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Perceiving animacy purely from visual motion cues involves intraparietal sulcus

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ABSTRACT

Distinguishing animate from inanimate objects is fundamental for social perception in humans and animals. Visual motion cues indicative of self-propelled object motion are useful for animacy perception: they can be detected over a wide expanse of visual field, at distance and in low visibility conditions, can attract attention and provide clues about object behaviour. However, the neural correlates of animacy perception evoked exclusively by visual motion cues, i.e. not relying on form, background or visual context, are unclear. We aimed to address this question in four psychophysical experiments in humans, two of which performed during neuroimaging. The stimulus was a single dot with constant form that moved on a blank background and evoked controlled degrees of perceived animacy through parametric variations of self-propelled motion cues. BOLD signals reflecting perceived animacy in a graded manner irrespective of eye movements were found in one intraparietal region. Additional whole-brain and region-of-interest analyses revealed no comparable effects in brain regions associated with social processing or other areas. Our study shows that animacy perception evoked solely by visual motion cues, a basic perceptual process in social cognition, engages brain regions not primarily associated with social cognition.

1. Introduction

The ability to infer the mental states of others is an essential process in human social interaction (Premack and Woodruff, 1978). Thinking about other minds is contingent upon identifying entities that are likely to possess a mind, a process termed animacy perception (Scholl and Tremoulet, 2000). Consequentially, identifying the neural mechanisms involved in animacy perception is an essential question in social neuroscience. Humans rely strongly on visual cues to perceive animacy, such as the form and the movements of entities to be categorised. Visual motion cues of animacy are particularly helpful because they are informative about action; accordingly, perceiving the actions of others is considered a central precursor for mentalising (Blakemore and Decety, 2001; C. D. Frith and U. Frith, 1999). Visual motion cues are particularly useful for detecting living beings when form information is poor due to low visibility, small object size or great distance.

Neural representations of an animate-inanimate continuum based on static visual cues (shape, color etc …) have been identified in large expanses of the human visual cortex (Chao et al., 1999; Connolly et al., 2012; Hanson et al., 2004; Kiani et al., 2007; Konkle and Caramazza, 2013; Kriegeskorte et al., 2008; Mahon et al., 2009; Sha et al., 2015). Brain regions responding to the motion of animate beings have also been identified (Bonda et al., 1996; Castelli et al., 2000; Gao et al., 2012; Grossman et al., 2000; Grossman and Blake, 2002, 2001; Lee et al., 2014; Martin and Weisberg, 2003; J. Schultz et al., 2005, 2004; R. T. Schultz et al., 2003; Shultz and McCarthy, 2014; Wheatley et al., 2007). However, these studies of animate motion have relied on stimuli with animacy cues comprising both form and motion information. For example, the spatial arrangement of the dots in point-light displays of biological motion (Johansson, 1973) is essential for perceiving these movements (Beintema and Lappe, 2002; Casile and Giese, 2005; Giese and Poggio, 2003). In studies using simpler animations, animacy was evoked through interactions between objects or between objects and their environment (e.g. Castelli et al., 2000; J. Schultz et al., 2005; Wheatley et al., 2007). As a result, the neural correlates of animacy perception based on visual motion cues alone are still unknown.

Isolated moving objects can appear animate when “self-propelled”, i.e. when they appear to move by themselves (Bingham et al., 1995; Gelman and Spelke, 1981; Gergely et al., 1995; Gyulai, 2004; Heider and Simmel, 1944; Kotovsky and Baillargeon, 2000; Luo and Baillargeon, 2005; Michotte, 1946; Opfer, 2002; Premack, 1990; Rochat et al., 1997; Scholl and Tremoulet, 2000; Stewart, 1982; Szego and Rutherford, 2007;

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Tremoulet and Feldman, 2000). Here, we used a single-dot stimulus mimicking the movements of biological agents by appearing self-propelled (J. Schultz and Bülthoff, 2013) to identify the neural correlates of animacy perception from motion cues only (Fig. 1A). In the first of our four experiments, we piloted a version of our task adapted to fMRI; we then obtained BOLD signal from 20 participants performing this task and allowed to move their gaze (the “freeview” group), a natural tendency in this task (J. Schultz and Bülthoff, 2013). As eye movements could obscure BOLD responses to stimulus variations, the experiment was repeated in 20 additional participants fixating the display centre (“fixation” group). Individual differences in animacy perception, which we had previously reported to occur in this task (J. Schultz and Bülthoff, 2013), were investigated in relation to visual imagery in a fourth experiment.

We expected responses to motion cues and animacy percepts in regions sensitive to our stimulus and those previously associated with animacy perception in the superior and ventral temporal cortex, including the posterior STS, the Fusiform Face Area and the ventral temporal cortex (Castelli et al., 2000; Gao et al., 2012; Lee et al., 2014; Martin and Weisberg, 2003; Morito et al., 2009; J. Schultz et al., 2005, 2004; R. T. Schultz et al., 2003; Wheatley et al., 2007). We first localized these regions functionally or, in the case of the VTC, anatomically (Grill-Spector and Weiner, 2014), then investigated which were sensitive to motion cues of animacy and which reflected the animacy percept. We then searched the whole brain for additional regions sensitive to these factors using univariate and multivariate analyses. To exclude influences of eye movements, we only focus on effects consistent across participants with free and constrained eye gaze.

2. Materials and Methods

2.1. Participants

111 healthy participants (N = 63 female), mean age 26.4 years (ranging from 19 to 36) volunteered as participants for 12 Euro per hour. The study was approved by the ethics committee of the University of Tübingen. All observers except for those in Experiment 1 were naïve

