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Action anticipation in human infants reveals assumptions about anteroposterior body-structure and action

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Animal actions are almost universally constrained by the bilateral body-plan. For example, the direction of travel tends to be constrained by the orientation of the animal's anteroposterior axis. Hence, an animal's behaviour can reliably guide the identification of its front and back, and its orientation can reliably guide action prediction. We examine the hypothesis that the evolutionarily ancient relation between anteroposterior body-structure and behaviour guides our cognitive processing of agents and their actions. In a series of studies, we demonstrate that, after limited exposure, human infants as young as six months of age spontaneously encode a novel agent as having a certain axial direction with respect to its actions and rely on it when anticipating the agent's further behaviour. We found that such encoding is restricted to objects exhibiting cues of agency and does not depend on generalization from features of familiar animals. Our research offers a new tool for investigating the perception of animate agency and supports the proposal that the underlying cognitive mechanisms have been shaped by basic biological adaptations in humans.

1. Introduction

The majority of both modern and prehistoric animal species are bilateria [1]. Their bodies are organized according to a bilateral body-plan with a front (anterior end), a back (posterior end) and the body's main axis: the anteroposterior axis. Notably, animal *behaviour* is thus almost universally constrained by the body's anteroposterior structure. The simplest example of this comes from animal locomotion: the direction of travel tends to be constrained by the position of the main axis (locomotion path tends to be axis aligned) and by its anteroposterior organization (locomotion forwards is more common than backwards).

Across evolutionary time, both of these stable co-relations between anteroposterior body-structure and behaviour might have been incorporated into the perceptual systems of some (if not many) species, for tracking animate agents and predicting their actions [2,3]. For instance, several authors hypothesized that the human visual system 'assumes' alignment between the main axis of any elongated bilaterally symmetrical object and its direction of movement. Indeed, misalignment between the two affects observers' estimates of the object's trajectory [4–6] and ratings of its perceived animacy [7]. Moreover, consistent with the notion that bilateria are by default expected to move forwards, the direction of movement supports attributing anteroposterior organization to stimuli that are otherwise ambiguous in this respect [8–10] (see also [11]). Furthermore, the featurally marked anteroposterior structure of a stimulus (e.g. an outline of an animal) biases perception of its ambiguous apparent motion towards forward-movement [12].

In this paper, we present a new test of the hypothesis that the constraints of bilateral body-plan on animal action are reflected in human perception of animate agency. In principle, an animal's actions can reliably guide disambiguating its anteroposterior organization (i.e. telling the front from the back), and

the animal's current orientation can reliably guide further action prediction. The prerequisites for these are (i) encoding the main axis of the animal as directional, and (ii) having an expectation of a stable relationship between this axial direction and action. We ask whether action anticipation in human infants is guided by these prerequisite skills. We tested whether infants exposed to a novel agent spontaneously map the direction in which it acts on the features of its main body-axis (resulting in a representation of an axial direction), and whether they rely on this encoding when anticipating the agent's subsequent actions. We predicted that, similar to other components of what has been referred to as the core-knowledge system of agency [13,14], the encoding and processing of axial direction in relation to action should be evident early in ontogeny despite infants' lack of experience with the particular morphologies of novel agents we adopted as experimental stimuli.

There are several ways in which infants' capacity for action representation may support encoding of an axial direction. In principle, a novel agent's locomotion defines a direction, which can then be mapped on its morphological features. In fact, motion direction can reliably disambiguate the actual front from the back (i.e. the leading end of an unfamiliar locomoting agent is likely to be its front). Indeed, in some species, actions directed at another animal's anterior end (e.g. preferential attacks on the head and neck of the prey) are guided not only by the morphological features of the target but also by its direction of movement [15–19]. Furthermore, results of classic ethological studies, which used ambiguous hawk/goose silhouettes (appearing goose-like when flown in long-end-first direction, but hawk-like when flown in the opposite, short-end-first, direction), suggest that several bird species are able to encode the morphological features of the silhouette in relation to its direction of movement [20,21].

Expectations about how agents are typically oriented during particular types of actions [22,23] could also support attributing direction to the axis. For example, upon recognizing an instance of contingent turn-taking communication, infants may extract direction by observing which end of a novel agent is closer to the communicative partner [24]. By a similar token, there may be expectations about the orientation of agents in goal-directed actions, even regardless of movement direction [25]. For example, if an instance of chasing is identified [26], axial direction of the chaser can be extracted from its orientation with respect to the chasee.

Finally, an agent's axial direction could be encoded in relation to a constrained pattern of reactions to distal stimuli [27], for example when the agent responds more often to stimuli directed at its one end than at the other. In this case, expectation of stability is warranted in virtue of cephalization, an evolutionary trend consisting in the accumulation of neuronal tissue (including perceptual organs) towards the anterior ends of organisms, often resulting in perception being constrained along the anteroposterior body-axis (e.g. a visual field of less than 360°).

