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5 **Capacity for movement is an organisational principle in object representations**
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29 Stimuli, analysis scripts, results and anonymised raw EEG data are publicly available at <https://osf.io/jxhcs/>
30 (online stimulus validation), <https://openneuro.org/datasets/ds003885> (Experiment 1) and
31 <https://openneuro.org/datasets/ds003887> (Experiment 2).
32

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Abstract

49

The ability to perceive moving objects is crucial for threat identification and survival. Recent neuroimaging

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evidence has shown that goal-directed movement is an important element of object processing in the brain.

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However, prior work has primarily used moving stimuli that are also animate, making it difficult to

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disentangle the effect of movement from aliveness or animacy in representational categorisation. In the

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current study, we investigated the relationship between how the brain processes movement and aliveness by

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including stimuli that are alive but still (e.g., plants), and stimuli that are not alive but move (e.g., waves). We

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examined electroencephalographic (EEG) data recorded while participants viewed static images of moving or

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non-moving objects that were either natural or artificial. Participants classified the images according to

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aliveness, or according to capacity for movement. Movement explained significant variance in the neural data

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over and above that of aliveness, showing that capacity for movement is an important dimension in the

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representation of visual objects in humans.

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Keywords: electroencephalography, MVPA, animacy, movement

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70 1. Introduction

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

77 One way of investigating human categorical knowledge is to examine how the brain distinguishes
78 objects in the visual world. The human visual system can automatically categorise stimuli, from low-level
79 visual features, to individual object identity, to increasingly abstract conceptual categories in fractions of a
80 second (Cichy et al., 2014; Contini et al., 2017; Mohsenzadeh et al., 2018; Potter et al., 2014; Potter &
81 Haggmann, 2015; Robinson et al., 2019). Categorical distinctions such as animacy are rapidly and
82 subconsciously processed by the brain (Carlson et al., 2013; Cichy et al., 2014; Connolly et al., 2012; Contini
83 et al., 2017; Grootswagers et al., 2018; Konkle & Caramazza, 2013; Ritchie et al., 2015). The representations
84 of higher-order categorical distinctions like animacy have been localised to the inferotemporal cortex (Haxby
85 et al., 2001; Kriegeskorte et al., 2008), and is observable from patterns of brain activity from approximately
86 100-160ms after stimulus onset (Contini et al., 2020; Goddard et al., 2016; Grootswagers, Robinson, &
87 Carlson, 2019; Grootswagers et al., 2021). In addition to higher-order conceptual processing, some of this
88 separation can be explained by differences in low and mid-level visual features between animate and
89 inanimate stimuli (Grootswagers, Robinson, Shatek, et al., 2019; Long et al., 2018; Wang et al., 2022). Even
90 at rapid presentation rates, and when subjects are completing an unrelated task, animate stimuli are
91 distinguishable from inanimate stimuli in patterns of EEG recordings (Grootswagers et al., 2021). This
92 automatic identification of animacy has also been shown behaviourally in children as young as 7 months old
93 (Träuble et al., 2014), leading to suggestions that learning about animacy early in development is
94 evolutionarily adaptive (Aslan & John, 2016). Neuroscience research has supported this idea, demonstrating
95 that both the adult brain (Bao et al., 2020; Konkle & Caramazza, 2013; Kriegeskorte et al., 2008) and the
96 infant brain (Bayet et al., 2020; Deen et al., 2017) represents whether something is animate as part of core
97 visual processing (DiCarlo et al., 2012).

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98 However, more recent research has shown that the structure of object representations in the brain is
99 more complex than a simple animate/inanimate dichotomy and may be influenced by an object's ability to
100 move independently. Recent neuroimaging work has shown that movement and agency are important in
101 animacy judgements, and visual stimuli may be better represented in the brain as a spectrum, according to
102 their similarity to humans (Contini et al., 2020) or their capacity for agency and goal-directed movement
103 (Connolly et al., 2012; Grootswagers et al., 2022; Jozwik et al., 2021; Sha et al., 2014; Thorat et al., 2019).
104 These findings suggest that motion, particularly animate motion, is an important property of object processing
105 in the brain. Areas active when perceiving motion are also active when viewing a still photograph taken mid-
106 motion, also known as implied motion (Kourtzi & Kanwisher, 2000). Studies of implied motion have shown
107 that the speed of implied motion has differential effects on brain activity based on the category of the object
108 being shown, suggesting that movement is an important factor in category distinctions (Lu et al., 2015).
109 Collectively these findings suggest that the brain represents both movement and aliveness.

110 Behavioural work further demonstrates how movement and aliveness are used to categorise objects.
111 Theoretical models of life status, such as the animistic-anthropocentric construction model (Yorek & Narli,
112 2009), suggest that our conception of what is alive is shaped by similarity to humans, particularly in terms of
113 the overlapping concept of motion, with animals most similar to humans, then plants and then other non-living
114 things. Most things that are alive can move, yet movement and aliveness are not the same: not all moving
115 objects are alive (e.g., cars, clouds), and not all objects that are alive move on a time scale that humans can see
116 (e.g., plants). The co-occurrence of movement and aliveness is so common that it is often a cause for
117 classification error. For example, adults often mistake natural moving things (e.g., waves) for being alive
118 when under time pressure to make a decision (Goldberg & Thompson-Schill, 2009). This co-occurrence
119 makes it difficult to interpret prior neuroimaging literature on how the brain might represent movement, given
120 it is so often confounded by aliveness. Is movement a relevant characteristic of an object for the brain to
121 process, and if so, is this solely because it most commonly co-occurs with animacy? Investigating these cases
122 that violate the intuitive association between aliveness and movement can provide insight into how these
123 characteristics are coded by the brain.

124 In the current study, we investigated the relationship between movement and aliveness in neural
125 categorisation by taking advantage of unusual cases of natural movement that are often misclassified by
126 children, and adults under time pressure. We used naturalistic static image stimuli, including typical animate

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127 and inanimate stimuli as in prior research, and also included natural moving objects (e.g., waves, fire) and
128 plants (e.g., trees, vines). These natural stimuli that violate the association between movement and aliveness
129 (i.e., they are moving but not alive, or alive but not moving) allow us to investigate how movement and
130 aliveness are processed in the brain. We first ran an online study to clarify behavioural classifications of the
131 stimuli. In two experiments, we gathered electroencephalography (EEG) data obtained while participants
132 classified images according to whether they were alive or not (Experiment 1), or whether they could move or
133 not (Experiment 2). Using multi-variate pattern analysis techniques, we examined similarities and differences
134 in the temporal dynamics of visual processing and decision-making based on a stimulus' capacity for
135 movement, and whether it is alive or not. These methods were used to examine if, and when, movement
136 (including natural, non-agentive movement such as from fire, or waterfalls) is represented in the brain, and
137 whether this is dependent on the categorisation task being completed. We find that capacity for movement
138 explains significant variance in the EEG data, even after controlling for low-level visual factors and aliveness.
139 The findings suggest that movement is an important organisational principle for object representation in the
140 brain.

