Capacity for movement is an organisational principle in object representations

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A B S T R A C T

The ability to perceive moving objects is crucial for threat identification and survival. Recent neuroimaging evidence has shown that goal-directed movement is an important element of object processing in the brain. However, prior work has primarily used moving stimuli that are also animate, making it difficult to disentangle the effect of movement from aliveness or animacy in representational categorisation. In the current study, we investigated the relationship between how the brain processes movement and aliveness by including stimuli that are alive but still (e.g., plants), and stimuli that are not alive but move (e.g., waves). We examined electroencephalographic (EEG) data recorded while participants viewed static images of moving or non-moving objects that were either natural or artificial. Participants classified the images according to aliveness, or according to capacity for movement. Movement explained significant variance in the neural data over and above that of aliveness, showing that capacity for movement is an important dimension in the representation of visual objects in humans.

1. Introduction

The ability to categorise objects is crucial for efficiently interacting with our environment and vital for survival. Knowing that objects in the same category share properties promotes efficient decision-making, such as aiding in deciding which animals to approach and which to flee, or determining which plants are edible and which are poisonous. Generalising object properties to new objects in the same category is an efficient way to make use of our limited memory capacity, and this generalisation permeates all interactions with the visual world.

One way of investigating human categorical knowledge is to examine how the brain distinguishes objects in the visual world. The human visual system can automatically categorise stimuli, from low-level visual features, to individual object identity, to increasingly abstract conceptual categories in fractions of a second (Cichy et al., 2014; Contini et al., 2017; Mohsenzadeh et al., 2018; Potter et al., 2014; Potter and Hagmann, 2015; Robinson et al., 2019). Categorical distinctions such as animacy are rapidly and subconsciously processed by the brain (Carlson et al., 2013; Cichy et al., 2014; Connolly et al., 2012; Contini et al., 2017; Grootswagers et al., 2018; Konkle and Caramazza, 2013; Ritchie et al., 2015). The representations of higher-order categorical distinctions like animacy have been localised to the inferotemporal cortex (Haxby et al., 2001; Kriegeskorte et al., 2008), and are observable from patterns of brain activity from approximately 100–

160 ms after stimulus onset (Contini et al., 2020; Goddard et al., 2016; Grootswagers et al., 2019, 2021). In addition to higher-order conceptual processing, some of this separation can be explained by differences in low and mid-level visual features between animate and inanimate stimuli (Grootswagers et al., 2019; Long et al., 2018; Wang et al., 2022). Even at rapid presentation rates, and when subjects are completing an unrelated task, animate stimuli are distinguishable from inanimate stimuli in patterns of EEG recordings (Grootswagers et al., 2021). This automatic identification of animacy has also been shown behaviourally in children as young as 7 months old (Träuble et al., 2014), leading to suggestions that learning about animacy early in development is evolutionarily adaptive (Aslan and John, 2016). Neuroscience research has supported this idea, demonstrating that both the adult brain (Bao et al., 2020; Konkle and Caramazza, 2013; Kriegeskorte et al., 2008) and the infant brain (Bayet et al., 2020; Deen et al., 2017) represents whether something is animate as part of core visual processing (DiCarlo et al., 2012).

However, more recent research has shown that the structure of object representations in the brain is more complex than a simple animate/inanimate dichotomy and may be influenced by an object's ability to move independently. Recent neuroimaging work has shown that movement and agency are important in animacy judgements, and visual stimuli may be better represented in the brain as a spectrum, according to their similarity to humans (Contini et al., 2020) or

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their capacity for agency and goal-directed movement (Connolly et al., 2012; Grootswagers et al., 2022; Jozwik et al., 2021; Sha et al., 2014; Thorat et al., 2019). These findings suggest that motion, particularly animate motion, is an important property of object processing in the brain. Brain regions active when perceiving motion are also active when viewing a still photograph taken mid-motion, also known as implied motion (Kourtzi and Kanwisher, 2000). Studies of implied motion have shown that the speed of implied motion has differential effects on brain activity based on the category of the object being shown, suggesting that movement is an important factor in category distinctions (Lu et al., 2015). Collectively, these findings suggest that the brain represents both movement and aliveness.

Behavioural work further demonstrates how movement and aliveness are used to categorise objects. Theoretical models of life status, such as the animistic-anthropocentric construction model (Yorek and Narli, 2009), suggest that our conception of what is alive is shaped by similarity to humans, particularly in terms of the overlapping concept of motion, with animals most similar to humans, then plants and then other non-living things. Most things that are alive can move, yet movement and aliveness are not the same: not all moving objects are alive (e.g., cars, clouds), and not all objects that are alive move on a time scale that humans can see (e.g., plants). The co-occurrence of movement and aliveness is so common that it is often a cause for classification error. For example, adults often mistake natural moving things (e.g., waves) for being alive when under time pressure to make a decision (Goldberg and Thompson-Schill, 2009). This co-occurrence makes it difficult to interpret prior neuroimaging literature on how the brain might represent movement, given it is so often confounded by aliveness. Is movement a relevant characteristic of an object for the brain to process, and if so, is this solely because it most commonly co-occurs with animacy? Investigating these cases that violate the intuitive association between aliveness and movement can provide insight into how these characteristics are coded by the brain.

In the current study, we investigated the relationship between movement and aliveness in neural categorisation by taking advantage of unusual cases of natural movement that are often misclassified by children, and adults under time pressure. We used naturalistic static image stimuli, including typical animate and inanimate stimuli as in prior research, and also included natural moving objects (e.g., waves, fire) and plants (e.g., trees, vines). These natural stimuli that violate the association between movement and aliveness (i.e., they are moving but not alive, or alive but not moving) allow us to investigate how movement and aliveness are processed in the brain. We first ran an online study to clarify behavioural classifications of the stimuli. Then, in two experiments, we gathered electroencephalography (EEG) data obtained while participants classified images according to whether they were alive or not (Experiment 1), or whether they could move or not (Experiment 2). Using multi-variate pattern analysis techniques, we examined similarities and differences in the temporal dynamics of visual processing and decision-making based on a stimulus' capacity for movement, and whether it is alive or not. These methods were used to examine if, and when, movement (including natural, non-agentive movement such as from fire, or waterfalls) is represented in the brain, and whether this is dependant on the categorisation task being completed. We find that capacity for movement explains significant variance in the EEG data, even after controlling for low-level visual factors and aliveness. The findings suggest that movement is an important organisational principle for object representation in the brain.

2. Methods

This section reports two EEG studies (Experiments 1 and 2) with very similar methodology. Stimuli, analysis scripts, results and anonymised raw EEG data are publicly available at https://doi.org/10.18112/openneuro.ds003885.v1.0.7 (Experiment 1) and https://doi.org/10.18112/openneuro.ds003887.v1.2.2 (Experi-

ment 2). Stimuli, analysis scripts, results and data from the online stimulus validation study are also publicly available at https://osf.io/jxhcs/.

To investigate how aliveness and movement are represented in the brain, we recorded electroencephalography (EEG) in two experiments, each consisting of a categorisation task in which participants classified images, and passive viewing, in which participants viewed stimuli in rapid streams. The structure of both experiments was identical, including the passive viewing blocks. The only difference was the categorisation task. In Experiment 1, participants classified images based on "whether they are alive or not". In Experiment 2, participants classified images based on "whether they can move or not". Different participants completed each experiment. Unless stated otherwise, the description of the methods below applies to both EEG experiments.

2.1. Participants

In Experiment 1, 24 undergraduate psychology students (15 women, 9 men) at the University of Sydney, Australia, participated in exchange for course credit. The mean age was 19.58 (range 18–26), and all but one were right-handed. In Experiment 2, a separate group of 24 undergraduate psychology students (16 women, 7 men, 1 non-binary person) at the University of Sydney participated for course credit. One additional subject was excluded from Experiment 2 with incomplete data as a result of a technical error during data collection. The mean age was 19.71 (range 18–26), and all but one were right-handed. All participants in both experiments had normal or corrected-to-normal vision, were neurologically healthy, and were not colour-blind. Informed written and oral consent was obtained from all participants prior to participation. The study was approved by the University of Sydney Ethics Committee.

2.2. Apparatus

Images were shown in the centre of a 1920 × 1080 pixel Asus gaming monitor with a refresh rate of 60 Hz. Participants responded using the two outermost buttons on a four- button box produced by The Black Box ToolKit Ltd (layout as shown in Fig. 1C, D). They were seated 55 cm away from the screen and stimuli subtended approximately 5° of visual angle. EEG was recorded at 1000 Hz on a 128 channel BrainVision Acti-Cap system (Brain Products GmbH), with electrodes located in positions consistent with the 10–5 extension of the 10–20 system (Oostenveld and Praamstra, 2001). Data were recorded with an online reference of FCz.

