Title: **Mugs and Plants: Object Semantic Knowledge Alters Perceptual Processing with Behavioral Ramifications**

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Abstract

Neural processing of objects with action associations is thought to recruit dorsal visual regions more than objects without such associations. We hypothesized that because the dorsal and ventral visual pathways have differing proportions of magno- and parvo-cellular input, there should be behavioral differences in perceptual tasks between manipulable and non-manipulable objects. This hypothesis was tested using gap detection task, suited to the spatial resolution of the ventral parvocellular processing, and object flicker discrimination task, suited to the temporal resolution of the dorsal magnocellular processing. Directly predicted from the cellular composition of each pathway, a non-manipulable object advantage was observed in tasks relying on spatial resolution, and a manipulable object advantage in temporal discrimination. We also show that these relative advantages are modulated by either reducing object recognition through inversion or by suppressing magnocellular processing using red light. These results establish perceptual differences between objects dependent on prior knowledge and experience.

Object perception and recognition underlies effective engagement with our complex environment. When looking at a potted plant, for example, precise access to long term semantic memory may be needed to facilitate a more detailed identification of the plant to know how often it needs to be watered. However, when reaching for a mug to have your morning coffee, detailed identification may be less important (e.g., which one of your 10 favorite mugs it is), but what is more pertinent is computing a motor plan to bring the mug to your mouth without spilling. The visual object processing necessary to identify plants and to drink from mugs is understood to progress along two distinct but interacting neural processing pathways, each of which is understood to subserve different end goals (Mishkin & Ungerleider, 1982; Kravitz et al., 2011). While the hypothesis of biased processing across the two pathways is widely accepted, it is unclear whether there are behavioral ramifications that are directly related to object processing being biased to different pathways. Here, we provide evidence that object semantic knowledge evokes differences in object perception based on the recruited regions across the dorsal or ventral streams. Importantly, we gain insight into neural processing by using purely behavioral methods that are custom tailored to the response properties of the neurons in both the dorsal (higher temporal resolution) and ventral pathways (higher spatial resolution).

The ventral pathway, commonly referred to as the 'what' pathway, is characterized by object feature selectivity and projects anteriorly from the occipital visual areas toward the hippocampus and the inferior temporal cortex (Kravitz et al., 2013). Damage to cortical regions along the ventral pathway results in visual agnosia, evidenced by difficulties in object recognition but preserved motor interactions with objects (Goodale & Milner, 1992; 1994; Karnath et al., 2009). Patients with ventral pathway damage but an intact dorsal pathway continue to manipulate, move, and reach for objects without much difficulty, while their ability to identify objects is

59 greatly impaired (James et al., 2003). The dorsal pathway, in turn, colloquially known as the
60 'where' or 'how' pathway, courses from the occipital visual areas into the parietal cortex. The
61 dorsal pathway is commonly understood to subserve object processing for the purposes of
62 reaching, grasping, and manipulation. While both pathways contribute to visual perception, the
63 demands of perceiving a specific object can differentially engage the two pathways such that the
64 dorsal pathway provides greater contribution for visual processing of objects that are directly
65 relevant for object manipulation (e.g., a hammer, a plunger, or a mug). Evidence for dynamic
66 recruitment of processing from one pathway more than the other has been garnered from a wide
67 range of techniques and paradigms. For example, while presenting participants with objects of
68 various categories, including tools, places, animals, and faces, an increase in dorsal pathway
69 processing, specifically in the left ventral premotor and left posterior parietal cortices, has been
70 observed exclusively in response to tool presentation (Chao & Martin, 2000). Similar results
71 which evidence a dorsal bias for manipulable objects have been found in functional magnetic
72 resonance imaging studies (Noppeney et al., 2006a; Mahon et al., 2007, Almeida et al., 2013,
73 Chen et al., 2018) and with various other paradigms including interocular suppression (Fang and
74 He, 2005) and continuous flash suppression (Almeida et al., 2008; Almeida et al., 2010).
75 While neuroimaging and neurophysiological evidence has been convincing in showing
76 selectivity for objects in various areas across the two streams, the impact that differential
77 processing across the two pathways has on object perception and subsequent behavior has not
78 been characterized. Hypotheses regarding how dynamic recruitment of the dorsal and ventral
79 pathways differentially influences perception and behavior are based on the anatomy and
80 physiology of the two visual pathways. Considering cellular physiology, there is an asymmetry
81 in innervation of the two pathways that overlaps with the separate magnocellular and

