Testing Domain Specificity: Conceptual Knowledge of Living and Non-living Things

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Among current theories regarding the organization of conceptual knowledge, there is an accepted distinction between living and non-living things in ventral stream processing. Less clear, however, is what drives the organization of concepts and whether "living" is a unitary, coherent concept category. Using functional neuroimaging and three behavioral paradigms, this study aimed to test how verbal association differentially affects the categorization of plants, how animacy affects the categorization of animals, and how motor production affects the categorization of manipulable non-living things. The results reveal that linguistic labels may not strongly influence the organization of categories. Moreover, motor production only shows some differential effect between category domains (non-living more than living) and no effect within category domains (manipulable compared to non-manipulable objects). Animacy, however, does differentially affect the categorization of animals and no other category items, implicating a shared mechanism for the detection of biological motion and the categorization of animals. Finally, a meta-analysis of previous functional imaging literature reveals significant neural overlap between cortical areas responding to animals and those responding to "socialness." This finding supports the theory that social concepts might better explain the living/non-living dichotomy through shared mechanisms responsible for detecting animacy, thereby implying causality and intentionality within the domain of agency. Still unclear is how object categories such as plants, which are living but non-social, fit into the organization of conceptual knowledge.

INTRODUCTION

The organization of conceptual knowledge is a much-debated area of study motivated by research from fields including neuropsychology, cognitive neuroscience, and developmental psychology. Neural processing of concept categories is localized in the ventral stream. While current researchers accept a dichotomy between living and non-living objects, significant deliberation surrounds the origins of these distinctions (e.g., Caramazza & Shelton, 1998; Martin, 2007; Martin, Ungerleider, Haxby, 1996; Moore & Price, 1999; Warrington & McCarthy, 1987; Warrington & Crutch, 2003; for a review, see Mahon & Caramazza, 2003). This dichotomy has been observed in both neuropsychological patient data (e.g., Caramazza & Shelton, 1998; Warrington & McCarthy, 1987) and functional neuroimaging data, in the form of a lateral-to-medial organization of categories in the fusiform gyrus (Mahon & Caramazza, 2009). Lesion data has indicated that lateral regions of the fusiform gyrus show more activation for living things such as animals and faces, whereas medial areas show more activation for non-living things such as tools and vehicles (e.g., Chao, Haxby, & Martin, 1999; Mahon, Millevill, Negri, Runiati, & Caramazza, 2007; Noppeney, Price, Penny, & Firston, 2006; for a review, see Mahon & Caramazza, 2009). The debate within this field of study regards *why* patient deficits and functional neuroimaging data reveal this particular pattern of conceptual knowledge organization. Since the first case of a category-specific deficit was reported, over 100 such cases have been observed; the most common pattern of category-specific deficits is an impairment in either biological living categories or non-biological inanimate objects (Martin & Caramazza, 2003). Two major theories that attempt to provide an explanation include the Sensory/Functional Theory (S/FT; Warrington & McCarthy, 1987; Warrington & Crutch, 2003) and the Domain Specific Hypothesis (DSH; Caramazza & Shelton, 1998). Originally developed around the observation of neuropsychological patient testing, each theory attempts to explain the origin of category-specific deficits exhibited by these patients.

Sensory/Functional Theory attempts to explain category specificity as a product of

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experience-based semantic knowledge of object properties. More specifically, S/FT posits that conceptual knowledge is organized into clusters of common sensory features for living things (e.g., shape, form, color) and common functional properties for non-living things (e.g., behaviors with regard to use or purpose of use; Warrington & McCarthy, 1987). In a foundational study, Warrington and McCarthy (1987) observed a patient, Y.O.T., who suffered from severe global aphasia and noted selective impairments not only for broad categories of semantic knowledge, but also for very specific subsets of these categories. Y.O.T. demonstrated a significant impairment for categories of non-living objects as compared to foods or living things, and small manipulable objects as compared to large man-made objects. Research in support of S/FT specifically sought to identify categories that were impaired together to find similarities between objects within these categories. For example, earlier work by Warrington and Shallice (1984) showed that categories of animals, plants and foods ("living" things) tended to be impaired or spared together. These types of observations led researchers to hypothesize a system of multiple processing channels based on an interactive network of relative weighted inputs, which now forms the basis of the S/FT (Warrington & Crutch, 2003). The weightings are thought to be based on modality-specific experience such as visual features, which are assumed to be a more critical component for identifying and differentiating a living animal, versus functional use, which is assumed to be more important in the identification of a non-living object such as a tool (Warrington & McCarthy, 1987; Warrington & Crutch, 2003). Further support for this theory has come from more recent studies, such as Borgo and Shallice (2001; 2003), who reported an association between impairment for living things and impairments for sensory-quality categories. Thus, for S/FT theorists, category-specific deficits occur because information is organized according to its sensory inputs, which results in a categorical organization of objects in the ventral stream.

As an alternative explanation for the observed organization of conceptual knowledge, Caramazza and Shelton (1998) outlined the Domain Specific Hypothesis (DSH), which draws upon the principle of modularity (Fodor, 1983). Specifically, the DSH suggests that the information is constrained by evolutionary processes in the human brain (Caramazza & Shelton, 1998; Mahon & Caramazza, 2009). In this manner, category-specific deficits exhibited by patients are examples of broad category domains formed through pressures of natural selection and evolutionary relevance and importance (Martin & Caramazza, 2003; Mahon & Caramazza, 2009; Caramazza & Shelton, 1998). The basis for the DSH comes from the observation of a patient, E.W., who exhibited modality independent, category-specific deficits for animals, vis-à-vis other livings things and all non-living things (Caramazza & Shelton, 1998). These observations lead to the idea that conceptual knowledge is domain-specific. Rather than being organized by sensory features, the DSH argues that domains are defined by evolutionary processes that have acted on the semantic content of information. Thus, category-specific deficits in patients should reflect impairments with all types of knowledge about the domain (Mahon & Caramazza, 2009). A case study by Farah and Rabinowitz (2003) supports this idea: Adam, who suffered a stroke at 1 year of age, failed to acquire both visual and non-visual knowledge about living things, but displayed normal levels of understanding about non-living things 15 years later. Further support for the DSH comes largely comes from work in developmental psychology, which demonstrates innate "knowledge" in human infants that is not mediated by experience with modality-specific associations (e.g., Mandler & McDonough, 1993; Carey & Spelke, 1994; Gelman, 1990).

Despite the differences between the theories, S/FT and the DSH agree that there is substantial evidence of a neural dissociation between the processing of living and non-living things in both neuropsychological and functional neuroimaging data (e.g., Chao, Weisberg, & Martin, 2002; Mahon, Anzellotti, Schwarzbach, Zampini, & Caramazza, 2009; Martin & Chao, 2001; Warrington & Crutch, 2003). Whereas S/FT and the DSH attempt to explain *why* category-specific deficits emerge, the focus of the study at hand is *what drives* the organization of concepts. That is, what types and forms of inputs are relevant to categorizing objects as living or non-living?

Early work by Piaget (1929/1960) pointed to the importance of "animism" (animacy) or biological motion in the emergence of a concept of "living." He described how children often attribute life to things that move or seem to move. For example, a child thinks that a bicycle is alive just as a cat is alive because it "goes," but a table is not alive because it cannot move (Piaget, 1929/1960). In his work, Piaget also showed that children have particular difficulty considering plants as alive. He argued that since plants are stationary and acted upon (rather than being actors), they are typically considered non-living by young children (Piaget, 1929/1960). In addition to animacy, Carey (2009) describes the importance of "agency"; the cognitive representation of action intentions, goals, causality and self-directed motion is important in the categorization of something as alive. For example, infants show surprise when non-living objects, such as a beanbag, seem to be capable of self-motion, and seek an external causal explanation, such as a human hand (Saxe, Tzelnic, & Carey, 2006). In another study, Wagner and Carey (2005) reported that after viewing various scenes of object motion, infants show an understanding of action intentions (that one ball is trying to "chase" another) through habituation to the appropriate end scenes.