If the anteroposterior structure of an agent is familiar, its orientation can reliably guide anticipation of the agent's actions (i.e. it is more likely to act in the direction revealed by its front). In the case of novel agents, the axial direction derived from the observation of previous actions supports anticipation just as well: the agent is more likely to move in the direction of its formerly leading end, to communicate in the direction of its formerly 'communicative' end, to react

to stimuli at its formerly reactive end, and so on. Several non-human primate species display evidence of sensitivity to human actors' orientations when begging or stealing food from them—a skill that may operate independently from the sensitivity to (often overlapping and more subtle) cues to visual access, such as head- and gaze-orientation [28–30]. It is not known whether primates' reliance on orientation is limited to the contexts of highly familiar actions and body morphologies or stems from more general inferences about body- and action-directions of bilaterian agents.

Developmental psychology so far presents a rather limited and unclear picture regarding human infants' abilities to process actions in relation to body structure of agents. Towards the end of their first year, infants are sensitive to the body orientation of human actors interacting with each other [22,23]. Six-month-olds can rely on a human actor's orientation when determining which objects are available to her reaching action [31], and 25-month-olds can take averted orientation as a cue to the lack of epistemic access [32]. When it comes to morphologically unfamiliar agents, numerous studies implicitly take it for granted that infants expect such agents to move forwards and along the main body-axis [33]. However, infants apprehend goal-directed actions even when a novel agent's anteroposterior structure is indiscernible [34], or if there is no consistency between the orientation of the novel agent's axial direction or apparent front and its action-directions [35,36]. Thus, whether infants readily map action-directions onto the agent and rely on this encoding of the axial direction in action anticipation remains an open empirical question.

Here, we report a series of experiments with a common structure. First, infants were provided with a limited opportunity to observe the behaviour of a novel agent (an animated box-like shape) with unfamiliar bilaterian morphology, which was engaged in a contingent goal-directed action (chasing a target). Previous research [34,37,38] suggests that similar familiarization events give 1-year-olds ample opportunity to recognize the goal of the chasing action (i.e. to reach the target) and to form expectations about the agent's further actions towards the target (i.e. that it is likely to move in the direction of the target). Next, in two consecutive test trials, the box did not resume the chase while being oriented with either its *leading end* or its *trailing end* towards the entering target. (Note that we use these particular trial labels for the sake of brevity, as the box's leading-end could be just as appropriately described as its 'goal-directed end' or 'reactive end', etc.)

During test trials, we measured infants' *anticipatory waiting*: the amount of time it took participants to stop fixating the motionless box and target, and move attention elsewhere. We reasoned that if infants spontaneously encoded the axial direction of the box during familiarization and expect it to constrain the agent's behaviour, they should judge the commencement of the chasing action more likely (and thus be prone to longer anticipatory waiting) on the leading-end test trial, when the action-direction derived from the box's axial direction and that derived from the anticipated chasing action are consistent, than on the trailing-end trial, when they are inconsistent.

Experiment 1 tested (i) whether infants take the agent's anteroposterior orientation into account when anticipating its actions towards the target and (ii) whether they spontaneously encode the agent's axial direction even in the absence of familiar features

