RESEARCH REPORT

A simple rule to describe interactions between visual categories

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Abstract

Humans can rapidly categorise visual objects when presented in isolation. However, in everyday life we encounter multiple objects at the same time. Far less is known about how simultaneously active object representations interact. We examined such interactions by asking participants to categorise a target object at the basic (Experiment 1) or the superordinate (Experiment 2) level while the representation of another object was still active. We found that the "prime" object strongly modulated the response to the target implying that the prime's category was rapidly and automatically accessed, influencing subsequent categorical processing. Using drift diffusion modelling, we show that a prime, whose category is different from that of the target, interferes with target processing primarily during the evidence accumulation stage. This suggests that the state of category-processing neurons is altered by an active representation and this modifies the processing of other categories. Interestingly, the strength of interference increases with the similarity between the distractor and the target category. Considering these results and previous studies, we propose a general principle that category interactions are determined by the distance from a distractor's representation to the target's task-relevant categorical boundary. We argue that this principle arises from the specific architectural organisation of categories in the brain.

KEYWORDS

category interactions, drift diffusion model, priming, representation similarity, visual categorisation

1 | INTRODUCTION

Visual categorisation of natural stimuli can be performed extremely rapidly and efficiently (see Fabre-Thorpe, 2011 for a review). This ultra-rapid object categorisation is probably supported by feed-forward activity in the ventral stream, particularly in the infero-temporal cortex (ITC; see DiCarlo, Zoccolan, & Rust, 2012 for an analysis). Most studies on object recognition and categorisation have examined objects belonging to a single category. However, in the real world, we routinely encounter multiple objects belonging to different categories. Since category-level processing of various kinds

of objects occurs in the same neural substrate, the ITC, it is vital to understand how the processing of one category affects the simultaneous processing of other categories, or in other words, how does concurrent categorical analysis of one object in the ITC affect categorical processing of another. For example, when looking at a bird, if a cat suddenly appears, how does the representation of the bird influence the processing of the cat representation? The bird representation could either (a) not influence the processing of the cat, the two categorisation processes being independent of each other, (b) interfere with it, perhaps by adding noise to the signal, or (c) facilitate it by pre-activating some of the neurons that represent the cat category (perhaps by a "spread of activation" because the two representations are semantically close). Each of these seemingly logically exclusive possibilities receives evidence from and is grounded in different domains of research.

In the visual domain, interactions between object categories have been explored only in a few studies. Using intracranial human recording, Agam et al. (2010) showed that categorical representations in the ITC are largely unaffected when two objects from different categories are presented simultaneously. That is, categorical representations are very robust and do not interact with each other. On the other hand, other studies suggest that object representations interfere with each other. Cohen and colleagues (Cohen, Konkle, Rhee, Nakayama, & Alvarez, 2014) found that participants' performance in a multiple object change detection task was worse when objects belonged to the same category than when they belonged to different categories. Importantly, the authors also showed that the strength of this behavioural interference could be predicted by the difference in the neural activity (particularly in the occipito-temporal cortex) elicited by each object presented in isolation to the same participants. That is, the more similar the two patterns of neural activity, the worse the performance in the behavioural task. The degree of separation between neural patterns has also been correlated with performance in visual search (Cohen, Alvarez, Nakayama, & Konkle, 2017) and the effectiveness of masking between objects belonging to different categories (Cohen, Nakayama, Konkle, Stantić, & Alvarez, 2015). These sets of results are contradictory: one set (Agam et al., 2010) finds, using intracranial recordings, that representations of object categories in the ITC are robust and do not interfere, whereas the other set finds evidence of behavioural interference between visual representations that could be predicted by the degree of separation between their neural pattern in fMRI.

In the language domain, interference effects between object categories have been explored more thoroughly. Such studies typically use a picture–word interference paradigm (PWI) in which a to-be-named picture is presented along with (or soon after) a distractor word. Their results show that participants are slower at naming the picture (e.g., a *dog*) while ignoring a superimposed written label of a related object

(e.g., *horse*) than a word unrelated to the picture (e.g., *table*) (Hantsch, Jescheniak, & Mädebach, 2012; Kuipers, La Heij, & Costa, 2006). However, the same studies have also reported that, under other circumstances, responses can be facilitated when the picture is presented with a related word. For example, participants are faster in naming the image of a dog as an animal when presented with the word *horse* than with the word *table*. Further, the interference effect appears to be absent when the distractor is a picture (Damian & Bowers, 2003; La Heij, Heikoop, Akerboom, & Bloem, 2003), suggesting that contrary to words, visual representations might not interfere automatically. Thus, the nature of representations (picture or word) and the specific task being performed might have different effects on inter-category interactions.

This study aims to shed light on whether and how visual categories interact. To do so, it will be important to manipulate the relatedness between visual representations as well as the level at which the categorisation task is performed by the participants. We were particularly interested in uncovering which processes are influenced (or not) when visual representations interact and if there were systematic rules that they follow. To determine these, we used drift diffusion modelling to assess and quantify the cognitive processes that are affected during multiple object processing.

1.1 | Drift diffusion model

Drift diffusion models (DDM) allow us to uncover the cognitive mechanisms underlying binary decisions such as in two-alternative force-choice paradigms (see Ratcliff & McKoon, 2008 for a review). This set of models attempts to capture the entire range of behaviour exhibited in a binary decision paradigm by positing that evidence accumulates stochastically over time towards one of two decisions (e.g., category A or B). Once sufficient evidence accumulates and reaches a specific threshold, it triggers a decision and subsequent behaviour. This accumulation is considered to be a directed random walk, as the perceptual and decision-making systems are noisy. The models estimate a range of parameters to describe the observed behaviour. These parameters map on to specific cognitive processes, such as the speed of evidence accumulation, setting the decision threshold, presence of pre-existing bias towards one decision and non-decisional factors such as motor preparation. The models allow the contributions of these cognitive processes to behaviour to be robustly estimated (see the Data Analysis section in Experiment 1 for more details). However, the application of these models is not straightforward in many experimental conditions.

The vast majority of PWI or priming paradigms studying interactions in language processing typically require participants to *name* the target word. Hence, DDM analyses cannot be applied to such studies, where the behavioural response

is not restricted to two options. Consequently, even though a large number of studies have been conducted on linguistic interactions, uncovering their cognitive mechanisms has proved to be difficult and has engendered different theories and vigorous debate (Kuipers & La Heij, 2012; Mahon, Costa, Peterson, Vargas, & Caramazza, 2007; Mulatti & Coltheart, 2012). Nevertheless, there have been a few PWI and priming studies that tested participants on 2AFC categorisation tasks and hence were amenable to DDM analyses.

Such studies have found that responses are faster and/or more accurate when a prime shares the same response as the target compared to when they convey different responses (Glaser & Düngelhoff, 1984; Lupker & Katz, 1981). For example, participants are faster at categorising the word *friend* as a person after seeing the word *murderer* than after seeing the word *chocolate*. This facilitation has been termed *response congruency* or *response priming*. DDM analyses (e.g., Voss, Rothermund, Gast, & Wentura, 2013) have revealed that this modulation occurs at the non-decisional stages (response competition or non-decision time, parameter t), probably during response execution. This is in line with electrophysiological findings that response congruency is mediated by pre-activation of the response associated with the prime (Bartholow, Riordan, Saults, & Lust, 2009; Eder, Leuthold, Rothermund, & Schweinberger, 2012). Response congruency seems to be a major contributor to priming in categorisation tasks, particularly when the primes are masked (for a meta-analysis see Van den Bussche, Van den Noortgate, & Reynvoet, 2009). In our study, we abstain from using masks as we do not want a mask to interfere with the neural response elicited by the prime and the target, and also because we are interested in examining the effect of relatedness between categories and not just the response congruency effect.

On the other hand, behaviour is also modulated by the similarity or relatedness between primes and targets (Alario, Segui, & Ferrand, 2000; Rahman & Melinger, 2007). For example, participants are faster at categorising the word *friend* as positive after seeing the word *chocolate* than after seeing the word *murderer*. This effect is termed *prime relatedness* or *associative priming*. DDM analyses have pinned this effect to decisional processes (drift rate or speed of accumulation of evidence, parameter v), that is, the ease of access to target information (Voss et al., 2013). Voss et al. suggest that this facilitation could be explained by the "spreading of activation" hypothesis (Collins & Loftus, 1975). The prime would activate associated representations, including the target, and because the target will be pre-activated, its processing will be facilitated.

Thus, according to these findings, the interactions between linguistic categories take place not only at the response selection and execution stages but also at the stage where words are represented, that is at the evidence accumulation stage. We will use a similar approach, applied to the visual domain, to examine the mechanisms that might be involved when (and if) two visual categories interact. We will assess the contributions of each of these processes (response congruency and, importantly, prime relatedness) and their corresponding cognitive mechanisms to behavioural performance.

1.2 | Our approach

In our study, we used sequential presentation of objects where a distractor object (the "prime") is presented just before the target object. This paradigm has the advantage that we can control the order in which the two stimuli are processed. It ensures that both stimuli are processed without the requirement of moving spatial attention, either overtly or covertly, to different locations. Additionally, it allows the assessment of the temporal dynamics of the interaction between object categories by varying the time interval between the presentation of the prime and the target (Stimulus Onset Asynchrony, SOA). For example, it has previously been found that the interference effect of a distractor word (e.g., "boat") on a picture (e.g., "train") was present at short but not at long SOA (Alario et al., 2000). Similarly, Kinoshita, de Wit, Aji, and Norris, (2017) found that when two stimuli convey incompatible responses, the strength of interference increases with time when the conflicting information is simultaneously presented (0 ms SOA), but the interference remains stable over time at longer SOA (500 ms). Finally, because we are interested in visual interactions, we minimised the involvement of language areas and its effects by testing participants in a manual yes/no categorisation task using a rapid picture-picture priming paradigm. Because this task involves a binary decision, drift diffusion modelling can and will be used to analyse the results.

We will examine the interactions between two pictures by manipulating the relatedness between them and assessing its effect on behavioural responses. By performing drift diffusion analysis on this data, we hope to determine the cognitive processes that drive interactions between categories. If the presence of a task-irrelevant picture interacts with the processing of the target category, it could influence decisional or/and non-decisional processes. If the prime influences motor processes or other non-decisional mechanisms, it should be visible in a change in the parameter t of the model (response congruency). This would imply that the prime does not affect the categorical processing of the target object but affects downstream processes, possibly by the pre-activation of a motor command. In this case, we would expect faster responses when prime and target share the same response than when they do not. The prime could also interact with decisional processes such as the efficiency or the ease of access to the target features (prime relatedness). This would be observed as a change in

evidence accumulation (parameter *v*). Such a finding would imply that target processing in the cortex is modulated by concurrent activity elicited by other objects. This effect of relatedness could be positive or negative. The study by Voss et al. (2013) could be taken to suggest that a related prime could aid the processing of a target category by pre-activating its representation. Similarly, one might expect that the target category's features will be processed more efficiently and faster since target and prime share common features. For example, seeing a cat might quicken the processing of a bird, as they are both animate, have legs, eyes, etc. Conversely, the results of Cohen et al. (2014) suggest that relatedness might lead to interference in the processing of similar features by making it hard to distinguish between targets and other objects. The results of this study will thus reveal the nature of the interactions between simultaneously active visual representations and (a) indicate how the relatedness between the prime and target images influences the categorisation of the target and (b) reveal the cognitive mechanisms underlying these interactions.

2 | EXPERIMENT 1: BASIC-LEVEL (BIRD) CATEGORISATION

In Experiment 1, we tested participants in a bird/non-bird categorisation task. A to-be-ignored prime was presented 80 or 180 ms before a target image. The prime could convey the same (congruent prime) or a different (incongruent prime) motor response as the target picture. Crucially, to study the effect of semantic distance between objects, incongruent primes were of two different types: they could belong to a category related to the bird target (e.g., another animal; i.e., they shared the same superordinate category) or to an unrelated category (e.g., a vehicle; i.e., they belonged to different superordinate categories).

2.1 | Methods

2.1.1 | Participants

13 volunteers (9 women, 1 left-handed; mean age 25 ± 2 years; including the first author) participated in this experiment. The two experiments have been carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) and received the approval of the French Ethical Committee (comité de protection des personnes Sud-Ouest et Outre-Mer I, protocol 11015). All participants had normal or corrected to normal vision and provided written informed consent. Data from both experiments are accessible on the OSF website (OSF. IO/ASB4E).

Although the number of participants in both experiments might seem limited at first glance, we believe that the data analysis that we performed is robust for several reasons. First, unlike in previous studies of priming, participants performed a large number of trials in each of the tested conditions. That is, in Experiment 1, each condition comprised at least 128 trials, and in Experiment 2, each condition consisted of 192 trials. Thus, the measurement of each participant's performance should be much more precise than in previous studies. Second, and more importantly, we utilised drift diffusion analysis to examine the behavioural data. This analysis takes into consideration every single trial, not just an average, in each participant, to estimate the model parameters. Further, the specific implementation we utilised was based on hierarchical Bayesian analysis, which parcels out variance at the individual level (Wiecki, Sofer, & Frank, 2013) to determine the drift diffusion parameters. Additionally, we report the Bayesian probabilities of whether one condition is different from another. Thus, contrary to the *p*-values used in frequentist statistics, this analysis gives a *direct* probability (*P*) measure that one condition is different from another given the data. This measure is not dependent on sample size as *p*-values are, but on the precision of measurement and overall variance. Therefore, we are confident that any reported *P* (probability of overlap between conditions) value of <.05 reflects a strong effect irrespective of sample size.