2.3. Stimuli

Stimuli were 400 realistic colour images collected from free online image databases (www.pixabay.com, www.pexels.com) under Creative Commons 0 licenses, and were used in all studies. All text in images (e.g. brand names on cars) was blurred manually using GIMP (v2.10.14, 2020), then each image was cropped and resized to 256 by 256 pixels. Stimuli were gathered in six categories based on those in Goldberg and Thompson-Schill (2009): animals, plants, still artificial things, still natural things, moving artificial things, and moving natural things (shown in Fig. 1A). For animals (bee, cat, dog, dolphin, eagle, horse, lemur, pigeon, tiger, whale) and plants (cactus, clover, fern, flower, grass, lemon tree, moss, palm tree, tree, vine), there were 10 objects. For all other categories, still artificial things (bench, clothes peg, headphones, lock, mug), still natural things (cliff, crystal, rock, sand, shell), moving artificial things (boat, bus, car, helicopter, train), and moving natural things (fire, hot spring, river, waterfall, waves), there were five objects. The extra plant and animal categories were included to ensure there was an equal number of images that were alive and not alive, as well as equal numbers of moving and still images. Within each category (e.g., cat, bench), there were 10 different images (e.g., cat1, cat2, … cat10). There were 400 images in total, each classified according to aliveness (200 living and 200 non-living), movement (200 moving and 200 still), and naturalness (300 natural and 100 artificial). For objects that are able
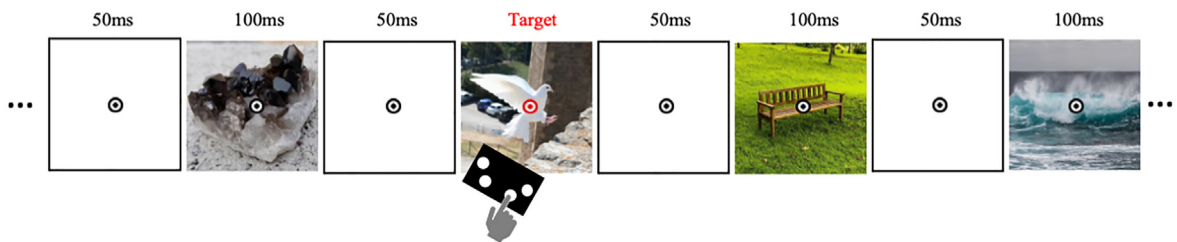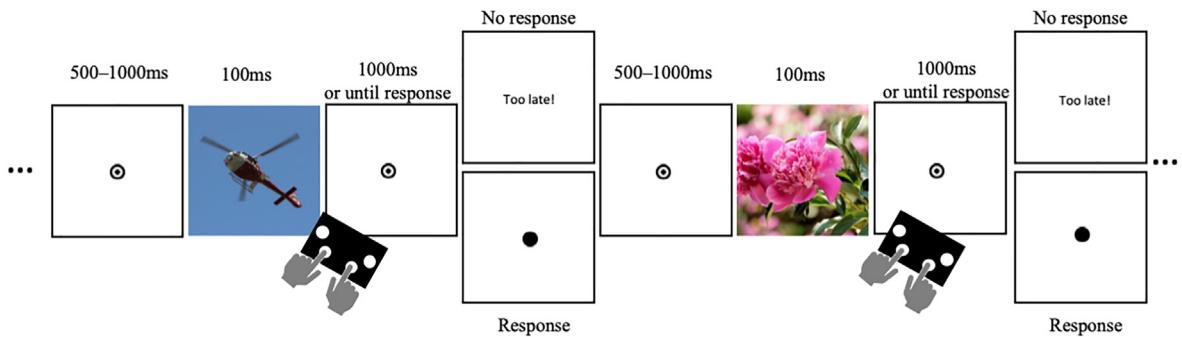
(A) Sample stimuli
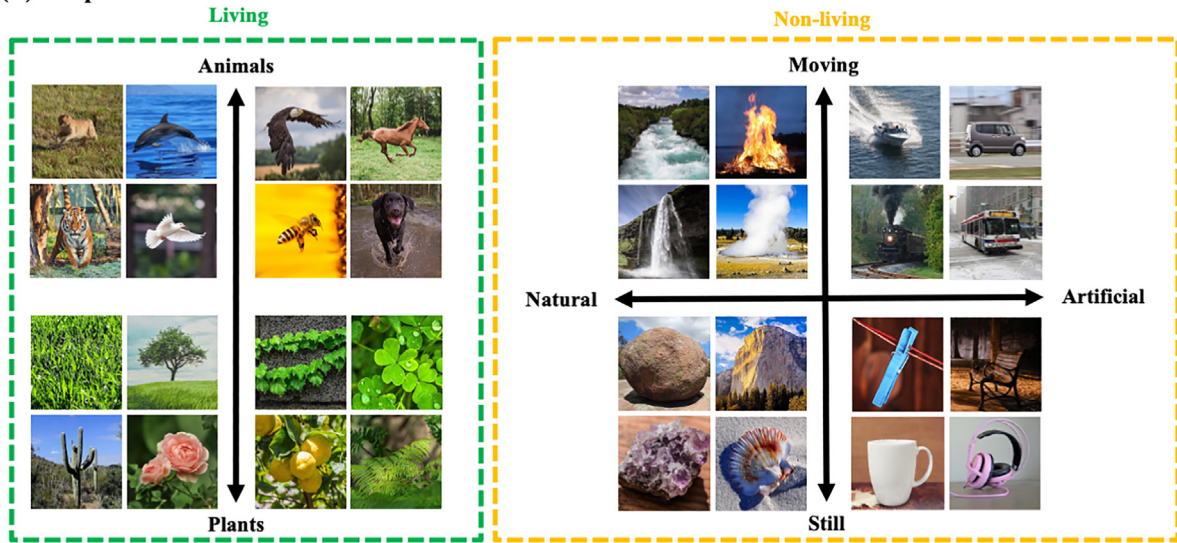
(B) Online stimulus validation (alive/not alive, moves/still, natural/artificial)
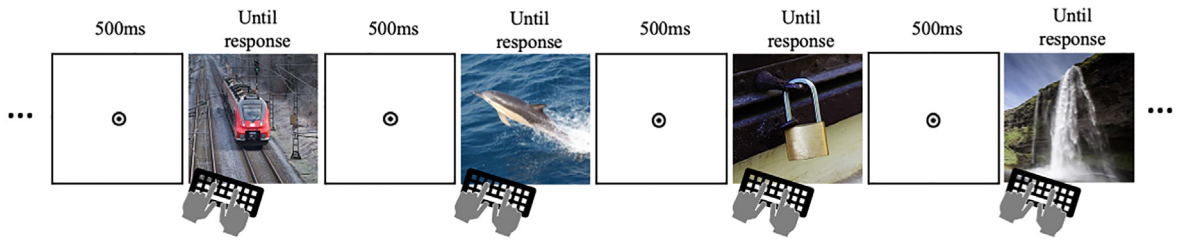
(C) Experiments 1 and 2: EEG (passive viewing)

(D) Experiment 1: EEG categorisation (alive/not alive) and Experiment 2: EEG categorisation (moves/still)

Fig. 1. Experimental paradigm for our online stimulus validation, and Experiments 1 and 2 with EEG. Sample stimuli are shown in (A). For the online stimulus validation experiment shown in (B), participants classified images by either aliveness, capacity for movement, or naturalness. During passive viewing trials of both EEG experiments in (C), participants viewed a rapid stream of images and responded to the fixation spot changing to red by pressing a button. During categorisation trials for both EEG experiments in (D), participants rapidly categorised images. In EEG Experiment 1, participants responded based on whether each image depicted something that was alive or not alive. In EEG Experiment 2, participants responded based on whether each image showed something that could move or could not move. Note that all images are magnified here for clarity; for presentation they occupied a smaller proportion of the screen.

to move, the stimulus was shown in motion in the image (e.g., birds and helicopters shown flying, see Fig. 1A), though all stimuli were static images.