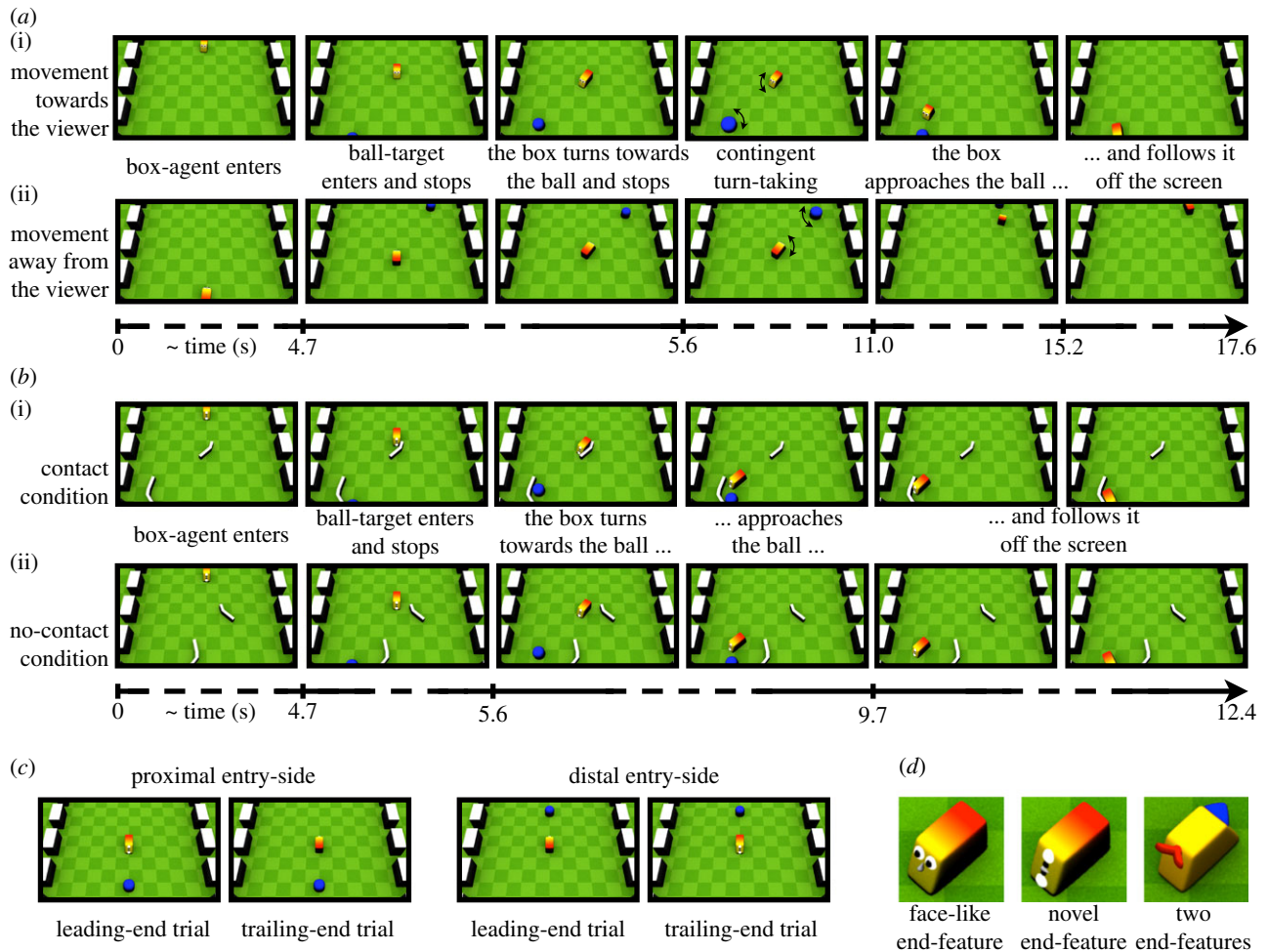


Figure 1. Illustrations of the stimuli used across experiments. (a) Events in the familiarization movies for Experiment 1. In each experiment, infants watched the box-agent travelling both (i) towards and (ii) away from the viewer. (b) Comparison of the familiarization stimuli for the (i) contact and (ii) no-contact conditions in Experiment 2. (c) Examples of still-frames during which anticipatory waiting was timed on test trials. In each condition of each experiment, for half of the participants the ball-target entered the plane from the side proximal to the viewer and for the other half from the distal side. (d) Close-ups of the box-agent with either face-like leading-end feature (Experiment 1), novel leading-end feature (Experiments 1 and 2) or two end-features (Experiment 3).

revealing anteroposterior organization. Experiment 2 tested an alternative perceptual-association account of the results by investigating (iii) whether the observed effects are specific to the domain of agency. Finally, in Experiment 3, we asked (iv) whether an agent's actions alone provide sufficient information for infants to support attributing direction to its axis.

2. Experiment 1: perceived axial direction affects anticipatory waiting

(a) Participants

The final sample in Experiment 1 consisted of 32 twelve-month-olds (face-like-feature group: $n = 16$, six females, age range 351–388 days, $m = 375$; novel-feature group: $n = 16$, seven females, age range 366–387 days, $m = 377$). See the electronic supplementary material, table S1, for information on exclusions in all experiments.

(b) Procedure and stimuli

All stimuli were three-dimensional animations created beforehand with the open-source software BLENDER (www.blender.org). All events took place on the same horizontal checkerboard-patterned plane viewed from a 30° angle (figure 1).