Language, propositions, and verbal labeling have been proposed as additional means for children to group objects with feature-based similarities (e.g., Waxman & Markow, 1995; Woodward & Markman, 1998). For example, studies have shown the importance of words in the "formation of sortal concepts" (Bloom & Keil, 2001; Xu, 1999; Xu & Carey 1991), and several researchers have argued that "language is used to partition the world" into meaningful units (Berlin, 1992; Goldberg & Thompson-Schill, 2009). Waxman and Markow (1995) have shown that children as young as 12-months of age, during early stages of lexical acquisition, use words and object names to guide the formation of categories.

More recent studies provide further evidence that motion processing and verbal learning influence the categorization of living things. For example, several studies have recently shown that children can correct the kinds of errors that they exhibit in Piaget's living/non-living studies once they understand the difference between types of motion and animacy; once children understand the cause of an object's movement and the different kinds of motion exhibited by living and non-living things, they reshape their living object category to include non-moving, living objects such as plants (Goldberg & Thompson-Schill, 2009; Opfer & Siegler, 2004). This developmental change in the organization of the "living" concept (i.e., to include plants) is thought to reflect a qualitative difference between mature systems of knowledge organization employed by adults and undifferentiated child based systems, with the assumption that the child system no longer "plays any role in the adult conceptual system" (Carey, 1988, 1999). Surprisingly, however, adults and even domain-specific experts exhibit remnants of child-like errors, especially in their response times, when performing a category decision task involving animals and plants (Goldberg & Thompson-Schill, 2009). Using a word-based speeded category decision task (living or non-living), Goldberg and Thompson-Schill reported significantly lower accuracy and longer response times for the categorization of plants as living things as compared to animals in a population of college undergraduates and biology professors (domain-specific experts). Although the difference between plants and animals was reduced by nearly two thirds for professors, the authors suggested that experience and expertise may only provide a "subtle reconstruction of conceptual knowledge." Additionally, they argued that conceptual categorization involves perceptual similarities based on "coarsely coded associations" that are largely established in early development and mediated through the use of language. These studies are important in highlighting the role of biological motion in the categorization of animals as living things and the role of verbal or propositional processing in the categorization of plants as living things.

A final domain in which different input variables appear to influence the categorization of living and non-living things is the domain of "tools." Recent studies have shown that information relevant for action (motor preparation and planning) plays a differential role in the categorization of tools compared to other non-living objects (e.g., Mahon et al., 2007). This evidence is based primarily on fMRI data wherein people exhibit greater functional connectivity between parietal action regions and "non-living" object processing regions of the ventral stream when the stimulus is a tool than when it is a non-manipulable object (Mahon et al., 2007). The central argument here is that motor-relevant processing contributes more toward the categorization of tools than other objects within the "non-living" domain.

If there is a pure dissociation between living and non-living things in the organization of conceptual knowledge, then why do plants cognitively dissociate from animals within the domain of "living"? And, why do tools engage neural structures that are not engaged by other non-living objects? Are different input variables important for the categorization of animals, plants, tools, and non-living things? To answer these questions, we aimed to test whether verbal associations, motor information, and animacy each play a unique role in the categorization of animals, plants, tools, and other objects. We used a generic behavioral categorization paradigm based on Goldberg and Thompson-Schill's (2009) study, coupled with a series of cognitive distracter tasks (verbal, motor, and biological motion judgment tasks), to test whether these tasks would differentially impact category judgments of living and non-living things. In light of previous research, we hypothesized that verbal distraction would differentially impair the categorization of plants, motor distraction would differentially impair the categorization of tools, and animacy distraction would uniquely impair the categorization of animals.

STUDY 1: NEURAL CORRELATES OF CATEGORY DIFFERENCES

A novel re-analysis of fMRI data collected by Mahon, Anzellotti, Schwarzbach, Zampini, & Caramazza (2009) was performed to compare neural activation related to processing animals and plants within the domain "living," in the ventral stream. It was hypothesized that if category domains are organized as living and non-living, then animals and plants should not differ significantly in the cortical activation within lateral areas of the fusiform gyrus (which have been associated with processing living things in prior neuropsychological and neuroimaging studies as described above).

Methods

Participants

Twenty-one participants (9 males; 12 females; ages 20-51 years old, $M = 31.2$) were recruited from the Center for Mind/Brain

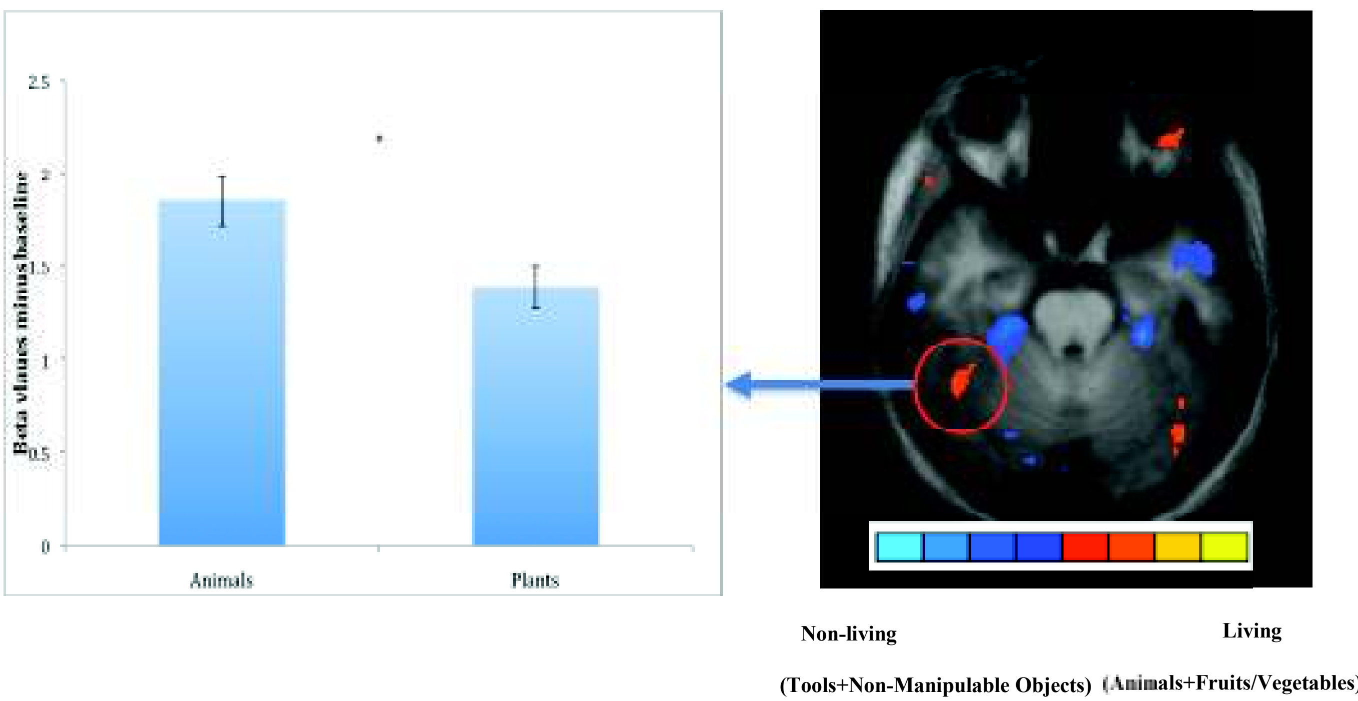


Figure 1. Shown on the right is the activation contrast for lateral (living) and medial (non-living) areas in the ventral occipital-temporal cortex. On the left is the comparison between activation for animals and activation for plants within the lateral ROI (peak activation 42, -46, -20; $t(19) = 3.13$, $p < .001$), which are significantly different, $t(19) = 4.7$, $p < .001$, and indicate more activation for animals than plants.