82 parvocellular processing pathways identified in anatomical architecture of visual processing
83 (Maunsell et al., 1990; Baizer et al., 1991; Ferrera et al., 1992). The asymmetry in cellular
84 composition across the two pathways endows each pathway with different response properties in
85 accordance with cell stimulus preferences within the magno- and parvo-cellular pathways. The
86 magno- and parvo-cellular pathways originate from different types of ganglion cells within the
87 retina and course separately through different layers of the lateral geniculate nucleus (Leventhal
88 et al., 1981; Perry et al., 1984), innervating separate layers of V1 (Blasdel & Lund, 1983). From
89 V1, the parvocellular pathway can be followed into area V2, through area V4, and then into the
90 inferior parietal cortex while the magnocellular pathway can be traced into different regions of
91 area V2, through areas V3d and MT, and then into the posterior parietal cortices (DeYoe & van
92 Essen, 1988; Livingstone & Hubel, 1988).
93 Differentiation in cellular innervation of the two processing pathways leads to different
94 response properties that convey information of different spatial and temporal resolutions. The
95 magnocellular channel is derived from the parasol ganglion cells with relatively large receptive
96 fields, spanning large regions of the retina (Nassi & Callaway, 2009). The cells of the
97 magnocellular channel are more myelinated, and have less neuronal convergence than the
98 parvocellular channel (Maunsell et al., 1999a). The features of the parasol retinal ganglion cells
99 enable the dorsally biased magnocellular pathway to encode information with a higher temporal
100 resolution than that of the parvocellular channel (Pokorny and Smith, 1997; but see Maunsell et
101 al., 1999b). Conversely, the parvocellular channel is derived from the midget retinal ganglion
102 cells, which receive input primarily from cone receptors and have smaller receptive fields (Nassi
103 & Callaway, 2009). The features of the midget retinal ganglion cells enable the ventrally biased
104 parvocellular channel to encode information with a higher spatial resolution than that of the

magnocellular channel (Derrington & Lennie, 1984; Leonova et al., 2003; McAnany & Alexander, 2008).

Due to the asymmetric contributions of the magno- and parvo-cellular pathways to the dorsal and ventral pathway processing pathways, we hypothesize that semantic knowledge of object utility (manipulable or non-manipulable) determines processing bias to either dorsal or ventral pathway processing and thus has consequences for perceptual processing. Thus, if semantic knowledge of an object's utility determines to which of the two pathways the bias will accrue, then: (1) manipulable objects, that elicit a higher degree of magnocellularly biased dorsal processing, should be processed with higher temporal resolution; and (2) non-manipulable objects, that rely more on parvocellularly biased ventral processing, should be processed with higher spatial resolution. Across five experiments, this hypothesis is tested by comparing processing of temporal and spatial resolution in two object groups: manipulable and non-manipulable objects. Each group consisted of ten line-drawings of objects which were carefully controlled for low-level perceptual differences (width of the gap line, luminance, size, and aspect ratio which a measure of elongation; see Methods for details). Due to the fact that our hypotheses are predicated on the idea that action associations bias processing across the two streams, the objects were chosen based on how often they are manipulated with the hands when they are encountered rather than by their association to any particular semantic grouping. The manipulable object set included objects that are typically manipulated by the hands when they are encountered, such as a hammer, a plunger, and a mug (Fig. 1A). The non-manipulable object set included objects that are rarely manipulated with the hands when they are encountered, such as a fire hydrant, a picture frame, and a potted plant (Fig. 1A).