First, we presented 12-month-old infants with two familiarization movies (each 17.6 s long) showing a box-agent and a ball-target engaging in a contingent goal-directed pursuit-action (figure 1a; electronic supplementary material, Movies S1 and S2). The animations were designed specifically to provide infants with multiple opportunities to perceive action-direction conveyed by locomotion, goal and contingent reactivity. The box entered the plane and moved towards its centre, where it turned towards the ball-target upon its entry from the opposite side of the plane, and stopped. Next, the box reacted contingently to the two expand-and-contract actions of the ball: first by raising and lowering its fore-end and then by approaching the ball. The ball exited before the arrival of the box. The box adjusted its path to the exit-path of the ball and followed it off the screen. The box moved in an animate, caterpillar-like pattern of locomotion [39,40], its main axis being always aligned with its direction of movement. There was a symmetrical set of black and white marks (end feature) on the fore-end of the box. The end-feature was different for the two groups of participants (figure 1d). In the *face-like-feature* condition, the marks at the box's leading end formed an iconic face-like pattern. In the *novel-feature* condition, the same marks were arranged in a vertical pattern that did not resemble a face.

The only difference between the movies in each pair was that for the second movie, the movement trajectories were rotated by 180° in the horizontal plane around its midpoint. Thus, if the first familiarization movie showed the box travelling *towards the viewer* and exiting through the left-proximal corner, then the second movie showed the agent travelling *away from the viewer* and exiting through the right-distal corner (figure 1a). Thus, across the familiarization phase, the box was presented equally often oriented towards and away from the viewer at each point along its motion-path.

After familiarization, infants were exposed to two test trials (figure 1c). Each trial started with the box present at the plane centre, its main axis aligned with the screen's vertical axis. After 1 s, the ball entered, stopped next to the screen's edge and performed one expand-and-contract action (2.2 s). The only difference between the two test trials was in the orientation of the stationary box, with either its leading end (*leading-end* trial) or trailing end (*trailing-end* trial) towards the entering ball. The trial continued as a still frame (for 20 s or till the infant looked away from the screen), giving us an opportunity to time infants' anticipatory waiting operationalized as the latency of the first saccade away from the box-and-ball dyad. Infants' looking behaviour was recorded for offline coding at the speed of 25 fps. The time-window for recording the anticipatory-waiting started 1 s after the ball finished contracting. See the electronic supplementary material for more details.

The following factors were fully counterbalanced across participants in each condition: order of familiarization movies (first movie: movement towards versus away from the viewer; figure 1a), the entry side of the ball in test (proximal versus distal edge of the plane; figure 1c), test event order (first trial: leading end versus trailing end; figure 1c). See the electronic supplementary material for more details.

(c) Results and discussion

In this and all later experiments, the anticipatory-waiting times were log-transformed for all parametric analyses, because of the positive skew, which rendered their distribution significantly different from normal. All the p -values reported in the paper represent two-tailed tests. All p -values for non-parametric tests represent exact probabilities.

Preliminary analyses found no significant effects of the controlled factors nor interactions with test event. A 2 (condition: face-like versus novel feature) \times 2 (test event: leading end versus trailing end) ANOVA found no significant effect of condition ($F_{1,30} = 0.005$, $p = 0.94$) or condition by test event interaction ($F_{1,30} = 0.98$, $p = 0.33$; figure 2). However, it revealed a main effect of test event: infants displayed longer anticipatory waiting in the leading end than the trailing end test trials ($F_{1,30} = 15.84$, $p = 0.0004$, $\eta_p^2 = 0.35$). Planned comparisons found this pattern in each condition separately (face-like feature: $t_{15} = 3.29$, $p = 0.005$, Cohen's $d = 0.92$; novel feature: $t_{15} = 2.28$, $p = 0.038$, Cohen's $d = 0.60$). Thirteen out of 16 babies showed the predicted longer anticipatory waiting on leading end than on trailing end trial in both the face-like-feature ($Z_{\text{Wilcoxon}} = -2.30$, $p = 0.019$) and novel-feature ($Z_{\text{Wilcoxon}} = -2.07$, $p = 0.039$) conditions.

Twelve-month-old infants thus appeared to spontaneously encode the novel agent's main axis as directional, even when its anteroposterior organization was not given away by familiar frontal morphology. In both conditions, it took longer

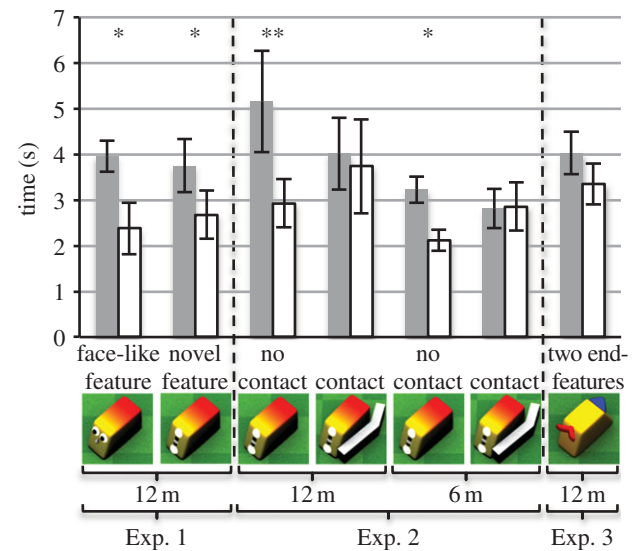


Figure 2. Mean anticipatory-waiting times on leading-end (grey bars) and trailing-end (white bars) test trials across conditions and age groups in the three experiments. Error bars represent s.e.m. * $p < 0.05$, ** $p < 0.005$ by Wilcoxon signed-rank test.