Science volunteer pool at the University of Trento, Italy, and were paid for their participation.

Materials and procedure

Stimuli consisted of four object categories of 24 pictures each: animals, tools, non-manipulable objects, and fruits/vegetables. While BOLD responses were recorded, participants passively viewed pictures in 20 second blocks, followed by 20 seconds of blank screen (fixation). Each block contained 24 pictures of the same category, each stimulus presented for 50 refreshes of the monitor, and each category block (24 pictures) was repeated three times per run. The order of blocks was randomized; each run lasted approximately 10 minutes.

Imaging procedure

Cerebral images were acquired by Mahon et al. (2009) on a Bruker BioSpin MedSpec 4T MRI machine. They collected functional data using an echo planar 2D imaging sequence with phase over-sampling (Image matrix: 70 × 64, TR: 2250 ms TE: 33 ms, Flip angle: 76°, Slice thickness = 3mm, gap = .45mm, with 3 × 3 in plane resolution). Volumes were acquired in the axial plane in 37 slices and the acquisition order was ascending interleaved odd-even.

Data analysis

Images were pre-processed (slice time correction, realignment, normalization) and transformed into Talairach space by Mahon et al. (2009) using Brain Voyager QX. The authors applied BOLD activity to the individual subject data, which included parameters for stimulus onsets and motion parameters. This individual-subject regression model provided an estimate of the strength of activation related to each category for each subject. We used these estimates to determine regions that responded to Living Things > Non-living Things at the group level. That analysis defined our regions of interest (ROIs). Then, we looked at the individual-subject responses within these ROIs to test the relative activation to plants versus animals at the group level, thresholded at $p < .05$.

Results and Discussion

Cortical activation was mapped for areas representing living things (animals and fruits/vegetables) and non-living things (tools and non-manipulable objects). As shown in the right panel of Figure 1, data were representative of previous functional imaging findings with significant lateral-to-medial dissociation of living and non-living things in ventral occipital-temporal cortex, $p = .05$, uncorrected (e.g., Chao et al., 1999, 2002; Mahon & Caramazza, 2009; Martin, 2007; Martin, et al., 1996). Additionally, a significant difference was observed between animals and plants within the lateral ROI in right hemisphere ($t(19) = 4.7$, $p < .001$). However, as shown in the left panel of Figure 1, animals exhibited significantly greater activation in this area than plants, suggesting that not all living objects contribute equally to cortical activation of the lateral regions of the ventral stream. Thus, cortical organization may not be indicative of a "living versus non-living" dissociation because not all living objects carry an equal weight within this domain. To further investigate why plants are not represented like animals in the ventral stream and to test what drives the organization of concepts of living and non-living, we performed a series of behavioral interference experiments.

STUDY 2a: VERBAL ASSOCIATIONS AND PLANTS

The first experiment was designed to test whether verbal learning accounts for the difference in performance when categorizing plants and animals as living things as reported by Goldberg and Thompson-Schill (2009). This was performed by first replicating the previous study and then by adding a secondary verbal distracter condition. Distraction was created by asking participants to sing the children's nursery rhyme "Twinkle, Twinkle, Little Star" while simultaneously completing the living-non-living categorization task. It was hypothesized that if verbal learning and linguistic labels are employed as a method of associating plants with the "living" domain, then performance for judging them as such should be significantly worse when a verbal distracter is employed.

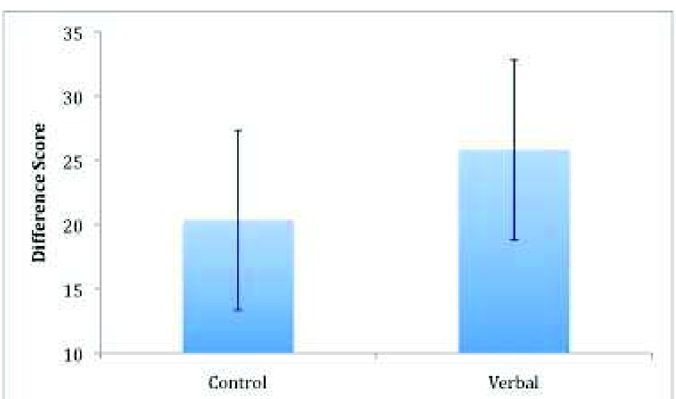
Methods

Participants

Twenty-one participants (10 males; 11 females; ages 18-21 years old, M = 19.8) were recruited from the undergraduate subject pool of the departments of Psychology and Brain and Cognitive Sciences (BCS) at the University of Rochester. Subjects were asked to participate in a 1-hour behavioral BCS study, which was held at the Rochester Center from Brain Imaging, and were paid $8 for their participation.

Materials

Word items were taken from Goldberg and Thompson-Schill (2009) and contained 140 items in six different categories. The set consisted of 30 animals, 30 plants, 20 non-moving artifacts (e.g., towel), 20 non-moving naturals (e.g., rock), 20 moving artifacts (e.g., bus), and 20 moving naturals (e.g., river). All words within each domain (living and non-living) were matched and



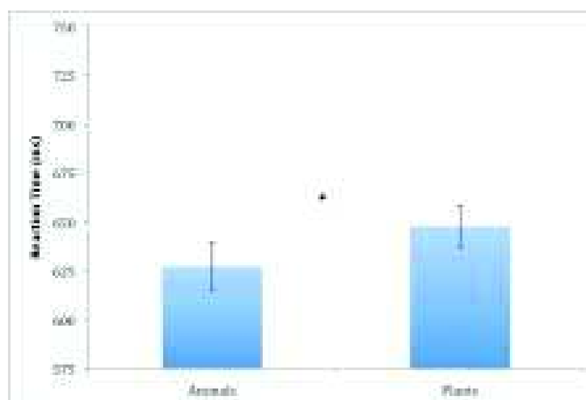


Figure 2. Results from Study 2a: (a) Participants' mean reaction times for identifying plants (M = 647.6 +/- 48.25) and animals (M = 627.2 +/- 54.45) as living (correct trials only). A significant difference was observed between animals and plants, $t(20) = 2.62$, $p < .05$. (b) Difference scores for the control condition (M = 20.34 +/- 7.76) and the verbal distracter task (M = 25.79 +/- 6.47). No significant difference was observed. Error bars represent standard error of the mean.

balanced for number of letters, syllables and frequency (for details refer to Goldberg & Thompson-Schill, 2009).

Procedure

Participants were told to follow onscreen instructions, which appeared in two varieties. In the control condition participants were instructed to indicate, as quickly and accurately as possible, whether the word that appeared onscreen represented a living or non-living object, by pressing either of two keys using their dominant hand. In the verbal distracter condition, participants were instructed to perform the same judgment task while at the same time holding a small microphone with their non-dominant hand and singing "Twinkle, Twinkle, Little Star" aloud. Each trial began with the presentation of a visual fixation-cross for a random duration between 500-1500 milliseconds followed by a random word from the stimuli set for a maximum of 1000 ms. If subjects did not make a decision within the allotted time, "no response detected" appeared on the screen for 500 ms. Each trial ended with a visual word mask (e.g., #####) for 500 ms.