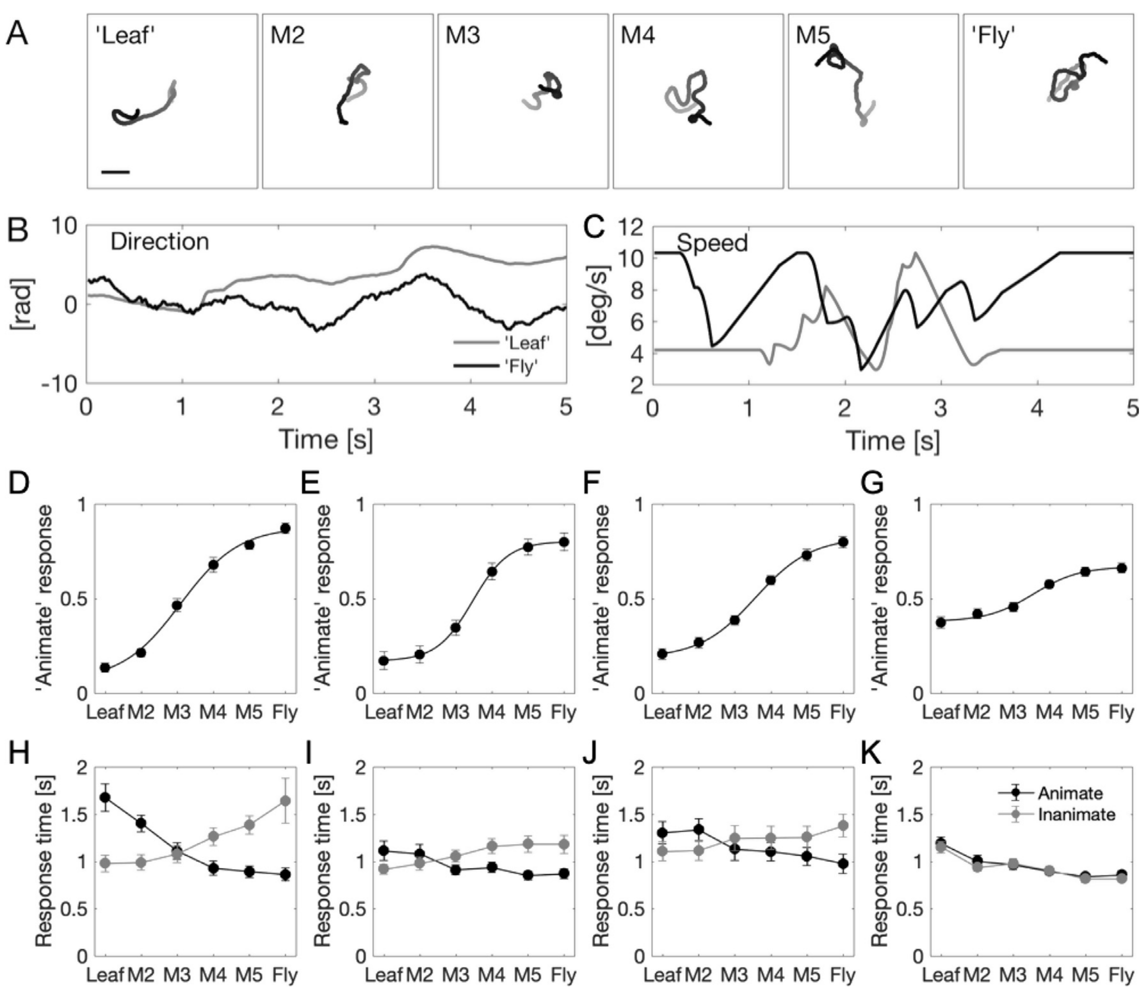

Fig. 1. Stimuli and behavioural results. A single dot mimicking the motion of natural living and non-living objects evoked animacy percepts. **(A)** Example dot movement patterns generating different degrees of animacy. Animacy varied across six morph levels (=six levels of parameter β) between “leaf” and “fly” through four intermediary stimuli (M2-M5) shown on white background. Calibration line represents one visual degree. Changes in dot direction **(B)** and speed **(C)** during one example trial. These changes determined whether the stimulus mimicked the motion of a “leaf blown by the wind” (inanimate) or “an insect like a fly or mosquito (animate)”, or some intermediate stimulus. Different changes across trials prevented trajectory learning. **(D)** Psychophysical pilot data acquired prior to scanning (Experiment 1, N = 11, 30 trials per condition). The probability of animacy percept increased monotonically from “leaf” to “fly” across the six morph levels. The line shows best-fitting cumulative Gaussian function for the group data for illustrative purposes; for analysis, this function was fit on individual data. **(E)** Psychophysical data acquired during scanning from participants free to move their eyes (Experiment 2, “freeview” group, N = 19, 49 trials per condition) or **(F)** fixating the screen centre (Experiment 3, “fixation”, N = 19, 49 trials per condition). **(G)** Psychophysical data acquired from 59 participants outside the scanner (Experiment 4, 10 trials per condition). **(H,I,J,K)** Response times obtained in Experiments 1–4. Response times increased with morph level when participants responded “inanimate” and decreased when participants responded “animate” in Experiments 1–3. Data show mean ± standard error of the mean.

about the experiment design and the stimulus manipulations, had no history of neurological or psychiatric illnesses, and for those participating in the neuroimaging experiments, were informed in writing of the safety precautions necessary for fMRI scanning. All participants provided written consent prior to the start of the experiment.

2.2. Experimental design and procedure

Four experiments were performed, all based on our previous study (J. Schultz and Bülthoff, 2013). The participants' task in all experiments was to indicate whether a single moving dot appeared alive to them or not by pressing one of two buttons with their right hand as soon as the stimulus disappeared (button assignments were counterbalanced across participants). The instructions were intentionally kept minimal: "Imagine you are looking through a window at objects moving outside. Half of them are alive, half of them are not. Both are shown as a white dot, but they differ by their movement. Please decide for each object whether it is alive or not."

In Experiment 1 we aimed to replicate our previous findings (J. Schultz and Bülthoff, 2013) and demonstrate percept stability over time, and tested eleven participants known to be sensitive to our stimuli.

We then used the same paradigm to select 40 participants sensitive to our stimuli (termed "responders") to be included in the fMRI experiments; the criterion was that a psychometric function (cumulative Gaussian) fitted to their responses could significantly explain the variation in animacy judgments (linear regression, $p < 0.05$; see J. Schultz and Bülthoff, 2013). 20 participants were included in the first fMRI experiment (Experiment 2) in which participants were free to move their eyes (the "freeview" group). 20 participated in the second fMRI experiment (Experiment 3), in which participants were asked to fixate a cross at the centre of the display throughout each trial (the "fixation" group). The fixation performance was recorded and trials in which participants made eye movements deviating more than 2° from the centre of the screen for more than 10% of the trial duration were coded separately in the fMRI data analysis and discarded from the results.

In Experiment 4, 60 new participants were asked to perform the same task, to give written reports about how they decided that a stimulus appeared inanimate or animate to them, and to complete the 16-question Vividness of Visual Imagery Questionnaire (VVIQ) (Marks, 1973). In this questionnaire, 4 situations are described (thinking of a friend, a rising sun, a shop front, a landscape scene) and 4 questions relating to mental visual images are asked about each situation. The mental images experienced were reported using the following rating scale: Perfectly clear and vivid as real seeing = 5; Clear and reasonably vivid = 4; Moderately clear and lively = 3; Vague and dim = 2; No image at all, you only "know" that you are thinking of the object = 1. The sum of the 16 ratings yielded a total score, with higher values indicating stronger tendencies for mental imagery. The contents of each participant's written reports were coded with 1 if they contained references to flying animals (mostly insects were reported) and/or objects moved by an external force (mostly objects moved by the wind were reported) and 0 otherwise; participants of the first category are henceforth termed "imagers", participants of the latter category "non-imagers". The rating was performed by a person who did not interact with the participants and had no knowledge of their animacy perception data. The point of subjective equivalence was determined as the morph level at which 50% of trials were perceived as animate.

In all experiments, one trial lasted 5s and was followed by a black screen during a variable inter-stimulus interval (Gaussian distribution, mean = 1s, sd = 1s). In Experiment 1 there were 30 trials in each of the 6 stimulus conditions, all presented in randomized order, with breaks every 60 trials. In Experiments 2 and 3 there were 49 trials in each condition, spread over three runs lasting about 11.5 min each. The order of the trials was pseudo-randomized so that each condition was preceded by each other condition equally often (2-back history matching). This design is optimized for estimation of the shape of the hemodynamic response (Liu, 2004), which we chose in order to investigate response timecourses in regions of interest and to minimise stimulus-order effects on perception. In Experiment 4, the number of trials was reduced to 10 trials per condition, acquired in one run, to accelerate data collection.

2.3. Stimuli

The stimulus consisted of a single moving white dot moving on a black background, as described in our previous behavioural study (J. Schultz and Bülthoff, 2013). The moving dot mimicked the movement of a leaf or a fly. The leaf was created by simulating the influence of an external force on the motion of the dot, which reduces the impression of self-propelled motion. The fly motion was simulated by creating motion trajectories with seemingly random but smooth changes in movement direction. The dot moved along pre-calculated movement trajectories, generated anew for every trial to prevent trajectory learning by a movement equation with one free parameter, referred to as β, which controlled the amount of animacy cues contained in the stimulus. Specifically, β is a weight that allows morphing in parameter space between two kinds of motions (animate and inanimate) by acting on several variables of the movement equation. Across six levels of the β parameter, which determined six stimulus morph levels spanning the range of possible stimuli (from "leaf" to "fly", Fig. 1A), the participants decided in a psychophysical procedure whether the moving dot appeared alive or not. Example variations of motion direction and speed are shown in Fig. 1B. Thus, animacy perception was operationalized here as a psychophysical yes/no task and amounted to discriminate visual cues characteristic of the movements of animate versus inanimate objects. As participants were not told what these cues were or what to look for, they were required to access their own representations of animate and inanimate motion to solve the task. We assessed their conscious use of representations using a questionnaire after Experiments 2&3 and in more detail in Experiment 4 (see below). The stimuli (dot size: 0.2°) moved within a two-dimensional "box" subtending about 9° × 9° visual angle. A static dot placed at the centre of the display served as a control stimulus. The experiment was run (in both behaviour-only and fMRI experiments) on a Windows PC and implemented in Matlab (Version R2010A, The MathWorks, Natick, MA) using the PsychToolbox extensions (www.psychtoolbox.org) (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

2.4. fMRI experiment procedure

Observers lay supine on the MRI scanner bed. The stimuli were back projected onto a screen situated behind the observers' head and reflected into their eyes via a mirror mounted on the head coil, situated 140.5 cm away from the projection screen. A JVC LCD projector with custom Schneider-Kreuznach long-range optics, a screen resolution of 1280 pixels × 1024 pixels, and a 60 Hz refresh rate were used. We used a magnet-compatible button box to collect participants' responses (The Rowland Institute at Harvard, Cambridge, USA). For participants in the fixation group, eye movements were recorded at 60 Hz using an ASL camera-based eyetracker 60 Hz with long-range optics (ASL, Bedford, MA).

2.5. MRI data acquisition

Participants were scanned at the MR Centre of the Max Planck Institute for Biological Cybernetics, Tübingen, Germany. All anatomical T1-weighted images and functional gradient-echo echo-planar T2*-weighted images (EPI) with BOLD contrast were acquired on a Siemens TIM-Trio 3T scanner with an 8-channel phased-array head coil (Siemens, Erlangen, Germany). The imaging sequence for functional images had a repetition time of 1920 ms, an echo time of 40 ms, a flip angle of 90°, a field of view of 256 mm × 256 mm and a matrix size of 64 pixels × 64 pixels (no parallel imaging was used). Each functional image consisted of 27 axial slices, of 3 mm thickness with 1 mm gap between slices. In-plane resolution was 3 × 3 mm. Volumes were positioned to cover the whole brain based on the information from a 13-slice parasagittal anatomical localizer scan acquired at the start of each scanning session. An average of 1084 functional images were acquired per observer in three sessions. The first four of these images were discarded to allow for equilibration of T1 signal. A T1-weighted anatomical scans was acquired after the functional runs (MPRAGE; TR = 1900 ms, TE = 2.26 ms, flip angle = 9°, image matrix = 256 mm [Read direction] x 224 mm [Phase], 176 slices, voxel size = 1 × 1x1 mm, scan time = 5.59 min).