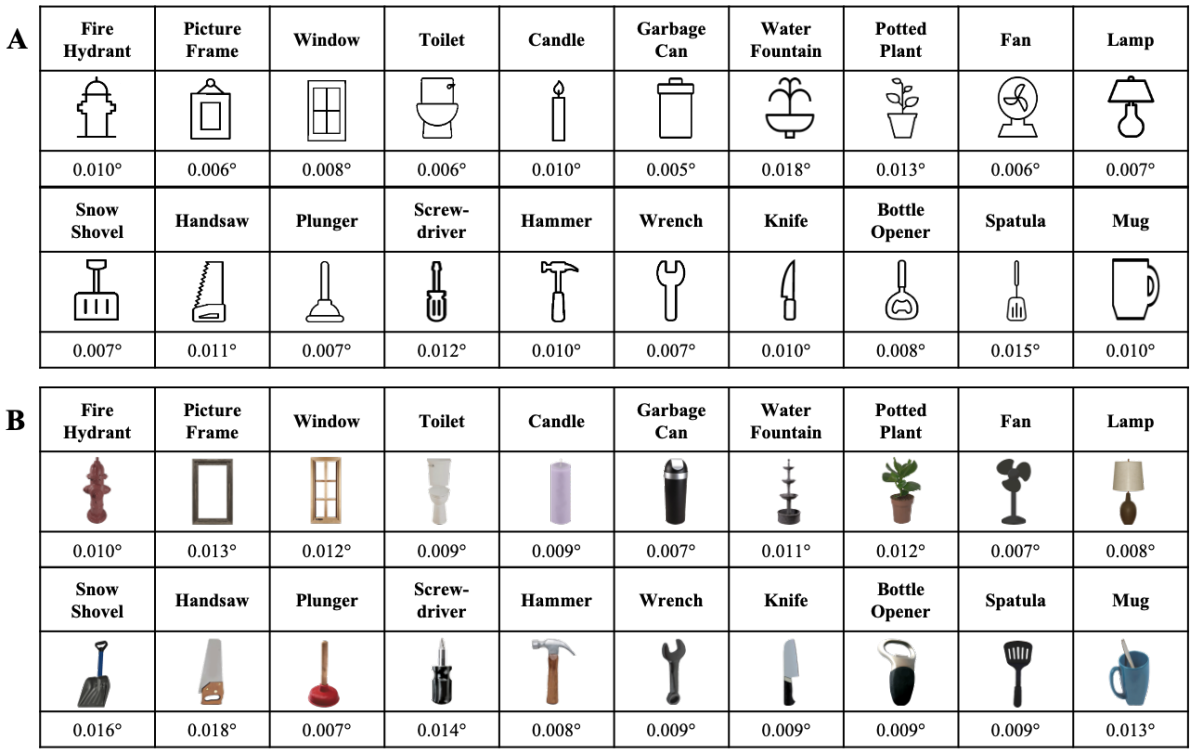

Figure 1 *Stimulus set used in the experimental paradigms. (A) Line drawings of manipulable and non-manipulable objects used in Exp. 1. (B) Pictures of real-world manipulable and non-manipulable objects used in the second control manipulation for Exp. 1. The numbers beneath each set of objects correspond to the size of the spatial gap titrated to each object.*

Experiment 1 employed two paradigms, each designed to take advantage of the unique stimulus response properties of the two visual processing pathways and their corresponding cellular composition. To measure ventral pathway engagement a gap detection task was employed. Each object appeared to the left or the right of fixation, and would either have an uninterrupted bottom contour or have a small spatial gap in the center of the bottom line of the object (Fig. 2A). Object group was counterbalanced such that manipulable objects were seen as commonly as non-manipulable objects, and objects within each group were counterbalanced such that all objects were seen an equal number of times. The size of the gap was titrated, in a separate procedure for each object individually in an independent group of participants, to a specific threshold making the task difficult but not impossible (See Methods for details). Participants' task was to report the presence or absence of the gap. If object semantic knowledge

determines the route of processing, then the presence of a spatial gap on non-manipulable objects will be detected with higher sensitivity as compared to manipulable objects because processing will be biased to ventral pathway's parvocellular processing.

To measure dorsal pathway engagement, a blink detection task was used. Similar to the spatial gap detection task, participants detected the presence of a short blink. During a blink trial, the object was presented for 80 ms, then removed for the short duration of 16 ms, then redisplayed for additional 48 ms. The duration of the blink was titrated with a staircase procedure, with the shortest titrations limited by the lower bound of the monitor's refresh rate. Thus, shortest blink duration was set to 16 ms. During a non-blink trial, the objects remained on the screen for the total duration of 144 ms. Similar to the spatial gap paradigm, participants responded with a button press to indicate whether a blink was detected. If object semantic knowledge determines the route of processing, then the presence of a temporal gap during the presentation of manipulable objects will be detected with higher sensitivity as compared to non-manipulable objects because processing will be biased to magnocellularly-dominated dorsal pathway. For both tasks, participants were given feedback on incorrect trials. Each participant performed both tasks (3 blocks each), in a counterbalanced order, across six blocks.