2.1.2 | Design and stimuli

The experiment consisted of a total of 16 blocks of 96 trials each. The target-prime SOA was 80 ms in half of the blocks and 180 ms in the other half. The order of the blocks was randomised. Within each block, half of the target images were birds, ¼ were non-bird animals and ¼ were vehicles. As target images included other animals, the bird/non-bird categorisation had to be performed at the basic-level (not at a superordinate-level; see Macé, Joubert, Nespoulous, & Fabre-Thorpe, 2009). For each target image, half of the primes were congruent (both prime and target conveyed the same motor response), and half were incongruent (prime and target conveyed different motor responses). Moreover, for bird target images, incongruent primes were divided into two equal groups: they were either related (non-bird animal) or unrelated (vehicle) to the bird target category. Thus, each block consisted of 48 bird targets and 48 non-bird targets. The bird targets were preceded by congruent primes in 24 trials, incongruent related primes in 12 trials, incongruent unrelated primes in another 12 trials. In the 48 non-bird target trials, 24 were non-bird animal targets preceded in half of the trials (12) by a bird prime and in the other half by a non-bird animal prime, and 24 were vehicle targets preceded in

12 trials by bird primes and in the other 12 trials by vehicle primes. The type of trial was intermixed within each block.

Contrary to usual practice in priming studies, we used each image only once in an experiment. All 3,072 images were un-altered, coloured natural images chosen from the image sets used in a previous study (Poncet & Fabre-Thorpe, 2014) and from the Internet. The set of images was also chosen so that it included one or several objects of various orientations, positions and sizes, ruling out the possibility that our results could be explained by simple image learning (low or high level) or familiarity due to image repetition. Furthermore, the stimuli were picked randomly for each participant, so the effect found in our study could not have been driven by specific pairs of stimuli. The bird category (1,536 images) included birds of different species (songbirds, owls, parrots, pigeons, ducks, etc.) in different environments (flying in the sky, perched on a tree, on the water, etc.). The non-bird animal category (768 images) included mammals (dog, bear, elephant, etc.; 384 images) and fish (redfish, shark, etc.; 384 images). The vehicle category (768 images) was also diverse and included planes, cars, boats, etc. Each image subtended $8° \times 8°$ visual angle and was seen only once by each participant either as a prime or as a target (its status was randomly assigned for each participant).

2.1.3 | Procedure

Participants were seated in a dimly lit room, approximately 60 cm from a CRT screen (refresh rate: 100 Hz). Stimuli were displayed using Matlab with Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007) and were synchronised with the refresh rate of the monitor. Participants were asked to perform a bird/non-bird categorisation task (chance level was 50%). At the beginning of a trial, a white fixation dot was presented at the centre of a black screen for 500 ms. The prime image was then presented at the centre of the screen for 20 ms followed by a blank screen. The target image was presented for 100 ms and appeared either 80 or 180 ms after the onset of the prime (Figure 1). The shorter SOA (80 ms) was long enough to allow participants to correctly perceive the order of the stimuli (Theeuwes & Van der Burg, 2013). Participants were told to ignore the first image and report whether the second image contained a bird or not by pressing the left ("yes" response) or right ("no" response) arrow key using the same hand. At the end of the trial, an auditory beep (negative feedback) signalled an incorrect response or an absence of response in the allowed time. The next trial started right after the participant's response or after a maximum of 1.2 s after the onset of the target image. Before the experiment began, participants were trained on 20 trials with a separate set of images.
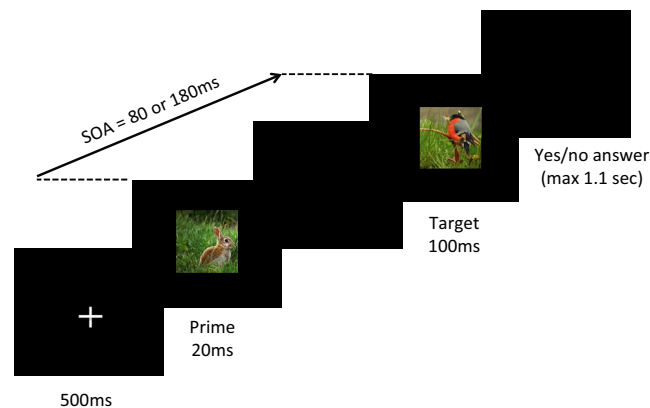
FIGURE 1 Illustration of a trial in Experiments 1 and 2. In Experiment 1, participants were asked to perform a bird/non-bird categorisation on the target image whereas in Experiment 2 they were asked to perform an animal/non-animal categorisation. In both experiments, participants were told to ignore the first image

2.1.4 | Data analysis

For each participant, behaviour was assessed using median reaction time (RT) for correct yes responses (Hits) and mean error rates (ER) on bird target images (misses). Anticipatory responses (RT faster than 150 ms) and trials without any response (no response within 1.2 s) were excluded from the analysis (0.4% of trials were rejected). We focused our analysis on bird target images because the non-bird category was undefined. Participants were asked to report whether the target image belonged to a bird or not. Presumably, their response was based on the (correct or incorrect) detection of certain target features (e.g., beak, feather). However, the basis for participants' responses to non-bird images is not clear. It could have been driven by the absence of bird features or the presence of a combination of attributes for the distractor category that might vary substantially between participants. Importantly, responses to non-bird animals and vehicles might be different to such an extent that the role of the prime would be difficult to assess. Nonetheless, for completeness, we present the results for responses to non-bird images (correct rejections and false alarms) and report relevant statistical analysis in Appendix S1. These data and analyses corroborate the results reported for bird images.

We define the priming effect as *the difference in performance between incongruent and congruent trials*. We calculated priming effects for the two target-prime relatedness (related and unrelated prime) conditions and two SOAs (80 and 180 ms) using both RT and ER measures (henceforth referred to as RT and ER priming). As a first step, we compared this difference to zero, using one-sample *t* tests, after pooling related and unrelated trials for the two SOAs separately. This comparison reflects the role of response congruency on

performance. Then, to investigate the effect of relatedness on the interaction between categories, we performed a two-way repeated measures ANOVA with prime relatedness and SOA as factors on RT and ER priming. All follow-up paired t tests were conducted with appropriate Bonferroni corrections applied for multiple comparisons.

A different approach would be to conduct signal detection theory (SDT) based analysis, where unbiased discrimination (d-prime) and possible biases (criterion shift) in the different conditions can be computed. This can allow us to verify, for example, if performance differences (e.g., priming effects) are driven by differences in processing the stimuli (d-prime) or instead by biases induced by the prime (prime inducing more liberal or more conservative responses; criterion). This approach, although frequently deployed in categorisation studies, is generally not used in priming studies. One substantial reason for the absence of its usage is that the effects of multiple factors tend to be pooled together and become hard to distinguish when applying STD analysis to priming studies. First, both the prime and the test image can influence performance and the two effects are difficult to separate using STD analysis. For example, the characteristics of the responses to vehicles and non-bird animal images might be different regardless of their status as prime or test image. Therefore, a difference in d-prime between conditions might be due to the category of the prime and/or the test image. Second, the comparison between different conditions involves multiple confounds. For example, if one wants to compare the effect of a bird prime with the effect of a vehicle prime, Hits are based on congruent trials in one condition (correct responses on trials with a bird prime preceding a bird image) but on incongruent trials in the other condition (correct responses on trials with a vehicle prime preceding a bird image, see Table 3). Similarly, false alarms would be incongruent trials in one condition (incorrect responses on trials with a bird prime preceding a vehicle image) and congruent trials in the other condition (incorrect responses to trials with a vehicle prime preceding a vehicle image). That is, there are clear response congruency differences between the two conditions. This confound is inextricable. Therefore, the origin of the potential differences in d-primes calculated with these Hits and FAs would be unclear. Finally, there is no obvious way to determine which false alarms should be assigned to which Hit rates. For example, instead of keeping the prime constant between Hits and FAs as in the previous example, one can instead keep response congruency constant (see Table 3). However, in this case it is not possible to separate out the effect of the kind or relatedness of the prime, and consequently, we cannot ascertain the bias induced by that prime. Since we are interested in the effect of both congruency and prime relatedness, we felt that SDT analysis would not help address our questions. Altogether, these issues raise difficulties in interpreting the results of SDT analysis and can easily lead to confusions and misinterpretations. This analysis is not central to test our questions but readers well-versed and interested in SDT can find it in a separate section.

To get a better understanding of the cognitive mechanisms underlying the observed effects, we performed two additional analyses. The first consisted of a quantile analysis of RTs to determine whether the priming effect changes across a range of RTs. One could imagine that the priming effect is smaller for fast RT compared to slower responses as observed by Kinoshita et al. (2017). For each participant and each condition separately, the quantiles were estimated using the quantileIOSR function in Matlab (R-8 type). For each bin, we then computed the RT priming (quantile in the incongruent condition *minus* quantile in the congruent condition) which was then averaged across participants. In a second analysis, we used the diffusion model developed by Ratcliff, (1978) to analyse our data. The goal of this analysis, described in more details in the following section, was to utilise the full distribution of behavioural data (RT and ER) to shed light on the cognitive mechanisms underlying the decision process in the categorisation task.

2.1.5 | Drift diffusion modelling

The drift diffusion model (DDM) is a sequential sampling model for analysing response-time data in a two-alternative forced choice task. It has been used in a range of tasks including categorisation and priming tasks (e.g., McKoon & Ratcliff, 2012; Nosofsky & Palmeri, 1997; Voss et al., 2013). In such models, the two choices are represented as an upper and a lower threshold. The model assumes a single process accumulating evidence until one of the decision thresholds is reached. This process is chiefly characterised by four parameters:

1. a, the distance between the two boundaries; it reflects how much evidence is required for a decision to be reached,
2. t, the set of all non-decisional processes such as encoding, memory access, movement initiation and execution,
3. v, the speed at which evidence accumulates (drift rate); it is low when stimuli are harder to discriminate,
4. z, an a-priori response bias affecting the starting point of the accumulation of evidence.

In addition to these four mains parameters, three inter-trial variability parameters (for the inter-trial variability in a, t and v) can be included. However, these parameters require a very large amount of data to estimate and their influence on the model output is usually very small. More importantly, the hypotheses we consider do not make any specific predictions (or provide a clear path to interpretation) for these

parameters. Hence, increasing the complexity of the models to assess these parameters is not desirable. Thus, as recommended by a large consortium of researchers using drift diffusion modelling (Boehm et al., 2018), we did not estimate inter-trial variability parameters in our models.

DDM has been successfully applied by Voss et al. (2013) to examine the distinction between response congruency and prime relatedness in a word priming task. The authors showed that whereas congruency effects are mapped onto non-decisional processes (response competition, t), prime relatedness (or semantic congruency) affects the speed of information uptake (drift rate, v). In other words, the congruency effect is mainly the result of motor response competition, which does not affect target processing. However, prime relatedness affects how well the target stimulus is processed.

In our experiment on the interaction between visual categories, we expect response competition to be larger for incongruent primes than for congruent primes. However, we are mostly interested in exploring the cognitive mechanisms that underlie the priming effect for related versus unrelated primes when both primes elicit the same incongruent response relative to the target. Indeed, this comparison should determine whether and what kind of interactions take place during the early stages of target processing, possibly in the visual system when non-decisional processes (t) are kept the same.

In terms of the DDM, if the activity elicited by the prime modulates the neural processing of the target, we would predict that the speed of evidence accumulation (v) will be different for the two incongruent primes and there should not be a difference in non-decisional processes (t) between them. Further, related primes could interact with target processing more than unrelated primes. They could facilitate the processing of the target by pre-activating the neural population of the target (higher v). On the contrary, because related but incongruent primes share features with the target, evidence could accumulate towards either decision boundary. This should slow down the processing of the target (lower v) for the related prime compared to the unrelated prime.

The parameter a (response threshold) was also allowed to vary in our model. This parameter can reflect a speed–accuracy trade-off between conditions. When instructed to be fast at the expense of accuracy, participants decrease their response criterion, that is, they lower their decision threshold (Zhang & Rowe, 2014) and hence require less evidence to trigger a response. On the other hand, with a high response criterion, participants are more accurate but also respond slower. In our paradigm, both accuracy and speed were emphasised with a negative feedback and a response deadline, respectively. However, recent studies have shown that the response threshold could change on a trial by trial basis (Domenech & Dreher, 2010; Steinweg & Mast, 2017). Including this parameter in the model should inform us about

different speed–accuracy trade-off strategies in response to different kinds of primes.

The analysis was performed using the HDDM toolbox developed by Wiecki et al. (2013). The parameters of the model (a, t, v) were fitted using an accuracy-coding procedure on the bird target trials for the three different primes and two SOA conditions simultaneously. In this procedure, the upper threshold represents correct responses (Hits) and the lower threshold incorrect responses (misses).[1]

We generated 20,000 posterior samples and discarded the first 2,000 samples as burn-in (see Wiecki et al., 2013 for details about the HDDM procedure). We evaluated the model first by visually inspecting the traces of the posteriors, the autocorrelation and the marginal posterior, as recommended by Wiecki et al. (2013). This inspection demonstrated the expected patterns for a converged model. We further assessed the convergence of the model with the Gelman–Rubin diagnostic (Gelman & Rubin, 1992). This statistic compares, for each parameter, the estimated between- and within-Markov chain variances for different runs of the same model (in this study we compared 5 runs). These differences ($\hat{R}$ values) should be close to 1; large differences indicate non-convergence. In our model, all $\hat{R}$ were less than 1.0013, showing that the model converged very well. We also performed posterior predictive checks, which consist of simulating new data from the fitted model and comparing it to the original data. The observed and predicted RT distributions for correct and incorrect responses in the different conditions are shown in Figure 2. The summary statistics of the posterior predictive checks can be found in Appendix S1 (Table S1). They confirm that the predicted RT distribution falls within the 95% credible interval of the observed RT distribution. That is, the model produces data that closely mimics the observed data, indicating that the model fit was excellent.