for infants to stop looking at the motionless box and ball when the leading end of the box was facing the ball than when it was directed away from it. This difference is consistent with the proposal that infants' looking behaviour in our task reflects their anticipation of the agent's action and that current orientation of the agent is taken into account in developing action expectations. However, the results are also consistent with a simpler explanation. As the leading end of the box was always closer to the ball during familiarization, infants might have learned to associate the front features and the ball in spatial proximity. Thus, the observed difference in looking behaviour at test could reflect relatively higher perceptual familiarity of the leading-end test trial (with the leading end again closer to the ball) over the trailing-end test trial (with the box's trailing end closer to the ball for the first time). In Experiment 2, we addressed this issue by manipulating the presence of the agency cues that the box exhibited. On the perceptual familiarity account, withdrawing agency cues from the box during familiarization should not affect infants' anticipatory waiting at test. If it does, this would not only falsify the alternative explanation but would also suggest that the expectations captured in our task are restricted to certain perceptual input conditions, which constitute instances of agency [13]. In order to explore earlier ontogeny of agent-orientation processing, in Experiment 2 we tested both 12- and six-month-olds.

3. Experiment 2: specificity to the agency domain

(a) Participants

In Experiment 2, there were 32 twelve-month-olds (contact group: $n = 16$, 11 females, age range 367–395 days, $m = 376$; no-contact group: $n = 16$, 10 females, age range 367–394 days, $m = 378$) and 48 six-month-olds (contact group: $n = 24$, 14 females, age range 182–212 days, $m = 197$; no-contact group: $n = 24$, 14 females, age range 182–212 days, $m = 196$). See also the electronic supplementary material, table S1.

(b) Procedure and stimuli

The procedure was identical to Experiment 1, but the events presented in familiarization movies (each 12.4 s long) were simplified versions of those used in Experiment 1 (novel-feature condition): the box moved at a constant speed without a caterpillar-like locomotion pattern and it started approaching the ball immediately upon the ball's entry (figure 1b; electronic supplementary material, Movies S3 and S4). The ball showed no expand-and-contract actions.

Crucially, there were two additional objects (wall-like structures) on the plane during familiarization. Their exact location was the only difference between stimuli for the two groups of participants. In the *contact* condition, the walls were located in the path of the box, so that all changes in the direction of its movement (the turn towards the entering ball and the adjustment of the path to the exit-path of the ball) could be interpreted as resulting from the contact with the walls. In the *no-contact* condition, the walls were located away from the path of the box, so that it made no contact with them at any time, and thus the changes of its path could be seen as self-generated reactions contingent on the behaviour of the ball [41].

One second after the onset of each test trial, the ball entered and stopped (0.8 s). The time window for recording the anticipatory waiting started 2 s from the trial onset. See the electronic supplementary material, Methods, for discussion.

(c) Results and discussion

During the test trials, six-month-olds showed overall shorter anticipatory waiting times than twelve-month-olds ($F_{1,76} = 4.22$, $p = 0.043$, $\eta_p^2 = 0.05$; figure 2). However, we found no significant interactions between age and any other analysed factor, and so we collapsed the age groups in further analyses. No significant effects of the controlled factors were found except for a significant test event by test order interaction ($F_{1,76} = 5.74$, $p = 0.019$, $\eta_p^2 = 0.07$). See the electronic supplementary material, Additional analyses, for a full account of presentation-order effects in Experiment 2.

A 2 (condition: contact versus no-contact) \times 2 (test event: leading end versus trailing end) ANOVA found no significant effect of condition ($F_{1,78} = 0.18$, $p = 0.67$), a significant effect of test event ($F_{1,78} = 9.43$, $p = 0.003$, $\eta_p^2 = 0.11$) and a marginally significant interaction between them ($F_{1,78} = 3.92$, $p = 0.051$, $\eta_p^2 = 0.05$). A non-parametric test confirmed significantly different patterns of anticipatory waiting (expressed as difference scores: $\text{waiting}_{\text{leading-end}} - \text{waiting}_{\text{trailing-end}}$) between the two conditions ($U_{\text{Mann-Whitney}} = 567.0$, $p = 0.025$). Contrast analysis revealed longer waiting on leading-end than on trailing-end test trial in the no-contact condition ($F_{1,78} = 12.75$, $p = 0.0006$, $\eta_p^2 = 0.14$), but not in the contact condition ($F_{1,78} = 0.60$, $p = 0.44$).