2.4. Stimulus validation and model generation

To validate the stimulus set and generate behavioural models to compare to the EEG data, we ran an online experiment using Amazon's Mechanical Turk platform, guided by Grootswagers (2020), programmed using jsPsych (de Leeuw, 2015) and hosted on Pavlovia (Peirce et al., 2019, https://www.pavlovia.org/). Stimuli, analysis scripts, results and data are publicly available at https://osf.io/jxhcs/. Categorisation responses served to ensure that people generally agreed upon stimulus category and were used to construct independent behavioural models.

Mechanical Turk (MTurk) workers were recruited from the U.S.A. and Canada to complete the 15 min experiment in return for cash payment. Participants were randomly allocated to answer one of three questions about each of the 400 stimuli: (1) "Is the thing in the image alive, or not alive?", (2) "Can the thing in the image move, or is it still?", or (3) "Is the thing in the image naturally occurring or man-made?" Data was gathered from 50 participants for each question. Participants were shown one image at a time and instructed to press the 'F' and 'J' keys on their keyboard to indicate their response for that image. The instructions stated that participants should "try to be fast and accurate." Each image appeared after a 500 ms fixation cross and remained on the screen until participants responded (Fig. 1B).

To ensure we were only using data where participants were completing the task properly, we removed seven subjects whose overall accuracy (based on expected classification) was less than 50%. We also removed 15 participants who responded in less than 100 ms on more than 25% of images, as participants are unlikely to be making valid responses in such a short time period. These exclusion rates are within the range expected from online samples (Thomas and Clifford, 2017). After these exclusions, there were 42 participants who classified by aliveness, 48 participants who classified by movement capacity, and 38 participants who classified by naturalness. For these included participants, any trial that had a reaction time more than 3 standard deviations longer than the mean of all trials pooled across all participants (on average, less than one trial per participant) or less than 100 ms (on average, less than one trial per participant) was also removed.

To investigate how neural activity was related to behavioural classifications of the stimuli, we used Representational Similarity Analysis (RSA) to generate models of categorical and visual attributes of the images (Kriegeskorte et al., 2008). Behavioural models were generated from responses of online participants by averaging the percentage of responses towards the affirmative decision ('alive', 'moves', or 'natural') for each image and calculating the Euclidean distance between each pair of images. This 400 × 400 matrix was then averaged over all images within a category to create a 40 × 40 Representational Dissimilarity Matrix (RDM). These RDMs are shown in Fig. 2A–C.

2.5. EEG experiment procedure

Participants in both EEG experiments completed 8 blocks of trials, alternating between a passive viewing task (4 blocks) and a categorisation task (4 blocks), and always beginning with passive viewing.

2.5.1. Categorisation task

To see how focusing on aliveness and movement affected neural processing, participants completed a categorisation task (Fig. 1D). Each trial consisted of a fixation cross for a random duration between 500 ms and 1000 ms, followed by an image in the centre of the screen for 100 ms. Participants had 1000 ms from stimulus offset to respond on the button box. For Experiment 1, participants decided whether the image was alive or not alive. For Experiment 2, participants decided whether the stimulus could move or not. The response mapping changed over each

block, such that the side of the button corresponding to 'alive' or 'able to move' switched between left and right every block, and the order of the mapping was counterbalanced across participants. When a participant responded, the fixation spot filled in to indicate that a response had been recorded (Fig. 1D). If there was no response in this time, the screen displayed "Too late!", and advanced to the next trial. For each of the four categorisation blocks, trials (single image presentation and response, as described above) were chunked into 10 sequences. One sequence contained 40 trials, so that each sequence contained one image from each category (e.g., one dog, one fire). Thus, across the 10 sequences in each block, all 400 images were shown. Each sequence lasted approximately 1–2 min, and participants were told to take a break between sequences and advance at their own pace.

2.5.2. Passive viewing task

In passive viewing blocks, participants viewed a series of rapid presentation sequences and responded by pressing a button when a fixation spot changed colour (Fig. 1C). Images were shown for 100 ms each, followed by a 50 ms inter-stimulus interval. This non-category related task was included to provide baseline neural activity for each image in order to assess whether movement was processed as a higher-order characteristic, or a lower-level visual attribute. The collection of the same passive task across both experiments also allows the experiments to be directly compared.

In each of the four passive viewing blocks, participants were shown three repetitions of each image during passive viewing sequences, equating to 12 total repetitions of each stimulus across the experiment. These were split into 15 short sequences of 80 images each (~12 s each), to minimise fatigue and eye blinks. All 400 images were displayed in the first five sequences, then shuffled and repeated over the next five, and shuffled and repeated over the final five sequences. This ordering ensured that no image appeared twice in the same sequence, and that images were distributed within each block.

Participants were instructed to press a button as quickly as possible whenever they saw the fixation spot (a bullseye, two concentric black circles, shown in Fig. 1) change colour to red. There were two to four randomly located colour changes in the middle 60 presentations of each sequence of 80 images. The concentric circles of the bullseye were used to ensure there was sufficient contrast with all stimuli to distinguish colour changes. This task ensured that participants maintained a central fixation and paid sufficient attention to the screen but were not explicitly focused on the semantic properties or categories of the images.

2.6. EEG data analysis

2.6.1. EEG preprocessing

We used a minimal pre-processing pipeline, based on prior work (Grootswagers et al., 2021, 2019, 2019; Robinson et al., 2019; Shatek et al., 2019). Using custom scripts for EEGLab (Delorme and Makeig, 2004) in MATLAB (The MathWorks Inc, 2020, version 2020a), data were re-referenced to an average reference, low pass filtered at 100 Hz, high pass filtered at 0.1 Hz, then down-sampled to 250 Hz. Epochs of data were created from 300 ms before each stimulus appeared on the screen to 1000 ms after stimulus onset.

2.6.2. Decoding image category

To investigate how the different object categories are represented in the brain, we used multivariate decoding applied to the EEG data in response to each image. All decoding analyses were run in MATLAB using functions from the CoSMoMVPA toolbox (Oosterhof et al., 2016), using all 128 channels from each participant. To test if individual images (e.g., tree1, cat1) and categories (e.g., plant, animal) were distinguishable from the EEG recording, we conducted pairwise decoding analyses. All analyses were conducted timepoint by timepoint relative to when each image was displayed. At the individual image level (e.g., tree1, cat1), we trained a Linear Discriminant Analysis (LDA) classifier on each pair
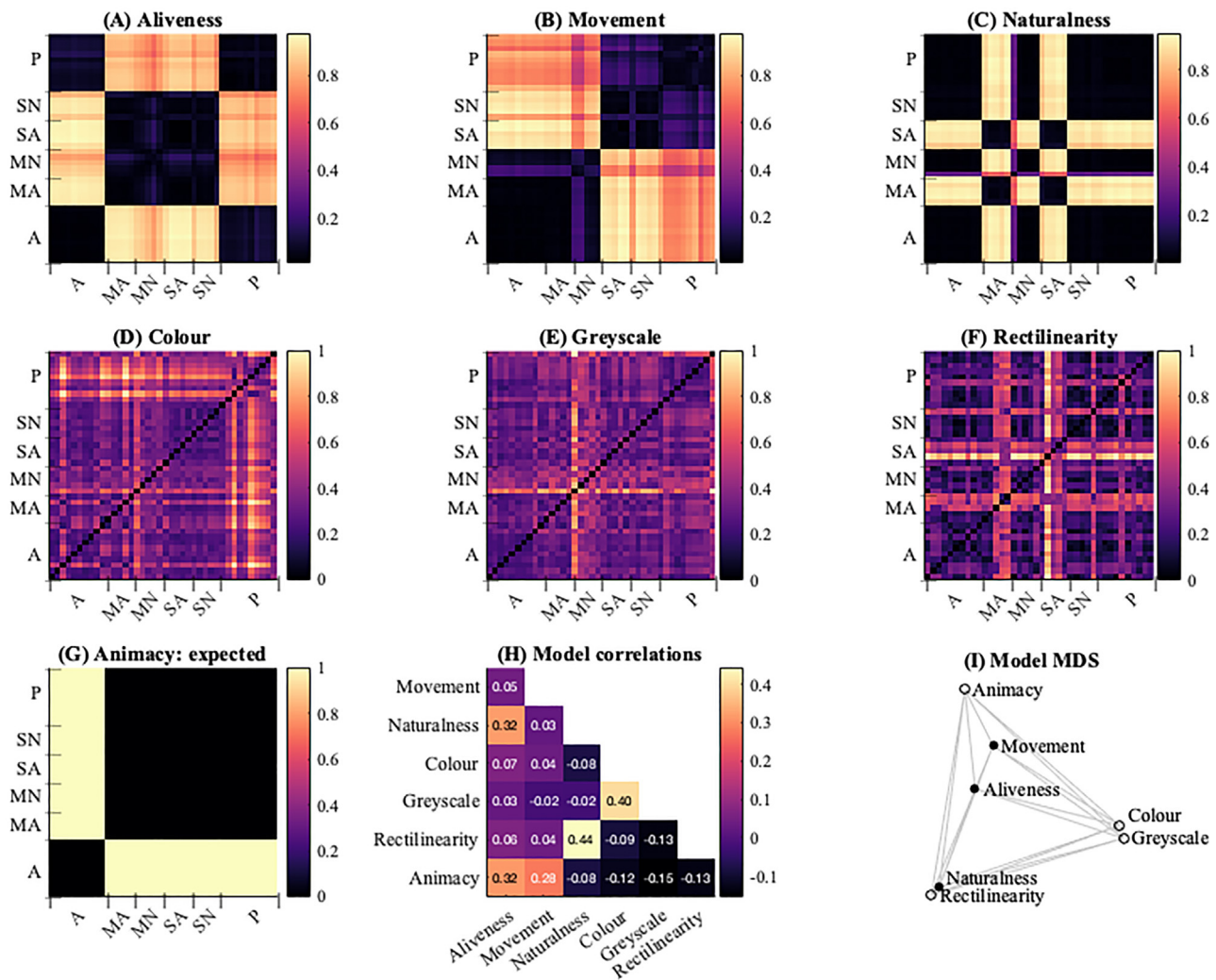
Fig. 2. Representational dissimilarity matrices (RDMs) generated from behavioural ratings of stimuli and image-level analysis of stimuli. Areas that are more purple (darker) indicate low dissimilarity (more similar). Areas that are more orange (lighter) indicate high dissimilarity (less similar). Each category (e.g., cat, tree) is shown in a single row/ column. Panels (A), (B), and (C) illustrate models generated from behavioural ratings of the stimuli from an online stimulus validation task. Panels (D), (E), and (F) show models generated by analysis of the low-level features of the stimuli, and panel (G) shows the experimenter-derived expected animacy model. Model correlations between these models are shown in (H), and the relationships between the models are shown using Multi-Dimensional Scaling (MDS) in (I). Abbreviations on panels (A) – (G) indicate categories; Plants (P), Still Natural (SN), Still Artefacts (SA), Moving Natural (MN), Moving Artefacts (MA), and Animals (A). (For interpretation of the references to color in this figure, the reader is referred to the web version of this article).