Hypothesis testing was performed by taking advantage of the Bayesian estimation of the DDM parameters provided by the HDDM toolbox. We analysed the probability, P, that two conditions are different from each other by determining how much the difference between two conditions overlaps

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[1] A different, "stimulus coding" procedure, where the upper threshold corresponds to the target category (bird images) and the lower threshold to the distractor category (non-bird images), can be used to include the parameter z in the model. This model includes all the data collected (for bird and non-bird images, correct and incorrect answers). However, the parameters fitted with this procedure are not always easy to interpret and it requires assumptions that are difficult to justify in our paradigm (in particular, a similar drift rate for bird and non-bird responses). Nevertheless, we report this procedure in Supplementary Materials (Figure S7). It revealed that responses were biased (parameter z in the model) towards a bird response if the trial included a non-bird image (as prime and/or target) and towards a non-bird response if the trial included a vehicle image. All the other parameters (a, t, v) were highly similar to the model presented here. Thus, our results cannot be accounted by a difference in response bias.
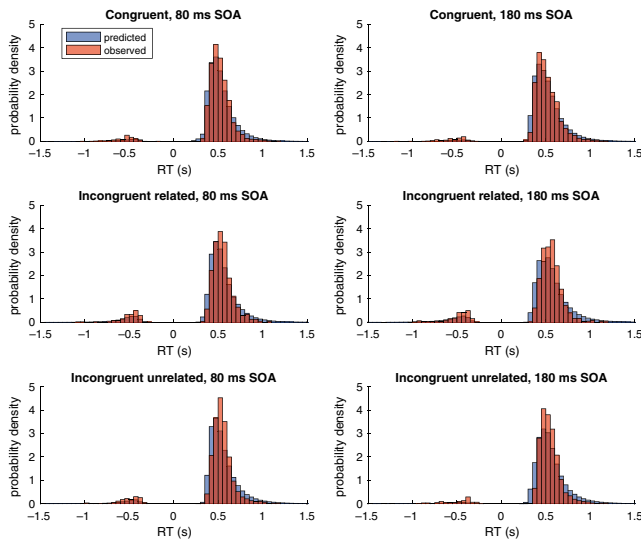
FIGURE 2 Observed (red histograms) and HDDM predicted (blue histograms) RT distributions in the different prime and SOA conditions in Experiment 1. Incorrect responses are represented with negative RTs

with 0. If the distribution of the difference is centred around 0, $P = .5$ (50% of the distribution is on one side and 50% on the other side). If the distribution of the difference is not centred around 0, that is if one condition is higher than the other one, P will move away from 0.5 towards 0. For example, if 10% of the difference distribution is on the left side of 0 and 90% is on the right side, it will result in $P = .1$. The minimum P value between two conditions is $P = 0$, when the distribution difference does not include 0; that is, the two conditions do not overlap at all. Contrary to *p*-values used in frequentist statistics, this analysis gives a *direct* probability measure, but it can still be interpreted in a similar way as *p*-values.

2.2 | Results

2.2.1 | Priming effect

The main goal of the study was to test interactions between visual categories. To this end, we compared the priming effect between conditions. Average median RT and mean ER for bird images are displayed in Table 1. We define the priming effect as the difference between congruent (bird prime and bird target) and incongruent (non-bird prime and bird target) trials. The priming effect was computed separately for the two relatedness and the two SOA conditions (Figure 3). To test the effect of response congruency, the two relatedness conditions were pooled. For non-bird images, congruent trials were trials with non-bird animal or vehicle images preceded by a non-bird animal or a vehicle image,

respectively, whereas incongruent trials were trials with non-bird images preceded by a bird prime (Table 2). The statistical analysis of these data are presented in Appendix S1 and show results closely resembling the ones presented here for bird images.

Effect of response congruency

Error rates. ER priming was positive at both 80 and 180 ms SOA meaning that when primes and targets map on to different motor responses (incongruent trials), participants made more errors than when they map on to the same motor responses (congruent trials). ER was higher by on average 3.3 percentage points when categorising bird targets preceded by non-bird primes than if preceded by bird primes ($t(12) = 3.94$, $p = .004$ and $t(12) = 4.29$, $p = .002$ at 80 and 180 ms SOA, respectively).

Reaction times. At both SOAs, RT priming was positive. Participants categorised congruent target images faster than incongruent target images by on average 31 ms at 80 ms SOA ($t(12) = 8.13$, $p < .001$) and 41 ms at 180 ms SOA ($t(12) = 6.89$, $p < .001$).

Effect of relatedness

Error rates. ER priming was larger for non-bird animal (related) primes than for vehicle (unrelated) primes ($F(1,12) = 10.41$, $p = .007$, $_p\eta^2 = 0.46$). That is, participants made more mistakes when incongruent primes belonged to the same superordinate category (animal) as the target (bird) than when they belonged to a different one (vehicle). There was no main effect of SOA ($F(1,12) = 0.19$, $p = .67$, $_p\eta^2 = 0.02$). Further, there was no interaction between relatedness and SOA ($F(1,12) = 3.24$, $p = .10$, $_p\eta^2 = 0.21$). The effect of relatedness can be observed (unchanged) at both long and short SOAs indicating that relatedness affects categorisation very early on.

Reaction times. We found no strong evidence for the effect of prime relatedness ($F(1,12) = 4.00$, $p = .07$, $_p\eta^2 = 0.25$) and SOA ($F(1,12) = 4.02$, $p = .07$, $_p\eta^2 = 0.25$) on RT priming. However, there was a significant interaction between these two factors ($F(1,12) = 10.21$, $p = .008$, $_p\eta^2 = 0.46$). At 80 ms SOA, there was no effect of prime relatedness: RT priming was the same for non-bird animal and vehicle primes ($t(12) = 1.07$, $p = .61$); whereas at 180 ms SOA, there was a noticeable effect of relatedness: RT priming was larger for non-bird animal than for vehicle primes ($t(12) = 3.80$, $p = .006$). In other words, the type of incongruent prime (related or unrelated) had no influence on RTs at 80 ms SOA, but at an SOA of 180 ms, incongruent related primes (non-bird animals) slowed down the categorisation of the target picture (bird) more than incongruent unrelated primes (vehicles).
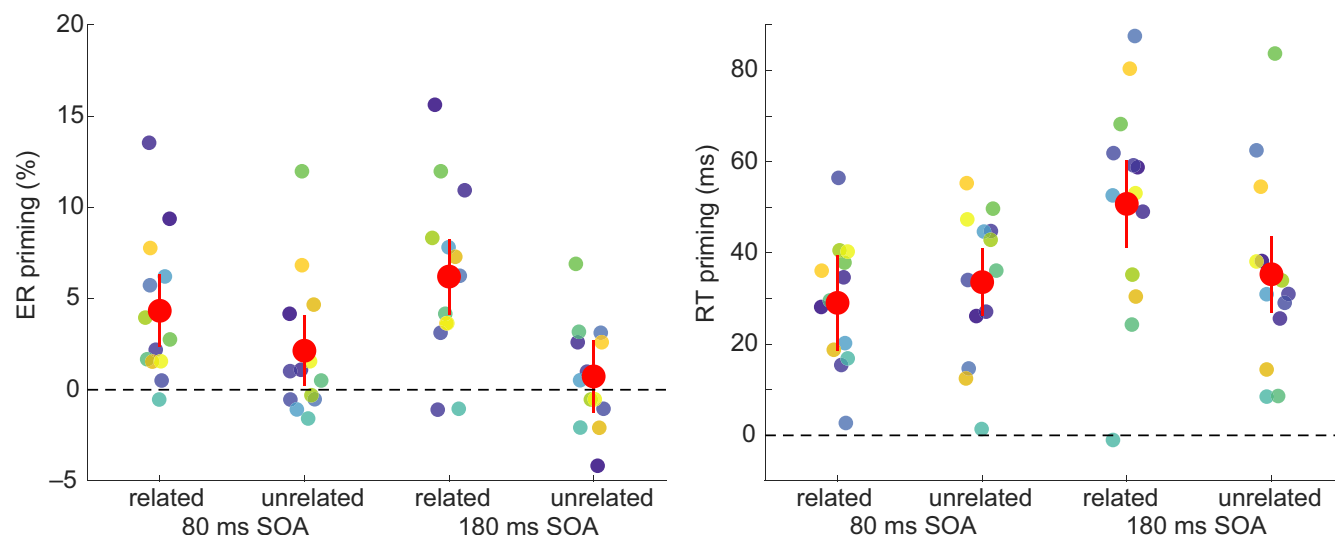
FIGURE 3 Priming effect (incongruent–congruent) in bird/non-bird categorisation task for error rates (ER, left panel) and reaction times (RT, right panel) in Experiment 1. A priming effect of 0 (dashed horizontal line) shows no effect of response congruency while a positive priming means that responses are worse in the incongruent than in the congruent condition. Each coloured dot represents one participant's performance in the specified condition. The mean priming effect and within-subject 95% confidence interval (CI) are represented in red. All CI is calculated using the Cousineau–Morey method (Cousineau, 2005; Morey, 2008)

TABLE 1 Average of median RT in ms and mean ER in % for categorising a bird image in Experiment 1

	80 ms SOA			180 ms SOA		
	Congruent	**Incongruent related**	**Incongruent unrelated**	**Congruent**	**Incongruent related**	**Incongruent unrelated**
RT	504 (15)	533 (14)	538 (15)	497 (20)	548 (17)	532 (18)
ER	4.94 (0.68)	9.27 (1.41)	7.08 (1.20)	4.42 (0.75)	10.63 (1.81)	5.16 (0.89)

Note: The bird image was preceded by a congruent (bird), an incongruent related (non-bird animal) or an incongruent unrelated (vehicle) image with a SOA of 80 or 180 ms. SEM are reported in parentheses.

Summary

Participants were faster and more accurate in congruent than incongruent trials. This suggests that even though they knew that they had to ignore the first (prime) image, they automatically processed its basic-level category, which then affected their categorisation responses to the bird target image. Importantly, the priming effect was larger for related primes than for unrelated primes and this effect increased with longer SOA.

2.2.2 | Signal detection analysis

SDT analysis can be useful for separating the ability to discriminate between stimuli from potential biases in participants' response criterion. Towards this end, a reviewer requested that we calculate criterion using the Hits and FAs on trials with different types of prime (bird, non-bird animals, vehicles, separately) to uncover any biases that might arise from specific kinds of primes. However, as discussed above in the data analysis section (2.1.4), if the prime category is

kept constant across Hits and FAs, response congruency cannot be the same between Hits and FAs and therefore one cannot exclude or assess the effect of congruency on d-primes. On the other hand, we could compute the d-primes according to consistent response congruency. When response congruency is the relevant framework across Hits and FAs, the primes are not the same, so it is not possible to calculate the effect of the prime category on the criterion. Another difficulty with SDT analysis in priming studies is that it can be unclear whether the prime or the test image is driving the changes in d-primes and criteria. With these caveats in mind, we report SDT analysis (Table 3) following both approaches outlined above: that is, while a) prime category is consistent for Hits and FAs and while b) response congruency is consistent for Hits and FAs.

In the approach, where the prime is consistent across Hits and FAs, at first glance it seems that vehicle primes lead to biased responses towards a "no" response (conservative criterion) compared to non-bird animal primes. This finding can be taken to argue that the effect of the prime category on participants' performance is due to differences in bias. However,

TABLE 2 Average of median RT in ms and mean ER in % for non-bird images (non-bird animals or vehicles) in Experiment 1

	Animal test stimulus				Vehicle test stimulus			
	80 ms SOA		180 ms SOA		80 ms SOA		180 ms SOA	
	Congruent	Incongruent related	Congruent	Incongruent related	Congruent	Incongruent unrelated	Congruent	Incongruent unrelated
RT	545 (15)	573 (17)	532 (20)	555 (17)	485 (16)	510 (16)	483 (20)	516 (20)
ER	6.26 (0.92)	9.00 (1.63)	4.98 (0.65)	11.27 (1.63)	1.21 (0.37)	2.93 (0.87)	1.37 (0.27)	4.20 (1.06)

Note: A non-bird image was either preceded by a bird prime (incongruent condition) or by the same image category (congruent condition), which was a non-bird animal prime for non-bird animal test stimuli or a vehicle prime for vehicle test stimuli. SEM are reported in parentheses.

there are several reasons to think that this is not the case. First, even though the criteria were different for non-bird animals and vehicle primes, the d-primes were also higher for vehicle primes than non-bird animal primes. That is, there is clear evidence for a difference in sensitivity due to the prime category. Second, this bias was also found for bird primes: with the prime always being a bird, participants' responses were more conservative to vehicle test images than to non-bird test animal images. This shows that criterion can change even when the prime is kept constant, indicating that a criterion change is not necessarily attributable to the prime. We take these findings to reflect a general difference in responses to non-bird animal and vehicle images, not a specific effect of the prime.