Statistical testing

Data analysis was performed on reaction times for responses to correct trials only in both conditions. In the control condition (replication), data were analyzed using a paired sample t-test between reaction times to animals and plants. In the experimental condition (verbal distracter), difference scores were calculated for each category (plant RT-animal RT) and conditions were compared using a paired sample t-test.

Results

As shown in Figure 2, the results of Goldberg and Thompson-Schill (2009) were replicated successfully. Participants exhibited a significantly slower reaction time of 20.4 ms for plants ($M = 647.6$ +/- 10.53) as compared to animals ($M = 627.2$ +/- 11.88), ($t(20) = 2.62$, $p < .05$). However, when control difference scores ($M = 20.34$ +/- 7.76) were compared to the difference scores in the verbal distracter condition ($M = 25.79$ +/- 6.47), no significant difference was observed, ($t(20) = .62$, $p = .55$), suggesting no further impairment of either category judgment through the use of a verbal distracter task.

Discussion

Despite previous research indicating the importance of language use in forming certain categories during development (e.g., Bloom & Keil, 2001; Waxman & Markow, 1995; Xu, 1999; Xu & Carey 1991), our results do not support this theory for the categorization of animals and plants. Results were expected to indicate a greater difference between reaction times for animals and plants in the verbal distracter condition based on the idea that language is used as an association tool to link plants to the domain of living things along with animals (Goldberg & Thompson-Schill, 2009; Woodward & Markman, 1998). However, it seems that there is no significant change in reaction time for the categorization of living and non-living things during verbal distraction. Thus, an inability to access verbal processes does not disrupt the categorization of plants as living things, and verbal learning is not necessarily something driving the organization of conceptual knowledge in this case.

STUDY 2b: BIOLOGICAL MOTION AND ANIMALS

The aim of the second experiment was to test the importance of animate processing on the categorization of conceptual knowledge. Here, we used a dual-task paradigm to test the interference of biological motion processing on the categorization of living and non-living things. Subjects were asked to judge the gender of a point-light-walker (PLW) immediately preceding a categorical judgment of a word as living or non-living. We manipulated the distance between the point-light-walker judgment and the categorical judgment in a stimulus onset asynchrony (SOA) design to assess interference effects during the psychological refractory period (PRP). To help clarify the methods, predictions, and results of this experiment, it is important to first explain the SOA paradigm, the PRP, and the bottleneck model of cognitive processing.

Dual-Task Interference and the SOA paradigm

Starting with the early work of Telford (1931), the PRP effect was shown to be the delaying of response to a second stimulus in an experimental design where the delay between two stimuli is asynchronous. This delayed response becomes greater as the distance between the stimuli is reduced and occurs even when the response types are of differing modalities (Pashler, 1994). Although many theories have been proposed as to the reason for the effect, one of the most prominent and relevant to the study at hand is the bottleneck or task-switching model (Sternberg, 1969). This model describes that if two stimuli require the same type of mechanism to be processed, then when both stimuli require the use of that mechanism simultaneously, a processing bottleneck occurs; because the first stimulus occupies the mechanism first, delays occur in the processing of the second stimulus until the first has been finished processing due to the necessary mechanism switching (Pashler, 1994; see Figure 3).

Many studies have replicated this effect and have shown that the bottleneck is not a voluntary aspect of stimulus processing and therefore cannot be explained by such things as temporal uncertainty or physical limitations (e.g., Bertleson, 1967; Broadbant & Gregory, 1967; Pashler & Christian, 1994; Pashler & Johnston, 1989; Sternberg, 1969; Telford, 1931; for a review, see Pashler, 1994). Additionally, key outcomes of an SOA paradigm include a high correlation between reaction time to the first and second stimulus at short SOAs (Gottsdanker & Way,

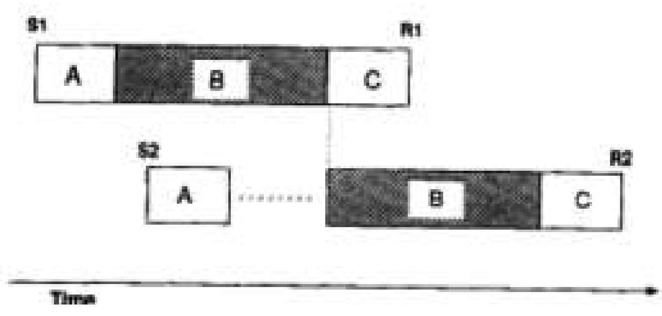


Figure 3. A central bottleneck model schematic: the shaded part of stimulus 2 (mechanism-based processing) cannot occur until the shaded part of stimulus 1 is complete (Pashler, 1994).

1966; Pashler, 1994; Pashler & Johnston, 1989; Welford, 1967), as well as a change in reaction time to the second stimulus, which approaches a slope of -1 (Pashler, 1994; Telford, 1931). Both of these characteristics are predicted by the bottleneck model. They occur because the necessary processing mechanism is occupied by the first stimulus, rendering this mechanism temporarily unavailable for processing the second stimulus and thereby introducing a delay (Pashler, 1994).

For these reasons, the SOA paradigm was chosen for Study 2b to test the hypothesis that a system or mechanism that is used to process biological motion (animacy) is also used in the categorization of animals as living things. If this hypothesis is true, then the results should show an effect of SOA on the categorization of animals only, and the difference in performance between categorizing animals and plants as living things (observed in the previous experiment) should be eliminated.

Methods

Participants

Twenty-two participants (12 males; 10 females; ages 19-22 years old, *M* = 20.1) were recruited from the undergraduate subject pool of the departments of Psychology and Brain and Cognitive Sciences (BCS) at the University of Rochester. Subjects were asked to participate in a 1-hour behavioral BCS study, which was held at the Rochester Center from Brain Imaging and were paid $8 for their participation.

Materials

Subjects performed two tasks separated by a brief SOA: a biological motion judgment on PLWs and a living/non-living categorization on words. The same word stimuli that were used in the previous experiment for presentation were used for the second task, and 3second video clips of left- and right-facing "male" and "female" PLWs were used for the first task (Biomotion Lab at Queen's University, Kingston, Ontario). PLWs were chosen because of their accepted use as representations of biological motion in experimental testing paradigms (e.g., Chang & Troje, 2008; Troje, Westhoff, & Lavrov, 2005; Zhang, & Troje, 2005). Based on pilot testing performed prior to the experiment, the SOAs used included: 96 ms, 208 ms, 400 ms, 800 ms, 1600 ms, 2000 ms. In order to produce the strongest statistical PRP effect, the distribution of SOAs was normalized within each stimulus category, such that the greatest number of SOAs included those in the range of 200-800 ms.

Procedure

Participants were told to follow a set of on-screen instructions, which came in two varieties: a control condition, which was the same as the control condition in the previous experiment, and an experimental condition in which participants engaged in the dual-task SOA paradigm. Each experimental trial began with a fixation-cross presented at a random interval from 500-1500 ms followed by the first stimulus, the PLW, presented for 3000 ms in total. Participants were required to judge whether the PLW on screen was a male or female and indicated their response by pressing one of two buttons with their right hand. During this time, a random word stimuli appeared after a specific SOA duration and participants had the remainder of the time (800 ms – 3000 ms based on the length of the delay) to indicate whether the word represented a living or non-living thing, by pressing one of two buttons with their left hand.