141

142 **2. Methods**

143 This section reports two EEG studies (Experiments 1 and 2) with very similar methodology. Stimuli, analysis
144 scripts, results and anonymised raw EEG data are publicly available at
145 <https://doi.10.18112/openneuro.ds003855.v1.0.0> (Experiment 1) and
146 <https://doi.10.18112/openneuro.ds003857.v1.0.0> (Experiment 2). Stimuli, analysis scripts, results and data
147 from the online stimulus validation study are also publicly available at <https://osf.io/jxhcs/>.

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

156

157 2.1 Participants

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

167

168 2.2 Apparatus

169 Images were shown in the centre of a 1920x1080 pixel Asus gaming monitor with a refresh rate of 60Hz.
170 Participants responded using the two outermost buttons on a four-button button box produced by The Black
171 Box ToolKit Ltd (layout as shown in Figure 2C, 1D). They were seated 55cm away from the screen and
172 stimuli subtended approximately 5° of visual angle. EEG was recorded at 1000Hz on a 128 channel
173 BrainVision ActiCap system (Brain Products GmbH), with electrodes located in positions consistent with the
174 10-5 extension of the 10-20 system (Oostenveld & Praamstra, 2001). Data were recorded with an online
175 reference of FCz.

176

177 2.3 Stimuli

178 Stimuli were 400 realistic colour images collected from free online image databases (www.pixabay.com,
179 www.pexels.com) under Creative Commons 0 licenses, and were used in all studies. All text in images (e.g.
180 brand names on cars) was blurred manually using GIMP (v2.10.14, 2020), then each image was cropped and
181 resized to 256 by 256 pixels. Stimuli were gathered in six categories based on those in Goldberg &
182 Thompson-Schill (2009): animals, plants, still artificial things, still natural things, moving artificial things, and
183 moving natural things (shown in Figure 1A). For animals (bee, cat, dog, dolphin, eagle, horse, lemur, pigeon,
184 tiger, whale) and plants (cactus, clover, fern, flower, grass, lemon tree, moss, palm tree, tree, vine), there were

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185 10 objects. For all other categories, still artificial things (bench, clothes peg, headphones, lock, mug), still
186 natural things (cliff, crystal, rock, sand, shell), moving artificial things (boat, bus, car, helicopter, train), and
187 moving natural things (fire, hot spring, river, waterfall, waves), there were five objects. The extra plant and
188 animal categories were included to ensure there was an equal number of images that were alive and not alive,
189 as well as equal numbers of moving and still images. Within each category (e.g., cat, bench), there were 10
190 different images (e.g., cat1, cat2, ... cat10). There were 400 images in total, each classified according to
191 aliveness (200 living and 200 non-living), movement (200 moving and 200 still), and naturalness (300 natural
192 and 100 artificial). For objects that are able to move, the stimulus was shown in motion in the image (e.g.,
193 birds and helicopters shown flying, see Figure 2A), though all stimuli were static images.

194

195 **2.4 Stimulus validation and model generation**

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

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

210 To ensure we were only using data where participants were completing the task properly, we removed
211 seven subjects whose overall accuracy (based on expected classification) was less than 50%. We also removed
212 15 participants who responded in less than 100ms on more than 25% of images, as participants are unlikely to
213 be making valid responses in such a short time period. These exclusion rates are within the range expected

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214 from online samples (Thomas & Clifford, 2017). After these exclusions, there were 42 participants who
215 classified by aliveness, 48 participants who classified by movement capacity, and 38 participants who
216 classified by naturalness. For these included participants, any trial that had a reaction time more than 3
217 standard deviations longer than the mean of all trials pooled across all participants (on average, less than one
218 trial per participant) or less than 100ms (on average, less than one trial per participant) was also removed.

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

226

227 *2.5 EEG Experiment procedure*

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

230

231 *2.51 Categorisation task.*

232 To see how focusing on aliveness and movement affected neural processing, participants completed a
233 categorisation task (Figure 1D). Each trial consisted of a fixation cross for a random duration between 500ms
234 and 1000ms, followed by an image in the centre of the screen for 100ms. Participants had 1000ms from
235 stimulus offset to respond on the button box. For Experiment 1, participants decided whether the image was
236 alive or not alive. For Experiment 2, participants decided whether the stimulus could move or not. The
237 response mapping changed over each block, such that the side of the button corresponding to 'alive' or 'able
238 to move' switched between left and right every block, and the order of the mapping was counterbalanced
239 across participants. When a participant responded, the fixation spot filled in to indicate that a response had
240 been recorded (Figure 1D). If there was no response in this time, the screen displayed "Too late!", and
241 advanced to the next trial. For each of the four categorisation blocks, trials (single image presentation and
242 response, as described above) were chunked into 10 sequences. One sequence contained 40 trials, so that each

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243 sequence contained one image from each category (e.g., one dog, one fire). Thus, across the 10 sequences in
244 each block, all 400 images were shown. Each sequence lasted approximately 1-2 minutes, and participants
245 were told to take a break between sequences and advance at their own pace.