It might be possible to assess the effect of prime with an alternative comparison. For example, if we consider trials where the test images are consistent but the primes are varied across conditions, we find differences in criterion but not in d-primes (e.g., when comparing bird prime related and non-bird animal prime conditions, the test images are consistent, birds and non-bird animals in Hits and FAs, respectively, for both conditions, but primes are either birds in the bird prime related condition or non-bird animals in the non-bird animal prime condition). This change in criterion can be argued to drive performance. However, once again, there are several confounds in this comparison, which makes any conclusion unreliable. First, response congruency is confounded in the two cases. When the prime is a bird, Hits are congruent and FAs are incongruent, whereas the opposite is true for non-bird primes. That is, the differences can be attributed to different congruency relationships and not type of prime. Second, even when the prime is the same (bird), criterion shifts from liberal to conservative depending on the type of test image that elicits FAs (non-bird animal versus vehicle). This indicates that it is not the prime that drives the shift in criterion and further supports the inference made above that general differences in processing non-bird animal and vehicle affect both d-primes and criterion. It is therefore very difficult to interpret any differences in d-primes or criterion between bird and non-bird prime trials.

In the approach, where congruency is consistent across Hits and FAs, we observe a bias towards "no" responses in related trials (including a vehicle) compared to unrelated trials (including a non-bird animal). This bias is also found in the parameter z for a DDM based on a stimulus coding procedure (see Appendix S1). We nevertheless observe a difference in d-primes between related and unrelated conditions, suggesting that despite a difference in criterion, congruency affects sensitivity. The results of this approach also suggest that vehicle images are processed differently than non-bird animal images. Indeed, d-primes and criterion were higher in the unrelated than in the related congruent condition, and since Hits were the same in both

TABLE 3 Signal detection analysis in Experiment 1

	Hit trials	FA trials	80 ms SOA		180 ms SOA	
			d-prime	Criterion	d-prime	Criterion
Consistent prime						
Bird prime related	BB	BA	3.11 (0.13)	−0.14 (0.05)	3.09 (0.16)	−0.24 (0.07)
Bird prime unrelated	BB	BV	3.72 (0.12)	0.18 (0.07)	3.66 (0.14)	0.05 (0.09)
Non-bird animal prime	AB	AA	2.97 (0.13)	0.10 (0.05)	3.02 (0.14)	0.17 (0.06)
Vehicle prime	VB	VV	3.81 (0.15)	0.38 (0.05)	3.94 (0.13)	0.26 (0.06)
Consistent congruency						
Congruent related	BB	AA	3.27 (0.11)	−0.05 (0.04)	3.47 (0.13)	−0.05 (0.04)
Congruent unrelated	BB	VV	3.96 (0.10)	0.30 (0.05)	4.00 (0.13)	0.23 (0.05)
Incongruent related	AB	BA	2.81 (0.16)	0.01 (0.05)	2.64 (0.18)	−0.02 (0.08)
Incongruent unrelated	VB	BV	3.58 (0.18)	0.25 (0.06)	3.57 (0.19)	0.08 (0.06)

Note: The analysis is based on whether the prime category or response congruency is kept constant between Hit and FA trials. For each condition, the exact trials for Hit and FA are described as prime-test image pairs, where B stands for bird, A for non-bird animal, V for vehicle. For example, AB is a trial where a non-bird animal is presented as a prime and a bird as the test image to be categorised. *SEM* is reported in parentheses next to mean d-prime and criterion.

conditions, this effect originates from FAs. This suggests that, with vehicle images, participants were more conservative and categorised them better than non-bird animal images.

2.2.3 | Quantile analysis

Quantile analysis allows us to investigate the dynamics of the RT priming effect depending on the speed of participants' responses. Kinoshita et al. (2017) found that when two stimuli convey incompatible responses, the interference increases with longer RTs. On the other hand, the interference is stable across time if the incongruent stimulus is presented 500 ms before the target. The authors argue that when both distractor and target are presented simultaneously, the interference between stimuli increases because the accumulation of evidence occurs simultaneously for both stimuli. With such concurrent accumulation, the mutual interference increases as time passes. When the distractor is presented 500 ms in advance of the target, the information about the distractor would have been fully accumulated, and hence, interference would be constant across time. In our paradigm, the prime and the target were presented 80 or 180 ms apart. It is possible that the prime, even if it was supposed to be ignored by the participants, was still being processed over time, especially since it was not masked. If it were the case, its interference with the target should increase with longer RTs. Such an increase should be observable particularly at short SOA, when the accumulation of evidence for the prime might still be ongoing.

The results show that the prime interferes with the processing of the target to the same extent across RTs (Figure 4). The priming effect is quite stable for all conditions except from the 6-7th decile at long SOA where it starts decreasing for both the unrelated (vehicle) and the related (non-bird animal) prime conditions. Indeed, the priming effect is close to 0 at long SOA for the slowest RT quantile bin when the prime was a vehicle. These findings suggest that the prime has been processed very quickly and automatically through a feed-forward pathway and is not processed further after the target appears. Its effect, either during processing in visual areas or at the motor level stage, is stable over time. Additionally, the interference seems to decrease with longer RTs and SOA, particularly for unrelated primes.

2.2.4 | Drift diffusion modelling

The priming effect that we observed can be the product of different cognitive processes. The DDM allows us to estimate the contributions of mechanisms such as non-decisional processes (t), speed of information processing (v) and decision threshold (a). Based on previous results (Voss et al., 2013), we might expect that the priming effect (the difference between congruent and incongruent primes) will be related to a difference in motor response (t). Our results also showed a difference between related and unrelated primes. This effect cannot be accounted by a difference in motor response as both primes are incongruent. However, it could be attributable to a difference in the speed of evidence accumulation (v), which would suggest that the neural processing of the target is affected differentially by the relatedness of the prime. We do not have any predictions for a but including it in the model should control for any difference in decision criteria (speed–accuracy trade-off) that could affect a specific condition. Please note that the results are presented with a Bayesian probability measure (P) that two distributions are
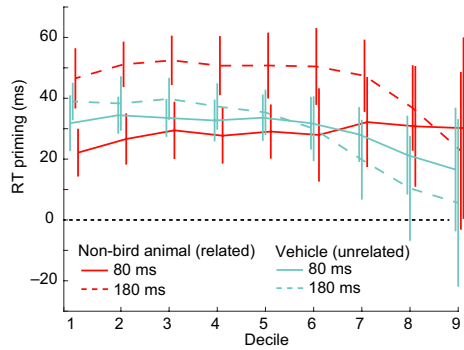
FIGURE 4 Evolution of the RT priming effect depending on the speed of the participants' responses. Error bars represent within-subject 95% CI
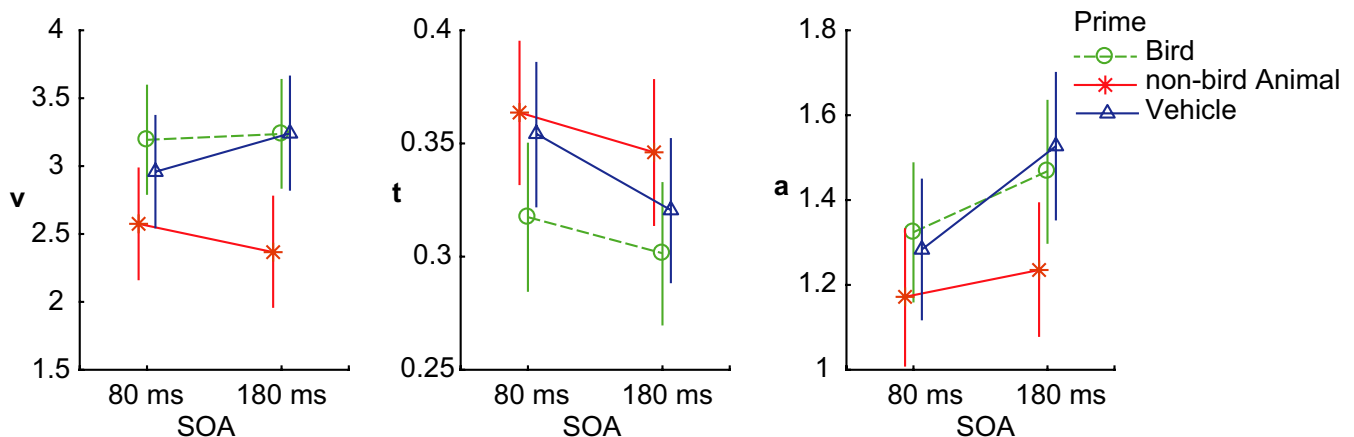
Non-decisional processes (t)

Non-decisional processes were faster following a bird than a non-bird animal prime ($P = .02$ and $P = .03$ at 80 and 180 ms SOA, respectively). For the vehicle prime, t was slower than for the bird prime at the short SOA ($P = .06$), but did not differ from that for the non-bird animal prime condition ($P = .34$). At the longer SOA, t in the vehicle prime condition became faster and was barely distinguishable from bird or non-bird animal prime conditions ($P = .20$ and $P = .13$, respectively). This finding is supported by the quantile analysis described earlier which shows a decay in the priming effect due to vehicle primes for the long SOA at long RTs (later quantiles). In short, primes eliciting different motor responses than the target slowed down behaviour. This effect was observed at both short and long SOAs although the difference was reduced for the unrelated prime at long SOA. This replicates the response congruency effect found by Voss et al. (2013).

Decision threshold (a)

The decision threshold was similar after bird and vehicle primes at both SOAs ($Ps > .46$). It was lower in the non-bird animal prime condition, particularly at long SOA ($Ps < .03$); there was less of a difference at short SOA ($P = .10$ and $P = .17$ compared to bird and vehicle prime condition, respectively). This suggests that incorrect responses were fast in the related incongruent prime condition compared to the other two conditions, particularly at long SOA. This might reflect the premature execution of an incorrect response, probably due to the high similarity between prime and target features.

different from each other. This can be interpreted in a similar way, but is not equivalent, to *p*-values estimated in frequentist statistics. Here, a probability (*P*) of less than .05 indicates that there is substantial evidence for a difference between the two conditions being compared and the strength of this difference is reflected in the probability value.

Drift rate (v)

In general, non-bird animal primes slowed down the accumulation of evidence of the target stimulus compared to the other primes (Figure 5). The accumulation of evidence was slower when the bird target was preceded by a non-bird animal than by a bird prime at both 80 ms ($P = .02$) and 180 ms ($P = .002$) SOA. The drift rate in the non-bird animal prime condition was also slower than in the vehicle prime condition at 180 ms ($P = .0015$) but only to a small extent at 80 ms ($p = .10$). There was no clear difference in v between bird and vehicle primes ($P = .21$ and $P = .51$ at short and long SOA, respectively).

Summary

The DDM results show that the priming effect for unrelated (vehicle) primes is mainly the result of longer non-decisional processes, indicating a likely interference in motor response.

FIGURE 5 Posterior estimates of the hierarchical drift diffusion model parameters: drift rate *v*, non-decision time *t*, decision threshold *a*, for the three different primes and the two SOAs. Larger *v* values correspond to faster decisional processes and therefore faster RTs while larger *t* values correspond to long non-decisional processes and therefore slower RTs. Error bars represent 89% credible intervals

For related primes (non-bird animal) in addition to response competition, decisional processes interfere with the categorisation of the target.

2.3 | Discussion

Our results showed that an image flashed for only 20 ms affected the categorisation of a subsequent image both in terms of response speed and accuracy. If the two images in the sequence contained a bird, even though not identical, participants were faster and more accurate than when the prime was a non-bird animal or a vehicle. This was true at short and long SOAs, implying that some information about the prime's category, perhaps sufficient to bias a motor response, had been processed automatically and very quickly.

As such, it can be argued that this priming effect is not the consequence of the interaction between different object categories but reflects stimulus-response binding between the bird category and a "yes" motor response (e.g., Denkinger & Koutstaal, 2009; Eckstein & Henson, 2012; Horner & Henson, 2009). This is probably the case to some extent and the results of the drift diffusion model support this idea showing slower non-decisional processes in the two incongruent conditions compared to the congruent condition. That is, the incongruent prime slows down response execution.

Importantly, our results showed that the priming effect was larger for related (non-bird animal) than unrelated (vehicle) primes. Both types of incongruent primes were presented the same number of times over the experiment and had the same stimulus–response association ("no" response). Thus, if the priming effect was only driven by stimulus–response association or a motor conflict, we should have observed the same amount of priming for related and unrelated incongruent primes. Our results suggest that at least part of the priming effect is directly caused by the relatedness between prime and target categories. Indeed, the DDM results show that the priming effect due to a vehicle prime could be explained mainly by non-decisional processes. However, the priming effect caused by non-bird animal primes was explained by non-decisional *and* decisional processes. Non-bird animal primes affected the accumulation of evidence v, the decision threshold a and non-decisional processes t.

The priming effect increases for related primes at longer SOA but not for unrelated primes. This could be explained by the combination of two mechanisms. First, the effect of unrelated primes decreases with longer SOA (the DDM parameters for unrelated incongruent primes become comparable to those of the congruent condition at the longer SOA). Second, the decision threshold does not increase at long SOA for non-bird animal primes compared to vehicle primes. That is, in the non-bird animal prime condition participants are fast but at the expense of accuracy, particularly at long SOA.

Taken together, these mechanisms can explain the increase in the priming effect for related compared to unrelated primes with longer SOA.