Statistical testing

Data from non-living categories were collapsed into only two categories: moving and non-moving objects. This was done to observe a possible interaction between animacy and the property of movement among non-living objects. Data analysis was performed first for the purpose of checking the effectiveness of the dual-task interference using a correlation between the reaction times to the first and second stimuli. Secondly, changes in slope between categories for the SOA range of 200-800 ms were observed. This range was chosen because of physical limitations on reaction time given the complexity of the task and because pilot testing had shown that for the stimuli used, this range best exhibited dual-task interference. Paired sample t-tests were performed comparing the changes in slope between all categories. In addition, a two-way repeated measures ANOVA was performed between the collapsed reaction times of the 200-800 ms SOA range and the control condition.

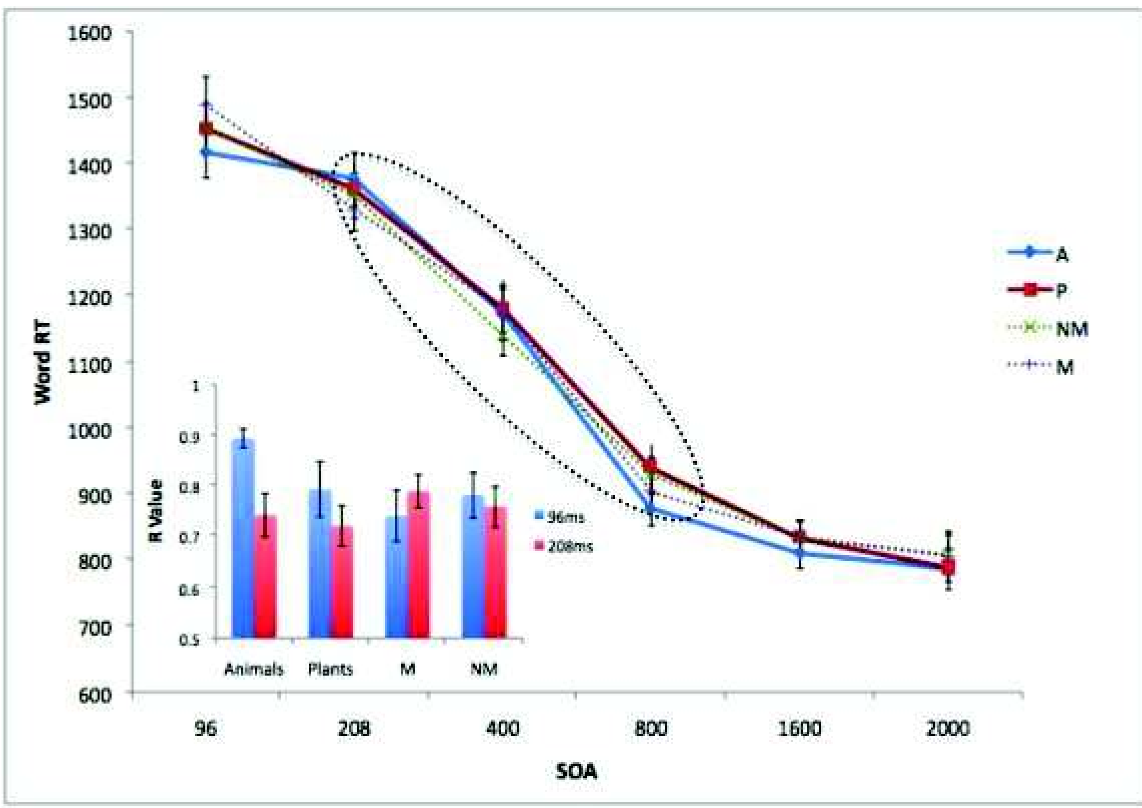


Figure 4. Results from the second experiment: correlations between reaction times for both stimuli were strong and positive $r(21) > .7$, $p < .05$, for all categories at short SOAs. Additionally, the change in reaction time (slope) for animals (M = -.84 +/- .04) was exclusively affected by dual-task interference compared to all other categories and showed the strongest PRP effect, approaching a slope of -1. A: animals; P: plants; NM: non-moving non-living things; M: moving non-living things.

Results

As indicated by Figure 4, correlations between reaction times for the biological motion and living/non-living stimuli were strong and positive ($r(21) > .7$, $p < .05$) for all categories at short SOAs, indicating a significant effect of dual-task interference. Upon comparison of slopes (within the 200-800 ms SOAs), significant differences were observed between animals (M = -.84 +/- .04) and plants (M = -.71 +/- .04, $t(21) = 2.85$, $p < .01$); animals and non-moving objects (M = -.72 +/- .04, $t(21) = 2.58$, $p < .05$); and animals and moving objects (M = -.72 +/- .03, $t(21) = 3.57$, $p < .01$). No significant differences were observed between plants and moving objects, ($t(21) = .16$, $p = .87$); plants and non-moving objects ($t(21) = .11$, $p = .91$); or moving and non-moving objects, ($t(21) = .08$, $p = .94$). These results suggest a specific effect of dual-task interference as a function of SOA on the categorization of animals only and not on the categorization of plants or non-living objects (irrespective of their motion properties).

A two-way analysis of variance for plants and animals (category × stimulus onset) yielded a main effect for stimulus onset ($F(1, 42) = 604.1$, $p < .001$), indicating a significant difference between the comparison of animals and plants in the control condition and in the SOA condition (200-800 ms). No main effect was observed for category ($F(1, 42) = .40$, $p = .53$) and there was no observable interaction ($F(1, 42) = .45$, $p = .50$). As

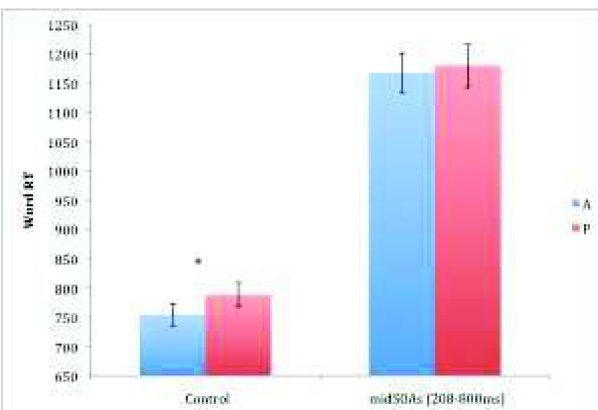


Figure 5. Comparison of animal and plant reaction time differences between control and SOA conditions. No significantly slower reaction time to categorizing plants as living, $t(21) = 4.25$, $p < .001$, was observed in the SOA condition, $t(21) = .75$, $p = .46$. A: animals; P: plants.