2.6. fMRI data preprocessing

Standard preprocessing of the fMRI data was carried out using the SPM8 software package (Wellcome Trust Centre for Neuroimaging, http://www.fil.ion.ucl.ac.uk/spm). Functional data were slice-time corrected, realigned and unwarped, coregistered with each participant's anatomical data, normalised into the standard Montreal Neurological Institute (MNI) space and spatially smoothed using a 6 mm full-width-at-half-maximum Gaussian kernel. One participant per experiment were excluded due to excessive head motion, bringing the number of participants to 19 in each experiment. Multivoxel pattern analysis (MVPA) was performed on unnormalized and unsmoothed data (see below).

2.7. fMRI data analysis

Pre-processed fMRI data were analysed using the general linear model (GLM) framework implemented in SPM8. A two-step mixed-effects analysis was used (Friston et al., 1999). After standard filtering, a linear combination of regressors in a design matrix was fitted to the data to produce parameter estimates which represent the contribution of a particular regressor to the data (first analysis step applied to individual data sets). The second step used a random-effects model to analyze the group aggregate of individual results (parameter estimate maps).

For each run, the GLM contained regressors for the six experimental conditions (the six morph levels), the control condition, rejected trials (in which participants of the fixation group deviated their gaze from the centre), two confound regressors modelling changes over time in the speed and acceleration of the stimulus and the realignment parameters (included to model movement artefacts). In a separate GLM model used for MVPA, trials were grouped instead by the percept they evoked (animate or inanimate). The regressors were constructed using standard procedures in SPM (event duration for all stimuli was 5s); for the confound regressors, delta functions were modulated according to the speed or acceleration of the stimulus before convolution with the HRF.

To identify regions responding to our stimulus, we searched for clusters of voxels showing, in both groups of participants, a higher response to at least one moving-dot stimulus condition compared with the control condition (static dot). This was implemented in a random effects ANOVA model that included all participants, as a "null conjunction" (Friston et al., 2005) across contrasts testing the effects of main interest in each participant group. These effects were calculated, for each participant, over the responses to each morph level minus the control condition (i.e. morph level 1 – fixation, morph level 2 – fixation, etc …). Results were thresholded at $p < 0.05$, corrected for family-wise errors due to multiple comparisons across the whole brain, and clusters greater than 10 voxels in size are reported. Individual regions of interest (ROIs) were identified as clusters of voxels within 10 mm of the group peak response showing a significant response at $p < 0.01$.

2.8. Regions of interest analysis

To test for effects of changes in stimulus properties (morph level) and animacy percept on the BOLD signal, we followed a regions-of-interest (ROI) approach. BOLD response timecourses were extracted from regions responding to dot motion (see above, Fig. 2 and Table S2), and from regions identified in separate localizer scans (see below and Table S1). ROIs were identified in each participant as contiguous voxels with significant responses (at $p < 0.01$ uncorrected) within 10 mm of the group response peak. Timecourses were extracted from these ROIs to test effects of stimulus and percept changes separately (see below). Coordinates are reported in MNI format. Anatomical structures were identified using the participants' anatomical scans, an atlas of human anatomy and the Anatomy toolbox for SPM8 based on probabilistic cytoarchitectonic maps (Eickhoff et al., 2005).

To identify regions of the superior temporal sulcus (STS) responding to biological motion, all participants completed an additional fMRI run in which they were presented with point-light displays of human actions, scrambled versions of these or only a fixation cross and were asked to press a button when two identical actions were presented consecutively (one-back repetition detection task). Stimuli were presented in blocks of 12 animations presented every 1.5 s, for a total of 76 trials per condition, and showed lateral views of four different full-body point-light actions (walking, marching, running and boxing) recorded from the motion of

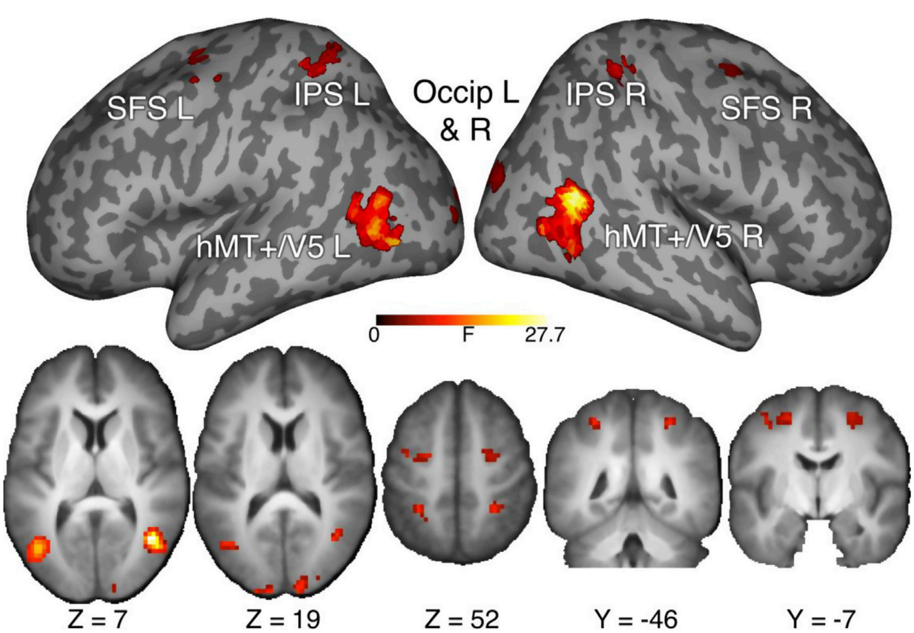

Fig. 2. Brain regions responding more to the moving dot stimulus than to the control static dot stimulus, irrespective of eye movements. Data are combined from participants free to move their eyes and those fixating the centre of the display using a conjunction contrast. Threshold: $p < 0.05$, whole-brain corrected for family-wise errors (FWE) at the voxel level. Activations are rendered on the inflated template MNI brain (top) and on sections of the average of our participants' brains ($N = 36$; bottom). Details of all clusters are reported in Table S1. IPS = intraparietal sulcus, SFS = superior frontal sulcus, hMT+/V5 = motion complex in lateral temporal cortex, Occip = occipital cortex (area V2d). Coordinates are in Montreal Neurological Institute space.

real actors and described in more detail elsewhere (Jastorff et al., 2006). Each action lasted 1.3 s, subtended about $3 \times 5°$ of the visual field and was shown as 10 dots of 0.2° in diameter located at the joints of the actor, plus a fixation cross located at the centre of the point-light figure. Scrambled actions were created by adding a constant random offset in horizontal and vertical direction to the trajectory of each dot; the offsets were chosen so that dot density and extension of the stimulus were matched with the original data but the shape of the actor was unrecognizable. Individual regions of interest (ROIs) were identified as clusters of voxels within 10 mm of the group peak responses to actions vs. scrambled actions (obtained in a whole-brain random-effects analysis, see Fig. S1) showing a significant response (see Table S1).

To localize regions responding to faces, we ran the following separate functional localizer experiment (e.g. Rossion et al., 2003). The experimental design consisted of 5 blocks each of faces, scrambled faces, objects, scrambled objects, and 4 blocks of fixation. Each block consisted of 6 stimuli covering about $6 \times 8°$ of the visual field presented for 1 s and followed by 2 s of fixation, for a total block length of 18 s. The block order was pseudo-randomized so that the immediate history of all conditions was matched (1-back history matching), in order to counterbalance their influence upon each other (see Buracas and Boynton, 2002). Stimuli were randomly sampled from a library of 160 faces (frontal views of faces only) and 76 everyday objects (from B. Rossion lab, https://face-categorization-lab.webnode.com/resources/natural-face-stimuli/). Scrambled objects were made by two-dimensional spatial Fourrier-scrambling. Subjects' task was to detect image repetitions of any image (one-back repetition detection task). In each subject, we looked for the Fusiform Face Area (FFA) (Kanwisher et al., 1997) by searching within the anatomical structure and close to the previously reported coordinate for voxels responding more to faces than to objects. The number of subjects for whom these ROIs were found and the coordinates are reported in Table S1. These face-sensitive regions were only defined in the free view group of participants due to loss of scan time in the fixation group related to setting up the eye tracker.

2.9. Timecourse data analysis

Trial-averaged BOLD timecourse data were computed as follows. Using in-house MATLAB code, raw BOLD signal data were extracted from each of the regions of interest, high-pass filtered (cutoff = 1/128 s), then averaged over voxels. Event-related responses from 5 s before trial onset to 25 s after trial onset were computed. The signal was expressed in units of the standard deviation (s.d.) of the activity in the 5s preceding stimulus onset, and it therefore represents the signal-to-noise ratio of the response. This approach compensates for differences in strength and noise of the BOLD signal across participants and has been successfully used before for fMRI data (Logothetis et al., 2001). We note that almost identical results are obtained by estimating event-related responses using a Finite Impulse Response model implemented in SPM8. The signal from the fixation trials was used as a baseline and subtracted from the signal obtained in the trials of interest, separately for each run. Mean and the standard error of the mean of the responses across participants are shown in the figures, and the peak response (observed at 6.7s post stimulus onset) was analysed using ANOVAs.