Planned comparisons confirmed longer anticipatory waiting in the no-contact condition during the leading-end test trials within each age-subgroup separately (twelve-month-olds: $t_{15} = 3.75$, $p = 0.002$, Cohen's $d = 0.96$; six-month-olds: $t_{23} = 2.61$, $p = 0.016$, Cohen's $d = 0.54$). However, no such effect was found in the contact condition (twelve-month-olds: $t_{15} = 0.65$, $p = 0.53$; six-month-olds: $t_{23} = 0.40$, $p = 0.69$). Thirteen of 16 twelve-month-olds ($Z_{\text{Wilcoxon}} = -2.79$, $p = 0.005$) and 17 of 24 six-month-olds ($Z_{\text{Wilcoxon}} = -2.37$, $p = 0.018$) in the no-contact condition waited longer on the leading end test trial, whereas in the contact condition only 7 twelve-month-olds and 13 six-month-olds did so.

Thus, the results of Experiment 2 not only replicated the findings of Experiment 1, but also extended them to six-month-olds, and suggest that infants' expectations reflect domain-specific encoding of the axial direction of agents. As the observed differences in looking behaviour during test trials depended on the agency of the box, they are more likely to reflect anticipatory waiting than to be driven by other factors (such as a preference for the layout of the leading-end-trial stimuli or its relative familiarity), as those should have affected looking behaviour in both conditions the same way.

4. Experiment 3: axial direction from actions alone

(a) Rationale

So far, we have discussed how directional information can be extracted from actions and support attributing direction to the agent's axis despite morphological novelty. But what is the role that the novel agent's actual morphology plays in this process? Our paradigm required that the two ends of the box-agent looked different from each other (so that the 180° orientation change across the test trials could be detected). Consequently, if the appearance of the leading end was somehow rendering it a good candidate for a front (and/or the appearance of the trailing end made it a suitable candidate for a back), it is in principle possible that axial direction was encoded in virtue of the box's appearance suggesting anteroposterior structure, without reference to its actions during familiarization.

Results of an additional control study suggested that differences in colours and tilts between the two ends of the box were not likely to have that effect; however, the presence of the articulated black-and-white end-feature might have been critical: twelve-month-olds familiarized to a box just like the one used in Experiments 1 and 2 but lacking the end-feature did not show longer anticipatory waiting on leading-end than trailing-end test trial (for details, see the electronic supplementary material, Additional findings and Movie S7). This null result may reflect general difficulties with differentiating the two ends by colour and tilt alone. However, it is also possible that the novel end-feature used in Experiments 1 and 2 played a bigger role in encoding axial direction than we had assumed.

Consider three ways in which novel morphological features can by themselves facilitate encoding of the axial direction. First, they may exhibit some recognizable instructive analogies to the bodies of familiar agents. For example, articulated end-parts may have spatial layouts or colour patterns analogous to those of some familiar anterior or posterior features: eyes, tail, etc. Second, these features may meet some general expectations about bodies with anteroposterior organization. For example, one may expect that the anterior end of an agent exhibit more complex articulated morphology than the posterior end. Third, some morphological features may be interpreted by the human perceptual system as inherently directional in virtue of their perceptual characteristics. For example, a distinctive feature located at one extremity of an object's main axis—a polar feature—has been argued to introduce directionality into the representation of an object [42]. Notably, all these three factors might have influenced directional representation of the box-agent in Experiments 1 and 2, because its end-feature

involved a colour contrast analogous to that of a human eye [43], its leading end was morphologically more complex than the plane trailing end, and the end-feature could act as polar feature [42].

Thus, even though Experiments 1 and 2 provided robust evidence for infants' reliance on the axial direction in action anticipation, they did not provide unequivocal evidence for infants' reliance on the actions of the box when encoding it as directional. Experiment 3 was designed specifically to address the question whether the actions of an agent can sufficiently guide its directional encoding. We approached this issue by exposing infants to the same behavioural sources of directionality as in Experiments 1 and 2 (i.e. locomotion, goal and contingent reactivity), while eliminating the hypothetical morphological cues.

(b) Participants

In Experiment 3, there were 32 twelve-month-olds (21 females, age range 349–376 days, $m = 361$). See also the electronic supplementary material, table S1.