of images from all but one block and tested on those same images from the left-out block. This was repeated over all pairs of images, for each block as the test data. Separate analyses were conducted for categorisation and passive viewing. At the category level (e.g., plant, animal), we conducted a similar pairwise analysis still leaving two images out to test on, but also excluded these two images from the training set. For example, to compare plants and animals, a classifier was trained on blocks 1–3 using all plants and animals except a pair of images (e.g., tree1 and cat1), and then tested on these left-out images (tree1, cat1) from remaining block (block 4). This process was repeated so each pair of images was left out in each block, then averaged over all pairs.

2.6.3. Representational similarity analysis

To investigate how movement and aliveness are represented in the brain, we used Representational Similarity Analysis (RSA) to relate neural activity to behavioural responses as well as lower-level visual features that might differ across categories (Kriegeskorte et al., 2008). Behavioural Representational Dissimilarity Matrices (RDMs) were calculated for aliveness, movement and naturalness based on the online stim-

ulus validation study, and low-level visual models were calculated for colour, rectilinearity and patterns of shadow using a greyscale model. For the colour model, each pixel of each image was allocated values within CIELab colour space, and these values were averaged over all images in a category to form a single vector of values for each category. The Euclidean distance between categories could then be calculated. For the greyscale model, each pixel of each image was converted to a single greyscale value. These values were averaged over all images in a category, and the Euclidean distance between categories was calculated to form the 40×40 RDM. To control for rectilinear differences in animacy, we also included a measure of rectilinearity from Nasr et al. (2014), calculated using publicly available code from [https://github.com/cechava/Rectilinearity_Toolbox]. As with the colour and greyscale measures, we calculated the amount of rectilinearity in of each image, then averaged across each category. We then calculated the Euclidean distance between each category to form a model of rectilinearity.

To calculate RDMs for the neural data, we used an LDA classifier at every time point to compute decoding accuracy for each pair of cate-

gories (e.g., cats vs rocks), resulting in a 40×40 neural dissimilarity matrix for each time point. This classifier used the same partitioning structure as category decoding above, in which each pair of images was left out as the testing set for each block and for each pair of categories. Separate neural RDMs were created for passive viewing and categorisation trials.

2.6.4. Linear modelling

To investigate how categories of aliveness and movement account for neural responses to objects, we ran a series of general linear models to see which characteristics best explained the neural processes over time in both the categorisation and passive viewing tasks. For the categorisation data, eight predictor variables were included: aliveness, naturalness, movement, colour, greyscale, rectilinearity, animacy, and stimulus-driven neural responses from the passive viewing trials. All of these models (except the passive viewing neural models) are shown in Fig. 2. These eight predictor variables were used to run separate linear models for each time point, with outcome variable as the neural RDM of the categorisation task at that time point. This process was repeated with the passive viewing data as the outcome variable, including the first seven predictor variables: aliveness, naturalness, movement, colour, greyscale, rectilinearity, and animacy.

The behavioural models of movement, aliveness, and naturalness (Fig. 2A–C) were included in the GLMs to assess how these different image categories influenced neural responses. We also included low-level visual models of colour, greyscale and rectilinearity (Fig. 2D–F), as prior evidence has shown that distinct patterns of neural activity arise at least to some extent as a result of similar low- and mid-level visual features such as rectilinearity (Grootswagers et al., 2019; Long et al., 2018; Wang et al., 2022). We also included a binary model of animacy (animals coded as 1, all other categories coded as 0; Fig. 2G), and the neural RDM of the passive viewing trials. For each time point, the passive viewing RDM was taken from the same time point as the categorisation task RDM (outcome variable) to account for stimulus-driven neural processes during the categorisation tasks. The combination of these models can highlight how stimulus movement and aliveness uniquely contribute to neural responses.

To ensure that multicollinearity was sufficiently low to interpret the output of the model, we calculated the variance inflation factors for each model based on a downloaded MATLAB function (Vasilaky, 2021). A measure of multicollinearity, the variance inflation factor indicates the impact on the variance of the model of adding a particular variable, compared to if it were independent to all the other variables (Montgomery et al., 2012). A variance inflation factor of one would indicate that the variable is independent from the other elements in the model, with factors close to one indicating fewer potential issues with multicollinearity and higher factors indicating more higher multicollinearity (Thompson et al., 2017). The variance inflation factors for all variables were low (ranging from 1.01 for movement to 1.40 for naturalness), indicating low multicollinearity between the models.

2.6.5. Neural network

To investigate whether the characteristics associated with movement are associated with lower-level visual processing, or more abstract categorical processing, we compared neural data to different layers of a neural network. CORnet (Kubilius et al., 2018, 2019) is a deep neural convolutional network designed as a model for the human visual system, where each convolutional layer represents a different area of the visual system. Feature weights for each image were extracted from the layers representing V1, V2, V4 and Inferotemporal cortex (IT). The distance between the feature weights for each image was calculated to form a 400×400 RDM, which was then averaged to 40×40 so it was the same size as the neural RDMs. This process was repeated over each brain region (layer). To examine which layer of CORnet most closely resembled neural activity over time, we examined the correlation between each layer and the neural data for each time point.

2.7. Statistical analysis

We used Bayesian inference to examine differences in accuracy and reaction time across stimulus categories.

For all comparisons, we used the BayesFactor package in R (Morey et al., 2018). Following recommendations in Teichmann et al. (2022), we used a JZS prior (Rouder et al., 2009) with a scale factor of 0.707. This is the default prior and scaling in the BayesFactor package because it makes minimal assumptions about the expected effect size, and serves as a "non-informative default" (Rouder et al., 2009, p. 232).

To calculate statistics for the differences in behavioural classification between animals and plants, we used the Bayesian equivalent of t-tests (Rouder et al., 2009). We also used Bayesian linear models to determine if naturalness and capacity for movement influenced reaction times or accuracy. Models were built to express all combinations of each variable, in addition to participant ID. To determine whether naturalness and movement had an effect on reaction times and accuracy, we compared an additive model (movement + naturalness + subject ID) to a model without each variable in turn (for movement, naturalness + subject ID). A larger Bayes Factor would indicate that the inclusion of that variable makes a model that is more likely given the data (Rouder et al., 2012). This can be interpreted similarly to the main effect in a traditional ANOVA.