2.10. Effect of perceiving animacy irrespective of stimulus

We used the timecourse data to evaluate differences due to animacy judgments independently of stimulus conditions. To this end, we extracted timecourses separately for trials which the participant considered animate and those they considered not animate. Most trials at morph level 1 (="leaf") were considered as not animate and most trials at morph level 6 (="fly") as animate. To ascertain a reasonable signal-to-noise ratio, we only assess the difference between the response to animate and non-animate trials for each condition in which there were at least 5 trials considered animate and 5 trials considered non-animate (these conditions were not met at one or both of the most extreme morph levels in 5 subjects). We then averaged the responses to trials with animate responses separately from those trials with inanimate responses for each of the six morph levels for each participant. The peak responses of those response timecourses were then assessed using a 3-way, mixed design ANOVA, with percept (animate or inanimate) and morph level as within-subjects factors, and participant as between-subjects factor.

2.11. Multivariate voxel activation pattern analyses (MVPA)

In order to find reliable MVP information, we searched for effects that would hold across several approaches. We ran ROI-based pattern correlations (Haxby et al., 2001), ROI-based Support Vector Machine (SVM) MVPA and whole-brain searchlight analyses implemented in the Searchmight toolbox (Kriegeskorte et al., 2006; Pereira and Botvinick, 2011). Input for these analyses were parameter estimate maps for each morph level and each run, or each percept and each run, estimated using the single-subject fixed-effects GLM models implemented for the univariate analyses, estimated from non-normalised, unsmoothed data. For ROI-based pattern correlation MVPA, we tested whether activation patterns evoked by stimuli of the same morph level would elicit more similar activation patterns across runs than stimuli of different morph levels (all possible pairings between runs were assessed: run 1 vs run 2, run 1 vs run 3, and run 2 vs run 3). The same analysis was performed for the animacy percept (animate or inanimate, irrespective of morph level) and for the leaf and fly stimuli only. Results of pattern correlation analyses were assessed for each ROI using Bonferroni-Holm-corrected paired t-tests. For ROI-based MVPA using SVM, a SVM (LIBSVM for MATLAB downloaded from http://www.csie.ntu.edu.tw/~cjlin/libsvm, used with default cost and gamma parameters) was trained on the parameter estimate maps of two runs to distinguish between the 6 different morph levels and tested on the data of the third run, in a leave-one-run-out cross-validation scheme. LIBSVM implements multi-class classifications as a series of $k(k-1)/2$ binary models, where k is the number of classes, and returns model parameters that achieve the highest overall performance. We then ran a similar analysis to test activation pattern similarity as a function of the percept or between the leaf and fly stimuli. Results were assessed for each ROI using Bonferroni-Holm-corrected one-sample t-tests vs. chance.

Searchlight classifiers, implemented in the Searchmight toolbox (Pereira and Botvinick, 2011), were run on all gray-matter voxels for which BOLD data were acquired. Classifiers were trained to distinguish fMRI data from two runs (parameter estimate maps) obtained in the 6 stimulus conditions, only the extreme stimulus conditions or to distinguish stimuli considered animate from those considered inanimate, and were tested on the data of the third run according to a leave-one-out cross-validation approach. Searchlights were defined using radii of 2, 3 or 4 voxels, with best results obtained at 3 voxels, which generated searchlights of 150 voxels on average. We used both Support Vector Machine (SVM) and Gaussian Naïve Bayes (GNB) classifiers and applied default settings. These analyses were run on individual datasets in native space and resulted in decoding accuracy maps. To find regions with above-chance classification accuracy in our participant groups, we normalised the accuracy maps to MNI space and tested each searchlight centre with a random-effects *t*-test against the null hypothesis of chance accuracy (1/6 for stimulus conditions, ½ for percept and extreme stimuli), thresholded at $p < 0.001$ uncorrected (one-tailed). We used a bootstrap procedure to identify clusters significant after correction for multiple comparisons (Oosterhof et al., 2010).

2.12. Statistical analysis

Behavioural data (binary animacy decisions summarised in proportion of trials rated as "animate" and response times) as well as BOLD signal data from ROIs were analysed using two-tailed t-tests and repeated-measures analysis of variance (ANOVA) with linear trend, with Greenhouse-Geisser correction whenever Mauchly's test of sphericity indicated that the assumption of sphericity in the data was violated, using the software JASP Statistics Version 0.8.1.2 (U. of Amsterdam, http://jasp-stats.org). Non-significant results ($p > 0.05$) are labelled as n.s. In Fig. 1D–G, group data of proportion "animate" responses were fitted using a psychometric function using morph level as independent variable (a cumulative Gaussian function was used, fitted using the Levenberg-Marquardt algorithm implemented in MATLAB). In Experiment 4, a Bayesian Contingency Table Test implemented in JASP was used to assess the link between imagers and responders, by calculating the relative likelihoods of our results given the null hypothesis that being an imager and being a responder were not associated, and the alternative hypothesis that being a responder is associated with being an imager. Independent multinomial distributions (rows fixed) were assumed.

3. Results

3.1. Psychophysics

Psychophysical assessment prior to scanning (Experiment 1) and during scanning (Experiments 2&3) revealed that as expected, the animacy percepts changed reliably as a function of morph level (Fig. 1D–F; a 3-way, repeated-measures ANOVA with factors morph level, participant group and experiment (1–3) with Greenhouse-Geisser correction for non-sphericity revealed a main effect of morph level: $F_{(1.8,81.2)} = 214.3$, $p < 0.001$, $\eta_p^2 = 0.83$ but no variation across experiments or interaction, $F < 2$, $p > 0.1$; mean R^2 of the individual function fits: 0.97, 0.88, 0.93 for Experiments 1–3), confirming previous extensive psychophysical tests (J. Schultz and Bülthoff, 2013). Specifically, stimuli with high morph level values were more likely to be judged as animate than stimuli with lower morph levels (significant increase in probability of animacy judgment from one morph level to the next: Bonferroni-Holm-corrected planned pairwise t-tests comparing each morph level to each higher level were all significant at $p < 0.007$). The reported morph level effects did not vary significantly between "freeview" and "fixation" participant groups (no significant main effect of participant group or interaction with morph level: $F < 1.9$, $p > 0.11$). Thus, participants experienced reliable, graded subjective animacy percepts as a function of physical dot movement, irrespective of testing location or eye movements.

Response times (RT) varied as a function of morph level and percept (Fig. 1H–J): a 3-way, mixed between- and within-subjects repeated-measures ANOVA revealed main effects of morph level ($F_{(3.0,112.6)} = 3.0$, $p < 0.04$, $\eta_p^2 = 0.07$) and percept ($F_{(1,38)} = 16.1$, $p < 0.001$, $\eta_p^2 = 0.3$), and an interaction between morph level and percept ($F_{(2.2,81.8)} = 19.8$, $p < 0.001$, $\eta_p^2 = 0.34$): Response times increased with morph level when participants responded "inanimate" and decreased when participants responded "animate". There were no significant main effects of Experiment (1–3) or interactions between experiment and morph level or percept ($F < 1.8$, $p > 0.12$). As variations in response times may reflect differences in task difficulty and/or attention, we used response times as modulators in control analyses of our fMRI data (see below).

To confirm that animacy percepts were evoked because of similarity to naturally moving objects, we asked participants after scanning: "How did you decide whether the moving dot was animate or not?". More than 75% of participants reported that they considered the dot as animate if it reminded them of an insect (fly, mosquito), and inanimate if it reminded them of an object moved by the wind or another external force. These data corroborate previous findings, including similar verbal reports, that we obtained with these stimuli (J. Schultz and Bülthoff, 2013) and support the hypothesis that participants relied on representations of the motion of animate and inanimate objects to categorize the stimuli presented to them into animate or inanimate.