Considered together, our results show that the categorisation of a bird image is easier after a congruent than an incongruent prime due to an easier response selection process (t). Decisional processes were affected differentially depending on whether the prime was related or unrelated (shared the same superordinate animal category as the target or not). Unrelated primes marginally affected the accumulation of evidence while related primes caused both a lower decision threshold and a slower accumulation of evidence (corresponding to less accurate and slower responses, respectively). Thus, the efficiency of processing the target stimulus (bird) was almost unchanged by an unrelated prime (vehicle) but strongly affected by a related prime (non-bird animal). This specific effect can be understood as the processing of a noisy signal (which leads to both a slow drift rate and inaccurate responses) and is in accordance with the interference effect found by Cohen et al. (2014) but not with a facilitation effect from a spread of activation process. Our results suggest that the priming interference depends on how many attributes are shared between prime and target. When prime and target features are vastly different, such as in the unrelated condition, the prime marginally affects the accumulation of evidence. However, in the related condition, prime and target share many visual features (i.e., all animals have eyes), which renders the accumulation of evidence slower and noisier.

3 | EXPERIMENT 2: SUPERORDINATE-LEVEL (ANIMAL) CATEGORISATION

In the second experiment, we tested participants in an animal/non-animal categorisation task. We further tested the effect of shared attributes by examining more subtle relationships between objects. Instead of comparing objects that share or do not share the same superordinate category (and therefore many or almost no features), we tested attributes that are not inherent to a specific superordinate category and therefore not directly relevant for the task. In other words, we determined whether the sharing of non-essential features also modulates interactions between visual categories. These non-essential properties nevertheless varied the semantic connections between pairs of objects.

Orthogonal visual features, such as size, position, orientation, are processed automatically (Hong, Yamins, Majaj, & DiCarlo, 2016; Konkle & Oliva, 2012), and the function of objects also plays a role in how objects are represented (Greene, Baldassano, Esteva, Beck, & Fei-Fei, 2016; Huth, Nishimoto, Vu, & Gallant, 2012; Peelen & Downing, 2017). Here, we grouped animal and vehicle images into three subclasses: air,

ground or water. This should allow us to compare images that are a-priori more related to each other within a group than across groups. Further, this membership was not relevant for the animal/non-animal categorisation task and could be tested in both congruent and incongruent trials. To give a concrete example, a target dog, categorised as an animal, could be preceded by four types of primes: a cat (congruent related: same response and ground subclass), a bird (congruent unrelated: same response, different subclass), a truck (incongruent related: different response, same ground subclass), or a plane (incongruent unrelated: different response and subclass).

3.1 | Method

3.1.1 | Participants

13 new volunteers and the first author (8 women, all right-handed; mean age 24 ± 3 years) participated in this experiment. All participants had normal or corrected to normal vision and provided written informed consent. Experiment 2 participants were different from Experiment 1 participants (except for the first author) so that the stimulus–response association was uncontaminated within each experiment. This was done to prevent introducing confounds due to task-switching (Denkinger & Koutstaal, 2009; Druey, 2013; Horner & Henson, 2008, 2009, 2011) ; that is, interference from an earlier task on the current one, for example interference due to a dog being a distractor in an earlier task but a target in the current one, was avoided.

3.1.2 | Design and stimuli

The experiment consisted of a total of 16 blocks of 96 trials. In half of the blocks, the SOA between the prime and the target image was 80 ms, and in the other half, it was 180 ms. The order of the blocks was randomised. Within a block, half of the target images contained animals and the other half vehicles. For each target type, half of the primes were congruent and half were incongruent. Furthermore, each stimulus could belong to one of three subclasses (air, ground or water). For each congruent or incongruent condition, half of the primes belonged to the same subclass as the target image (related prime) and half belonged to a different subclass (unrelated prime). Thus, in one block, participants performed 12 congruent related trials (e.g., cat–dog), 12 congruent unrelated trials (e.g., bird–dog), 12 incongruent related trials (e.g., truck–dog) and 12 incongruent unrelated trials (e.g., plane–dog) with an animal presented as the target image. Additionally, the same conditions with the same number of trials per block were used but with a vehicle presented as the target image.

Most of the stimuli were the ones used in Experiment 1 but for the purpose of this experiment, fewer images of birds and more images of vehicles and non-bird animals were included. The set of images was composed of 1,536 animals and 1,536 vehicles that could be presented as either the prime or the target image. These two categories were composed of three equal subclasses representing air, ground or water. In the animal category, 1/3 of the images were birds (pigeon, duck, etc.), 1/3 were mammals (cow, deer, etc.) and 1/3 were fish (shark, salmon, etc.). In the vehicle category, 1/3 of the images were air vehicles (plane, helicopter, etc.), 1/3 were ground vehicles (motorbike, truck, etc.), and 1/3 were water vehicles (boat, canoe, etc.). Within each subclass, the object was presented in various contexts, for example a bird could be flying in the sky, standing on the ground or on a lake.

3.1.3 | Procedure

The same procedure as in Experiment 1 was used but participants were asked to perform an animal/non-animal categorisation task (Figure 1).

3.1.4 | Data analysis

We calculated ER and median RT on animal target pictures for each participant. The analysis for responses to vehicle images can be found in Appendix S1. Trials with anticipatory responses or the absence of response within 1.2 s (0.8% of all trials) were excluded from the analysis. As in Experiment 1, we defined the priming effect as the difference in performance between incongruent and congruent trials. We determined the priming effect for related images (e.g., car/dog trial *minus* cat/dog trial) and for unrelated images (e.g., plane/dog *minus* fish/dog), separately. We first compared these differences, pooled over related and unrelated trials, to 0 using one-sample *t* tests to determine the effect of response congruency on performance. Then, a 2×2 repeated measures ANOVA (SOA x relatedness) was applied to RT and ER priming to determine the role of relatedness on performance. All reported paired *t* tests are Bonferroni corrected. We also included signal detection analysis while keeping in mind the caveats introduced in Experiment 1 (see section 2.1.4). Finally, we conducted a quantile analysis of RT and modelled our data with HDDM using the same procedure as in Experiment 1. Gelman–Rubin diagnostics showed that all 5 chains converged well: all $\hat{R}$ values were below 1.0065. Posterior predictive checks also showed a good fit between observed RT and predicted RT from the model (see Figure 6 and Table S2).[2]

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[2]As in Experiment 1, the results of a stimulus-coding procedure which includes responses to animal and non-animal images are reported in Supplementary Materials (Figure S8). This model revealed no difference in response bias, z, between conditions and produced very similar output as reported here with an accuracy-coding procedure.
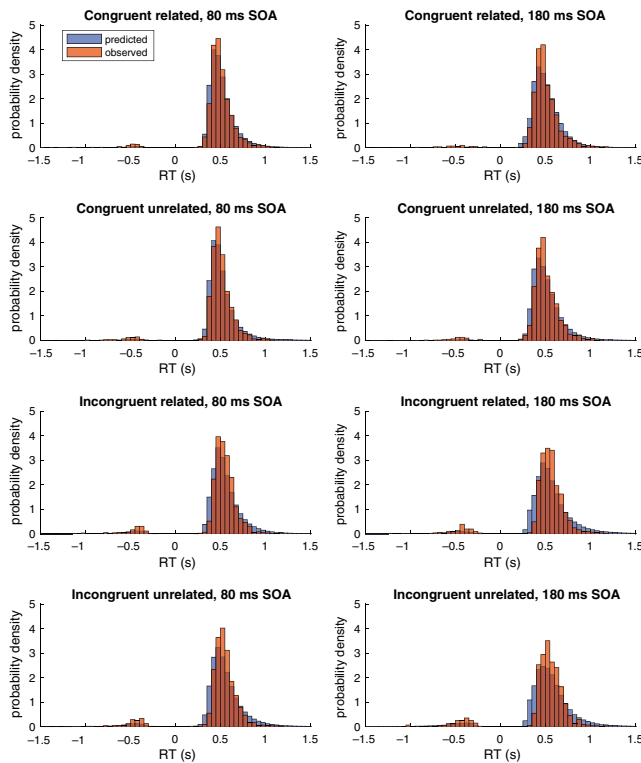
FIGURE 6 Observed (red histograms) and HDDM predicted (blue histograms) RT distributions in the different prime and SOA conditions in Experiment 2. Incorrect responses are represented with negative RTs

3.2 | Results

3.2.1 | Priming effect

As in Experiment 1, we were interested in studying the influence of the prime category and SOA on the priming effect (Figure 7). To test the effect of response congruency, the two relatedness conditions were pooled. We report the raw RT and ER for the target category "animal" in Table 4 and for the distractor category "vehicle" in Table 5. We present the statistical analysis of responses to vehicle images in the Appendix S1. This analysis shows comparable results to that of animal images.

Effect of response congruency
Error rates. ER was in general higher in incongruent than in congruent trials. At 80 ms SOA, ER was on average 3 percentage points higher in the incongruent compared to the congruent condition ($t(12) = 3.20$, $p = .02$), and at 180 ms, it was around 5 percentage points higher ($t(12) = 3.72$, $p = .006$).

Reaction times. RTs were on average 41 ms slower in the incongruent compared to the congruent condition at 80 ms SOA ($t(12) = 6.77$, $p < .001$) and 61 ms slower in

the incongruent condition at 180 ms SOA ($t(12) = 6.45$, $p < .001$).

Effect of relatedness
Error rates. The RM-ANOVA on ER priming revealed no difference between related and unrelated primes ($F(1,12) = 0.26$, $p = .62$, $_p\eta^2 = 0.02$). There was also no effect of SOA ($F(1,12) = 1.60$, $p = .23$, $_p\eta^2 = 0.12$) or interaction between relatedness and SOA ($F(1,12) = 0.42$, $p = .53$, $_p\eta^2 = 0.03$).

Reaction times. RT priming was higher at longer SOA ($F(1,12) = 8.83$, $p = .01$, $_p\eta^2 = 0.42$) but there was no effect of relatedness ($F(1,12) = 0.13$, $p = .52$, $_p\eta^2 = 0.03$) or an interaction ($F(1,12) = 3.50$, $p = .09$, $_p\eta^2 = 0.23$).

Summary
As observed in Experiment 1, the prime category was processed automatically by the participants leading to better performance in the congruent condition than in the incongruent conditions. However, prime relatedness, when not task-relevant, did not seem to have modulated responses, confirming previous results (Evans, Horowitz, & Wolfe, 2011).

3.2.2 | Signal detection analysis

As mentioned in Experiment 1, SDT analysis is not easily applicable to our paradigm and its interpretation can be unclear. Nevertheless, we report d-prime and criterion (Table 6) using the two approaches discussed earlier: when the kind of prime is consistent across Hits and FAs (confounding the effect of congruency) and when congruency is consistent across Hits and FAs (confounding the effect of prime category).

According to the approach where the prime is kept constant, participants showed a bias towards "yes" responses when presented with an animal prime and towards "no" responses with a vehicle prime. d-primes were otherwise very similar in all conditions. Given that accuracy is very high, comparing animal and vehicle primes consists primarily in comparing Hits for animal prime trials, which are congruent, with Hits for vehicle prime trials, which are incongruent. Thus, not surprisingly, participants were more conservative in incongruent trials than in congruent trials. On the contrary, according to the approach where congruency is kept constant, d-primes were higher for congruent than for incongruent trials. Importantly, no response bias was observed suggesting that the effect of congruency was perceptual. Overall, these results support the findings that, with the current set of manipulations, congruency strongly affects performance, whereas relatedness between two categories has little to a mild effect on behaviour.
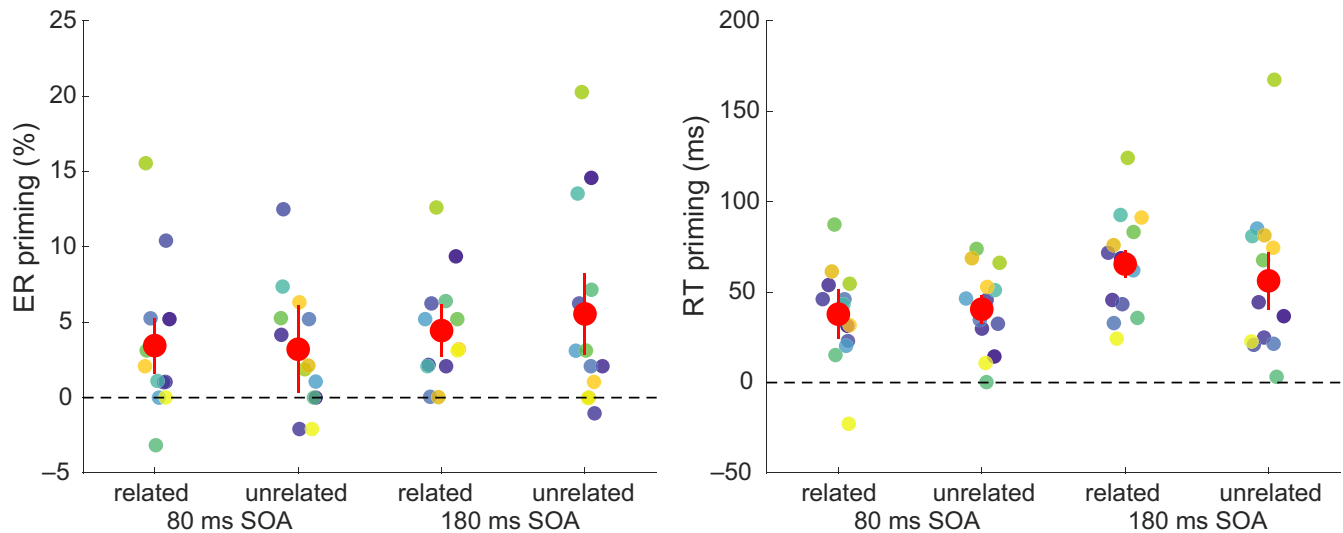
FIGURE 7 Priming effect in Experiment 2 (animal/non-animal categorisation task) for ER (left panel) and RT (right panel). Each coloured dot represents one participant's performance. The average across participants is represented in red with within-subject 95% CI

TABLE 4 Average of median RT in ms and mean ER in % in Experiment 2 for categorising an animal image

	80 ms SOA				180 ms SOA			
	Congruent related	Incongruent Related	Congruent Unrelated	Incongruent Unrelated	Congruent related	Incongruent Related	Congruent Unrelated	Incongruent Unrelated
RT	496 (17)	534 (16)	497 (17)	538 (17)	488 (19)	553 (19)	492 (20)	549 (20)
ER	2.59 (0.74)	6.04 (1.55)	3.50 (0.79)	6.71 (1.17)	2.35 (0.66)	6.80 (1.47)	3.03 (0.63)	8.58 (2.21)

Note: Animal images were presented after a congruent related, an incongruent related, a congruent unrelated or an incongruent unrelated prime with a SOA of 80 ms or 180 ms. SEM are reported in parentheses.