246

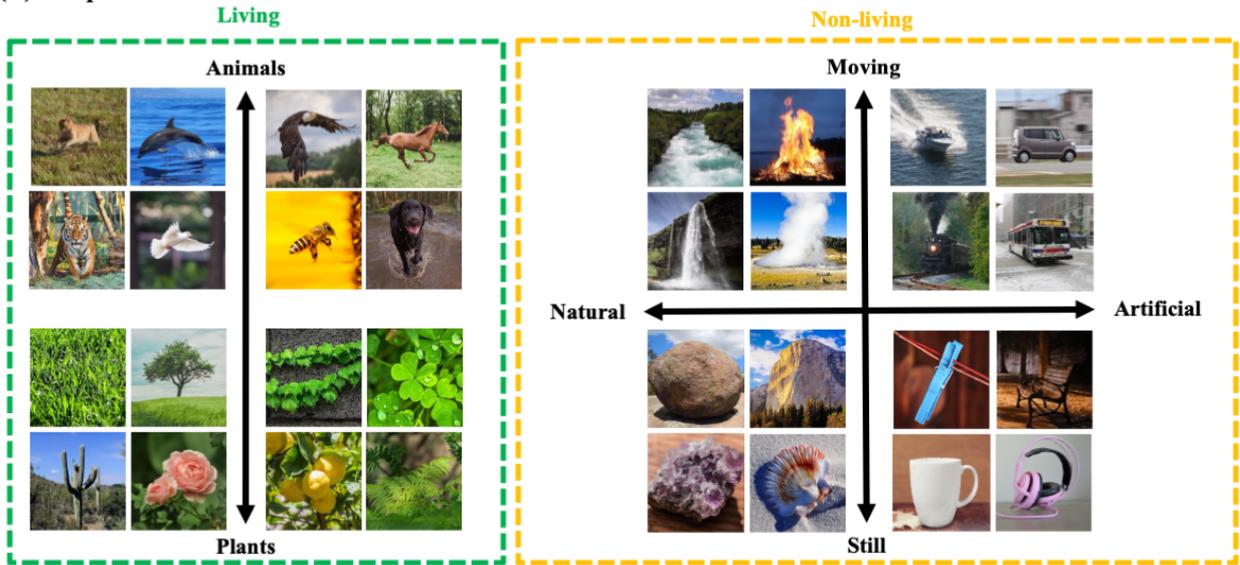
247 *2.52 Passive viewing task.*

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

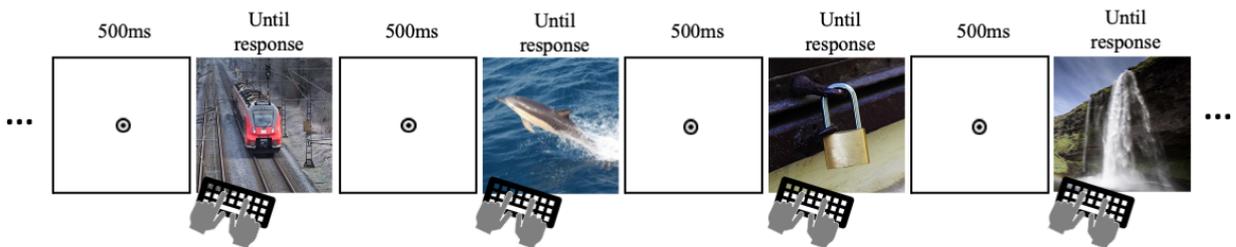
253 In each of the four passive viewing blocks, participants were shown three repetitions of each image
254 during passive viewing sequences, equating to 12 total repetitions of each stimulus across the experiment.
255 These were split into 15 short sequences of 80 images each (~12 seconds each), to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

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

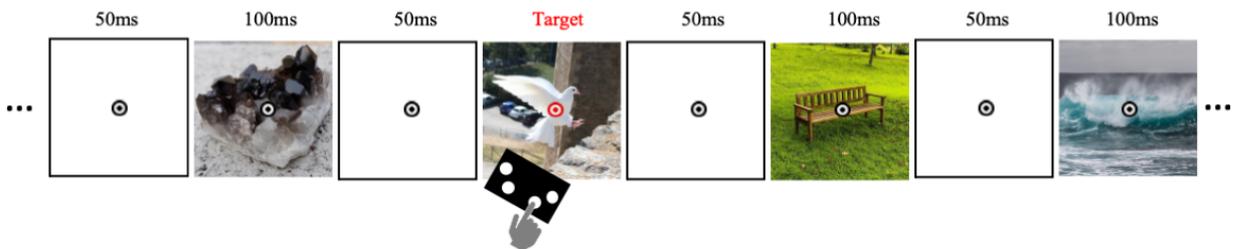
(A) Sample stimuli



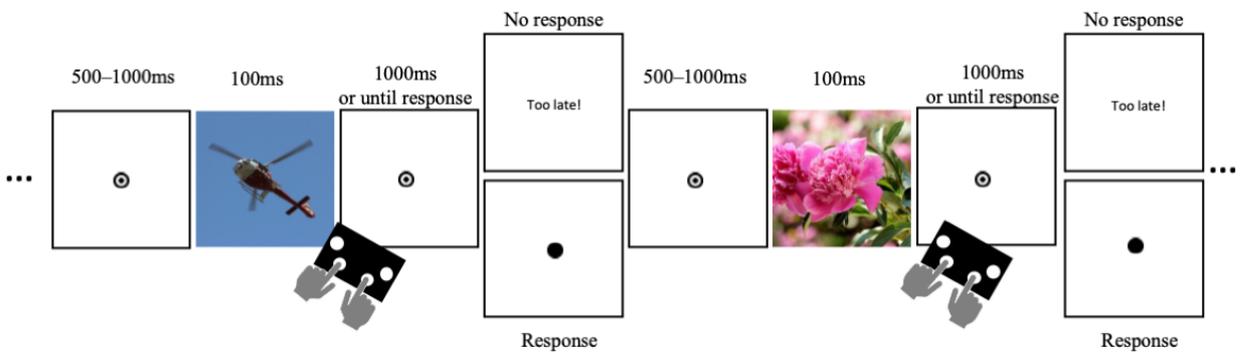
(B) Online stimulus validation (alive/not alive, moves/still, natural/artificial)



(C) Experiments 1 and 2: EEG (passive viewing)



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



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Figure 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.

267

268 *2.6 EEG Data Analysis*

269 *2.61 EEG preprocessing.*

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

276

277 *2.62 Decoding image category.*

278 To investigate how the different object categories are represented in the brain, we used multivariate decoding
279 applied to the EEG data in response to each image. All decoding analyses were run in MATLAB using
280 functions from the CoSMoMvpa toolbox (Oosterhof et al., 2016), using all 128 channels from each
281 participant. To test if individual images (e.g., tree1, cat1) and categories (e.g., plant, animal) were
282 distinguishable from the EEG recording, we conducted pairwise decoding analyses. All analyses were
283 conducted timepoint by timepoint relative to when each image was displayed. At the individual image level
284 (e.g., tree1, cat1), we trained a Linear Discriminant Analysis (LDA) classifier on each pair of images from all
285 but one block and tested on those same images from the left-out block. This was repeated over all pairs of
286 images, for each block as the test data. Separate analyses were conducted for categorisation and passive
287 viewing. At the category level (e.g., plant, animal), we conducted a similar pairwise analysis still leaving two
288 images out to test on, but also excluded these two images from the training set. For example, to compare
289 plants and animals, a classifier was trained on blocks 1-3 using all plants and animals except a pair of images

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290 (e.g., tree1 and cat1), and then tested on these left-out images (tree1, cat1) from remaining block (block 4).