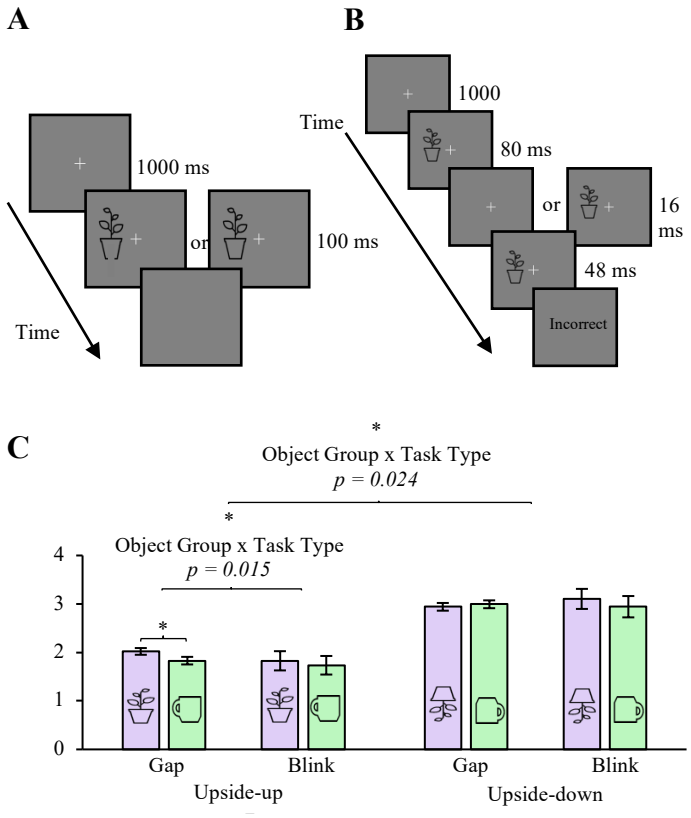

Figure 2. The paradigm and results for Experiments 1 and 2. Participants maintained fixation on the center cross. An object appeared to the left or right of fixation. A) For the spatial-gap paradigm, participants indicated by keypress if the bottom line of the presented object contained a gap. B) for the temporal paradigm, participants were to indicate whether the object flickered. C) Results for Experiment 1 (n=26) and 2 (n=30). For Experiment 1 (C, left), there was a significant main effect of task type ($F(1, 25) = 50.953$, $p < 0.001$, $\eta_p^2 = 0.671$) such that d' sensitivity was higher for blinks than for gaps ($M_{gaps} = 1.93$; $M_{blinks} = 2.97$); and a significant two-way interaction between object group and task type ($F(1, 25) = 6.772$, $p = 0.015$, $\eta_p^2 = 0.213$), driven by the difference between object groups in the gap condition ($F(1, 25) = 9.888$, $p = 0.004$, $\eta_p^2 = 0.283$, with non-manipulable objects having a higher d' for gaps than manipulable objects ($M_{non\text{-}manipulable} = 2.021$; $M_{manipulable} = 1.831$). For Experiment 2 (C, right), there was a significant main effect of object group ($F(1, 25) = 5.860$, $p = 0.023$, $\eta_p^2 = 0.190$) such that d' was higher for non-manipulable objects than for manipulable objects ($M_{non\text{-}manipulable} = 2.466$; $M_{manipulable} = 2.340$) (Fig. 2C, right). There was also a significant main effect of task type ($F(1, 25) = 82.298$, $p < 0.001$, $\eta_p^2 = 0.767$) such that d' was higher for blinks than for gaps ($M_{gaps} = 1.782$; $M_{blinks} = 3.024$). There was no significant interaction between object group and task type ($F(1, 25) = 0.508$, $p = 0.483$, $\eta_p^2 = 0.020$). Additionally, across the two experiments, with orientation as a between subjects factor, there was a significant three-way interaction between object group, task type, and orientation ($F(1, 50) = 5.381$, $p = 0.024$, $\eta_p^2 = 0.097$) such that orientation significantly reduced the effect for the inverted objects.

The spatial and temporal paradigms used d' as a measure of perceptual sensitivity (Fig. 2). A two-way repeated-measures analysis of variance (ANOVA) was conducted on d' with object group (manipulable, non-manipulable) and stimulus type (gap, blink) as within-subject variables (Fig. 2C, left). The ANOVA revealed no significant main effect of object group ($F(1, 25) = 2.342$, $p = 0.138$, $\eta_p^2 = 0.086$), and a significant main effect of task type ($F(1, 25) = 50.953$, $p < 0.001$, $\eta_p^2 = 0.671$) such that d' sensitivity was higher for blinks than for gaps ($M_{gaps} = 1.93$; $M_{blinks} = 2.97$). Importantly, and consistent with the hypothesis of differential engagement of two pathways depending on object utility, a significant two-way interaction

167 between object group and task type ($F(1, 25) = 6.772$, $p = 0.015$, $\eta_p^2 = 0.213$) was observed,
168 driven by the difference between object groups in the gap condition ($F(1, 25) = 9.888$, $p = 0.004$,
169 $\eta_p^2 = 0.283$), with non-manipulable objects having a higher d' for gaps than manipulable objects
170 ($M_{non\text{-}manipulable} = 2.021$; $M_{manipulable} = 1.831$). The interaction effect and the driving main effect are
171 consistent with the prediction that non-manipulable objects, given reliance on ventral pathway
172 processing, should yield higher sensitivity in the detection of spatial gaps than manipulable
173 objects. Notably, the expected higher sensitivity to temporal gaps in the manipulable object set
174 was not supported. Given the high sensitivity for the temporal task type (d' = 2.941 for non-
175 manipulable objects and d' = 2.993 for manipulable objects), the lack of difference between the
176 object groups in the blink condition was likely due to the temporal task being overly easy (i.e.,
177 ceiling effect; see Exp. 4 for a manipulation that avoids ceiling effects).

178 While Experiment 1 provides evidence for biased engagement of the ventral pathway for
179 non-manipulable object perception during a temporal task, it could be argued that despite careful
180 low-level feature controls (e.g., luminance, size, elongation) an uncontrolled low-level difference
181 between manipulable and non-manipulable objects is responsible for driving the manipulable vs.
182 non-manipulable advantage in the spatial gap task. In order to rule out this possibility and,
183 simultaneously, to further probe the hypothesis that semantic knowledge of object utility
184 (manipulable or non-manipulable) biases the pathway that will ultimately process the object, we
185 conducted two control experiments. In addition to serving as a low-level control and a further
186 test of the hypothesis, these experiments provide internal replications of the reported finding (see
187 Open Science Collaboration, 2015).