3.1.1. Link between animacy percept and visual imagery

In Experiment 4, we tested a separate group of participants to assess the link between animacy perception and visual imagery. Participants completed the animacy perception task, gave written reports about their categorisation strategy and completed the VVIQ. One participant was excluded because of incomplete data, leaving 59 participants. Animacy percepts (Fig. 1G) again changed reliably as a function of morph level (same ANOVA design as above; main effect of morph level: $F_{(2.8,162.7)} = 22.1$, $p < 0.001$, $\eta_p^2 = 0.28$), and response times (Fig. 1K) showed a main effect of morph level ($F_{(4.2,179.4)} = 12.1$, $p < 0.001$, $\eta_p^2 = 0.22$) but no effect of percept ($F_{(1,43)} = 0.7$, $p > 0.4$, $\eta_p^2 < 0.02$) and no interaction between morph level and percept ($F_{(3.9,170.7)} = 0.6$, $p > 0.6$, $\eta_p^2 < 0.02$). The amplitudes of the variations in percept were lower compared to Experiments 1–3 (comparing data across all 4 experiments revealed an interaction between experiment and morph level: $F_{(7.6,259.6)} = 9.6$, $p < 0.001$, $\eta_p^2 = 0.22$) and the pattern of response times was also different in Experiment 4 (comparing data across all 4 experiments revealed an interaction between experiment and morph level: $F_{(12.4,334.5)} = 2.6$, $p < 0.004$, $\eta_p^2 = 0.09$ and an interaction between experiment and animacy: $F_{(3,81)} = 3.2$, $p > 0.03$, $\eta_p^2 < 0.1$). We attributed these differences to the reduced number of trials per condition (10 instead of 30 or 49 in Experiments 1–3), but note that across all experiments, varying the stimulus morph level influenced the animacy percept in the expected manner. Consistent with previous results (J. Schultz and Bülthoff, 2013), we found that 61% of our participants (36 of 59) showed the expected gradual changes in animacy perception (these were termed "responders", see Materials and Methods; the average R^2 of their function fits was 0.89 compared to 0.65 for the entire 59 participants). Again consistent with previous results, 73% of our participants (43 of 59, termed "imagers") reported that they considered the dot as animate if it reminded them of a flying animal (fly, mosquito, bee, bird), and inanimate if it reminded them of an object moved by the wind or another external force. The remaining participants described that they referred to physical aspects of the motion of the dot, such as shapes of motion trajectories or speed profiles, to determine its animacy. We found that there were more imagers among responders than among non-responders (32 of 43 vs. 4 of 16, respectively; χ^2 value = 11.97, $p < 0.002$; 4 participants were responders but not imagers, and 11 were imagers but not responders). The Bayesian contingency table test revealed that the log odds ratio was 2.0 (95% credible interval: 0.85, 3.4) in favour of the alternative hypothesis that being a responder is associated with being an imager, and the Bayes Factor (BF_{+0}) was 186. Among responders we found a weak link between tendencies to experience visual imagery (higher VVIQ score) and sensitivity to animacy cues (i.e. lower point of subjective equivalence in the animacy task; $R^2 = 0.11$, $F_{(1,34)} = 4.8$, $p < 0.04$) that was driven by an outlier: the effect was not significant anymore once the outlier was removed ($R^2 = 0.10$, $F_{(1,33)} = 3.9$, $p = 0.06$). However, VVIQ values were not higher in imagers than non-imagers ($t_{(58)} = -0.13$, n.s.; 2-sample *t*-test) or in responders than non-responders ($t_{(58)} = 0.38$, n.s.). Our data thus support the idea that participants were more likely to experience changes in animacy percept when their mental representations of the flying insects and objects moved by external forces were triggered by our stimuli, but that animacy perception is not linked to general vividness of visual imagery.

3.2. Neuroimaging

3.2.1. BOLD signals evoked by physical dot motion

The first analysis step identified brain regions responding to the single moving dot stimulus. A whole-brain analysis identified voxels with a greater response to the moving compared to the static dot stimulus (control) in one or more morph levels (See Materials and Methods). As animacy percepts did not vary significantly between participants free to move their eyes and those fixating the centre of the display (see Psychophysics section, above), we combined their data in a random-effects analysis using a conjunction contrast. This procedure isolated regions activated by our stimulus independently of eye movements. We found bilateral activations in brain regions typically involved in visual motion processing and visuo-spatial attention, including area hMT+/V5 (the Anatomy toolbox indicated that these ROIs included 76% and 89% of left and right hMT+/V5, respectively), superior occipital gyri/dorsal part of visual area V2, intersection of intraparietal and postcentral sulci, and intersection of superior frontal and precentral sulci (likely frontal eye fields (Blanke et al., 2000; Corbetta and Shulman, 2002)) (Fig. 2; Table S2), as seen in previous studies using complex moving stimuli (Culham et al., 1998; Jovicich et al., 2001). These results confirm the efficacy of our stimulus for activating widespread visual cortical areas.

3.2.2. BOLD signals reflecting physical movement parameter (morph level)

The second analysis step aimed at identifying regions responding to changes in the physical movement pattern of the single dot, which was determined by the parameter β (morph level). Following a region-of-interest approach, we investigated regions activated by our stimulus or previously associated with animacy perception (see Materials and Methods, Fig. S1 and Table S1). Voxel-averaged BOLD responses from each ROI were entered into a repeated-measures ANOVA with factors morph level, ROI and participant group. BOLD signal significantly changed across ROIs (main effect of ROI: $F_{(15,432)} = 10.7$, $p < 0.001$, $\eta_p^2 = 0.27$), with morph level (main effect of morph level: $F_{(5,2160)} = 6.1$, $p < 0.001$, $\eta_p^2 = 0.01$), and morph level had different effects across ROIs (interaction morph level x ROI: $F_{(75,2160)} = 1.61$, $p < 0.05$, $\eta_p^2 = 0.06$; all other effects n.s.).

To reveal the origin of these effects, we ran subsequent separate repeated-measures ANOVAs with factors morph level and participant group for each ROI, which revealed significant effects of morph level only in the dorsal occipital cortex (right: $F_{(5,170)} = 4.7$, $p_{corr} < 0.02$, $\eta_p^2 = 0.12$; left: $F_{(5,170)} = 5.5$, $p_{corr} < 0.003$, $\eta_p^2 = 0.14$; p values corrected for multiple comparisons using Bonferroni-Holm method; data displayed in Fig. 3). The BOLD signal in these ROIs generally increased with morph level towards animacy. We note that while signal in V2d increased as a function of morph levels (significant linear trend), the signal changes were not monotonic, indicating other influences on activation than stimulus characteristics. Activation showed inverted-U-shaped quadratic trends, compatible with increased task difficulty at the middle morph level (=most uncertainty concerning the animacy percept). BOLD response in this region may thus reflect processing of visual cues of self-propelled motion combined with effects of task difficulty. In both hemispheres, responses changed across participant groups (right: $F_{(1,36)} = 25.27$, $p < 0.001$, $\eta_p^2 = 0.43$; left: $F_{(1,36)} = 16.16$, $p < 0.012$, $\eta_p^2 = 0.32$). This group effect is due to a smaller difference between responses to the moving vs static stimulus in the fixation compared to the freeview group (Fig. S2).

Next, we used MVPA to investigate whether the BOLD signal activation pattern, separately from univariate response differences, contained sufficient information to decode morph levels from each other. We thus subtracted the mean activation per condition in each ROI (in order to remove univariate differences between conditions) and performed correlation and classifier-based analyses searching for systematic changes in activation patterns across morph levels. Results revealed such information in the occipital regions, and additionally revealed effects in the correlation-based analysis in IPS, MT+/V5, SFS and VTC (Fig. 5A and B). Next, we attempted to decode only the extreme stimuli (leaf & fly) from the activation pattern, as these represent the largest changes in stimulus characteristics. Indeed, we found that activation patterns in IPS and in SFS evoked by the same stimuli were significantly higher than between activation patterns evoked by different stimuli (Fig. 5C), suggesting that some information about the differences between these stimuli is contained in the activation pattern of these regions. Classifier-based decoding results did however not reach significance (Fig. 5D). These results support the findings obtained in the univariate analyses suggesting an involvement of the dorsal occipital cortex (V2d) in processing the physical motion cue that determined the degree of perceived animacy.

Whole-brain multivariate analyses using the searchlight approach (Kriegeskorte et al., 2006) that we used in a previous study (Kim et al., 2015), using Support Vector Machines or Gaussian Naïve Bayes classifiers, revealed voxels whose surrounding activation pattern allowed to decode the stimulus morph level (Figs. S3A and C); while some such voxels were found in early visual cortex and lateral occipital cortex, only 2 voxels showed effects significant at $p < 0.001$ uncorrected using the GNB classifier and none in the SVM-based analysis, and none survived any type of correction for multiple comparisons (FWE, FDR). Thus, no additional regions showed systematic variations in their activation pattern with morph level.

3.2.3. BOLD signals distinguishing between animate and inanimate percepts

The crucial third analysis concerned the animacy percept, which relied on the morph level of the stimulus and was assessed by psychophysics during scanning. We compared BOLD responses from trials classified as “animate” and as “inanimate” irrespective of stimulus morph level. By design, this contrast is not influenced by any known, systematic physical differences between stimuli across morph levels (see Materials and Methods). As in the analysis of the effects of the movement parameter above, we ran a region-of-interest analysis of the BOLD signal in regions responding to physical dot motion and regions previously associated with animacy perception. A repeated-measures ANOVA with factors percept (animate/inanimate), ROI and participant group revealed that BOLD signals significantly changed across ROIs (main effect of ROI: $F_{(15,432)} = 11.5$, $p < 0.001$, $\eta_p^2 = 0.29$), between perceived animacy and inanimacy (main effect: $F_{(1,432)} = 17.1$, $p < 0.001$, $\eta_p^2 = 0.04$), with different effects of animacy across ROIs (interaction percept x ROI: $F_{(15,432)} = 1.7$, $p < 0.05$, $\eta_p^2 = 0.06$; all other effects n.s.).