TABLE 5 Average of median RT in ms and mean ER in % in Experiment 2 to non-animal (vehicle) images

	80 ms SOA				180 ms SOA			
	Congruent related	Incongruent Related	Congruent Unrelated	Incongruent Unrelated	Congruent related	Incongruent Related	Congruent Unrelated	Incongruent Unrelated
RT	488 (18)	538 (19)	501 (17)	541 (19)	495 (21)	553 (22)	507 (20)	555 (23)
ER	1.80 (0.56)	5.64 (1.02)	1.47 (0.48)	5.99 (1.26)	1.45 (0.40)	7.14 (2.47)	2.51 (0.52)	7.13 (2.39)

Note: At 80 ms and 180 ms SOA depending on the prime congruency and relatedness. SEM are reported in parentheses.

3.2.3 | Quantile analysis

The results of the quantile analysis show that the priming effect is stable across RTs in both related and unrelated conditions (Figure 8). There might be a small decrease at the slowest quantile for the unrelated prime at long SOA but this observation is based on just one data point. In general, the analysis suggests that the prime is not processed further once the target object is presented. The interference that the prime induces is present from the onset of the target and does not change at longer RTs.

3.2.4 | Drift diffusion modelling

As in Experiment 1, to compare the experimental conditions, we calculated a Bayesian probability measure (P) that two distributions are different from each other.

Drift rate (v)
The accumulation of evidence was much faster after a congruent than an incongruent prime (all Ps < .01; Figure 9). However, the drift rate was not affected by the relatedness of the prime (all Ps > .14) or by the SOA (all Ps > .19).

TABLE 6 Signal detection analysis in Experiment 2

	Hit trials	FA trials	80 ms SOA		180 ms SOA	
			d-prime	Criterion	d-prime	Criterion
Consistent prime						
Animal related	AA related	AV related	3.73 (0.19)	−0.21 (0.05)	3.79 (0.24)	−0.21 (0.08)
Animal unrelated	AA unrelated	AV unrelated	3.61 (0.17)	−0.13 (0.07)	3.67 (0.24)	−0.13 (0.06)
Vehicle related	VA related	VV related	3.85 (0.20)	0.26 (0.04)	3.79 (0.15)	0.33 (0.05)
Vehicle unrelated	VA unrelated	VV unrelated	3.79 (0.13)	0.34 (0.06)	3.59 (0.19)	0.25 (0.08)
Consistent congruency						
Congruent related	AA related	VV related	4.21 (0.18)	0.06 (0.06)	4.29 (0.16)	0.08 (0.06)
Congruent unrelated	AA unrelated	VV unrelated	4.12 (0.15)	0.18 (0.06)	3.98 (0.14)	0.03 (0.06)
Incongruent related	VA related	AV related	3.39 (0.23)	−0.02 (0.03)	3.27 (0.25)	0.06 (0.07)
Incongruent unrelated	VA unrelated	AV unrelated	3.25 (0.16)	0.05 (0.07)	3.26 (0.31)	0.08 (0.04)

Note: Mean d-prime and criterion are reported with their *SEM* in parentheses.

Abbreviations; A, animal image; V, vehicle image.
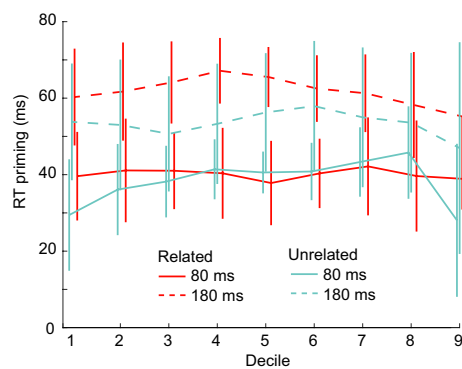
FIGURE 8 Evolution of the RT priming effect in Experiment 2 depending on the speed of the participants' responses. Error bars represent within-subject 95% CI

Non-decisional processes (t)

Non-decisional processes were similar across conditions, except that it decreased in the congruent related condition at longer SOA ($P = .01$). With an increase in SOA, there might be better preparation of the motor response in the congruent conditions. However, *t* does not decrease as much after a congruent unrelated prime ($P = .15$). Thus, response congruency alone cannot account for the acceleration of non-decisional processes with longer SOA. The relatedness of the prime also needs to be taken into consideration.

Decision threshold (a)

At short SOA, the decision threshold was similar across conditions (all $Ps > .18$). *a* increased (less noisy signal, more accurate responses) in the congruent related condition at longer SOA compared to short SOA ($P = .04$) such that there was a clear difference at long SOA between related congruent and incongruent conditions ($P = .009$). In other words, when the prime was from the same category and class as the target,

responses became more accurate at long SOA. This effect was absent in other prime conditions.

Summary

The priming effect observed in Experiment 2 is the result of a strong congruency effect on the drift rate. Although we would have expected an effect on non-decisional processes (*t*), the congruency effect is explained by a slower *v* in incongruent than in congruent conditions. With our results, it is difficult to determine whether the congruent prime facilitates the accumulation of evidence (*v*) or if the incongruent prime slows it down. However, given that in Experiment 1 the accumulation of evidence was slowed down only in the incongruent related condition, it is more likely that incongruent primes slow down the accumulation of evidence.

There was no effect of relatedness in the incongruent conditions. However, in the congruent condition, related primes facilitated target processing at long SOA for *a* and *t*. This suggests that when prime and target are very similar, the prime can speed up target processing with long enough SOA. That is, this facilitation is a late effect and seems to build up with more time between prime and target.

3.3 | Discussion

As in Experiment 1, the presentation of a brief image influenced the categorisation of a following image in an animal/non-animal task. Despite a large diversity of images (animals and vehicles) used in this study, we found a large congruency effect. Participants were slower and less accurate in categorising an animal target after a vehicle prime than after an animal prime and this effect increased with SOA.

Our DDM analyses show that the difference between congruent and incongruent primes was not explained by
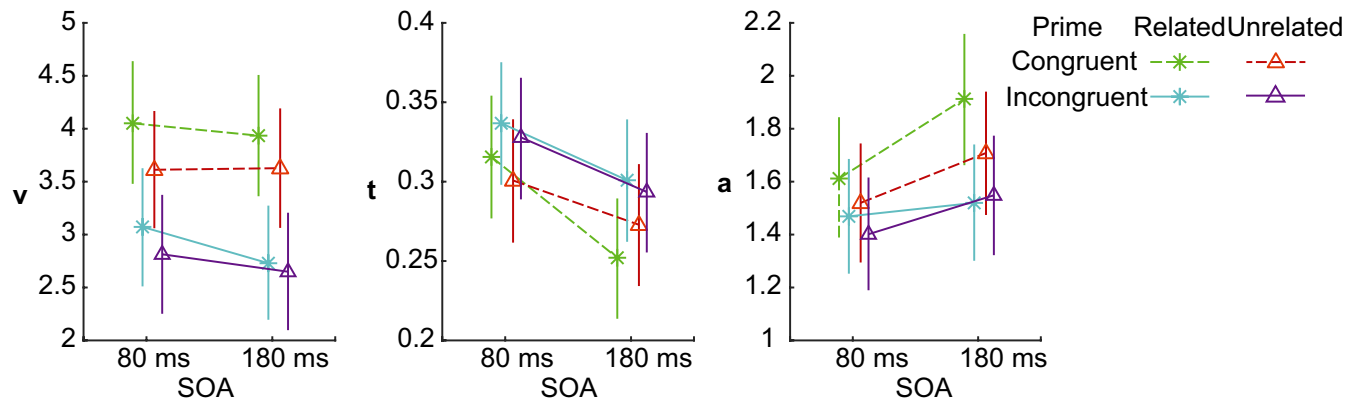
FIGURE 9 Posterior estimates of the hierarchical drift diffusion model parameters in Experiment 2: drift rate v, non-decision time t, decision threshold a, for the four different primes and the two SOAs. Error bars represent 89% credible intervals

non-decisional processes (motor preparation) but by a slower drift rate in the incongruent conditions. Even if prime and target do not belong to the same subclass, as long as they share the same superordinate category, the drift rate is faster than for a prime that belongs to a different superordinate category. It is somewhat surprising that we did not find a noticeable difference in non-decisional time between congruent and incongruent trials even though this effect was clearly visible in Experiment 1. t was in general lower (faster) in the congruent condition compared with the incongruent condition (the extent of overlap between conditions varied between 0.77 and 0.96, with 0.5 being complete overlap and 1 no overlap) but this difference was stronger in Experiment 1 (where the probabilities were above 0.95, except at long SOA when comparing vehicle and bird primes). This suggests that the association between an object category and its corresponding motor response was stronger in Experiment 1 than in Experiment 2. One possible explanation for this stimulus–response mapping difference is that the target category (bird) is better defined (less broad and diverse) in the first than in the second (animal category) experiment. Therefore, the mapping between the response and the stimulus could have been based on only a few bird features in Experiment 1 which would accentuate the effect of non-decisional processes.

Relatedness had only a small effect in this experiment. This could be because these attributes were task irrelevant and/or because the (semantic) relationship between the objects (e.g., within *air* animals as opposed to between *air* and *ground* animals) was not very strong. Nevertheless, the results of the DDM suggest that relatedness seems to have an effect at long SOA on congruent primes. We found that related congruent primes facilitated target categorisation, particularly at long SOA, through modulating a and t.

Interestingly, task requirements have a major impact on the priming effect. In Experiment 1, categorising a bird target was much faster and more accurate when preceded by a bird than by a non-bird animal. On the other hand, in Experiment

2, there was no difference when air animal (birds) were preceded by either air animals or other animals (non-birds) (RT priming: $t(12) = 0.55$, $p = .59$; ER priming: $t(12) = 0.39$, $p = .70$). This difference between the two experiments, despite these conditions using the same stimulus pairings, can be explained by response congruency: in Experiment 1, non-bird animal primes were incongruent with a bird response whereas in Experiment 2 non-bird animal primes were congruent with an animal response.

However, response congruency alone cannot explain all our results. For example, the amount of priming was different for the two incongruent primes in Experiment 1. Further, consider the following results. A vehicle prime in Experiment 2 interfered more than an animal prime when categorising an animal target. In Experiment 1, a vehicle prime interfered less than an animal prime when categorising a bird target. This set of findings cannot be explained by response congruency, since vehicles were incongruent in both experiments. Hence, this outcome must depend on the specific categorisation task. In Experiment 1, the target category is set around only birds, whereas in the second the target category encompasses a larger set of objects, all animals. We discuss how this difference in task requirements can explain our results in the General Discussion section.

4 | GENERAL DISCUSSION

The main goals of this study were to examine how visual categories interact when active within a short temporal window and to determine the cognitive mechanisms underlying these interactions. Our results show that a brief presentation of an image influenced categorisation performance of a subsequent test image at both basic and superordinate levels. Participants knew that they should ignore the first image (prime) but its processing was unavoidable. Thus, in agreement with previous observations (Evans et al., 2011),

a first conclusion of our study is that object attributes, particularly those that determine category membership, are automatically and rapidly processed and can influence the processing of other objects. Crucially, the relatedness between the prime and the subsequent image modulated performance. We discuss these findings and their implications in detail below (see section 4.1).

Additionally, our results show that when prime and target conveyed the same response (congruent condition) performance was better than when the two images conveyed conflicting responses (incongruent condition). This effect can partially be attributed to an interference at the motor response stage, which replicates previous findings (Voss et al., 2013), but more so, and interestingly, during the accumulation of evidence. This suggests that the prime sufficiently alters the state of category-processing neurons such that subsequent processing of the target is modulated by this changed state. This effect of the prime on the accumulation of evidence depends on how similar the prime is to the target category as defined by the task.

Finally, the SOA between the two images influenced the priming effect only in two specific conditions. In Experiment 1, the interference due to an unrelated incongruent prime (vehicle prime for a bird target) reduced with longer SOA. In Experiment 2, related congruent primes (bird prime for a bird target) facilitated target categorisation at the longer SOA. Interestingly, although these effects seem to be in opposite directions, the DDM results in both conditions reveal that the SOA effect was not driven by a difference in v but instead by faster t and higher a. This finding could be explained by a striking characteristic shared by these two conditions: they are the easiest conditions in terms of perceptual distance or similarity between the prime and the target. The primes are either extremely dissimilar to the target representation (vehicles in Experiment 1; maximal perceptual distance with the target exemplar) or extremely similar to it (congruent related primes in Experiment 2; minimal distance from the target exemplar). That is, SOA did not influence the processing of the target during categorisation, but participants modified their response criteria and motor preparation at longer SOAs in the easiest conditions. This suggests that the interaction between two objects is temporally stable, particularly with regard to the processing of categories in the visual system (accumulation of evidence). This conclusion is bolstered by the finding that the behavioural priming effect remains stable over a long range of response times, as revealed by the quantile analyses.