188 In the first control manipulation, the same paradigm and objects from Experiment 1 were
189 used with the manipulation of inverting objects (upside-down). The inversion preserved the low-

level features of each object while impairing participants' ability to rapidly recognize and access their semantic knowledge of the objects' function. Inversion has been found to interfere with recognition of faces and objects (Diamond and Carey, 1986). Following from the hypothesis that semantic knowledge of object's utility drives the perceptual difference between manipulable and non-manipulable objects, we predict that object inversion should reduce the difference between manipulable and non-manipulable objects. A two-way repeated-measures ANOVA was conducted on d' with object group (manipulable, non-manipulable) and task type (gap, blink) as within-subject variables. The ANOVA revealed a significant main effect of object group ($F(1, 25) = 5.860$, $p = 0.023$, $\eta_p^2 = 0.190$) such that d' was higher for non-manipulable objects than for manipulable objects ($M_{non\text{-}manipulable} = 2.466$; $M_{manipulable} = 2.340$) (Fig. 2C, right). There was also a significant main effect of task type ($F(1, 25) = 82.298$, $p < 0.001$, $\eta_p^2 = 0.767$) such that d' was higher for blinks than for gaps ($M_{gaps} = 1.782$; $M_{blinks} = 3.024$). As predicted, there was no significant interaction between object group and task type ($F(1, 25) = 0.508$, $p = 0.483$, $\eta_p^2 = 0.020$). In order to statistically demonstrate that results of the inversion experiment are indeed different from those observed in Experiment 1, data were subjected to a between-subject ANOVA with object orientation (upright, inverted) as a between subjects variable and object group and task type as within subject factors. The ANOVA revealed a significant three-way interaction between object group, task type, and orientation ($F(1, 50) = 5.381$, $p = 0.024$, $\eta_p^2 = 0.097$) such that, as predicted, orientation significantly reduced the effect for the inverted objects.

In the second control manipulation, line drawings were replaced by real-world images of corresponding objects, such that a line drawing of a candle was replaced with a picture of a candle, etc. (Fig. 1B). The prediction remained the same as in the original experiment, if object semantic knowledge determines which visual processing pathway object processing is biased to

then non-manipulable objects will be biased to the ventral pathway leading to higher sensitivity (as measured by d') in the spatial gap task, replicating the pattern of performance observed in Experiment 1. A two-way repeated-measures ANOVA was conducted on d' with object group (manipulable, non-manipulable) and task type (gap, blink) as within-subject variables. The ANOVA revealed a significant main effect of object group ($F(1, 29) = 28.211$, $p < 0.001$, $\eta_p^2 = 0.493$) with non-manipulable objects having a higher sensitivity than manipulable objects ($M_{non\text{-}manipulable} = 2.361$, $M_{manipulable} = 2.046$) (Fig. 3). There was also a significant main effect of task type ($F(1, 29) = 8.413$, $p = 0.007$, $\eta_p^2 = 0.225$) with blinks having a higher average sensitivity than gaps ($M_{blinks} = 2.409$, $M_{gaps} = 1.998$). Importantly, a two-way interaction between object group and task type was also significant ($F(1, 29) = 13.061$, $p = 0.001$, $\eta_p^2 = 0.311$), driven by a simple main effect in the gap condition ($F(1, 29) = 46.424$, $p < 0.001$, $\eta_p^2 = 0.616$) such that non-manipulable objects had a higher d' for gaps than did the manipulable objects ($M_{non\text{-}manipulable} = 2.238$; $M_{manipulable} = 1.758$). In order to statistically demonstrate that results observed using real objects are indistinguishable from the results observed using the line-drawings in Experiment 1, the data were subjected to a between-subject ANOVA with stimulus type (line drawings, real object images) as a between subjects variable and object group and task type as within subject factors. The ANOVA revealed no significant three-way interaction between object group, task type, and stimulus type ($F(1, 54) = 0.454$, $p = 0.503$, $\eta_p^2 = 0.000159$). These results replicate Experiment 1, providing strong additional support for the hypothesis that the perceptual differences between manipulable objects and non-manipulable objects is due to the semantic content of the objects rather than low-level features.

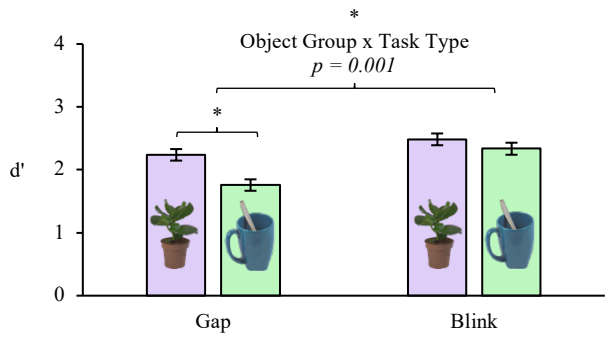

Figure 3. *Results from the second control manipulation of experiment one in which real object images were used instead of line drawing images. There was a significant main effect of object group ($F(1, 29) = 28.211$, $p < 0.001$, $\eta_p^2 = 0.493$) with non-manipulable objects having a higher sensitivity than manipulable objects ($M_{non\text{-}manipulable} = 2.361$, $M_{manipulable} = 2.046$) (Fig. 3). There was also a significant main effect of task type ($F(1, 29) = 8.413$, $p = 0.007$, $\eta_p^2 = 0.225$) with blinks having a higher average than gaps ($M_{blinks} = 2.409$, $M_{gaps} = 1.998$). The two-way interaction between object group and task type was also significant ($F(1, 29) = 13.061$, $p = 0.001$, $\eta_p^2 = 0.311$), driven by a simple main effect in the gap condition ($F(1, 29) = 46.424$, $p < 0.001$, $\eta_p^2 = 0.616$) such that non-manipulable objects had a higher d' for gaps than did the manipulable objects ($M_{non\text{-}manipulable} = 2.238$; $M_{manipulable} = 1.758$).*