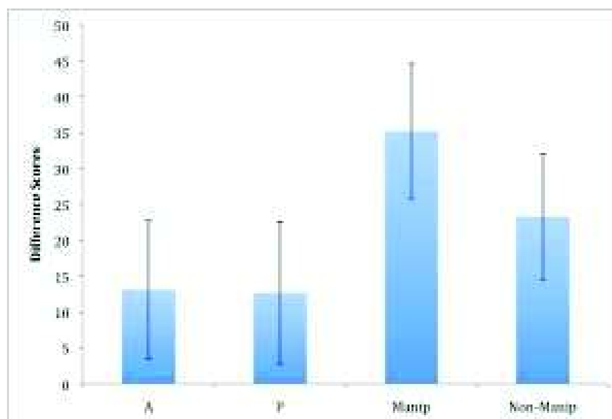


Figure 6. Difference scores between control and motor distracter task conditions for all category items. Significant differences were observed between manipulable objects and animals, $t(20) = 3.09$, $p < .01$, and plants, $t(20) = 2.41$, $p < .05$. However, no differences were observed between category items within the non-living domain (manipulable compared to non-manipulable words). A: animals; P: plants; Manip: manipulable non-living things; Non-Manip: non-manipulable non-living things.

seen in Figure 5, comparisons of animal (M = 1167.27 +/- 33.91) and plant (M = 1179.74 +/- 36.69) categorization reaction times for the SOA condition showed no significant difference ($t(21) = .75$, $p = .46$). This finding from the experimental condition contrasts with the comparison of animals (M = 753.9 +/- 18.98) and plants (M = 788.4 +/- 20.58) in the control condition, which, as expected, exhibited a significant difference of 34.5 ms, with plants being slower than animals, ($t(21) = 4.25$, $p < .001$). These results suggest that the dual-task biological motion SOA paradigm eliminated the previously observed categorization difference between animals and plants by slowing down judgments of animals to the level of plants.

Discussion

These findings implicate the role of a single mechanism used to detect biological motion in the categorization of living things. Dual-task interference was observed only for animals and not for plants or non-living categories, suggesting the occurrence of a processing bottleneck as two different stimuli called upon a single mechanism in succession (Pashler, 1994). If a processing bottleneck was not occurring, then results should have shown a more distributed and general dual-task interference across all categories. However, the exclusivity of the PRP effect observed for animals suggests that the mechanism used to detect animacy is also used to categorize animals as living things. Access to this mechanism creates a bottleneck of cognitive resources resulting in a performance deficit in categorization. These results, along with the lack of difference between performance in categorizing animals and plants during the biological motion dual-task paradigm, suggest that that the decrease in the performance gap occurs because of the impairment of animal categorization, not an improvement of plant categorization, during biological motion processing. This specific effect on animal categorization alone strongly suggests the importance of animacy detection as a mechanism for the formation of concept categories.

STUDY 2c: MOTOR ACTIONS AND MANIPULABLE OBJECTS

This experiment tested the relationship between motor action processing and the categorization of manipulable non-living things. Using the same general experimental design as Study 2a, a secondary motor distraction task was employed by asking participants to simultaneously draw concentric circles as they made living/non-living judgments on word stimuli. It was hypothesized that if the categorization of concepts pertaining to manipulable objects is influenced by systems responsible for carrying out motor actions, then interference would be observed exclusively for manipulable non-living objects compared to living objects in the motor distractor paradigm.

Method

Participants

The same twenty-one participants from Study 2a were tested in this experiment (10 males; 11 females; ages 18-21 years old, M = 19.8).

Materials

The same word items from the first two experiments, taken from Goldberg and Thompson-Schill (2009), were used in this experiment.

Procedure

Participants completed the motor action and living/non-living categorization task as a block of 140 (word) trials either before or after the sessions from Study 2a (order was counterbalanced). The control condition was the same control session as that of Study 2a. In the motor distracter condition, participants were instructed to perform the living-non-living judgment task with their dominant hand, while repeatedly drawing spirals on a sheet of paper with their non-dominant hand. As in Study 2a, each trial began with the presentation of a visual fixation-cross for a random duration between 500-1500 ms followed by a random word from the stimuli set for a maximum of 1000 ms. If subjects did not make a decision within the allotted time, "no response detected" appeared on the screen for 500 ms; each trial ended with a visual word mask (e.g., #####) for 500 ms.

Statistical testing

Data analysis was performed on reaction times for responses to correct trials only in both conditions and words were binned into four object categories: animals, plants, manipulable objects, and non-manipulable objects. Difference scores were calculated for each category RT (e.g., manip (motor distract) – manip (control)), and category scores were compared using paired sample t-tests.

Results and Discussion

As seen in Figure 6, there was a significant difference in performance between: manipulable objects (M = 35.20 +/- 9.37) and animals (M = 12.64 +/- 9.61; $t(20) = 3.09$, $p < .01$) and manipulable objects and plants (M = 12.72 +/- 9.90; $t(20) = 2.41$, $p < .05$). No significant difference was observed between performance for non-manipulable objects (M = 23.29 +/- 2.72) and animals, ($t(20) = 1.02$, $p = .32$); non-manipulable objects and plants ($t(20) = 1.04$, $p = .31$); or manipulable and non-manipulable non-living things ($t(20) = 1.41$, $p = .17$). These results suggest that motor information may be more important for the categorization of non-living things than living things as indicated by differential impairments in performance for non-living category words. However, these results are less transparent for interpreting the role of motor action on the categorization of manipulable versus non-manipulable objects. There was a measureable difference between living things and manipulable objects but not living things and non-manipulable objects. This lack of difference between manipulable and non-manipulable objects raises the question of whether motor actions specifically influence the categorization of manipulable objects within the non-living domain.

GENERAL DISCUSSION, STUDIES 2a-c

We performed three behavioral studies to test the hypothesis that verbal associations, animacy, and motor information are important in the development of the living/non-living dissociation. Taken together, our results indicate important influences of motor and biological motion information on the conceptual distinction between "living" and "non-living."

The results from Study 2a indicate that verbal distraction has no differential impact on the processing of semantic categories. Previous studies that suggest language, as a mechanism to create semantic associations and group objects with similarities, still provides a viable explanation for the formation of concept categories (e.g., Berlin, 1992; Bloom & Keil, 2001; Waxman & Markow, 1995; Xu, 1999; Xu & Carey, 1991; Woodward & Markman, 1998). As suggested by Goldberg and Thompson-Schill (2009), the "groups" produced through linguistic association may reflect developmental "roots" that are only partially modifiable by further experience. If this is case, then the findings observed in Study 2a are to be expected, as verbal distraction would have little impact on categories that are already well established. If this explanation is correct then we should expect to see a greater effect of verbal distraction on living/non-living categorization in children. Alternatively, it is also possible that subjects were not affected by verbal distraction in our task as the nursery rhyme could have been over-learned or subjects may have used the prosody of the melody ("Twinkle, Twinkle, Little Star"), instead of language in order to recite the rhyme.

Interestingly, the results from the motor interference paradigm of Study 2c indicate a disproportionate impact of motor input on the categorization of non-living things compared to living things. However, the within-category distinction between manipulable and non-manipulable objects is less clear. Although there is a greater effect of motor interference on manipulable objects than on non-manipulable objects, this difference in the interference effect only approaches significance. It is unclear as to why domain dissociations are observable for this experiment (living and non-living) but category distinctions are not (manipulable and non-manipulable). These results could be explained by two different theories: S/FT and the "grounding by interaction" hypothesis (Warrington & McCarthy, 1987; Mahon & Caramazza, 2008). S/FT provides an explanation for these results based on the hypothesis that functional information is more important than sensory features for the categorization of non-living things; objects such as tools, for example, will be categorized based on *perceptions* of characteristics about function and purpose, rather than shape or color (Warrington & McCarthy, 1987; Warrington & Crutch, 2003). In contrast, the "grounding by interaction" hypothesis suggests that conceptual knowledge, particularly for tools, is organized based on both an "abstract" and "symbolic" representation of the concept (knowledge about what it is) and interactions between this knowledge and sensory and motor systems (Mahon & Caramazza, 2008). Under this hypothesis, the instantiation of a concept may require the interaction of specific sensory and motor systems responsible for producing *actions*. Therefore, activation of a particular motor system may complement the "abstract" or "symbolic" knowledge about an object concept. In our study, the motor distracter task apparently interfered with a generic action mechanism that is necessary to categorize many non-living objects. In order to determine whether specific types of motor inference disproportionately impact manipulable objects relative to non-manipulable objects (as in the "grounding by interaction" hypothesis), further research would have to be conducted to specifically create motor interference with a task that is specific to tool manipulation (e.g., grasping, pounding).