For decoding analyses, we used a series of t-tests using the ttestBF function (Morey et al., 2018) from the BayesFactor package with the parameters described above. The alternate hypothesis is that the decoding is above chance (50%), and the null-interval was effect sizes from negative infinity up to 0.5, as effect sizes during baseline periods prior to stimulus onset from previous work have shown this to be most appropriate (Teichmann et al., 2022). This formed a one-sided hypothesis that the effect size for alternate hypothesis should be positive. For linear modelling, in which both negative and positive results are meaningful, we used the same procedure with the alternative hypothesis that the betas are different to zero, with a two-sided prior from −0.5 to 0.5.

Bayes Factors are interpreted according to (Jeffreys, 1998), where Bayes Factors larger than 30 are very strong evidence for the alternate hypothesis, Bayes Factors larger than 10 are strong evidence for the alternate hypothesis, Bayes Factors larger than 3 provide some evidence for the alternate hypothesis, and Bayes Factors smaller than 1/3 provide evidence for the null hypothesis.

3. Results

We used behavioural and neural measures to investigate how aliveness and movement are processed by the brain. In two experiments, participants rapidly classified images according to aliveness (Experiment 1) or capacity for movement (Experiment 2) while we measured neural responses with millisecond precision.

3.1. Behavioural: passive viewing

In the passive viewing task, participants performed an orthogonal fixation change task. Behavioural performance on the passive viewing blocks of both EEG experiments indicated that participants were engaged with the task. Participants correctly identified the target colour change within 600 ms on 93.77% of occurrences for Experiment 1 (SE = 0.93, range 79.07–100%) and on 95.76% of occurrences for Experiment 2 (SE = 0.54, range 88.04–98.89%).

3.2. Behavioural: categorisation task

To examine the relationship between movement and aliveness in categorisation of naturalistic image stimuli, we used behavioural metrics (reaction time, classification accuracy) and multivariate pattern analysis of neural data. The median reaction time for Experiment 1 was
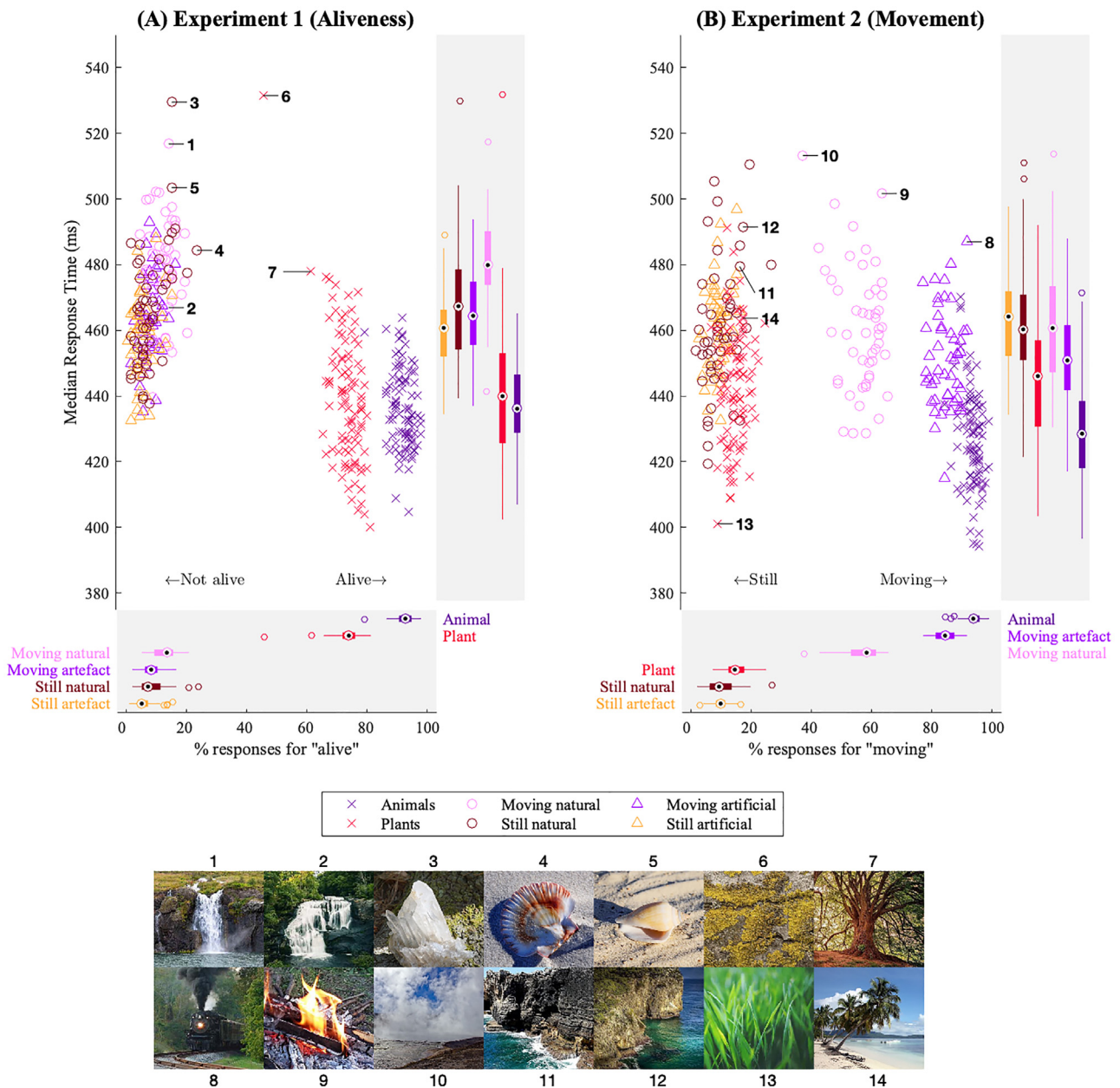
Fig. 3. Median response times and classifications of stimuli from EEG Experiments 1 and 2. Data from participants considering whether the stimulus was alive or not is shown in (A) and data from classifying images by capacity for movement are shown in (B). Sample images below correspond to the labelled data points, showing a selection of responses.

457 ms (SE = 10.7 ms, range of participant means 322 ms – 561 ms), and for Experiment 2 was 456 ms (SE = 11.53 ms, range of participant means 373 ms – 588 ms). Participants showed high accuracy in classifying the stimuli, with few trials (on average, ~16 of 1600 trials per participant) that timed out without a response (misses). In Experiment 1, the mean percentage of correct responses was 87.42% (SE = 1.4152, range 69.75–97.5%), with an average of 1.10% misses (SE = 0.26, range 0.13–5.94%). For Experiment 2, there were 82.97% (SE = 1.64, range 61.67–94.42%) correct responses, on average, with 0.97% misses (SE = 0.18, range 0.19–3.00%). Though some participants had low 'accuracy' scores, these always arose from consistent classification in the opposite direction from what was predicted (e.g., consistently responding that plants were not alive in Experiment 1, or consistently responding that moving natural stimuli did not move in Experiment 2).

3.3. Behavioural: experiment 1

We were interested in how image category influenced how participants categorised images according to whether they were alive or not in Experiment 1 (Fig. 3A) First, we assessed performance for the alive images, which consisted of animals and plants, as previous work has shown that animals are considered 'more alive' than plants (Yorek et al., 2009). Bayesian t-tests were used to evaluate whether there were differences in reaction time and classification between plants and animals. There was very weak evidence for differences in reaction time between plants and animals in the aliveness task of Experiment 1 (BF = 1.09) and some evidence that responses to animals were faster than plants in the movement task of Experiment 2 (BF = 3.17). However, there was strong evidence that plants were classified as "not alive" more often than ani-

mals (BF = 16.66), suggesting that plants are considered 'less alive' than animals, as predicted by behavioural models of aliveness (Yorek and Narli, 2009).

For the stimuli that are not alive, we used Bayesian linear modelling to investigate how moving and natural stimuli influenced aliveness judgements compared with still and artificial stimuli. Natural stimuli were mistakenly classified as alive more often (BF = 184.70) and more quickly (BF = 3757.79) than artificial stimuli. This is somewhat expected, given that all of the stimuli that are alive are also natural. Capacity for movement also influenced judgements of aliveness, with non-living moving stimuli classified as alive more often (BF = 132.28) and more slowly (BF = 667.90) compared to still stimuli. These results are in line with use of intuitive biological knowledge under time pressure (Goldberg and Thompson-Schill, 2009), mistaking moving and natural stimuli for being alive.