Together, our results suggest that a briefly presented image interacts with the categorisation of a following image. This interaction does not facilitate the processing of the image, as the pre-activation or the spread of activation hypotheses would suggest, but instead interferes with it, as the neural interference proposal would suggest (such as in Cohen et al., 2014). We outline, below, a general principle that can explain our and others' results, inspired by and incorporating the current understanding of the organisation of visual categories in the brain.

4.1 | Interactions are determined by the organisation of categories

Visual objects can be represented in a multi-dimensional space in which the distance between them is based on their perceptual similarity (Carlson, Ritchie, Ritchie, Kriegeskorte, Durvasula, & Ma, 2013; Mohan & Arun, 2012; Ritchie, Tovar, & Carlson, 2015; Sofer, Crouzet, & Serre, 2015). When these distances are mapped out, the resulting layout exhibits a hierarchical structure in which sub-categories are nested within more broad categories (see Figure 10). This sort of organisation has also been described in the language domain, particularly by McClelland & Rogers to illustrate their Parallel Distributed Processing theory (McClelland & Rogers, 2003; Rogers & Patterson, 2007).

Interestingly, this perceptual organisation accords well with the neural organisation of visual categories in the ITC (Carlson, Simmons, Kriegeskorte, & Slevc, 2014; Jozwik, Kriegeskorte, & Mur, 2015; Mur et al., 2013). Several studies have shown that real-world objects are represented in the ITC both in a continuous and a categorical manner (Bell, Hadj-Bouziane, Frihauf, Tootell, & Ungerleider, 2008; Kriegeskorte et al., 2008; Sato et al., 2013; Sha et al., 2014). Patterns of neural activity elicited by related objects (e.g., cat and bird) resemble each other more than those elicited by unrelated objects (e.g., cat and plane). The degree of (dis) similarity between objects can be depicted as a distance in a multi-dimensional continuous semantic or neural space (Kriegeskorte et al., 2008; Mur et al., 2012). Further, objects are represented in the ITC in categorical clusters. For example, there seem to be patches of neurons that specialise in processing specific categories such as animate and inanimate objects, or faces and body parts (e.g., Freiwald & Tsao, 2010; Grill-Spector, 2003).

Given this perceptual and neural organisation, to perform a categorisation task the system will need to determine a boundary around the set of object features or elements that define and distinguish the target category from other categories. For example, in a bird/non-bird categorisation task, the system needs to include features that are shared by other categories, such as "eye," but needs to specifically look for features that are found only in birds, such as "feather." This boundary might be thought of (but is not restricted to) as a linear separation between target and distractors as decoding studies might suggest (DiCarlo & Cox, 2007). We are
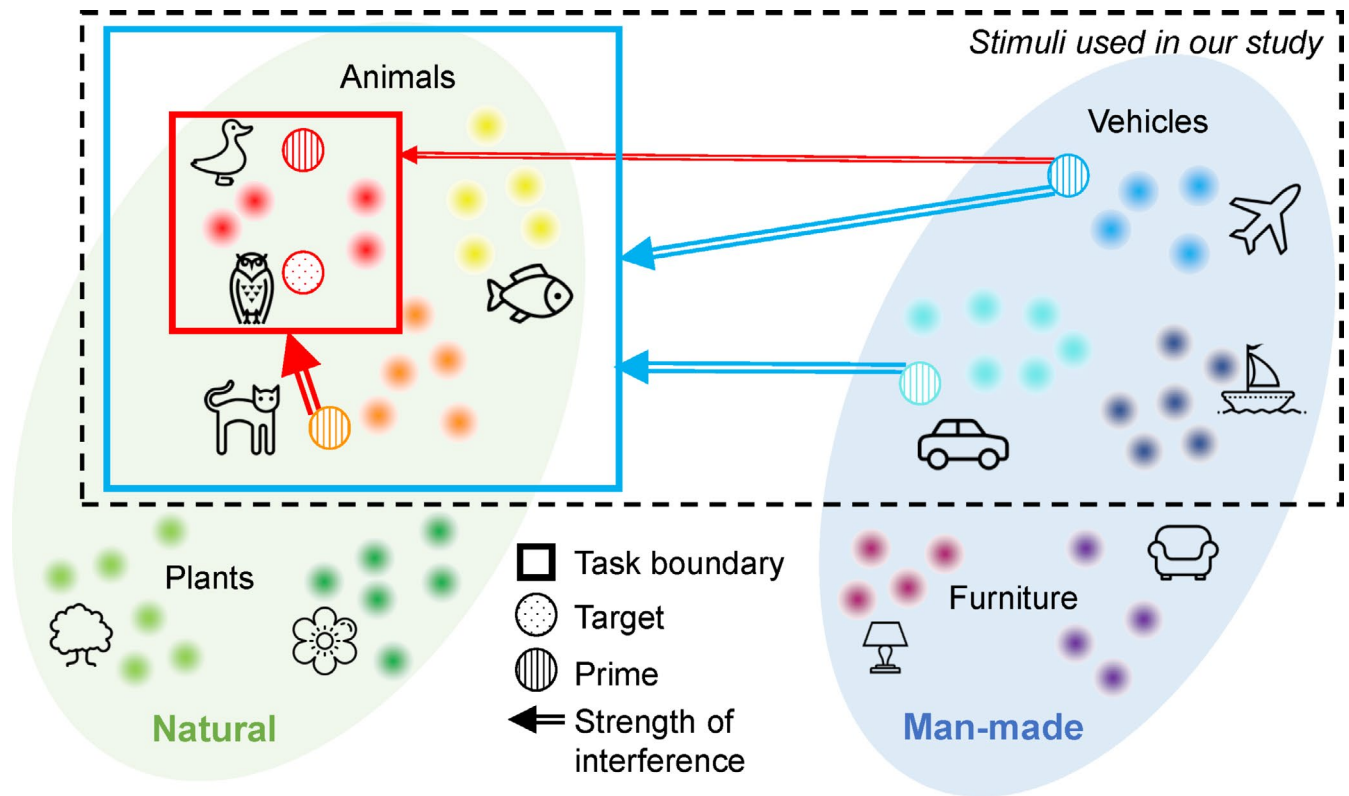
FIGURE 10 Schematic representation of object representations with their possible interactions. Each coloured circular blob represents an object. Different colours represent different basic categories from among natural and man-made categories. In Experiment 1, we asked observers to perform a bird/non-bird categorisation task. The task boundary in this case would be the red square that encloses bird representations but excludes all other. The task boundary in Experiment 2 (animal categorisation) is represented by the blue square. The different experimental conditions are illustrated with patterned circles. The red circle with dot patterns represents a bird (animal) target. The four circles with vertical lines represent possible primes. The red circle with vertical lines is a bird prime, the orange circle with vertical lines is a non-bird animal prime, and the two blue circles with vertical lines are vehicle primes. In Experiment 2, if we take the example of an air animal target (bird, dot-filled circle), the red circle with vertical lines represents a congruent related prime (bird), the orange circle with vertical line an unrelated congruent prime (cat), the two blue vertical blobs a related and an unrelated incongruent prime (plane and car respectively). The arrows indicate interference in Experiments 1(red arrows) and 2 (blue arrows). When the prime does not belong to the target category (the prime is outside the red or blue square), the closer it is to the boundary, the slower the target processing. In Experiment 1, the distance to the task boundary (red square) is close for non-bird animals but not for vehicles, explaining the large interference from the non-bird animal primes (larger arrow) but almost no interference from vehicle primes. In Experiment 2, the distance between vehicles and the task boundary (blue square) decreases compared to Experiment 1 such that vehicles interfere with the processing of an animal target. Icons from https://icons8.com

agnostic as to how exactly this separation occurs in the representational space.

In addition to changes in task-related boundary, the distance between representations itself might vary depending on the task. Several studies have shown that discriminability of neural representations is affected by task demands and it has been suggested that attention could selectively exaggerate the distance between them along relevant dimensions (Çukur, Nishimoto, Huth, & Gallant, 2013; Erez & Duncan, 2015; Harel, Kravitz, & Baker, 2014; Nastase et al., 2017). However, such effects cannot explain, on their own, the difference between facilitatory or interfering prime effects. A boundary or a maximal distance at which one representation cannot be considered as congruent (and becomes incongruent) needs to be set. Therefore, we focus our interpretation on the role of

task boundary in the priming effect without discussing the role of attention further.

The continuous and categorical organisation of categories influences participants' performance in single object categorisation tasks (Carlson, Ritchie, et al., 2013; Ritchie et al., 2015; Sofer et al., 2015). For example, Carlson, Ritchie, et al. (2013) have shown that the distance between the neural representation of an object and its task-defined category boundary predicts the speed at which it can be categorised. According to them, this finding explains why a highly discriminable object, which implies a large distance between it and its category boundary, can be categorised quickly. We will utilise this "distance-to-bound" approach (Ritchie & Carlson, 2016) in our explanation of the results. Specifically, we will consider the proposal that

the distance from a prime to the target category boundary modulates the strength of the interference in the accumulation of evidence.

In Experiment 1, participants were asked to perform a bird/non-bird categorisation. Here, the target category boundary would be set around birds. In this situation, non-bird animals are close to the boundary (since they are within the same superordinate animal category) while vehicles are further away from the target category boundary (since they belong to a distinct superordinate category). In accordance with the distance-to-bound principle's predictions, the accumulation of evidence was slower for a bird image when it was preceded by a related (non-bird animal) than by an unrelated (vehicle) prime. In Experiment 2, the task boundary was set around all animals. The vehicle category is now closer to the boundary. According to the distance-to-bound principle, it should interfere with the accumulation of evidence for an animal (such as a bird) target image, more than in Experiment 1, which is what we find. This raises the important point that it is not the distance between the prime and the specific target image that matters but the prime's distance to the task-relevant category *boundary*. Indeed, if the distance between prime and target images were the determining factor, the interference induced by a vehicle prime on a bird target should have been the same in both experiments; the distance between them remains the same in both tasks. However, there was hardly any interference in the speed of information accumulation in the basic-level categorisation task (Experiment 1), but a substantial reduction in the speed at the superordinate-level (Experiment 2). Thus, the rate of evidence accumulation depends on the prime's distance to the target boundary and therefore reflects the organisation of categories in the brain, presumably in the ITC (see Figure 10 for an illustration and examples).

This distance-to-bound approach is not incompatible with the neural overlap explanation developed by Cohen et al. (2014). In their studies, they argue that the interference from a distractor depends on the extent to which its neural activity overlaps with that of the target representation: the more similar the neural activity, the greater the interference. One can easily consider the amount of neural activity overlap to be in direct relation with the distance between representations, the explanatory principle that we utilise, since both reflect the perceptual similarity between the stimuli. That is, the extent of neural overlap between two objects might be strongly correlated with the perceptual distance between them. Extending this reasoning to our study, we can begin by assuming that the categories of both objects are processed and overlap in the ITC (the interpretation remains the same if the relevant processing occurs in other brain regions) since the SOA between the two images is relatively short (but long enough to not cause backward or forward masking). In incongruent

trials, a related incongruent prime (say a non-bird animal in Experiment 1) would elicit activity that is more similar to that of the target than an unrelated incongruent prime (a vehicle in Experiment 1). This increased similarity in neural activity of the related incongruent prime leads to more interference with the target, which would explain our current result.

Speaking in more general terms, when the prime is congruent with the target (bird–bird trial in Experiment 1 and animal–animal trial in Experiment 2), it evokes the same motor and similar neural response as the target. In an incongruent trial, the prime elicits activity outside the target category boundary, whereas the target elicits activity within it. The available information is therefore noisy as it conveys conflicting information and the system needs to separate out the two patterns of activity to reach a decision about the target's category. In this case, we would expect that the more similar the two representations are, the more the prime will interfere with the processing of the target, exactly as observed. Our findings therefore support Cohen et al.'s proposal. However, as mentioned above, there is a caveat. Cohen et al. considered the neural overlap between two objects, which translates to the distance between two objects. This distance is not sufficient to explain all our results. As discussed, it is the distance of the prime to the task-relevant boundary and not to the target representation that is relevant; otherwise, the vehicle prime would have had the same interference at both categorisation levels. Thus, we argue that Cohen et al. proposal is only applicable to the specific situation they tested and thus may not be a general principle to explain object interactions. In a categorisation task, the system is looking for any evidence (neural activity) that suggests that the image belongs to the target category. If there is activity outside the category boundary, as is the case for an incongruent prime, the distance-to-bound principle indicates that the processing time needed for the prime representation to be discounted (or parcelled out) increases the closer it is to the task-relevant category boundary.