The results from Study 2b suggest an alternative explanation as to how concept categories are organized. In light of Piaget's

(1929/1960) early work with children and animacy, as well as Carey's (1999, 2009) more recent work on agency, it is possible that the formation of concept categories is not dissociated along a dimension of living versus non-living things. The exclusivity of the PRP observed for animals and not for other category specific word stimuli in Study 2b suggests a common mechanism (a biological motion system) that is important for both the detection of animacy and the organization of conceptual knowledge for animals. Carey (1988, 1999) suggests that there exists a "qualitative difference" between the organization of a conceptual knowledge system of children and adults. In particular, she posits that understanding the difference between "alive" on the one hand, and "movement" or "naturalness" on the other, is a key component of this difference. The concept "alive" permits animals to be coalesced with plants into a common conceptual category (Carey, 1988, 1999). However, if animals and plants are combined as such, then children, adults, and especially domain-specific experts should not exhibit the category errors and performance differences for plants versus animals that we observed in Study 2a (see also Goldberg & Thompson-Schill, 2009). Our data indicate that differences between animals and plants are due to differences in the inputs that bear on their categorization: biological motion is more important for the categorization of animals as living things than that of plants. The implication of these findings is that adults are not so different from children in this context, in that animacy remains an important dimension for the categorization of living objects throughout the lifespan. The results from Study 2b and prior research suggest that animacy may be a more likely dimension along which conceptual knowledge is organized. Since animacy has been implicated as important to the property of "socialness," (i.e., social versus non-social; Martin & Weisberg, 2003; Ross & Olson, 2010; Zahn et al., 2007), this possibility is further explored in the following section.

STUDY 3: META-ANALYSIS OF CONCEPT CATEGORIES

Several researchers have hinted at the hypothesis that social relevance plays a role in the organization of conceptual knowledge with respect to the living/non-living distinction (e.g., Martin & Weisberg, 2003; Zahn et al., 2007). For example, in a neuroimaging study with social and mechanical vignettes, Martin and Weisberg (2003) implicated a "core system" that is particularly important for understanding social interaction. Their findings indicated the same lateral-to-medial activation for living and non-living objects in the ventral stream; areas associated with living things (i.e., lateral fusiform gyrus) also showed activation for social vignettes, and areas associated with non-living and manipulable objects (i.e., medial fusiform gyrus) also showed activation for mechanical vignettes controlled for visual form and properties (Martin, 2007; Martin & Weisberg, 2003). Similarly, Zahn et al. (2007) suggested that there could exist a specific neural network important for the representation of social concepts, which is mediated in part by the anterior temporal lobes. This network includes overlap with lateral areas of the fusiform gyrus, normally activated for living things. One possibility that emerges from these prior conclusions is that domain-specific processing in the ventral stream is organized according to the distinction of "socialness" rather than that of being "alive." If this were the case, then the results of Study 2b would be expected, in that animacy, a key component of "socialness" (e.g., Carey 1998; 1999; Martin & Weisberg, 2003; Ross & Olson, 2010) would be exclusively linked to categories within the domain of social (i.e., animals) rather than non-social (i.e., plants). To further investigate the possibility of "socialness" as a dimension along which concepts are organized, a meta-analysis of previous fMRI studies was conducted to examine neural overlap between living things, and social things (Chao et al., 1999, 2002; Martin & Weisberg, 2003; Noppeney et al., 2006; Ross & Olson, 2010). "Socialness," in these studies, was a dimension tested using social vignette stimuli modeled after stimuli created by Heider and Simmel (1944). These vignettes consisted of movie clips of shapes exhibiting biological motion as rated by behavioral testing data and previous literature (Martin & Weisberg, 2003; Ross & Olson, 2010).

Method

Activation maps

Stereotaxic foci representing Talairach coordinates from five different studies (fusiform gyrus and superior temporal sulcus activations) were projected onto a population-averaged brain using CARET (computerized anatomical reconstruction and editing toolkit; Van Essen et al., 2001; Van Essen, 2005; Van Essen & Dierker, 2007; see Figure 7). Foci were grouped by color-spectrum and shape according to category-based activation: circular represents "living" and square represents "socialness."

Statistical tests

Data analysis was performed using a 3 × 2 (Coordinates x Category) ANOVA for each hemisphere separately (analysis was modeled after Kaddosh, Lammertyn, & Izard, 2007). Means and standard deviations were computed for each category (within a hemisphere) separately. To keep the analysis balanced, only coordinate activations represented bilaterally were used in the ANOVA

Study	Category Activation	Task	Left			Right		
			X	Y	Z	X	Y	Z
Chao, Haxby & Martin, 1999	Living	picture-viewing	-38	-58	-10	38	-56	-12
Chao, Haxby & Martin, 1999	Living	picture-viewing	-49	-59	-10	39	-59	11
Chao, Haxby & Martin, 1999	Living	picture-viewing	-42	-59	19	36	-57	-10
Chao, Haxby & Martin, 1999	Living	picture-viewing	-39	-55	-8	53	-54	16
Chao, Weisberg & Martin, 2002	Living	picture-naming	-42	-59	19	53	-54	16
Noppeney et al., 2006	Living	picture/word viewing		n.s		39	-60	-21
Mean*			-42	-58	2	44	-56	4
S.D.*			4	2	16	9	2	14
Martin & Weisberg, 2003	Social	social vignette viewing	-44	-57	-23	41	-52	-15
Martin & Weisberg, 2003	Social	social vignette viewing	-49	-57	17	56	-58	19
Martin & Weisberg, 2003	Social	social vignette viewing	-40	-38	-20	40	-33	-21
Ross & Olson 2010	Social	Heider & Simmel animations	-40	-4	-13	54	-12	-12
Ross & Olson 2010	Social	Heider & Simmel animations	-40	-44	-14	36	-43	-14
Ross & Olson 2010	Social	social word semanticity	-31	-72	-17		n.s	
Mean*			-43	-40	-11	45	-40	-9
S.D.*			4	22	16	9	18	16

Figure 7. Activation foci for the meta-analysis and corresponding cortical maps (Figure 9). Noppeney et al. (2006) and Ross & Olson (2010; social word semanticity) coordinates not included in mean, S.D., or ANOVA analyses. Mean and S.D. rounded to nearest whole integer.