3.4. Behavioural: experiment 2

We were also interested in how image category influenced movement classification in Experiment 2 (Fig. 3B). There was weak evidence for no difference in reaction time (BF = 0.68) in classifying plants and animals as moving or non-moving. There was also weak evidence that animals were classified as moving more often than plants were classified as still (BF = 3.17). For non-living stimuli, we investigated the impact of capacity for movement and naturalness on movement classification using the Bayesian equivalent of an ANOVA. We found that natural stimuli were classified less accurately than artificial stimuli (BF = 66.50), and moving stimuli were also classified less accurately than still stimuli (BF = 1815.09). There was weak evidence for the null hypotheses that naturalness did not affect reaction times (BF = 0.92), and weak evidence for the null hypothesis that movement did not affect reaction times (BF = 0.29). Crucially, there was a significant interaction effect (BF = 168.7) for accuracy, suggesting that stimuli that are both moving and natural were responded to less accurately. This difference is clear in Fig. 3B (pale pink circles), showing the low agreement across participants on whether these natural moving stimuli are moving or not.

3.5. Decoding image category

We were interested in the temporal dynamics of visual information processing in the brain, from low-level image identity to category level representations. To test if individual images (e.g., tree1, cat1) and categories (e.g., plant, animal) were distinguishable from the EEG recording, we used a linear discriminant classifier to classify stimuli at these two levels. Neural responses contained information about image identity (e.g., dog1) and category (e.g., animal) from 90 to 120 ms after stimulus onset, characteristic of early-stage visual processing (Carlson et al., 2013; Cichy et al., 2014). Both when participants were passively viewing images (Fig. 4A, C) and when they were classifying them (Fig. 4B, D), information about stimulus identity remained present for more than 400 ms after stimulus offset. This is in line with prior work demonstrating enduring neural representation after stimulus offset in rapid serial visual presentation sequences (Grootswagers et al., 2019; Mohsenzadeh et al., 2018; Robinson et al., 2019).

In both EEG experiments, participants completed the same passive viewing task (Fig. 4A, C). At both levels of classification, neural data revealed similar information was present over time for the passive trials in both experiments. This similarity indicates that there are unlikely to be major differences in data quality between the two experiments.

3.6. EEG: linear modelling

To investigate how much the conceptual categories of movement and aliveness explained brain activity, we used linear modelling to see which theoretical models best explained patterns of brain activity over time (Fig. 5), in both the passive and categorisation tasks. These linear models

allowed us to assess how movement and aliveness account for the neural data both during task-related classification and passive viewing, once accounting for stimulus naturalness, animacy, low-level features such as colour and rectilinearity.

We also ran a model to predict the passive viewing neural data, to examine whether the same information about movement and aliveness was present without a relevant semantic task. For passive viewing, aliveness explained patterns of neural activity 120 ms after stimulus presentation (Fig. 5A), for a brief period of approximately 50 ms. In contrast, information about movement was present slightly later, from 200 ms for both experiments, and for a longer period of time (Fig. 5C).

During the categorisation task, aliveness explained patterns of neural activity for a very brief period from 120 ms to 150 ms after stimulus onset in Experiment 1 and 130 ms to 160 ms after stimulus onset in Experiment 2 (Fig. 5B). In contrast, movement explained variance in patterns of neural recordings from 180 ms in Experiment 1 and 200 ms in Experiment 2, with a peak at around 230 ms - 240 ms for both experiments, until approximately 320 ms after stimulus onset for Experiment 1 and 500 ms after stimulus onset for Experiment 2 (Fig. 5B). Though both aliveness and movement had a similar time course in both tasks, aliveness seems to have an earlier and less prolonged peak than movement.

3.7. Neural network

To further investigate whether the neural signal more closely resembled higher-order processing or lower-level visual processing, we examined the correlation between neural activity and layers of a neural network modelling the visual system, CORnet (Kubilius et al., 2018, 2019). CORnet includes layers that resemble processing in four visual areas: V1, V2, V4 and Inferotemporal cortex (IT). In both experiments, all four layers were correlated with neural activity from approximately 100–120 ms after stimulus presentation to approximately 180 ms after onset, with a peak at approximately 120–130 ms (Fig. 6). Notably, only the layer resembling IT is significantly correlated with neural activity after approximately 300 ms post-stimulus onset. This extended correlation with the IT layer suggests that the neural activity from around 300 ms is related to higher-order classification, and that the later significance of movement in the linear modelling may be attributed to higher-order categorisation processes.

4. Discussion

In this study, we used electroencephalography (EEG) to investigate the contribution of movement and aliveness in categorisation. Previous work has focused on animacy as a major dimension in visual object processing, but animacy tends to co-occur with movement, raising the question of how much these object features contribute to categorical object processing in the brain. Here, we show that movement is an important organisational principle in the brain. We use naturalistic image stimuli including moving elements of the natural landscape (e.g., waterfall, fire) to show that the brain processes movement associated with non-living kinds as well as movement from living things. EEG data revealed that information about capacity for movement was present in neural signals both during active classification as well as passive viewing of stimuli, after accounting for categorical similarities in colour, shape, naturalness, animacy, and aliveness. The results show that capacity for movement is an important dimension in human visual object perception.

Behavioural results from the categorisation task showed that moving things (waterfalls, clouds, etc.) were more likely to be judged as alive under time pressure, and that elements of the natural landscape tend to be perceived as still. These trends are in line with prior work showing that under time pressure, adults may rely on intuitions about the world (Goldberg and Thompson-Schill, 2009; Kelemen et al., 2013; Shtulman and Harrington, 2016; Shtulman and Valcarcel, 2012; Young and Shtulman, 2018). Our behavioural results build on these

Passive Viewing

Categorisation task
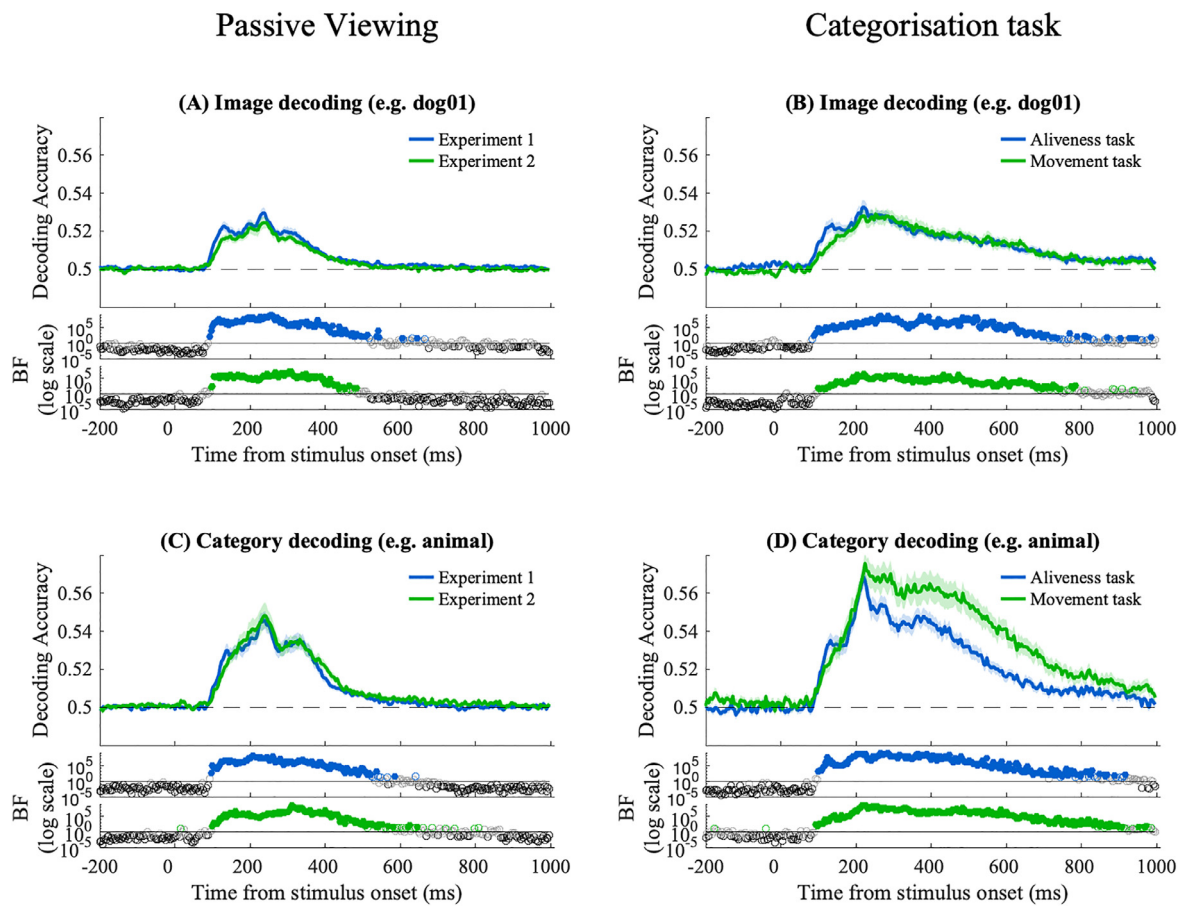
Fig. 4. Decoding stimulus identity. Plots show pairwise decoding accuracy from an LDA classifier over time for image-level (A, B), and category-level (C, D) classification. The dashed line at 0.5 indicates chance decoding, with higher values indicating more discriminability between classes of stimuli. Blue lines show data from Experiment 1 (aliveness task) and green lines show data from Experiment 2 (movement task). Shaded areas indicate standard error across subjects (N = 24 for each experiment). Bayes Factors (BF) above 30 (very strong evidence) are shown in the filled coloured dots, BF between 10 and 30 (strong evidence) are shown as unfilled coloured dots, BF between 1/3 and 10 are shown in grey, and BF below 1/3 (evidence for the null) are shown in black. For passive viewing blocks (A, C) the task was the same across both experiments. For categorisation trials (B, D) participants classified stimuli by aliveness in Experiment 1 (blue) and by capacity for movement in Experiment 2 (green). (For interpretation of the references to color in this figure, the reader is referred to the web version of this article).