4.2 | Locus of category interactions

There are good reasons to think that categories interact in the ITC, particularly when two objects are visually presented in rapid succession. First, ITC has been documented to represent categories, in a way that is similar to the perceptual organisation of categories (Jozwik et al., 2015; Kriegeskorte et al., 2008). Similarly, there is strong evidence that categorical information at the superordinate-level ("animal") and basic-level ("dog") can be accessed automatically (Li, VanRullen, Koch, & Perona, 2002; Poncet, Reddy, & Fabre-Thorpe, 2012; Rousselet, Thorpe, & Fabre-Thorpe, 2004). Therefore, it seems plausible that the category of a distractor

image could influence the processing of a subsequent target image. Second, the activity elicited by a stimulus persists in the ITC long after its presentation (Kovács, Vogels, & Orban, 1995; Rolls & Tovée, 1994). Rolls and Tovée, (1994) reported that neurons in ITC continued to respond for 300 ms to a stimulus presented for only 16 ms; they also noted that neuronal activity was sustained for even longer durations when stimulus presentation times were increased. Finally, accurate and robust information about object category can be decoded in the ITC as early as 100 ms after stimulus onset (Hung, Kreiman, Poggio, & DiCarlo, 2005; Liu, Agam, Madsen, & Kreiman, 2009) for multiple levels of categorisation (Carlson, Tovar, Tovar, Alink, & Kriegeskorte, 2013; Cichy, Pantazis, & Oliva, 2014). Thus, if two pictures are presented in rapid succession, categorical information will be processed very rapidly for both stimuli, allowing the possibility for them to interact.

On the other hand, it might be argued that interference between images instead takes place at earlier stages of the ventral pathway. For example, bird and non-bird animal images could interfere with each other more than bird and vehicle images because their low-level features are more similar in the former than in the latter case (Coggan, Liu, Baker, & Andrews, 2016; Oliva & Torralba, 2001). That is, the low-level image statistics might be enough to explain the interference in our results without the need to access category information. However, this is very unlikely for two main reasons. First, if early interference occurs between similar objects (e.g., animal–bird), but not between dissimilar objects (e.g., vehicle–bird), which is necessary to explain our results, then one would predict that the maximal interference should occur for congruent trials (e.g., bird prime followed by a bird target). The current evidence contradicts this prediction, and in fact, we get the best performance in those cases. Note that we never used the same image twice, and hence, the target and prime were distinct images (so the observed facilitation cannot be attributed to putative low-level facilitation from identical images). Second, the interference depends on the task: bird and animal images interfere in Experiment 1 but not in Experiment 2. This would be very unlikely if the effect was due to low-level image or feature interference. These findings argue against the possibility that the results can be explained by low-level (pre-categorical) interference.

Nevertheless, it is possible that these interactions take place at a step later than ITC, in the pre-frontal cortex (PFC). The ITC has strong projections to PFC (Ungerleider, Gaffan, & Pelak, 1989; Webster, Bachevalier, & Ungerleider, 1994) and it has been argued that while ITC encodes relevant object level properties needed to identify an object category, PFC categorises stimuli based on more abstract attributes (Freedman, Riesenhuber, Poggio, & Miller, 2003; Pan & Sakagami, 2012). However, it has been shown that monkeys with bilateral removal of PFC were still able to learn

and generalise perceptual categories of related stimuli rapidly without explicit instruction (Minamimoto, Saunders, & Richmond, 2010). In humans, damage to the ITC but not PFC leads to visual categories agnosias (Gainotti, 2000). Closer to our focus, in priming studies PFC seems to be mostly involved in the retrieval of stimulus–response associations (Horner & Henson, 2008, 2011; Thompson-Schill, D'Esposito, & Kan, 1999). Further, Cohen et al. (2014) found that behavioural interference from multiple object categories was correlated with the degree of separation between the neural patterns in the ITC but not in the PFC. These results, in conjunction with the extremely rapid reaction times observed in humans when performing categorisation tasks (Thorpe, Fize, & Marlot, 1996), lead to the conclusion that the interactions observed in our study are more likely to take place in the ITC than in the PFC. Nevertheless, the conclusions of our study are the same irrespective of whether the interaction takes place in the ITC or in other brain areas.

Another possibility is that the PFC reads out the ITC activity to perform the categorisation task. Indeed, there is evidence that object representations in the ITC are unaffected by the task, whereas PFC seems to represent only task-relevant information (Bracci, Daniels, & Op de Beeck, 2017; Erez & Duncan, 2015; McKee, Riesenhuber, Miller, & Freedman, 2014). One can imagine that the boundary between categories is set by the PFC depending on task demands. During the categorisation, the PFC will "look" at the activity in the ITC centres. If the neural activity is within the target category boundary, the decision process is fast; however, if the neural activity crosses the boundary, that is if the signal is noisier, the PFC will have to disentangle those patterns of activity and the categorisation process will be slower. Lower performance or a large priming effect would thus be the result of the difficulty to read-out the ITC signal by the PFC or in other words, it would be affected by the quality of the signal in ITC. This possibility implies that the interactions between categories are still occurring in the ITC and is constrained by its structure.

4.3 | Category interactions in the visual domain

Our proposal is consistent with recent advances in understanding categorisation mechanisms when only *one* object is presented at a time. Neuroimaging studies have shown that all visual features are extracted in parallel or at least around the same time after stimulus onset (Carlson, Tovar, et al., 2013; Cichy et al., 2014; Contini, Wardle, & Carlson, 2017). Our proposal incorporates this finding in assuming that information about all categories is accessed at the same time. However, results from behavioural studies have shown that

all categorisations are not the same. Performance (RTs and ERs) is better when a categorisation task involves pitting distant categories (e.g., bird and car) against each other than when it involves closer (e.g., bird and dog) categories (e.g., Bowers & Jones, 2008; Kadar & Ben-Shahar, 2012; Macé et al., 2009; Praß, Grimsen, König, & Fahle, 2013; but see Mack & Palmeri, 2015).

Sofer et al. (2015) proposed that such differences in behavioural performance could reflect differences in discriminability. With a computational model based on task-specific perceptual discriminability between images, they could accurately predict behavioural responses in categorisation tasks. In our proposal, task-specific perceptual discriminability would map onto the distance between the distractor and the task relevant (target) category boundary. The further away the distractor is from the boundary, the easier it is to reject it, which would explain the above results. Thus, well-established results in visual categorisation studies, such as the superordinate superiority (Joubert, Rousselet, Fize, & Fabre-Thorpe, 2007; Macé et al., 2009; Wu, Crouzet, Thorpe, & Fabre-Thorpe, 2015) or the effect of distractor variability (Bowers & Jones, 2008; Poncet & Fabre-Thorpe, 2014) can be explained by the distance-to-bound principle. An interesting corollary is that the farther away a specific target is from the (target) boundary, the easier (faster) it should be to reach the decision that it is a target. We did not test for this possibility in our study, but this prediction would fit well with our proposal.

Category interactions have also been reported in visual short-term memory studies. In a change detection task, Cohen et al. (2014) found that if multiple objects belong to the same category, changes are detected less often than if they belong to different categories. Further, they found that the similarity between neural activity patterns of these objects presented in isolation could predict the extent of interference in memory. In our study, participants do not actively maintain the prime representation in memory, but we expect similar interactions to take place due to the rapid succession of the prime and the target. Indeed, we found that the more related an incongruent prime was to the target, the more it interfered with the processing of the target. The similar set of findings across different tasks indicate that the distance between representations affects behaviour. We propose a more nuanced and general rule incorporating the finding that interactions between representations depend on task requirements and argue that the distance between the distractors and the target boundary (not the target itself) is an important determinant of outcomes. Cohen and colleagues did not manipulate task requirements and hence their findings can be easily accommodated by the more specific rule about the distance between target and distractors. However, when task requirements change from one level of categorisation to another, as in our study, the distance to the target representation is not enough to explain category

interference and the distance to task boundary must be taken into consideration.

4.4 | Category interactions in language

Interactions between objects and their categories have been studied quite extensively in the language domain, primarily using the picture–word interference (PWI) paradigm. PWI is a Stroop-like task (Starreveld & La Heij, 2017) where participants are usually asked to name a visual image while a distractor word is presented simultaneously. Different stimuli (pictures, line drawings, words), response modalities (oral or manual responses), and temporal windows (varying time intervals between the two stimuli) have been employed. Most studies, however, ask participants to name an object, unlike in our experiments, where the task was to categorise images. Typically, these studies have shown that a distractor word interferes with picture naming when image and word are related (e.g., a picture of a bird with the word *cat*) compared to when they are not related (e.g., a picture of a bird with the word *table*) (e.g.,La Heij & van den Hof, 1995; Lupker, 1979; Rosinski, 1977). On the other hand, recent studies have found that the interference effect caused by a related distractor word could be reversed when the word belonged to a different category (e.g., the word *nest* instead of *cat*) or when it was a subcategory of the expected response (such as *seagull*) (e.g., Costa, Alario, & Caramazza, 2005; Kuipers et al., 2006).

Several mechanisms have been proposed to account for these PWI results. The most dominant proposal currently invoked is the *response exclusion* hypothesis (Mahon et al., 2007). In their paper, the authors review several studies and report new data showing that the priming effect depends on (a) whether the distractor satisfies response-relevant criteria (if it contains features of the target such as being a verb or being an animal) and (b) distractor relatedness (how semantically close it is to the target). If both related and unrelated distractors share the same response-relevant criteria with the target, the related distractor facilitates target responses more than the unrelated one. However, if the related distractor satisfies response-relevant criteria and the unrelated distractor does not, then the related distractor interferes with the response more than the unrelated one. As such, our results are consistent with Mahon et al.'s (2007) proposal. When both primes share the same response as the target, as in the case of related and unrelated congruent primes in Experiment 2, the related prime facilitated target processing, although this effect was weak. On the other hand, when the related prime satisfies a response-relevant criterion and the unrelated prime does not, as is the case of a non-bird animal and a car prime in Experiment 1, the related prime (non-bird animal) interfered with target processing. The difference between our model and Mahon and colleague's hypothesis is that our results

show that the interference caused by distractors depends on the distance of the distractor to the task boundary, whereas their proposal implicitly accords with the dependence of performance on the distance between two objects. It is possible that the importance of the boundary was not visible in PWI paradigms since in naming tasks the boundary is not often manipulated but set at the basic-level (Hantsch, Jescheniak, & Schriefers, 2009, i.e., participants name a bird image as a bird, not as an animal or an owl, but see 2012; Kuipers et al., 2006; Kuipers & La Heij, 2012). Importantly, using drift diffusion analysis, we find that interactions between visual or semantic categories take place not only at the response selection stage (as proposed by Mahon et al., 2007) but also during perceptual and decisional processes. Additionally, we suggest that the amount of interaction has a clear origin: it depends on the neural organisation of the brain.

We should note that there are a few studies in the language domain that are more directly comparable to ours, such as those that used a picture–picture paradigm. These have reported that naming a picture presented shortly after a related distractor picture had no effect on naming speed (Damian & Bowers, 2003; Navarrete & Costa, 2005). This suggests that the task, naming versus categorising as in our study, affects the direction of the interaction between categories. One possibility is that in a naming task, the interaction takes place during language processing (lexical and phonological stages), not during visual processing. An alternative could be that the absence of effect in these picture–picture naming studies is the result of an interference between visual categories (as we found) *and* a facilitation from additional later stages involved in naming.

One of the rare studies using a categorisation task in a PWI paradigm (Lupker & Katz, 1981) found similar results as we report here. In their study, Lupker and Katz (1981) asked participants to respond "yes" or "no" whether an image was a dog while a distractor word was presented simultaneously. Participants responded to a dog target picture the fastest when the picture was presented with the word *dog* (486 ms), slower with a non-animal name (*truck*, 506 ms), and the slowest when the word was another animal name (*cat*, 523 ms). In our study, both prime and target were pictures such that the involvement of language processing was minimal. Indeed, this type of task can also be performed by monkeys (Thorpe et al., 1996), indicating that language is not necessary. This raises the question about how comparable the mechanisms that explain Lupker and Katz's (1981) results are to ours. It is possible that distractor words automatically produce visual representations (similar to imagery) that could then interfere with the representation of a target picture in the ITC. Indeed, it has been shown that concrete words interfere with target naming more than abstract words (Lupker, 1979) and that categorical interference in PWI paradigms seems to be correlated with an increase of activity in the middle temporal gyrus (Diaz et al., 2014). Other neuroimaging studies have also shown evidence that a word activates the referent's visual object representation in the occipito-temporal cortex (Kumar, Federmeier, Fei-Fei, & Beck, 2017; Simanova, van Gerven, Oostenveld, & Hagoort, 2010). Another possibility, brought forward by Carlson et al. (2014), is that the ITC might not just be a visual area but might also be involved in representing conceptual information. As they show in their study, the semantic relationships among words match with the representation of object similarity in the ITC.

4.5 | Conclusion

In this study, we show that visual object categories are automatically and rapidly processed and influence the processing of a following object. The interactions between two representations depend on the task and the semantic distance between them. When the two objects are from different task-relevant categories (incongruent), the distractor interferes with the processing of the target object, not just at the response selection stage but during the accumulation of evidence. The amount of this interference depends centrally on the distractor's distance to the task category boundary and increases the closer the incongruent object is to the boundary. We argue that these results are the direct consequence of the brain organisation and suggest that this principle can be used to describe category interactions in multiple domains of cognition.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHORS CONTRIBUTION
MP designed and ran the experiments. MFT provided the resources for running the experiments and commented on an early draft. MP and RC analysed the data and interpreted the results. MP wrote the first draft and revised the manuscript with RC.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/ejn.14890.

DATA AVAILABILITY STATEMENT
The programmes used to run the two experiments and the collected data are available on the OSF website (OSF.IO/ASB4E). A substantial proportion of the stimuli were sourced

from the copyright protected Corel database and thus cannot be shared on OSF.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Poncet M, Fabre-Thorpe M, Chakravarthi R. A simple rule to describe interactions between visual categories. *Eur J Neurosci*. 2020;00:1–28. https://doi.org/10.1111/ejn.14890