291 This process was repeated so each pair of images was left out in each block.

292

293 *2.63 Representational Similarity Analysis.*

294 To investigate how movement and aliveness are represented in the brain, we used Representational Similarity
295 Analysis (RSA) to relate neural activity to behavioural responses as well as lower-level visual features that
296 might differ across categories (Kriegeskorte et al., 2008). Behavioural Representational Dissimilarity Matrices
297 (RDMs) were calculated for aliveness, movement and naturalness based on the online stimulus validation
298 study, and low-level visual models were calculated for colour, rectilinearity and patterns of shadow using a
299 greyscale model. For the colour model, each pixel of each image was allocated values within CIELab colour
300 space, and these values were averaged over all images in a category to form a single vector of values for each
301 category. The Euclidean distance between categories could then be calculated. For the greyscale model, each
302 pixel of each image was converted to a single greyscale value. These values were averaged over all images in
303 a category, and the Euclidean distance between categories was calculated to form the 40 x 40 RDM. To
304 control for rectilinear differences in animacy, we also included a measure of rectilinearity from Nasr et al.
305 (2014), calculated using publicly available code from [https://github.com/cechava/Rectilinearity_Toolbox]. As
306 with the colour and greyscale measures, we calculated the amount of rectilinearity in of each image, then
307 averaged across each category. We then calculated the Euclidean distance between each category to form a
308 model of rectilinearity.

309 To calculate RDMs for the neural data, we used an LDA classifier at every time point to compute
310 decoding accuracy for each pair of categories (e.g., cats vs rocks), resulting in a 40x40 neural dissimilarity
311 matrix for each time point. This classifier used the same partitioning structure as category decoding above, in
312 which each pair of images was left out as the testing set for each block and for each pair of categories.

313 Separate neural RDMs were created for passive viewing and categorisation trials.

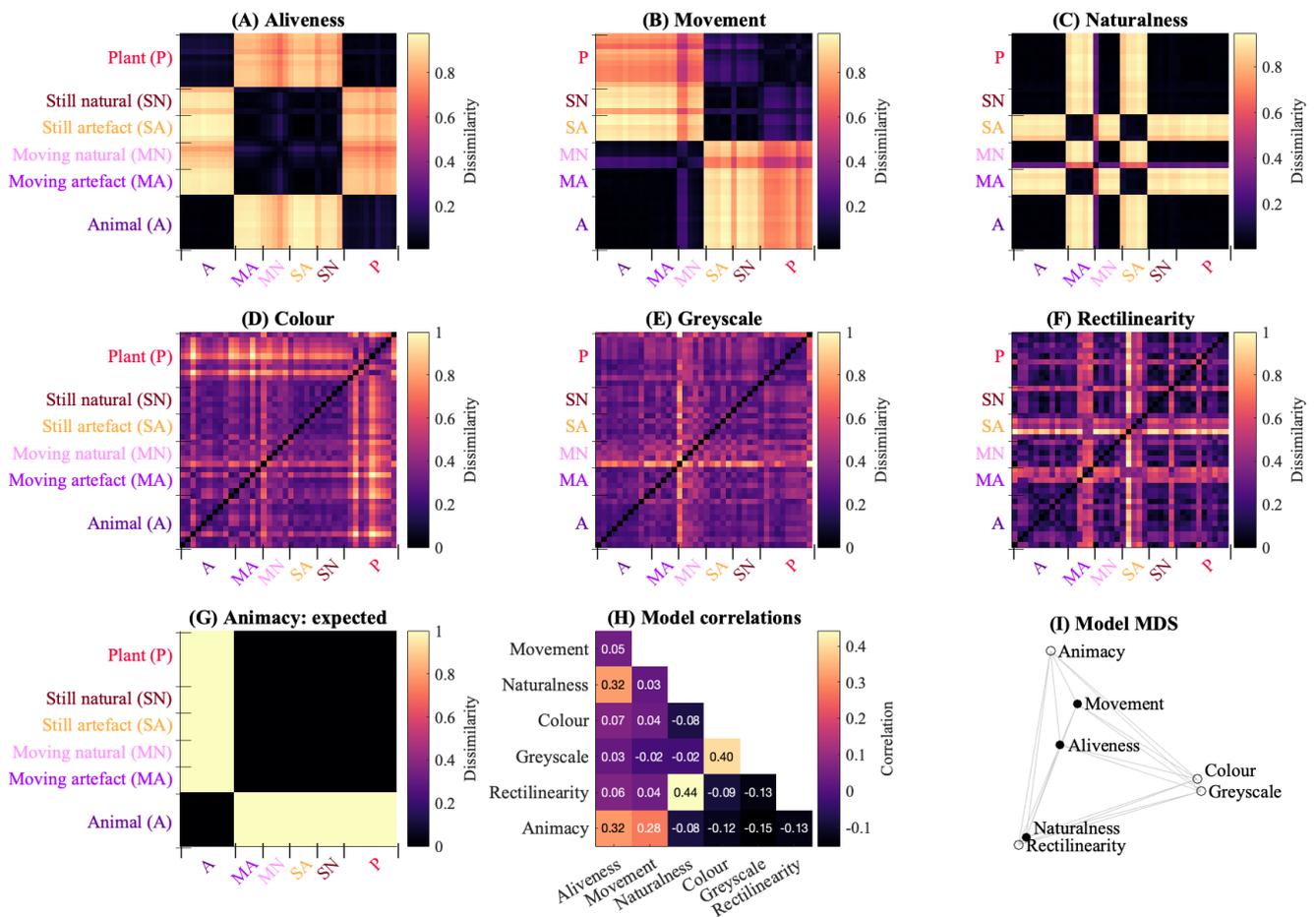


Figure 1. Representational dissimilarity matrices (RDMs) generated from behavioural ratings of stimuli and image-level analysis of stimuli. Areas that are more purple indicate low dissimilarity (more similar). Areas that are more orange indicate high dissimilarity (less similar). Each category (e.g., 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 veridical/ 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 Artefact (MA), and animals (A).

315

316

317 **2.64 Linear modelling.**

318 To investigate how categories of aliveness and movement account for neural responses to objects, we ran a
 319 series of general linear models to see which characteristics best explained the neural processes in the
 320 categorisation tasks over time. Eight predictor variables were included: aliveness, naturalness, movement,
 321 colour, greyscale, rectilinearity, animacy, and stimulus-driven neural responses from the passive viewing

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322 trials. Seven of these models (all except the passive viewing trials) are shown in Figure 2. These same eight
323 predictor variables were used to run separate linear models for each time point, with outcome variable as the
324 neural RDM of the categorisation task at that time point.