(c) Procedure and stimuli

We employed the materials and procedure used in Experiment 2 except for the following modifications: (i) we used a box-agent whose main body was uniformly yellow and fully symmetrical, while its two ends bore a novel feature each (figure 1d; electronic supplementary material, Movies S5 and S6). The two features were distinctively different in colour and shape (a red V-shaped feature and a blue triangular feature), yet matched in size and in precise location at their respective ends. Thus, the ends of the box were equated in terms of how morphologically complex they might appear as well as in terms of the presence of polar features [42]. (ii) We chose end-features that had no obvious similarities to facial features and were equated for their similarities to schematic end-morphologies, which twelve-month-olds might have encountered in storybooks, toys or cartoons. The feature-to-end assignment (V-shape at the leading and triangle at the trailing end, or *vice versa*) was counterbalanced across the participants. In addition, (iii) there were no walls on the plane through which the box travelled in the familiarization. (iv) The ball was dark grey to avoid confusion with a blue triangular end-feature. (v) As the familiarization movies in Experiment 3 were introducing twice as many novel features of the box as in Experiments 1 and 2 (two instead of one), we doubled the number of familiarization movies (four instead of two) to ensure that participants received enough opportunity to encode the novel information.

On test trials, the ball entered the plane immediately and the time window for recording the anticipatory waiting started 2 s after the trial onset (see the electronic supplementary material, Methods, for discussion).

(d) Results and discussion

Initial analysis found no significant effect of feature-to-end assignment (leading end: V-shape versus triangle) or interaction of this factor with test event (leading- versus trailing-end trial), so data were collapsed across this factor. No significant main effects or interactions were found for any other controlled factor, except for test order. A 2 (test event: leading- versus trailing-end trial) \times 2 (test order: leading-end trial first versus trailing-end trial first)

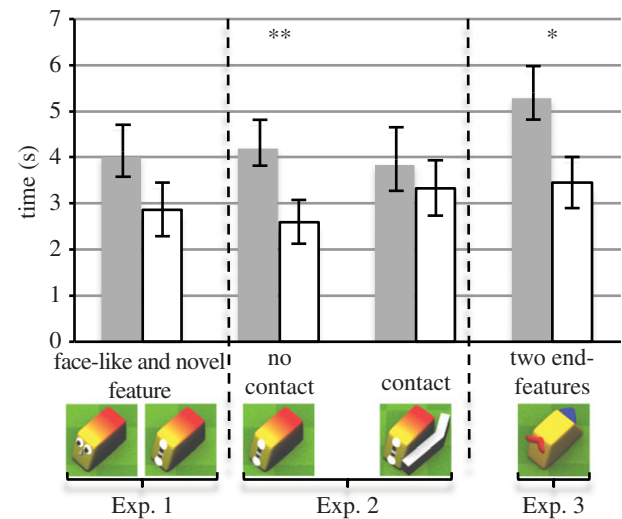


Figure 3. Mean anticipatory-waiting times on the first test trial (leading end, grey bars; trailing-end, white bars) across the three experiments. Error bars represent s.e.m. * $p < 0.05$, ** $p < 0.017$ (Bonferroni-corrected) by two-tailed t -tests.

ANOVA found no significant difference in anticipatory waiting between the test events ($F_{1,30} = 2.44$, $p = 0.13$) and no significant main effect of test order ($F_{1,30} = 1.91$, $p = 0.18$), but it revealed a significant interaction between them ($F_{1,30} = 8.79$, $p = 0.006$, $\eta_p^2 = 0.23$). Infants waited longer when watching a leading-end event than a trailing-end event when the leading-end event was presented on the first test trial ($F_{1,30} = 10.25$, $p = 0.003$, $\eta_p^2 = 0.25$), but not if it was presented on the second test trial ($F_{1,30} = 0.98$, $p = 0.33$). This pattern suggests that the longer waiting during the leading-end event was not merely an effect of the presentation order. Moreover, the leading-end event elicited significantly longer waiting if it was presented on the first than on the second test trial ($F_{1,30} = 13.15$, $p = 0.001$, $\eta_p^2 = 0.30$), but the trailing-end event did not ($F_{1,30} = 0.39$, $p = 0.54$). In order to investigate what caused this pattern of simple effects, we compared infants' waiting times on each test-trial separately in between-subject tests according to presentation order. The first test trial elicited significantly longer anticipatory waiting when it presented a leading-end event than when it presented a trailing-end event ($t_{23} = 2.3$, $p = 0.03$, d.f. corrected for non-homogeneous variances, Cohen's $d = 0.85$, $U_{\text{Mann-Whitney}} = 68.5$, $p = 0.024$), but the second test trial did not ($t_{30} = 0.12$, $p = 0.90$, $U_{\text{Mann-Whitney}} = 125.0$, $p = 0.92$).