While the first three experiments yielded strong supporting evidence that gap detection is better on non-manipulable objects than manipulable objects, perhaps resulting from bias toward the ventral pathway, manipulable objects failed to elicit an advantage in temporal resolution, failing to provide evidence of a dorsal pathway bias for manipulable objects. One explanation for the null effect is that the temporal gap detection task was too easy (ceiling effect), evidenced by high d' values in the temporal task. To increase task difficulty, and move away from the ceiling performance, the blink paradigm was re-designed to a discrimination task[1]. Objects were presented for 80 ms, removed from the screen for either a 16 ms or 48 ms blink, and redisplayed for 48 ms (Fig. 4). Participants' task was to indicate whether the blink duration was short or long. The prediction was that manipulable objects should have a performance benefit over non-manipulable objects due to the increased magnocellular input, and therefore temporal resolution, of the dorsal pathway. Due to the difficulty of the task (mean accuracy 77%), evidenced by low d' values, analyses were conducted on RT. A two-way repeated-measures ANOVA was

[1] We thank Ed Awh, from the University of Chicago, for the helpful suggestion.

conducted on RT with object group (manipulable, non-manipulable) and blink duration (short, long) as within-subject variables. Only the RTs for correct responses were analyzed.

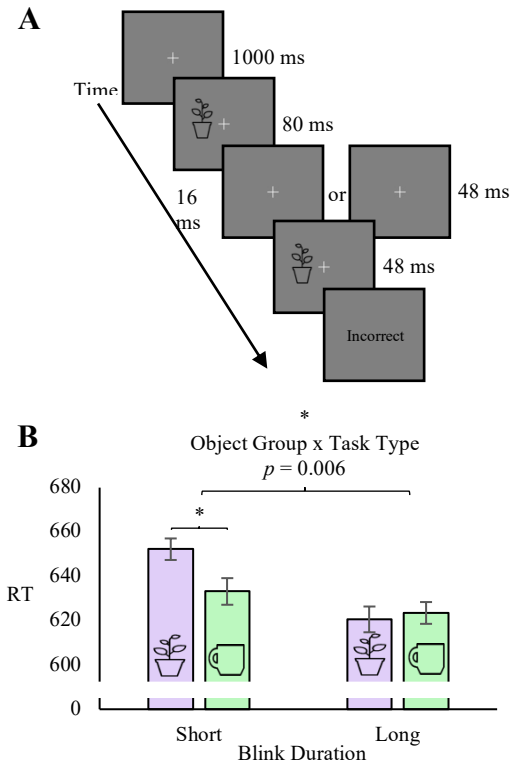

Figure. 4. *The paradigm and results for experiment 4. A) Participants maintained fixation on the center cross. An object would then appear to the left or right of fixation. The objects would flicker by being removed from the screen for 16 ms or 48 ms. Participants were to indicate by keypress if the object flicker duration was short or long. B) There was no significant main effect of object group (F(1, 24) = 4.080, p = 0.055,* $\eta_p^2 = 0.145$*). There was a significant main effect of blink duration (F(1, 24) = 4.850 p = 0.038* $\eta_p^2 = 0.168$*) such that the short duration elicited a higher RTs than did the long duration (*M_{short} *= 642.68 ms;* M_{long} *= 621.997ms). The two-way interaction between object group and blink duration was significant (F(1, 24) = 9.011, p = 0.006,* $\eta_p^2 = 0.273$*) driven by a simple main effect in the short blink condition (F(1, 24) = 11.710, p = 0.002,* $\eta_p^2 = 0.328$*) such that manipulable objects had a lower RT for short blinks than did the non-manipulable objects (*$M_{manipulables}$ *= 633.150;* $M_{non\text{-}manipulable}$ *= 652.210).*

The ANOVA revealed no significant main effect of object group ($F(1, 24) = 4.080$, $p = 0.055$, $\eta_p^2 = 0.145$) (Fig. 4). There was a significant main effect of blink duration ($F(1, 24) = 4.850$ $p = 0.038$ $\eta_p^2 = 0.168$) such that the short duration elicited a higher RTs than did the long duration ($M_{short} = 642.68$ ms; $M_{long} = 621.997$ ms). The two-way interaction between object group and blink duration was significant ($F(1, 24) = 9.011$, $p = 0.006$, $\eta_p^2 = 0.273$) driven by a simple main effect in the short blink condition ($F(1, 24) = 11.710$, $p = 0.002$, $\eta_p^2 = 0.328$) such that manipulable objects had a lower RT for short blinks than did the non-manipulable objects ($M_{manipulable} = 633.150$; $M_{non\text{-}manipulable} = 652.210$). In accuracy, no effect was observed for object group ($F(1, 24) = 3.666$, $p = 0.068$, $\eta_p^2 = 0.133$), blink duration ($F(1, 24) = 1.509$, $p = 0.231$, η_p^2