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

335 To ensure that multicollinearity was sufficiently low to interpret the output of the model, we
336 calculated the variance inflation factors for each model based on a downloaded MATLAB function (Vasilaky,
337 2021). A measure of multicollinearity, the variance inflation factor indicates the impact on the variance of the
338 model of adding a particular variable, compared to if it were independent to all the other variables
339 (Montgomery et al., 2012). A variance inflation factor of one would indicate that the variable is independent
340 from the other elements in the model, with factors close to one indicating fewer potential issues with
341 multicollinearity and higher factors indicating more higher multicollinearity (Thompson et al., 2017). The
342 variance inflation factors for all variables were low (ranging from 1.01 for movement to 1.40 for naturalness),
343 indicating low multicollinearity between the models.

344

345 *2.65 Neural network*

346 To investigate whether the characteristics associated with movement are associated with lower-level visual
347 processing, or more abstract categorical processing, we compared neural data to different layers of a neural
348 network. CORnet (Kubilius et al., 2018, 2019) is a deep neural convolutional network designed as a model for
349 the visual system, where each convolutional layer represents a different area of the visual system. Feature
350 weights for each image were extracted from the layers representing V1, V2, V4 and Inferotemporal cortex

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351 (IT). The distance between the feature weights for each image was calculated to form a 400 x 400 RDM,
352 which was then averaged to 40 x 40 so it was the same size as the neural RDMs. This process was repeated
353 over each brain region (layer). To examine which layer of CORnet most closely resembled neural activity
354 over time, we examined the correlation between each layer and the neural data for each time point.

355

356 *2.7 Statistical analysis*

357 We used Bayesian inference to examine differences in accuracy and reaction time across stimulus categories.
358 For all comparisons, we used the BayesFactor package in R (Morey et al., 2018). Following recommendations
359 in Teichmann et al. (2021), we used a JZS prior (Rouder et al., 2009) with a scale factor of 0.707. This is the
360 default prior and scaling in the BayesFactor package because it makes minimal assumptions about the
361 expected effect size, and serves as a “non-informative default” (Rouder et al., 2009, p. 232).

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

370 For decoding analyses, we used a series of t-tests using the `ttestBF` function (Morey et al., 2018) from
371 the BayesFactor package with the parameters described above. The alternate hypothesis is that the decoding is
372 above chance (50%), and the null-interval was effect sizes from negative infinity up to 0.5, as effect sizes
373 during baseline periods prior to stimulus onset from previous work have shown this to be most appropriate
374 (Teichmann et al., 2021). This formed a one-sided hypothesis that the effect size for alternate hypothesis
375 should be positive. For linear modelling, in which both negative and positive results are meaningful, we used
376 the same procedure with the alternative hypothesis that the betas are different to zero, with a two-sided prior
377 from -0.5 to 0.5.

378 Bayes Factors are interpreted according to Jeffreys (1961/1998), where Bayes Factors larger than 30
379 are very strong evidence for the alternate hypothesis, Bayes Factors larger than 10 are strong evidence for the

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380 alternate hypothesis, Bayes Factors larger than 3 provide some evidence for the alternate hypothesis, and
381 Bayes Factors smaller than 1/3 provide evidence for the null hypothesis.

382

383 **3. Results**

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

387

388 ***3.1 Behavioural: Passive viewing***

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

394

395 ***3.2 Behavioural: Categorisation task***

396 To examine the relationship between movement and aliveness in categorisation of naturalistic image stimuli,
397 we used behavioural metrics (reaction time, classification accuracy) and multivariate pattern analysis of neural
398 data. The median reaction time for Experiment 1 was 457ms (SE = 10.7ms, range of participant means 322ms
399 – 561ms), and for Experiment 2 was 456ms (SE = 11.53ms, range of participant means 373ms – 588ms).

400 Participants showed high accuracy in classifying the stimuli, with few trials (on average, ~16 of 1600 trials
401 per participant) that timed out without a response (misses). In Experiment 1, the mean percentage of correct
402 responses was 87.42% (SE = 1.4152%, range 69.75% - 97.5%), with an average of 1.10% misses (SE = 0.26,
403 range 0.13% - 5.94%). For Experiment 2, there were 82.97% (SE = 1.64%, range 61.67% - 94.42%) correct
404 responses, on average, with 0.97% misses (SE = 0.18, range 0.19% - 3.00%). Though some participants had
405 low ‘accuracy’ scores, these always arose from consistent classification in the opposite direction from what
406 was predicted (e.g., consistently responding that plants were not alive in Experiment 1, or consistently
407 responding that moving natural stimuli did not move in Experiment 2).

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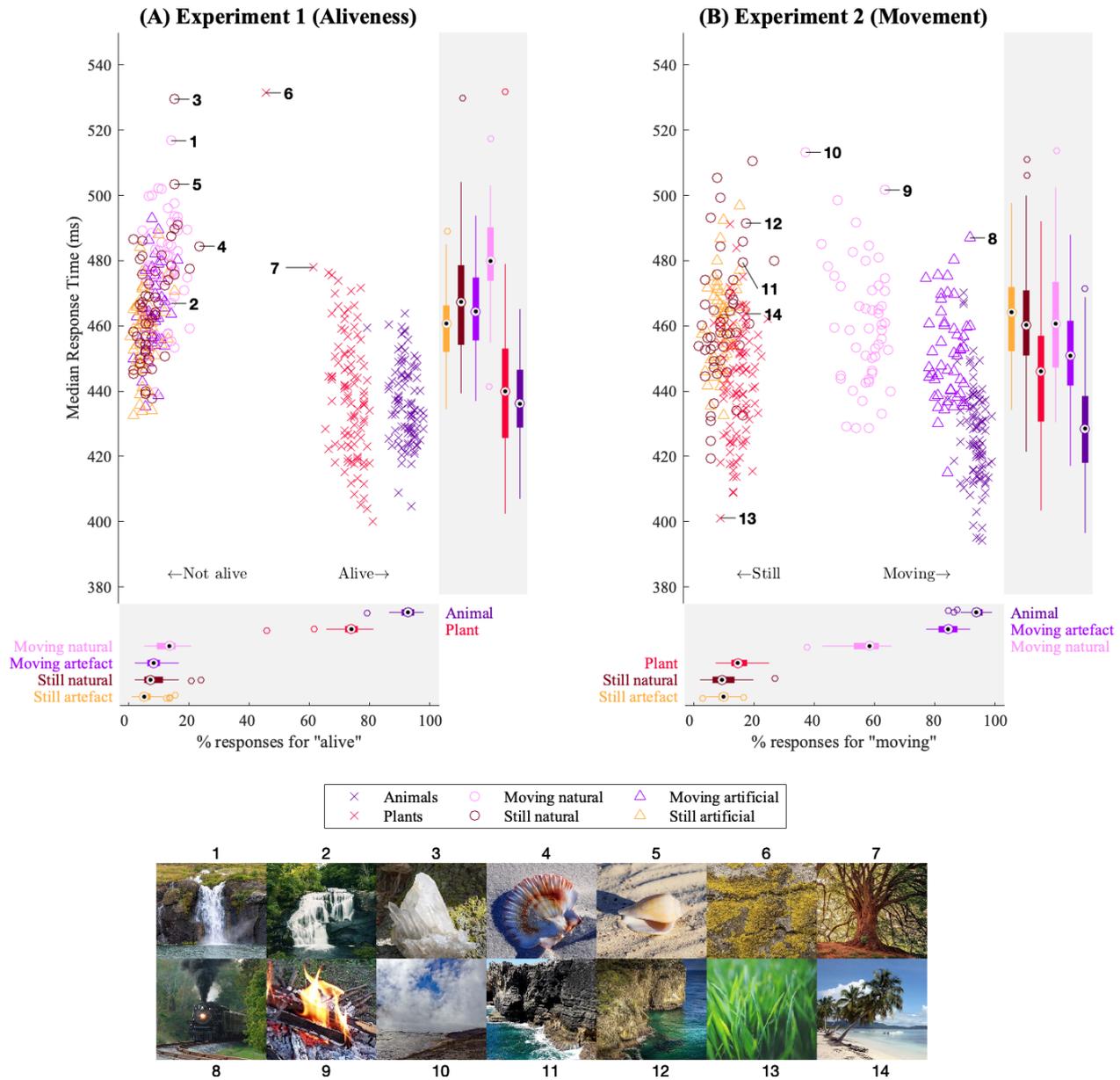