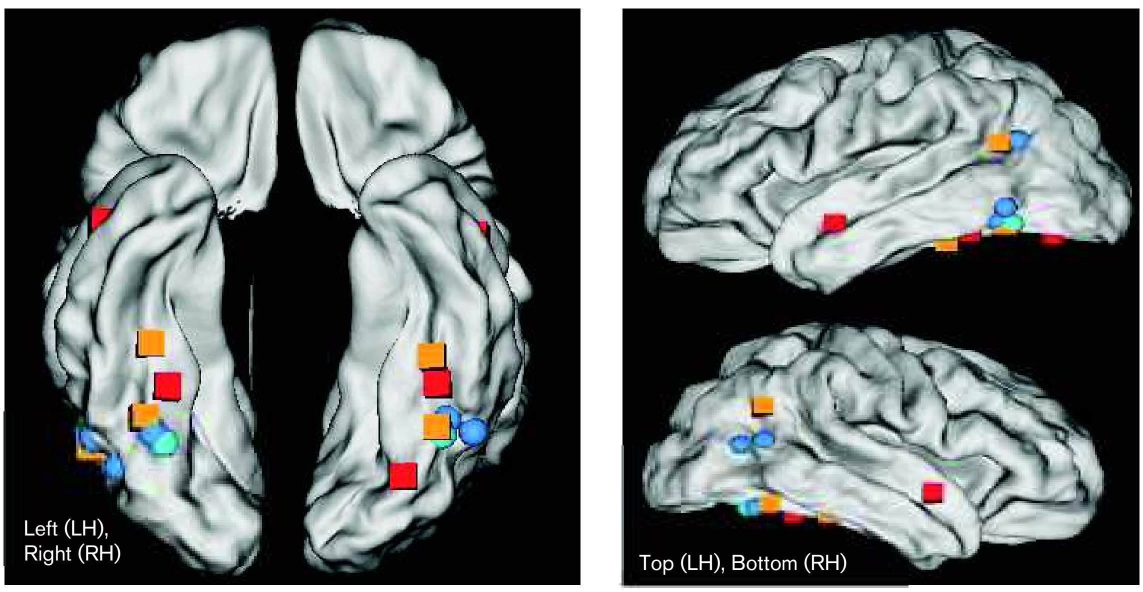
(that is, coordinates representing category specific activation for both hemispheres), and, as such, one set of coordinates per category was not used in testing (living: Noppeney et al., 2006; socialness (word stimuli): Ross & Olson, 2010).

Results

A two-way analysis for left hemisphere acti-

	Living			Social		
	X	Y	Z	X	Y	Z
LH						
Mean	-40	-58	2	-43	-44	-11
S.D.	2	2	16	4	23	16
RH						
Mean	44	-56	4	45	-40	-9
S.D.	9	2	14	9	18	16

Figure 8. Means and standard deviations rounded to the nearest integer for living and social foci coordinates. The main interaction observed in the RH seems to be driven by the difference in Y coordinates between living and social categories.



(a) (b)

Figure 9. A cortical mapping of studies reported in Figure 7. Squares represent social category activation; circles represent living category activations. (a) Ventral view foci. (b) Lateral view foci. No significant difference was observed for activation between categories, LH ((F(1, 24) = .01, p = .92), RH (F(1, 24) = .15, p = .71), and a significant interaction was observed in RH (F(2, 24) = 3.44, p < .05). Results suggest significant neural overlap between areas responsible for categories of living objects and categories of "socialness." Color code: *light blue*, Chao et al. (1999); *turquoise*, Chao et al. (2002); *light green*: Noppeney et al. (2006); *orange*: Martin & Weisberg (2003); *red*: Ross & Olson (2010).

vation yielded a main effect for coordinates ($F(2, 24) = 34.63$, $p < .001$), indicating a significant difference between all three dimensions (x,y,z) of the Talairach Coordinate System (Talairach & Tournoux, 1988; see Figure 8). No main effect was observed for category (($F(1, 24) = .01$, $p = .92$), and there was no interaction ($F(2, 24) = 2.57$, $p < .10$) suggesting that neural representations for both living and social categories are not significantly different in the left hemisphere. A two-way analysis for right hemisphere activation yielded a main effect for coordinates ($F(2, 24) = 137.6$, $p < .001$), again indicating a significant difference between all three dimensions. No main effect was observed for category ($F(1, 24) = .15$, $p = .71$), but a significant interaction was observed ($F(2, 24) = 3.44$, $p < .05$), which seems to be driven by the Y coordinate differences due to the more anterior location of social foci. These results suggest that neural representations of social and living categories in the right hemisphere are not significantly different.

Discussion

This meta-analysis suggests a significant neural overlap between areas that show activation for "socialness" and activation for living things. Social concepts are traditionally hard to define as they represent abstract semantic knowledge that enables us to describe our own as well as others' behaviors (Zahn et al., 2007). Neural regions representing "socialness" have most often been reported as cortical responses to social vignettes (e.g., Martin & Weisberg, 2003; Ross & Olson, 2010). These vignettes are based on the work of Heider and Simmel (1944), who first developed a movie clip of simple shapes that seemed to be capable of causal motion. When observers viewed this clip, they consistently attributed personality traits and emotions to the shapes regardless of the instructions that they were given (see also Scholl & Tremoulet, 2000). Follow-up studies on the phenomenon have repeated these findings and have demonstrated that these observations of animacy are consistent across cultures (Scholl & Tremoulet, 2000). Research in developmental psychology (e.g., Csibra, Gergely, Biro, Koos, & Brockbank,, 1999; Dasser, Ulbaek, & Premack, 1989; Gergely, Nadasdy, Csibra, & Biro, 1995; Premack, 1990) has shown that perceptual animacy is a phenomenon directly related to the elements of intentionality, goal-directed behavior, and causality, all of which make up the domain of agency, as described by Carey (e.g., 1988, 1999). Additionally, recent research has suggested that motion kinematics, and not feature properties of objects, are responsible for perceptual animacy and understanding agency (Scholl & Tremoulet, 2000).

Based on the behavioral evidence from studies such as these and functional imaging (e.g., Chao et al., 1999, 2002; Martin & Weisberg, 2003; Noppeney et al. 2006; Ross & Olson, 2010), "socialness," as observed through animacy and causal motion, seems to be an important factor in assessing the life state of an object. Castelli, Happé, Frith, and Frith (2000) reported findings in which goal-directed, and intentional movement, compared to random motion, elicited strong responses in fusiform gyrus and were accompanied by anthropomorphic language descriptions of stimuli. These findings, along with those discussed previously, indicate a strong relationship between areas linked to conceptual knowledge about living things and things that exhibit "socialness."

The Domain Specific Hypothesis can support animacy as an important factor for driving the organization of conceptual knowledge for living things, as well. Given that the DSH implicates evolutionary pressures as constraints on the development of concept categories (Caramazza & Shelton, 1998), animacy detection and social relevance are factors that would have been very important from an evolutionary standpoint. Therefore, understanding and parsing the environment into living and non-living things based on "socialness" would have been an effective means of survival and would have been promoted as a domain-specific mechanism. Plants, although living things, do not exhibit animacy or any other properties of the domain "social," and would therefore have been grouped as non-social objects, sharing properties similar to those of non-living objects.

CONCLUSION

Theories of conceptual knowledge organization agree on the dissociation between living and non-living things and are supported by both functional imaging and behavioral evidence. However, it is unclear whether the domain "living" is a coherent category representation. Results from this study show a dissociation between animals and plants in lateral, "living" regions of the ventral stream and a differential impact of animacy (biological motion) on the categorization of animals. If living things were a unitary concept category, then these findings would not be expected. On the other hand, intentional movement, causality, animacy, and agency seem to be important contributing factors in determining whether an object is alive (e.g., Piaget, 1929/1960; Carey, 1998, 1999, 2009; Scholl & Tremoulet, 2000; Martin & Weisberg, 2003; Ross & Olson, 2010). For these reasons, it may be the case that "socialness," a domain that represents elements of agency, animacy, causality and intentionality, better explains the organization of living and non-living things. The domain "socialness" fits well within the model of the Domain Specific Hypothesis as a cognitive mechanism that has been shaped by pressures of evolution. However, future studies are still required to understand the finer distinctions both between and within domains of "living" and "non-living." Specifically, studying an object category such plants, which is representative of both living and non-social things, might provide a more comprehensive understanding of the organization of conceptual knowledge.

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