Importantly, the analysis used to reveal the origin of these effects, which involved separate repeated-measures ANOVAs with factors percept (animate/inanimate) and participant group run on the data of each ROI, revealed that the right intraparietal sulcus (IPS R, MNI coordinates = [30–46 52], Fig. 4A) was the only region showing a significant change of BOLD signal as a function of percept: Signal was greater

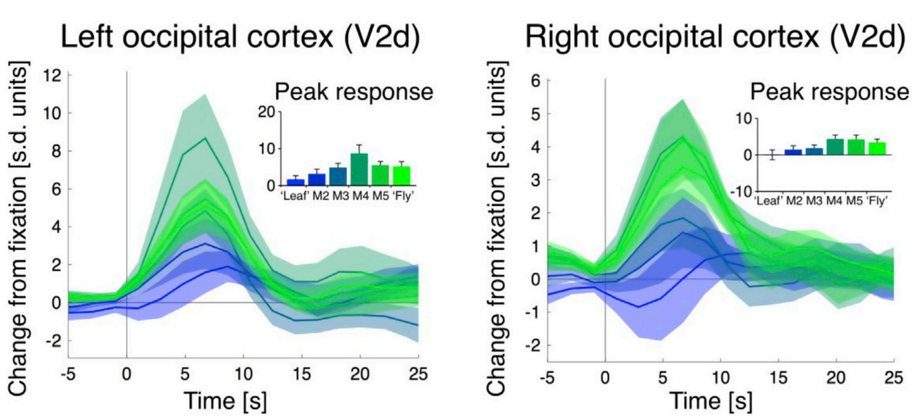

Fig. 3. BOLD signal in occipital cortex (V2d) reflecting physical dot motion pattern (morph level). BOLD signal in bilateral occipital cortex clusters (located in visual area V2d) changed as a function of morph level. These effects were found in both participants free to move their eyes and those fixating the centre of the display (Fig. S2). The displayed standard deviations (s.d.) represent signal-to-noise ratios of responses in the 5s preceding stimulus onset, averaged across all participants, N = 36. Shaded areas and error bars represent one standard error of the mean.

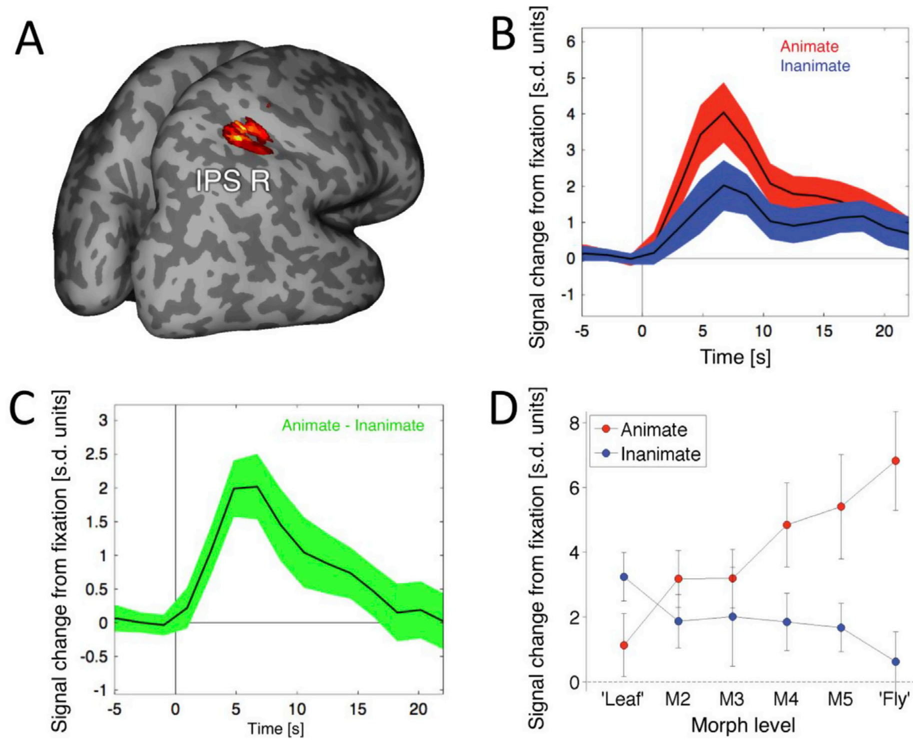

Fig. 4. BOLD responses in right intraparietal sulcus (IPS R) reflecting subjective animacy percept derived from single dot motion. (A) Location of the right IPS cluster, displayed at $p < 0.0005$ uncorrected (peak is significant at $p < 0.05$, voxel-wise FWE correction). This is the only brain region in which significant activations to changes in animacy percept were found. (B) Higher BOLD response in cluster shown in A when participants responded "animate" (red) compared to "inanimate" (blue). Mean and standard error of the mean across all participants (N = 38) (shaded area) are shown. (C) Animacy signal (same data as in B, but different display): Difference between BOLD signal from trials in which participants responded "animate" (red data in panel B) minus signal from "inanimate" response trials (blue data in panel B), calculated for each participant, then averaged. This procedure reveals that the difference in BOLD is quite substantial and significant (see small error of the mean). Mean and standard error of the mean (shaded area) across all participants (N = 38) are shown. (D) Peak BOLD signal response in cluster shown in A as a function of both animacy percept and dot motion pattern (morph level). The response increased with morph level only when the animacy percept occurred. This effect was found in the data combined across participants and in participants with controlled eye fixations. Mean response and standard error of the mean across all participants (N = 38) are shown. Responses from fixation and freeview participants are reported separately in Fig. S4.

during trials in which the moving dot was perceived as animate compared to trials in which it was perceived as inanimate (Fig. 4B and C, $F_{(1,30)} = 17.8$, $p_{corr} < 0.009$, $\eta_p^2 = 0.37$). There was no effect of eye movements (i.e. no main effect of participant group or interaction between percept and participant group: $F_{(1,30)} < 0.9$, n.s.; Fig. S4). The regions responding to biological motion or to faces did not show significant BOLD signal changes as a function of perceived animacy (Table S1).

Next, we used the same multivariate voxel activation pattern analyses (MVPA) as for the morph level analysis to investigate whether the BOLD signal activation pattern contained sufficient information in order to decode animacy and inanimacy percepts from each other. Results showed that activation patterns in SFS evoked by similar percepts were significantly higher than between activation patterns evoked by different percepts (Fig. 5E), suggesting that some information about the percept is contained in the activation pattern in this brain region. Decoding the percept using classifiers could however not be achieved using the data of any ROI (Fig. 5F).

Whole-brain multivariate analyses (searchlight MVPA; Kriegeskorte et al., 2006) revealed weak effects in insula, caudate and orbitofrontal regions, none of which survived correction for multiple comparisons. Thus, no additional regions contained significant information about the percept in their activation pattern (Figs. S3B and D).

3.2.4. BOLD signals coding physical movement parameter differently depending on subjective animacy percept

So far, we showed that the subjective animacy percept relied on the graded physical changes in the stimulus (morph level, Fig. 1), that BOLD response in the occipital cortex changed as a function of the morph level (Fig. 3), and that BOLD response in the right IPS differentiated between animate and inanimate percepts (Fig. 4A–C). As a next important step, we tested whether BOLD responses to changes in morph level in these ROIs depended on the animacy percept using a repeated-measures ANOVAs with factors percept (animate/inanimate), morph level and participant group. We found an effect only in the right IPS (Fig. 4D, interaction morph level x percept: $F_{(3.9,116.3)} = 5.7$, $p < 0.001$, $\eta_p^2 = 0.16$). There was no difference between participant groups (main effect and interactions: $F < 1.3$, n.s.). BOLD signal increased as a function of the morph level in trials with animacy percepts ($F_{(3.5,104.3)} = 4.6$, $p < 0.004$, $\eta_p^2 = 0.13$), but did not vary with morph level in trials without animacy percept ($F_{(2.8,83.5)} = 1.2$, n.s.).

These results suggest that the animacy BOLD signal in the right IPS increased linearly with the amount of physical visual motion cues about animacy contained in the stimulus, but only when the animacy percept occurred. In sum, our physical stimulus manipulation (i.e. the change in morph level) led to gradual, psychophysically measurable changes in animacy percept, which were accompanied, whenever the animacy percept occurred, by gradual increases in BOLD responses in the right IPS. Our experiment thus allowed us to determine a neural correlate for animacy perception based on visual motion cues of biological agents.