260 = 0.059), nor the interaction ($F(1, 24) = 2.000$, $p = 0.170$, $\eta_p^2 = 0.077$), suggesting that all
261 significant effects were absorbed by the response time measure and no speed-accuracy tradeoffs
262 were observed, indicating consistency with response time results. These results, specifically the
263 simple main effect in the short gap condition with manipulable objects having a lower RT than
264 non-manipulable objects, supports our hypothesis that manipulable object processing would
265 elicit higher temporal resolution than non-manipulable object processing. The lack of a
266 difference in the long duration condition is likely due to a ceiling effect, similar to the lack of
267 temporal effect in Experiment 1.

268 The last test of our hypotheses is derived from the neurophysiological differences
269 between the dorsal and ventral pathways. It was reasoned that if the differences in spatial gap
270 sensitivity for non-manipulable objects are mechanistically derived from the magnocellular and
271 parvocellular dichotomy of the two visual processing pathways, then the effect should be
272 modulated through manipulation of processing within the pathways. Ambient red light has been
273 shown to suppress activity in the magnocellular processing channel because of the large number
274 of visually responsive cells with red inhibitory surrounds in their receptive fields (Wiesel &
275 Hubel, 1966). Therefore, presenting objects with a red background should suppress the
276 contribution from the parietal magnocellular pathway, whereas a background of any other color
277 should have no impact on processing. To test this prediction, the spatial resolution paradigm
278 from Experiment 1 was used with the manipulation of background color varying between green
279 or red (Fig. 5A). Due to the suppression of the magnocellular channel by red light, it was
280 predicted that the color of the background should modulate the perceptual difference in spatial
281 gap detected observed in Experiment 1. Namely, suppressing the contribution of the dorsal
282 pathway should exacerbate the difference between manipulable and non-manipulable objects. A

two-way repeated-measures ANOVA was conducted on d' with object group (manipulable, non-manipulable) and background color (green, red) as within-subject variables. The ANOVA revealed a significant main effect of object group ($F(1, 25) = 17.171$, $p < 0.001$, $\eta_p^2 = 0.407$) with non-manipulable objects having a higher average than manipulable objects ($M_{non\text{-}manipulable} = 2.25$, $M_{manipulable} = 2.02$) (Fig. 5B). There was no significant main effect of background color ($F(1, 25) = 2.138$, $p = 0.156$, $\eta_p^2 = 0.079$) but, as predicted, there was a significant two-way interaction between object group and background color ($F(1, 25) = 4.444$, $p = 0.045$, $\eta_p^2 = 0.151$) such that the effect was increased with the red background. It was hypothesized that if the perceptual differences between manipulable and non-manipulable objects are mechanistically derived from the magno- and parvo-cellular processing in the two visual pathways, then suppression of the magnocellular processing with red light should modulate the effect. The results of Experiment 5 support our hypothesis by demonstrating an increase of the perceptual difference between manipulable and non-manipulable objects with red light.

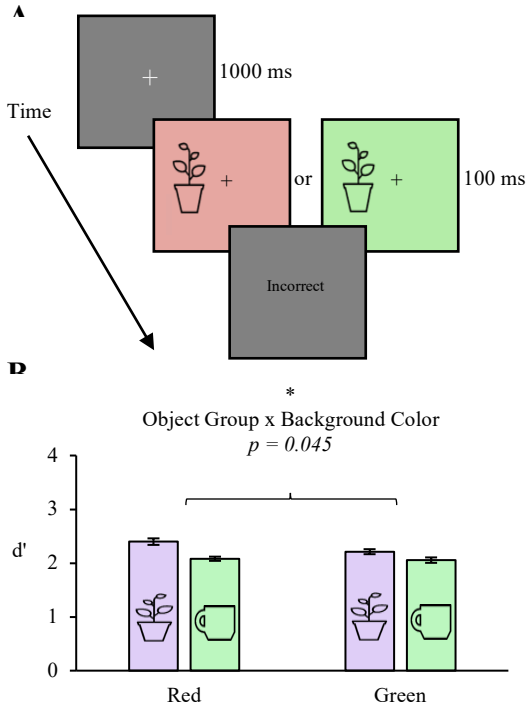

Figure 5. The paradigm and results of experiment 5. (A) Participants maintained fixation on the center cross. An object then appeared to the left or right of fixation. As in Experiment 1, participants were asked to detect the presence of small gap in the bottom outline of the object. The background color (red or green) was manipulated. (B) There was a significant main effect of object group ($F(1, 25) = 17.171$, $p < 0.001$, $\eta_p^2 = 0.407$) with non-manipulable objects having a higher average than manipulable objects ($M_{non\text{-}manipulable} = 2.25$, $M_{manipulable} = 2.02$). There was no significant main effect of background color ($F(1, 25) = 2.138$, $p = 0.156$, $\eta_p^2 = 0.079$) but there was a significant two-way interaction between object group and background color ($F(1, 25) = 4.444$, $p = 0.045$, $\eta_p^2 = 0.151$.