Figure 3. Median response times and classifications of stimuli from EEG Experiments 1 and 2. Data from participants considering whether the stimulus was alive or not is shown in (A) and data from classifying images by capacity for movement are shown in (B). Sample images below correspond to the labelled data points, showing a selection of responses.

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413 **3.3 Behavioural: Experiment 1**

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We were interested in how image category influenced how participants categorised images according to whether they were alive or not in Experiment 1. 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

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417 plants (Yorek et al., 2009). Bayesian t-tests were used to evaluate whether there were differences in reaction
418 time and classification between plants and animals. There was very weak evidence for differences in reaction
419 time between plants and animals in the aliveness task of Experiment 1 ($BF = 1.09$) and some evidence that
420 responses to animals were faster than plants in the movement task of Experiment 2 ($BF = 3.17$). However,
421 there was strong evidence that plants were classified as “not alive” more often than animals ($BF = 16.66$),
422 suggesting that plants are considered ‘less alive’ than animals as predicted by behavioural models of aliveness
423 (Yorek & Narli, 2009).

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

432

433 *3.4 Behavioural: Experiment 2*

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

446

447 **3.5 Decoding image category**

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

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

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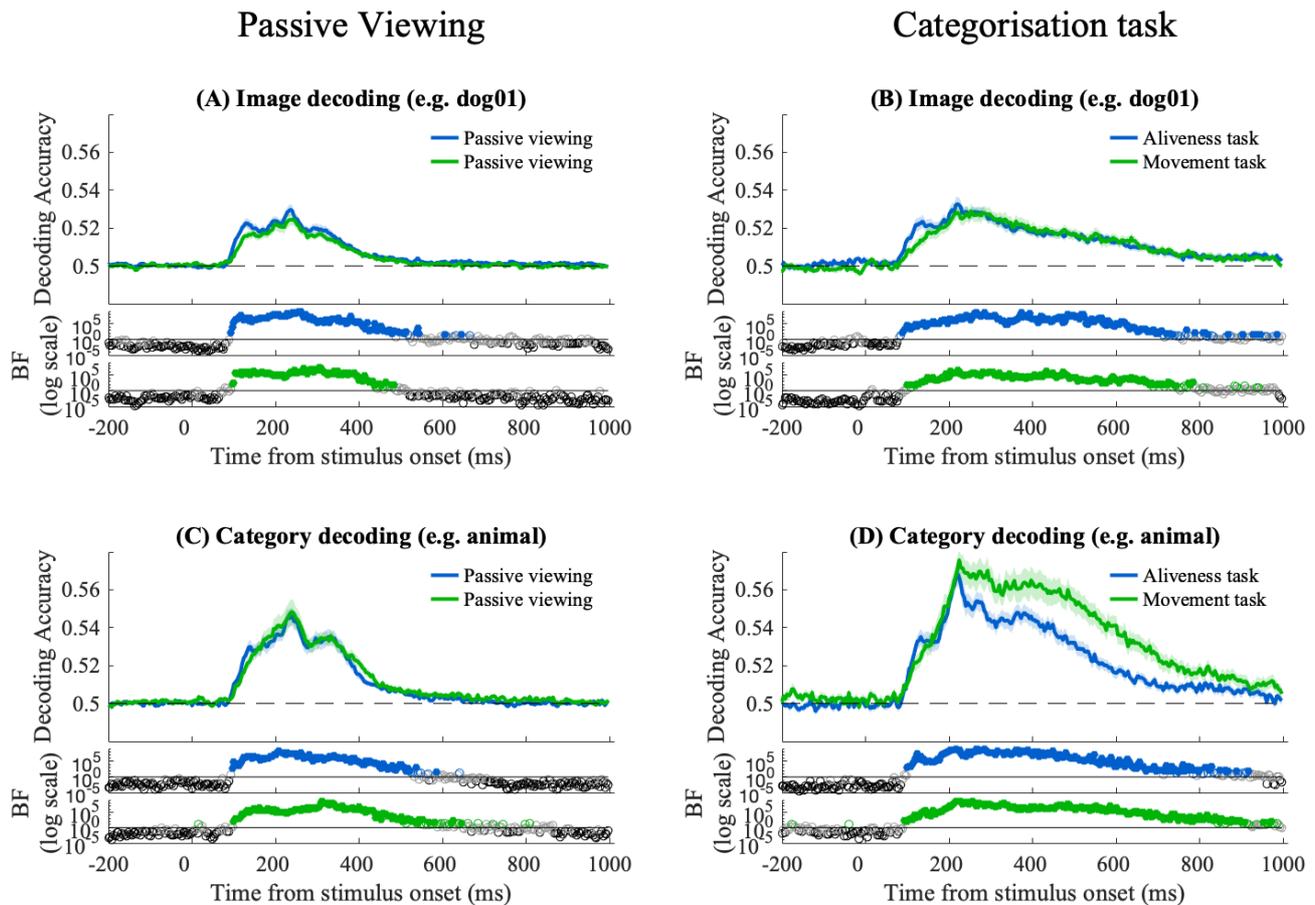


Figure 4. Decoding stimulus identity. Plots show pairwise decoding accuracy from an LDA classifier over time for image-level (A, B), and category-level (C,D) classification. The dashed line at 0.5 indicates chance decoding, with higher values indicating more discriminability between classes of stimuli. 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).