3.2.5. Control analysis: effects of response times on BOLD signal

To assess whether variations in response times (RTs, see Behavioural results above) could have influenced our neuroimaging findings, we repeated our first-level analysis but included each trial's RT as parametric modulator, and, in a separate analysis, included 1/RT as parametric modulator. This allowed to search for voxels whose activation changed as a function of response time, to look for different effects of response times across morph levels, and to assess whether our IPS R effects hold when separately accounting for variations in response times. Results are reported in Fig. S5: we found 2 clusters showing significant BOLD increases with RT (Temporoparietal junction/angular gyrus, MNI -42 -61 22, Z = 5.42; Precuneus, MNI -3 -52 28, Z = 5.25), and 3 clusters showing activation increasing with 1/RT (Right premotor cortex, MNI 45 8 34, Z = 5.01; right inferior parietal lobule, MNI 33–43 40, Z = 4.57; and right inferior frontal gyrus, MNI 48 38 16, Z = 4.33). The only ROIs showing significant variation of RT effects across morph levels or animacy were the left hMT+/V5 (animacy effect: $F_{(1,37)} = 5.72$, $p = 0.0220$, $\eta_p^2 = 0.02$; all other $F < 1.7$, $p > 0.15$, $\eta_p^2 < 0.05$), which also showed significant variation with 1/RT (animacy effect: $F_{(1,37)} = 6.32$, $p = 0.0165$, $\eta_p^2 = 0.02$), as did the left V2d (animacy effect: $F_{(1,37)} = 7.85$, $p = 0.0080$, $\eta_p^2 = 0.03$). These regions may therefore be sensitive to task difficulty, attention or other factors influencing RT, factors that were not a focus of

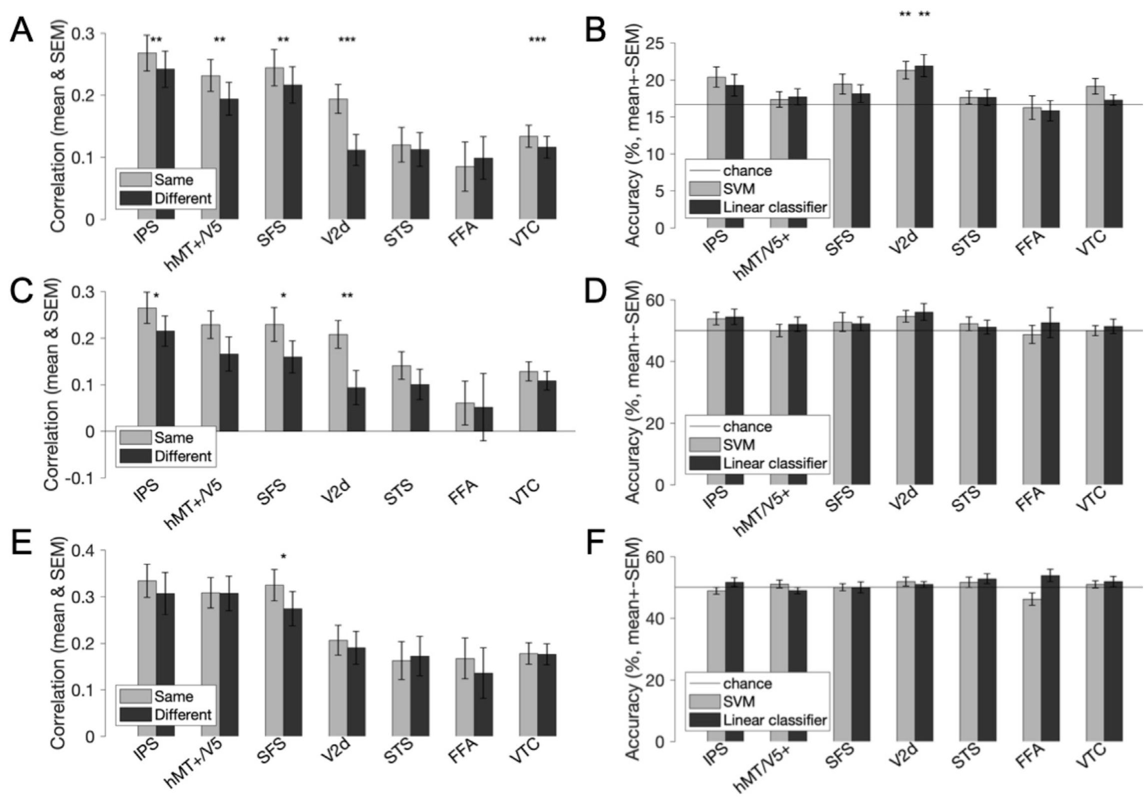

Fig. 5. Multivariate analysis of BOLD activation pattern in regions of interest. **(A)** Correlations of the activation pattern over voxels (parameter estimate maps) across runs were higher between trials of the same type compared to trials of different types (e.g. morph level 1 & morph level 1 vs. morph level 1 & morph level 2) in IPS, MT+/V5, SFS and early visual cortex. **(B)** Accuracy in decoding trial type using a support vector machine or linear discriminant classifier. Morph level could be decoded using both kinds of classifiers from activation in early visual cortex. **(C)** Same analysis as in A, attempting to distinguish fly from leaf stimuli only: significant results were obtained in IPS and SFS. **(D)** Same analysis as in B, attempting to decode fly from leaf stimuli; no significant results were found. **(E)** Same analysis as in A, conducted to distinguish animate from inanimate percepts. Correlations between SFS activation patterns evoked by similar percepts were significantly higher than between activation patterns evoked by different percepts. **(F)** Same analysis as in B, attempting to decode the reported percept (animate or inanimate); no significant results were found. Note that univariate differences between conditions were subtracted out prior to running multivariate analyses to restrict information to differences between activation patterns. ** = $p < 0.01$, *** = $p < 0.001$; paired t-tests were used to compare correlation coefficients (values were Fisher-Z-transformed prior to statistics) and 1-sample t-tests were used to compare decoding accuracy against chance; p values were corrected for multiple comparisons using Bonferroni-Holm. L. = left hemisphere, R. = right hemisphere, IPS = intraparietal sulcus, SFS = superior frontal sulcus, V2d = dorsal aspect of area V2, STS = superior temporal sulcus, FFA = fusiform face area, VTC = ventral temporal cortex.

our study. Crucially for our question of interest, the interaction between morph level and animacy observed in IPS R remained significant even when RT or 1/RT were included in the model ($F_{(5,185)} = 2.87$, $p = 0.0159$, $\eta_p^2 = 0.07$ and $F_{(5,185)} = 0.70$, $p = 0.6266$, $\eta_p^2 = 0.02$, respectively). Thus, we found no evidence suggesting that our findings associating the right IPS with animacy perception may have been influenced by variations in response times.

4. Discussion

Our study uncovered a region in the right intraparietal sulcus (IPS) involved in the perception of animacy from visual motion cues alone. Despite the fact that our stimuli were simplistic, the animacy percept was coded in both binary and graded fashion in the IPS, while physical stimulus parameters engaged occipital brain regions. Multivariate analyses revealed information about stimulus parameters in occipital cortex and (in less stable results) in hMT+/V5, IPS and superior frontal sulcus; the latter region also contained limited information about the animacy percept. Superior and ventral temporal regions previously activated by stimuli combining form and motion cues of animacy showed no significant responses to, or information about, animacy percepts evoked by our simple motion stimulus.

These unexpected findings could be due to our stimuli containing only very simple cues of animacy. Brain regions such as the posterior superior temporal sulcus (pSTS) and the temporo-parietal junction (TPJ) associated with animacy perception are involved in action observation (Grossman et al., 2000; Grossman and Blake, 2002) and are sensitive to animacy cues in observed actions (Mar et al., 2007). The pSTS might be particularly involved in processing complex stimuli displaying goal-directed, intentional action (Castelli et al., 2000; Gao et al., 2012; Jastorff and Orban, 2009; Lee et al., 2014; Martin and Weisberg, 2003; Saygin et al., 2012; J. Schultz et al., 2005; R. T. Schultz et al., 2003) or requiring form and motion integration (Castelli et al., 2000; Eickhoff et al., 2005; Gao et al., 2012; Giese and Poggio, 2003; Grossman et al., 2000; Jastorff and Orban, 2009; Lee et al., 2014; Martin and Weisberg, 2003; Oram and Perrett, 1996; J. Schultz et al., 2005, 2004; 2008; R. T. Schultz et al., 2003; Wheatley et al., 2007). Alternatively, pSTS may be more sensitive to top-down knowledge about the origin of the stimuli than to the stimulus characteristics themselves. The FFA, also associated with responses to animate entities (R. T. Schultz et al., 2003), may be associated with agency rather than animacy (Castelli et al., 2000; Gobbini et al., 2011). Our stimuli did not involve perception of human action or form-motion integration. Thus, perception of animacy in this most simple form may not engage pSTS or the ventral temporal regions we tested. The findings of reliable univariate but only inconsistent multivariate changes in signal associated with perceiving animacy suggests that this percept involves neural activity increases over a large group of neurons more than a state change in a distributed representation, at least at the spatial scale we investigated.

In right IPS, BOLD signal was associated with the percept of animacy: the signal was higher when participants perceived animacy compared to inanimacy (Fig. 4B and C) and increased linearly with the amount of physical animacy cues (Fig. 4D), but only when animacy was reported. Previous animacy-related IPS activations were found using stimuli combining form and motion cues, including point-light displays of human movements (Bonda et al., 1996; Thompson et al., 2005) or displays of interacting moving objects (Castelli et al., 2000; Gao et al., 2012; Lee et al., 2014; Martin and Weisberg, 2003; J. Schultz et al., 2005, 2004; R. T. Schultz et al., 2003; Wheatley et al., 2007). While such displays can evoke strong animacy percepts, how the cues combine to generate the percept can be difficult to untangle. The process of combining these cues itself is likely to recruit IPS, a visual association area. Our study revealed an animacy signal based solely on motion cues.