prior findings to show that application of scientific intuition in adulthood is not limited to judgements about the accuracy of complex statements about physics and chemistry, or judgement of words that are used in prior work, but also extends to basic judgements of aliveness and to naturalistic pictorial visual stimuli. The presence of these behavioural classification biases under time pressure may reflect that they are adaptive in most situations in both modern times and for our ancestors (New et al., 2007). For example, assuming that moving things are alive allows for rapid reactions even when these assumptions are wrong, such as moving away from an oncoming car. The behavioural results, therefore, suggest that natural movement is uniquely positioned in a spectrum of movement because of its ambiguous causal relationships.

Though here we consider all kinds of movement together, it is clear that moving natural things like fire and waterfalls move in different ways to animals and vehicles. Animate movement differs from inanimate movement, in terms of having a goal-directed trajectory (Gergely et al., 1995), predictability of movement (Pratt et al., 2010), and the speed and angle of directional changes (Tremoulet and Feldman, 2000), amongst other things. Given the evidence of neural processing of goal-directed movement and agency (Thorat et al., 2019) it is possible that difficulties and inconsistencies in classifying movement in the natural landscape (e.g., see pink dots in Fig. 3) occur because there is no obvious agent causing natural movement. This is in contrast to all the other moving stimuli, which can generate spontaneous goal-directed

movement (animals) or move with the intervention of humans (all the moving man-made stimuli were vehicles). Future studies may evaluate whether moving artificial stimuli that move without clear human intervention (e.g., clocks, fireworks) show similar response patterns.

Alternately, these difficulties in classifying the moving natural objects may be due to colloquial implications of the language we used in the instructions. For example, there were four participants in Experiment 1 who consistently responded that plants were not alive. The term 'alive' can colloquially be interpreted to mean 'animate' (Leddon et al., 2009) particularly in childhood, so it is possible that these participants interpreted the instructions as such. Similarly, in Experiment 2, some participants consistently classed the moving natural things as still, potentially because they interpreted 'can move' to refer only to self-generated movement, animate movement, or as movement of an item relative to the environment it is in. However, these same participants also reliably classified vehicles as moving, so it is unclear whether this is a semantic or lexical distinction that is important. Further research is required to fully understand the impact of lexical factors on classification behaviour in the current context.

Our behavioural results suggest movement and aliveness are related in making judgements about stimuli, yet our linear modelling showed that they are processed differently in the brain. Information about movement was present in neural activity around 180–200 ms after stimulus onset, regardless of the task (Fig. 5C, D). Even after accounting for visual

## Passive Viewing

Categorisation task
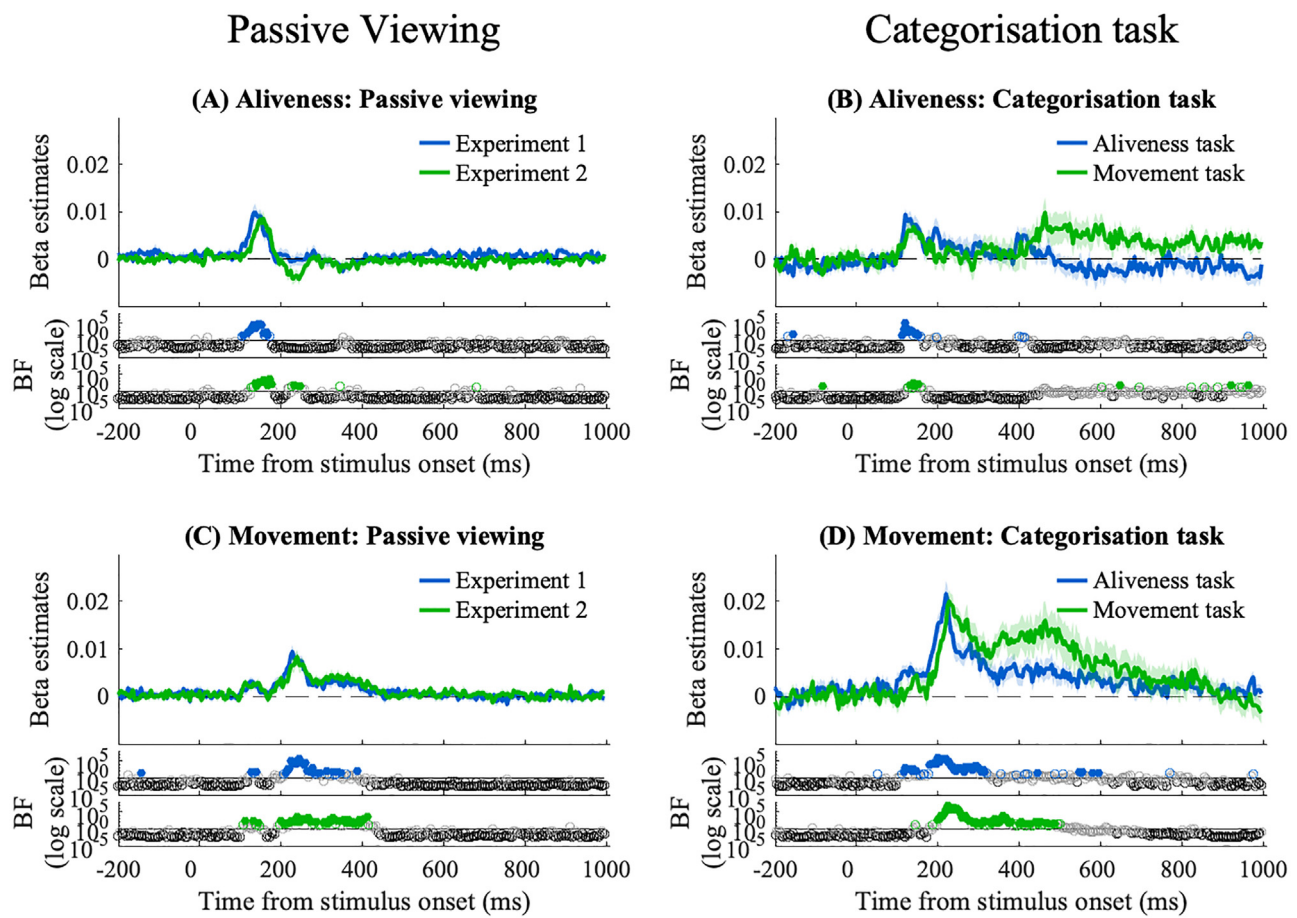
Fig. 5. Aliveness and movement explained a significant proportion of brain activity during categorisation and passive viewing tasks. Plots show beta estimates for aliveness (A, B) and movement (C, D) from linear modelling, which included behavioural (aliveness, movement, naturalness) and image-level (colour, greyscale, rectilinearity) models, as well as a model of animacy. For the categorisation task (right column), the passive viewing RDM from the corresponding time point was also included. Blue lines show data from Experiment 1 (aliveness task) and green lines show data from Experiment 2 (movement task). Shaded regions show standard error across subjects ($N = 24$ for each experiment). Bayes Factors (BF) above 30 (very strong evidence) are shown in the filled coloured dots, BF between 10 and 30 (strong evidence) are shown as unfilled coloured dots, BF between 1/3 and 10 are shown in grey, and BF below 1/3 (evidence for the null) are shown in black.