481

482 **3.5 EEG: Linear modelling**

483 To investigate how much the conceptual categories of movement and aliveness explained brain activity while

484 classifying object stimuli, we used a linear model to see which theoretical models best explained patterns of

485 brain activity over time (Figure 5). This linear model allowed us to assess how movement and aliveness

486 account for the neural data specifically during task-related classification, once accounting for stimulus

487 naturalness, animacy, low-level features such as colour and rectilinearity, as well as basic stimulus-driven

488 neural processes (as measured in the passive viewing trials).

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489 During categorisation tasks, aliveness explained patterns of neural activity for a very brief period from
490 120ms to 150ms after stimulus onset in Experiment 1 and 130ms to 160ms after stimulus onset in Experiment
491 2 (Figure 5A). In contrast, movement explained variance in patterns of neural recordings from 180ms in
492 Experiment 1 and 200ms in Experiment 2, with a peak at around 230ms - 240ms for both experiments, until
493 approximately 320ms after stimulus onset for Experiment 1 and 500ms after stimulus onset for Experiment 2
494 (Figure 5B). Though both aliveness and movement had a similar time course in both tasks, aliveness seems to
495 have an earlier and less prolonged peak than movement.

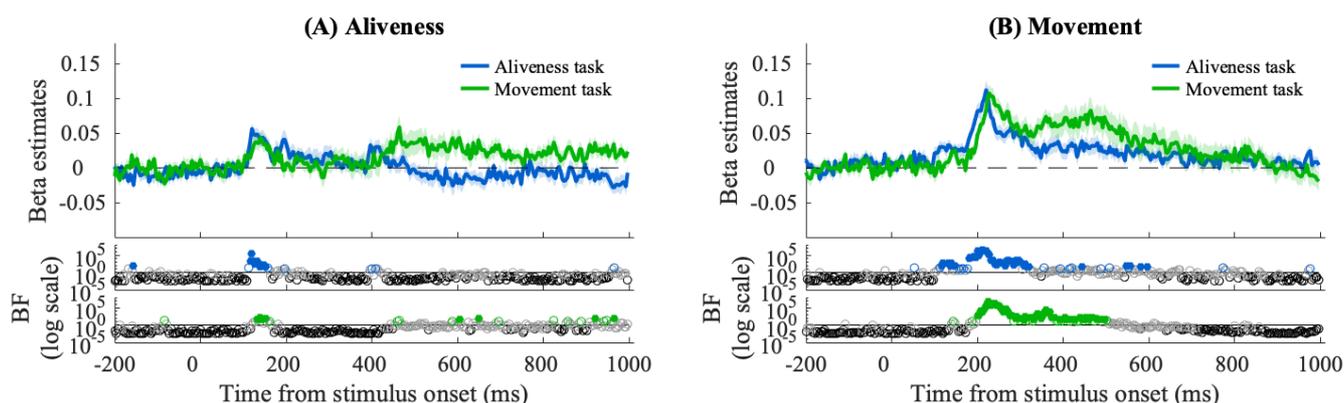


Figure 5. Aliveness and movement explained a significant proportion of brain activity during categorisation tasks. Plots show beta estimates for aliveness (A) and movement (B) from a linear model, which included behavioural (aliveness, movement, naturalness) and image-level (colour, greyscale, rectilinearity) models, as well as a model of animacy and the passive viewing RDM from the corresponding time point. 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.

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497 3.6 Neural Network

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

506 higher-order classification, and that the later significance of movement in the linear modelling may be
 507 attributed to higher-order categorisation processes.

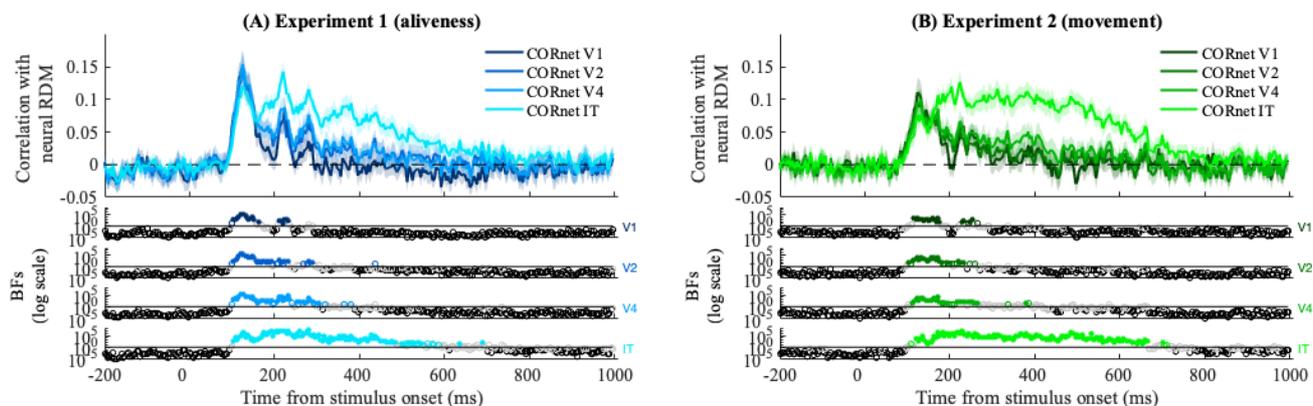


Figure 6. Correlation between neural activity and layers of CORnet (Kubilius et al., 2018, 2019) representing areas of the visual system, for Experiment 1 (A) and Experiment 2 (B) during the categorisation task. Shaded regions show standard error across subjects (N=24 for each experiment). Bayes Factors (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.

508

509 4. Discussion

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

520 Behavioural results from the categorisation task showed that moving things (waterfall, cloud, etc)
 521 were more likely to be judged as alive under time pressure, and that elements of the natural landscape tend to
 522 be perceived as still. These trends are in line with prior work showing that under time pressure, adults may
 523 rely on intuitions about the world (Goldberg & Thompson-Schill, 2009; Kelemen et al., 2013; Shtulman &

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524 Harrington, 2016; Shtulman & Valcarcel, 2012; Young & Shtulman, 2018). Our behavioural results build on
525 these prior findings to show that application of scientific intuition in adulthood is not limited to the complex
526 judgements about the accuracy of complex statements about physics and chemistry or judgement of words that
527 are used in prior work, but also extends to basic judgements of aliveness and to naturalistic pictorial visual
528 stimuli. The presence of these behavioural classification biases under time pressure may reflect that they are
529 adaptive in most situations in both modern times and for our ancestors (New et al., 2007). For example,
530 assuming that moving things are alive allows for rapid reactions even when these assumptions are wrong, such
531 as moving away from an oncoming car. The behavioural results, therefore, suggest that natural movement is
532 uniquely positioned in a spectrum of movement because of its ambiguous causal relationships.