In order to validate the robustness of the first test trial effect in Experiment 3, we re-analysed the data from first test trials of the earlier experiments applying a Bonferroni correction ($p = 0.017$). We found that—similarly to Experiment 3—the leading-end event elicited longer anticipatory waiting than the trailing-end event in the no-contact condition of Experiment 2 ($t_{29} = 3.04$, $p = 0.005$, d.f. corrected for non-homogeneous variances, Cohen's $d = 1.01$, $U_{\text{Mann-Whitney}} = 101.5$, $p = 0.007$), but not in the contact condition of Experiment 2 ($t_{38} = 0.98$, $p = 0.33$, $U_{\text{Mann-Whitney}} = 175.0$, $p = 0.51$) and not in Experiment 1 ($t_{30} = 2.11$, $p = 0.044$, Cohen's $d = 0.77$, $U_{\text{Mann-Whitney}} = 77$, $p = 0.055$; figure 3).

Altogether, this pattern of results in Experiment 3 suggests that infants were indeed able to extract axial direction of the box with two end-features from its actions alone. However, their reliance on this encoding for action anticipation was evident only during the first test trial, and

thus different from the within-group effects observed in Experiments 1 and 2, where the agent carried a feature only on its leading end. This difference may simply reflect infants' difficulties with differentiating two end-features (or their relations to action-directions) over the course of multiple test trials or indicate that an agent-morphology with features pronounced on one end (as in Experiments 1 and 2) indeed can sometimes facilitate the encoding of axial direction, perhaps by guiding the attribution of the anteroposterior organization (see also the electronic supplementary material, Additional findings).

5. Discussion

The proposal that there are basic cognitive adaptations for detecting and evaluating agency is at the focus of much theoretical and empirical work in psychology [13,34,35,41,44–47]. The adaptive value of such mechanisms relies on the existence of highly stable regularities among features (e.g. face-like patterns [44]), kinematic patterns (e.g. those preserved in otherwise impoverished point-light biological-motion displays [45]), and abstract behavioural characteristics (e.g. self-propulsion, goal-directedness, action efficiency [34,41,46,47]) of agents and actions. An increasing body of research suggests that sensitivity to such agency-specific factors emerges early in ontogeny, is evidenced in non-human animals, and may be largely independent of experience [44–46]. Consistent with this approach, we challenged human infants with novel instances of agents in order to test whether the ubiquity of the bilateral body plan and the regularity with which its anteroposterior organization constrains animal behaviour are reflected in early mechanisms of human agency perception.

The current series of studies provided robust evidence for a mechanism sensitive to the relationship between anteroposterior organization and action in preverbal human infants as young as six months of age. This mechanism supports encoding axial direction of an agent with respect to its actions and relying on it to constrain inferences about further actions. Moreover, encoding axial direction of an agent is spontaneous, and achieved despite the agent's morphological novelty and a relatively short exposure. Future experimentation is required to clarify what aspects of the agent's appearance can facilitate or hinder this processing and how. But the current results (Experiment 3) at least suggest that axial-direction encoding can be sufficiently supported by actions alone.

Perceived axial direction of an agent can be used not only for anticipating its action-directions but also for interpreting its communicative behaviours [24,27] and monitoring its epistemic states [32]. Functional relationships between these abilities are not yet fully understood. For instance, attribution of body directionality is often assumed to entail attribution of attention or perception [24]. However, a dissociation between these two abilities was documented recently in high-functioning adults with Asperger's syndrome, who spontaneously monitored the axial direction of novel agents [48] but failed to take averted human body orientation as a cue to not seeing [49]. Developmental trajectories for separate types of inferences from body orientations are not clear either. For instance, while even seven-month-olds may appreciate that not being present when some change occurs leads to not seeing it [50], 25-month-olds are presently the youngest age group to evidence inferring lack of perceptual access from averted orientation [24] (cf. [31], where the availability of a target-object to the human actor's vision and action are confounded). Such results call for a cautious interpretation of axial-direction processing exhibited by our twelve- and six-month-old participants. Accordingly, we propose a lean conclusion, according to which infants appreciate how the current orientation of an agent constrains directions in which an immediate action is likely to be commenced. The early developmental emergence of this skill supports the proposal that the cognitive mechanisms underlying perception of animate agency in humans have been shaped by basic biological adaptations for processing actions constrained by the anteroposterior organization of the bilateral body-plan.

The research was approved by the University College London Research Ethics Committee and United Ethical Review Committee for Research in Psychology (EPKEB), Budapest, Hungary and conducted in compliance with the Declaration of Helsinki. For all the experiments, infants were recruited from the laboratory's own database of parents who volunteered to participate in psychological research with their children. An informed consent from the parent was always obtained prior to testing.

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Data accessibility. The dataset is available in the electronic supplementary material.

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