controls, the movement model still explained a large portion of variance in brain activity, indicating that capacity for movement is an inherent feature of object representations. After an initial peak at approximately 230–240 ms, there was an extended period where movement explained a proportion of the variance in neural activity until around 500 ms after stimulus onset. The combination of an early peak and an enduring significance suggests that this 'movement' factor is capturing some elements of automatic early visual processing, as well as some higher-order cognitive influences in the later period while participants are making a decision on how to classify the stimuli. Similar temporal dynamics are present in the first 300 ms of linear modelling of neural processing during passive viewing (Fig. 5A, C), indicating that visual representations are inherently organised in terms of capacity for movement, even when it is not the focus of the task. It is also possible that these movement representations are driven by animacy differences within the living stimuli. However, when only considering the non-living images (moving and non-moving artefacts and natural things), movement remains decodable within both the passive viewing and the categorisation task, albeit more strongly in the categorisation task (Supplementary Fig. 1). Thus, visual representations appear to be organised in terms of capacity for movement, and these representations of movement may be enhanced when they are task-relevant.

To investigate whether the later periods of significance represent processing in brain areas associated with higher-order abstract object perception (Carlson et al., 2013), we compared the brain data to a

neural network. The correlations between brain activity and CORnet (Kubilius et al., 2018, 2019), a neural network designed to model the visual system, revealed that early neural activity correlated well with all layers (V1, V2, V4 and IT) with a peak at approximately 120–130 ms (Fig. 6). The earlier layers remain significant for a short period of time. In both experiments from approximately 300 ms onwards while participants were classifying the stimuli, patterns of brain activity were most similar to the IT layer, indicating that neural representations in this later time period were likely to be more abstract, higher-order classifications (Carlson et al., 2013). In particular, the movement task of Experiment 2 may engage more higher-order processing than the aliveness task in Experiment 1. The correlation between the IT layer of CORnet and neural activity appears to be sustained longer in the movement task (Fig. 6B) compared to the aliveness task (Fig. 6A), and it seems that movement may explain more variance in neural activity in Experiment 2 compared to Experiment 1 (Fig. 5D). Similarly, object category (e.g., animal, plant) was more separable in the neural responses during the movement task than the aliveness task (Fig. 4D), further suggesting that judgements about movement might inherently involve some higher-level category responses. The combination of these analyses suggests that the 'movement' factor in the current experiment represents some combination of more abstract features at later time points, in addition to some visual similarity at earlier time points between all things that move, such as blurred edges.
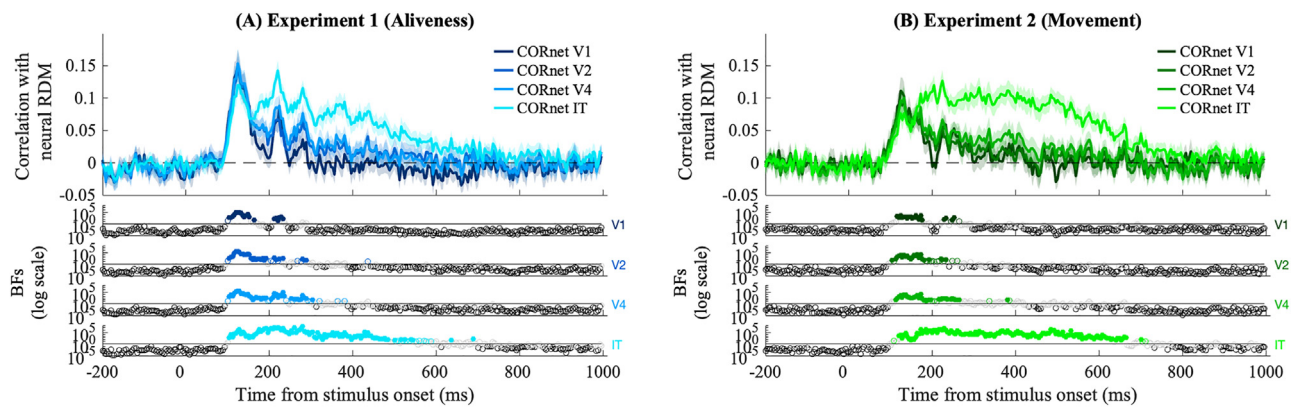
Fig. 6. Correlation between neural activity and layers of CORnet (Kubilius et al., 2018, 2019) representing areas of the visual system, for Experiment 1 (A) and Experiment 2 (B) during the categorisation task. Shaded regions show standard error across subjects (*N* = 24 for each experiment). Bayes Factors (BF) above 30 (very strong evidence) are shown in the filled coloured dots, BF between 10 and 30 (strong evidence) are shown as unfilled coloured dots, BF between 1/3 and 10 are shown in grey, and BF below 1/3 (evidence for the null) are shown in black.

It is notable that even when participants were classifying the images by aliveness, movement still explained variance in neural activity (blue lines in Fig. 5D). This suggests that when judging if something is alive, we may be using the quality and type of the movement to provide clues about aliveness. This would fit with an evolutionary explanation of the current effects; threats to our ancestors were primarily moving animate things, and thus detection and distinction of animals rapidly in the environment may have been advantageous for survival (New et al., 2007). As noted above, it is also the case that the quality and type of movement associated with animates differs from movement in the natural environment. It is possible that these differences in movement contribute to the decision-making about whether something is alive or not. This higher-order processing would fit with the hierarchy proposed in some behavioural and philosophical models of aliveness, which claim that we understand whether something is living based on similarity to a human prototype, from humans, to moving things and plants, and to non-living things (Yorek and Narli, 2009).

A particularly interesting finding was that aliveness only explained patterns of brain activity in a very brief period shortly after stimulus onset. Attention to particular features of a stimulus based on the task can affect neural representations (Harel et al., 2014), and thus we were surprised that aliveness did not account for more variance in brain activity in Experiment 1 when it was the focus of the task. There is little consensus about the degree to which aliveness explains patterns of brain activity in object representations, with some work showing that aliveness is a better correlate of brain activity than animacy (Contini et al., 2020), and others showing that it is important for behaviour but does not explain variance in brain representations (Jozwik et al., 2021). The fit of aliveness models may depend on the choice of stimuli; in Contini and colleagues' (2020) study, robots and toys appeared more animate than inanimate, reducing the fit of the animacy model compared to the aliveness model. In the current study, aliveness may have poor explanatory power in our linear models because the differences between living and non-living stimuli are captured by other variables in the linear models, particularly naturalness which is not evenly distributed across alive and non-alive stimuli, and the low-level visual correlates of aliveness such as rectilinearity (Nasr et al., 2014).

Converging evidence from neuroscience and behaviour has shown that animacy and aliveness are best described as represented on a continuum according to capacity for goal-directed movement (Connolly et al., 2012; Contini et al., 2020; Sha et al., 2014; Thorat et al., 2019; Yorek et al., 2009). In the current study, we show that capacity for movement is an important dimension in human visual object perception, not only for animate movement, but also for inanimate movement in the natural world. Our results support previous work showing that animacy processing in the brain is closely related to the capacity for self-initiated movement and extend this to show that natural movement may be a part of this spectrum. Overall, our results show that capacity for movement is an important dimension in the representation of visual objects in humans.

Data and code availability

Stimuli, analysis scripts, results and anonymised raw EEG data are publicly available at https://doi.org/10.18112/openneuro.ds003885.v1.0.7 (Experiment 1) and https://doi.org/10.18112/openneuro.ds003887.v1.2.2 (Experiment 2). Stimuli, analysis scripts, results and data from the online stimulus validation study are also publicly available at https://osf.io/jxhcs/.

Declaration of Competing Interest

The authors declare no conflicts of interest.

Credit authorship contribution statement

Sophia M. Shatek: Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Project administration. **Amanda K. Robinson:** Methodology, Formal analysis, Writing – review & editing, Supervision, Project administration. **Tijl Grootswagers:** Methodology, Writing – review & editing, Supervision, Project administration. **Thomas A. Carlson:** Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2022.119517.

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