533 Though here we consider all kinds of movement together, it is clear that moving natural things like
534 fire and waterfalls move in different ways to animals and vehicles. Animate movement differs from inanimate
535 movement, in terms of having a goal-directed trajectory (Gergely et al., 1995), predictability of movement
536 (Pratt et al., 2010) the speed and angle of directional changes (Tremoulet & Feldman, 2000), among other
537 things. Given the evidence of neural processing of goal-directed movement and agency (Thorat et al., 2019) it
538 is possible that difficulties and inconsistencies in classifying movement in the natural landscape (e.g., see pink
539 dots in Figure 3) occur because there is no obvious agent causing natural movement. This is in contrast to all
540 the other moving stimuli, which can generate spontaneous goal-directed movement (animals) or move with
541 the intervention of humans (all the moving man-made stimuli were vehicles). Future studies may evaluate
542 whether moving artificial stimuli that move without clear human intervention (e.g., clocks, fireworks) show
543 similar response patterns.

544 Alternately, these difficulties in classifying the moving natural objects may be due to colloquial
545 implications of the language we used in the instructions. For example, there were four participants in
546 Experiment 1 who consistently responded that plants were not alive. The term ‘alive’ can colloquially be
547 interpreted to mean ‘animate’ (Leddon et al., 2009) particularly in childhood, so it is possible that these
548 participants interpreted the instructions as such. Similarly, in Experiment 2, some participants consistently
549 classed the moving natural things as still, potentially because they interpreted ‘can move’ to refer only to self-
550 generated movement, animate movement, or as movement of an item relative to the environment it is in.
551 However, these same participants also reliably classified vehicles as moving, so it is unclear whether this is a

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552 semantic or lexical distinction that is important. Further research is required to fully understand the impact of
553 lexical factors on classification behaviour in the current context.

554 Our behavioural results suggest movement and aliveness are related in making judgements about
555 stimuli, yet our linear modelling showed that they are processed differently in the brain. Information about
556 movement was present in neural activity around 180-200ms after stimulus onset, regardless of the task (Figure
557 5B). Even after accounting for stringent visual controls, the movement model still explained a large portion of
558 variance in brain activity, indicating that capacity for movement is an inherent feature of object
559 representations, not just for animate stimuli but also for inanimate stimuli. After an initial peak at
560 approximately 230-240ms, there was an extended period where movement explained a proportion of the
561 variance in neural activity until around 500ms after stimulus onset. The combination of an early peak and an
562 enduring significance suggests that this ‘movement’ factor is primarily capturing some higher-order cognitive
563 influences in the later period while participants are making their decision.

564 To ensure these time-based assumptions about hierarchical processing were correct, that later periods
565 of significance do indeed represent processing in brain areas associated with higher-order abstract object
566 perception (Carlson et al., 2013), we compared the brain data to a neural network. The correlations between
567 brain activity and CORnet (Kubilius et al., 2018, 2019), a neural network designed to model the visual system,
568 revealed that early neural activity correlated well with all layers (V1, V2, V4 and IT) with a peak at
569 approximately 120 - 130ms (Figure 6). The earlier layers remain significant for a short period of time, and in
570 both experiments from approximately 300ms onwards, while participants were classifying the stimuli, patterns
571 of brain activity were most similar to the IT layer, indicating that neural representations in this time period
572 were likely to be more abstract, higher-order classifications (Carlson et al., 2013). In particular, the movement
573 task of Experiment 2 may engage more higher-order processing than the aliveness task in Experiment 1. The
574 correlation between the IT layer of CORnet and neural activity appears to be sustained longer in the
575 movement task (Figure 6B) compared to the aliveness task (Figure 6A), and it seems that movement may
576 explain more variance in neural activity in Experiment 2 compared to Experiment 1 (Figure 5B). Similarly,
577 object category (e.g., animal, plant) was more separable in the neural responses during the movement task
578 than the aliveness task (Figure 4D), further suggesting that judgements about movement might inherently
579 involve higher-level category responses. The combination of these analyses suggests that the ‘movement’

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580 factor in the current experiment represents a more abstract concept, as opposed to a visual similarity between
581 all things that move, such as blurred edges.

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

593 A particularly interesting finding was that aliveness only explained patterns of brain activity in a very
594 brief period shortly after stimulus onset. Attention to particular features of a stimulus based on the task can
595 affect neural representations (Harel et al., 2014), and thus we were surprised that aliveness did not account for
596 more variance in brain activity in Experiment 1 when it was the focus of the task. There is little consensus
597 about the degree to which aliveness explains patterns of brain activity in object representations, with some
598 work showing that aliveness is a better correlate of brain activity than animacy (Contini et al., 2020), and
599 others showing that it is important for behaviour but does not explain variance in brain representations
600 (Jozwik et al., 2021). The fit of aliveness models may depend on the choice of stimuli; in Contini and
601 colleagues' (2020) study, robots and toys appeared more animate than inanimate, reducing the fit of the
602 animacy model compared to the aliveness model. In the current study, aliveness may have poor explanatory
603 power in our linear models because the differences between living and non-living stimuli are captured by
604 other variables in the linear models, particularly naturalness which is not evenly distributed across alive and
605 non-alive stimuli, and the low-level visual correlates of aliveness such as rectilinearity (Nasr et al., 2014). It is
606 also possible that because the classification decision occurred at different points in each trial, the temporal
607 variation in the decision-making reduced the signal-to-noise ratio and made decoding more difficult.

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608 Converging evidence from neuroscience and behaviour has shown that animacy and aliveness are best
609 described as represented on a continuum according to capacity for goal-directed movement (Connolly et al.,
610 2012; Contini et al., 2020; Sha et al., 2014; Thorat et al., 2019; Yorek et al., 2009). In the current study, we
611 show that capacity for movement is an important dimension in human visual object perception, not only for
612 animate movement, but also for movement in the natural world. Our results support previous work showing
613 that animacy processing in the brain is closely related to the capacity for self-initiated movement and extend
614 this to show that natural movement may be a part of this spectrum. Overall, our results show that capacity for
615 movement is an important dimension in the representation of visual objects in humans.

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