment task (Parsons, 1987; Vannuscorps, Pillon & Andres, 2012). When asked to judge the laterality of hand drawings presented on a screen at different angles and postures, naïve observers often make more mistakes and are slower at judging the laterality of hands displayed in orientations that would be difficult to reach with their own hand (for instance, a stimulus depicting the palm of a left hand with the fingers pointing toward the left), than of hands displayed in orientations that would be easy to execute (for instance, a stimulus depicting the palm of a left hand with the fingers pointing toward the right).

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Knowledge of the biomechanical constraints has also been found to influence the perceived path of apparent body movement (Heptulla-Chatterjee, Freyd & Shiffrar, 1996; Funk, Shiffrar & Brugger, 2005; Shiffrar & Freyd, 1990, 1993; Vannuscorps & Caramazza, 2016b). In the seminal study of this effect, Shiffrar and Freyd (1990) showed their participants photographs of a human model whose hand alternated between two positions at different frequencies and asked them to report the perceived path of body movement. If body movements were processed like any other object, then the body should be perceived moving back and forth over the shortest distance between these two postures (Burt & Sperling, 1981). Instead, the participant's perception of apparent body movement sometimes followed biologically plausible paths rather than paths along the shortest distance. This was the case, in particular, when the shortest path between the hand positions was biomechanically impossible and the interval between the two hand pictures (ISI) was long enough for the longer movement to be plausible. Together with these previous findings, the results reported herein indicate that knowledge of the body movement capabilities influences not only the planning, control, and execution of one's own body movements, but also the perceptual processing of others' bodies and body movements.

Our findings also contribute new evidence that FD is influenced by knowledge of the typical motion of "objects". The results of previous studies addressing this issue were either unclear (Reed & Vinson, 1996; Vinson & Reed, 2002) or at odds with this conclusion (Nagai and Yagi, 2001). This raises the possibility that our finding may not generalize to other types of objects. Indeed, although the findings reported in this study provide new insights into the inner working of the mechanisms used by the visual system to predictively extrapolate the future location of moving upper-limbs, our conclusion is drawn from, and therefore limited

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to, the perception of upper-limb movements. This important issue will need to be explored in future studies. Given evidence that FD is modulated by visual expertise (Blättler et al., 2011), previous studies may simply have failed to document an influence of knowledge of the typical motion of objects on FD because they used objects (e.g., a rocket) that observers encounter much less often than bodies. If so, then, one should observe similar modulation of perceptual extrapolation by knowledge of the typical motion of more familiar objects. Yet, another possibility is that the perception of human body movements relies on predictive mechanisms that are fundamentally different from those involved in the perception of other objects. One specific feature that distinguishes the human body from other types of objects is that human body movements can be mapped onto the observer's own body representation. This mapping may allow the observer to use predictive mechanisms initially evolved to control the execution of one's own movements and, therefore, that are not available for the other types of objects (Wilson & Knoblich, 2005). This hypothesis is somewhat undermined by the finding that individuals born without upper limbs, and who therefore do not have upper limb motor representations, show the same differential FD for upper-limb movements away and toward the body (Vannuscorps & Caramazza, 2016a). However, the influence of knowledge of the body mechanics could not be discriminated from a mere landmark attraction effect in that study.

The importance of perceptual extrapolation of others' body movements can be appreciated by considering the relevance of this process on our ability to interact successfully with others despite the significant delays imposed by the transmission and transformation of the original visual information onto an interpretable percept. This process also likely contributes to the basic ability to perceive coherent continuous body movements despite the many brief

interruptions in the perceptual flow imposed by eye blinks. How the human mind and brain solve this engineering problem remains unclear. Here, we contribute to this issue by reporting evidence that perceptual extrapolation of observed body movements is tuned to knowledge of the body biomechanical constraints and, therefore, increases when an observed movement would be easy to continue along the same trajectory and decreases (or disappears) when the movements would be hard (or impossible) to continue along the same trajectory. Post-hoc analyses further suggested that this effect is specific to human bodies. This finding invites future research to try to determine the nature of the representations and processes underlying this perceptual bias. One possibility is that the biomechanical bias in body movement perception reflects the influence of knowledge of the body movement capabilities of others, accumulated in the course of perceptual learning (Tessari, Ottoboni, Symes, & Cubelli, 2010; Vannuscorps & Caramazza, 2016a). Alternately, this perceptual bias may rely on the observer's own body somatosensory and motor representations, learned through movement execution, which may feed back into perception and generate predictions of how the observed movements will most plausibly unfold (Wilson & Knoblich, 2005; Wilson et al., 2010).

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