What may be the role of this hitherto unreported right IPS region in animacy perception? We propose that it is involved in assessing complex visual motion signals for animacy cues. This may involve matching stimuli to stored representations of animate motion and could function as follows. With weak animacy cues (low morph levels) or cues not perceived (high morph level trials not evoking animacy), activation is low because stored representations of animate entities are not activated. The stronger the cues, the more likely their resemblance to stored representations of animate entities, leading to "activation" of these representations, increasing neural activity and a percept of animacy. This hypothesis is in part supported by findings from Experiment 4, which revealed a link between visual imagery and animacy perception. Thus, right IPS activation in our experiment may be related to the activation of representations of the motion of animate entities. This may be an example of the use of memory evidence during perceptual decision-making: recent human neurophysiological data has shown that aIPS mediates the transformation of memory evidence into choices (Rutishauser et al., 2018). Alternatively, one could consider that our IPS R activation findings reflect the sensory evidence for animate movements; a recent fMRI study reported that IPS activation increased with the sensory evidence for a given sensory state (Bang and Fleming, 2018). Studies using our stimuli and involving measures of confidence may allow to clarify the processes involved.

The IPS R response we observed could also reflect evidence accumulation for animacy decisions – an appealing hypothesis given the established link between evidence accumulation and the posterior parietal cortex (e.g. Roitman and Shadlen, 2002). Specifically, our response time findings (RTs increased with morph level when participants responded "inanimate" and decreased when participants responded "animate") may be compatible with two alternative, competing evidence accumulation processes triggered by our stimuli: one for cues of animate motion and another one for cues of inanimate motion. As occurrence time and noticeability of the cues varied across trials, participants searched longer for cues in some trials, leading to longer response times and sometimes to missing the cues completely. This may be similar to the effect observed in visual search tasks: response times are longer in signal-absent than signal-present trials (Chun and Wolfe, 1996; e.g.: Treisman, 1988). Because all trials contained both cues for animate and for inanimate motion, we would argue that trial types did not differ in attentional demands: RTs depended more on the way participants processed a given stimulus than on the trial type. This fits with the observed RT distributions: the effect sizes of the percept and the interaction between percept and morph level were both over 4 times larger than the effect size of morph level (η_p^2 of 0.3 and 0.34 for the former, 0.07 for the latter). If we assume that participants focused more on cues for animacy or on cues for inanimacy across trials (independently from the morph level), this could explain why response times for "animate" responses at low morph levels (designed to contain cues for inanimacy) were longer than for "inanimate" responses, and why the symmetric opposite pattern was observed at high morph levels. Importantly for the interpretation of our imaging findings regarding animacy perception, the IPS R activation we measured did not completely follow RT variations: while higher BOLD signal measured at higher morph level stimuli perceived as animate was accompanied by short response times, variations of response times in trials with inanimate percepts were not reflected in IPS R BOLD signal changes. These findings thus do not seem to be compatible with a non-specific, domain-general evidence accumulation process (Basten et al., 2010), as we did not find IPS R activation changes reflecting the amount of evidence for inanimacy.

Regarding the cues contained in our stimulus and used to make animacy decisions, we must acknowledge the possible involvement of representations of goal-directed motion. We used only one moving object showing different levels of self-propelled motion. While using no second object eliminated obvious cues of goal-directed motion such as chasing, we did design our stimuli to mimic naturally occurring entities (insects, objects moved by the wind), and an insect buzzing around a room could be considered to be following an (invisible) goal. In that sense, we cannot exclude that perceiving a moving object as an insect could have triggered representations of goal-directed behaviour. Therefore, it is possible that animacy perception as investigated in our experiment may have relied on representations of goal-directed motion.

What is the meaning of our findings for social cognition? Animacy perception is considered a precursor to social cognition (C. D. Frith and U. Frith, 1999; Waytz et al., 2010). While we investigate animacy here as a very low-level, mostly perceptual process, it is interesting to discuss the link to higher-level social cognitive processes. Interestingly, some brain regions previously associated with animacy perception (pSTS, TPJ) are considered part of the "social brain" (Adolphs, 2003; Brothers, 1990; C. D. Frith and U. Frith, 1999), in particular due to their association with mentalising. Perceiving animacy could trigger a mentalising process geared at inferring intentions behind the movement of the perceived animate object, as has been suggested for the perception of actions (Blakemore and Decety, 2001). Perhaps animacy perception from motion as investigated here is a purely high-level perceptual process involving perceptual association areas rather than the "traditional" social brain regions. This process may trigger social cognition networks involved in action observation or mentalising depending on other stimulus characteristics and task demands. This would fit well with a network view of the social brain, which proposes specialised networks for different functions exchanging information depending on task demands. Our study consciously adopted an almost extremely reductionist approach to isolate animacy perception from perceptual cue-combination (form-motion integration) and complex social cognitive processes. Our study has thus attempted to separate animacy perception from social cognition itself.

Are there alternative explanations for our findings? A key factor to consider is a potential variation in attention and task difficulty across stimulus conditions. Evidence for such effects is the variation in response times we observed (see discussion above). This suggests that processing of our stimuli was not identical across stimulus conditions, which is not surprising: we purposefully manipulated the amount of cues about animate or inanimate motion across conditions. Could variations in response times have nevertheless influenced our neuroimaging findings? Because IPS is associated with visuo-spatial attention to motion (Corbetta and Shulman, 2002; Culham et al., 1998; Culham and Valyear, 2006; Jovicich et al., 2001), and because the lateralization of our effect fits with the specialization of the right parietal lobe in visuo-spatial transformation and attention (Heilman and Abell, 1980; Milner and McIntosh, 2005), we ran additional control analyses on our fMRI data: while some brain regions did show variations in activation with response times or 1/response time, including hMT/V5 and early visual cortex (see Results and Fig. S5), we found no sign of an influence of variations in RT or 1/RT on our IPS R activation, and our IPS R effects remained significant when including RT or 1/RT as confound variables. Thus, we believe that our IPS R effects are not simply driven by variations in task difficulty or attention.

Furthermore, we considered a potential influence of eye movements on IPS R activation. While we observed in a previous study that participants tend to follow our stimulus with their gaze, eye movements were not found to vary with percept (J. Schultz and Bülthoff, 2013). Eye movements acquired during scanner did not vary across conditions (Main effects of with morph level, percept and interaction: all $p > 0.18$, 2-way repeated-measures ANOVA, same design as used for response time analysis). To nevertheless control for effects of eye gaze, we only report results combined across participants with free and constrained eye gaze.

Several other task components are known to engage IPS. Some were held constant across conditions and cannot explain our results, such as action observation and visual short-term memory (Culham and Valyear, 2006; Farah et al., 1991; Warrington and Shallice, 1984) or analysis of complex motion signals (Kriegeskorte et al., 2003; Vanduffel et al., 2002). IPS and the neighbouring inferior parietal regions have been associated with understanding action goals (Jastorff et al., 2010; Thompson and Parasuraman, 2012); while goal-directed motion is an important cue for animacy (Gelman and Spelke, 1981; Gergely et al., 1995; Luo and Baillargeon, 2005; Opfer, 2002), our stimulus did not contain these cues. The participants' task may have had a strong influence on our results: our participants actively *performed animacy judgments* rather than passively *experiencing animacy percepts*. Such conscious judgements might induce a top-down modulation on processing of animacy cues, while passively experiencing animacy cues would not. However, a passive experience has several shortcomings: even if presenting participants with undeniably animate- and inanimate-looking stimuli, animacy percepts are left unreported and may vary with focus of attention or across individuals with personality or perception styles. We thus believe that searching for neural activation reflecting participants' percepts was a valid approach. A possible next step could be to disentangle the influence of task effects from processing of animacy cues, for example by comparing BOLD signal evoked by stimuli unambiguously perceived as animate during animacy judgments and during passive perception or performance of an unrelated task. If our previous results are anything to go by (J. Schultz et al., 2005), findings would remain unchanged by the task.

Occipital cortex (likely visual area V2d; Fig. 3) showed both univariate and multivariate activation related to physical stimulus properties. Animacy-related activation was previously found in occipital cortex with stimuli depicting interactions between two dots (Morito et al., 2009; J. Schultz et al., 2005). Spatial relations between dots may constitute shape information, which can trigger these areas; this cue was absent in our current study. Speed and object position change with morph level (J. Schultz and Bülthoff, 2013) and may have influenced occipital cortex activation. Our findings may also reflect top-down influences on occipital cortex associated with prediction or attention (Muckli and Petro, 2013; Murray et al., 2002; Somers et al., 1999).

We must specify that animacy perception was operationalized as a simple psychophysical task, equivalent to discriminating cues characteristic of animate and inanimate objects. Because participants were not told what these cues were and had minimal instructions, we believe this task to be a valid, albeit very abstract, approximation of animacy detection. Our aim was not to demonstrate which visual cues are the most important for animacy perception or for the stimulation of higher-level visual areas; if so we should have tested other cues and modelled other object movements. Although we expect similar results, we have not run these experiments. An advantage of our stimulus is that it can be gradually developed to identify the factors necessary to trigger social brain regions by stepwise inclusion of other animacy cues. Such findings are likely to be essential in order to understand the initial stages of human social perception and cognition.

In conclusion, our results suggest that visual cues of self-propelled motion are processed early in the hierarchy of visual areas, and that right IPS is involved in processing these cues for the perception of animacy. Our findings show how animacy perception can be separated from social cognition and raise questions about the factors necessary for engaging the social brain.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.04.058.

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