We hypothesized that manipulable and non-manipulable objects, due to differential recruitment of the two visual pathways, would elicit perceptual differences stemming from the characteristic spatial and temporal resolutions associated with the magno- and parvo-cellular inputs. In five experiments we provide strong evidence in support of behavioral consequences driven by physiological and anatomical differences of the two visual pathways, and argue that semantic knowledge of object utility guides processing along a particular pathway. If an object has a strong action association, its processing will be largely determined by activity in the dorsal pathway which is not found with objects that lack strong action association (Chao & Martin, 2000; Noppeney et al., 2006; Mahon et al., 2007). The increased level of activity in the parietal regions endows the perception of action-associated objects with greater access to the information encoded in the magnocellular channel which preferentially courses through the dorsal pathway. Without the enhanced dorsal pathway activity evoked by action associations, object representation is more dependent on the ventral pathway, which has a higher ratio of parvocellular channel information than does the dorsal pathway (Maunsell et al., 1990; Baizer et al., 1991; Ferrera et al., 1992). Based on differential magno- and parvo-cellular input to the two pathways, we predicted that the perception of objects with strong action associations results in an increased temporal resolution and that the perception of objects without such associations results in an increased spatial resolution. In the experiments reported here, we offer evidence that objects are perceived with different spatial and temporal resolutions depending on object semantic knowledge (namely, whether the object is manipulable or non-manipulable). In two follow-up control experiments, further evidence was provided in support of the hypothesis that the difference between manipulable and non-manipulable objects in the spatial task was driven

by the semantic knowledge of the objects rather than possible low-level visual features. Namely, it was observed that the effect is curtailed by impeding the access of object semantic knowledge through inversion and it was observed that the perceptual differences between manipulable and non-manipulable objects replicated with a separate set of more realistic object images (with a different set of low-level object properties). Lastly, to test if the differing relative proportions of magno- and parvo-cellular input are responsible for the perceptual differences that were observed in our first four experiments, ambient red light was used to suppress activity of the magnocellular channel. It was observed that this increased the perceptual difference in the spatial task between manipulable and non-manipulable objects.

Results are strengthened by a set of various low-level controls imposed on the stimulus set. Manipulable and non-manipulable object groups were controlled for size, hue, saturation, visual clutter, and image value. Additionally, object groups were controlled for the degree of elongation difference (i.e., aspect ratio) as this factor has been shown to drive some amount of dorsal visual pathway selective for tools, which are a subset of manipulable object (Chen et al., 2018).

Based on the evidence provided, we argue that semantic knowledge of the manipulability of objects, as defined by strong associations with an action appropriate for the item, generates the perceptual differences between manipulable and non-manipulable objects. Previous studies have shown that manipulable objects evoke a larger degree of dorsal pathway processing than do non-manipulable objects (Chao & Martin, 2000; Almeida et al., 2013). However, the origin of this processing difference and consequent perceptual differences between manipulable and non-manipulable objects is poorly understood.

One possibility by which objects imbue semantic content related to manipulation is implied manipulability. A potentially provocative investigation suggested that hand proximity (a proxy for manipulability), leads to differences similar to the perceptual differences between manipulable and non-manipulable objects (Gozli et al., 2012). Implied manipulability was induced by varying the positions of participants' hands such that hands near the display implied manipulability, while hands far from the display implied low manipulability. Importantly, participants were presented with a simple circle shape, rather than manipulable or non-manipulable objects. It was observed that when the participants' hands were positioned near the experimental stimuli, participants' sensitivity to temporal blinks was heightened and when participants' hands were far from the stimuli sensitivity to spatial gaps was heightened. In effect, the placement of the participants' hand in this paradigm shifted the perception of the stimuli to resemble either the non-manipulable objects, if the hands were far from the stimuli, or the manipulable objects, if the hands were near the stimuli. It may be that when an object is learned to be a manipulable, the neural representation of that object becomes associated with the near hand effect reported by Gozli et al., (2012).

A possible mechanism linking the near-hand effect reported by Gozli et al. (2012) and the perceptual difference between manipulable and non-manipulable objects derive from the bimodal cells in the anterior parietal cortex (Graziano & Gross, 1993). The bimodal cells have a somatosensory receptive field covering a part of the hand and they have a visual receptive field corresponding to a part of the visual field near their associated hand area. When an object is shown, if that object does not have a strong action association, then the activity of the bimodal cells is unaffected. After the organism has learned to use the object with their hands, the bimodal cells will respond solely to the visual presentation of the object even in the absence of

364 somatosensory input (Zhou & Fuster, 2000). During object training, it has been shown that the
365 anterior parietal regions which contain the bimodal cells upregulate brain-derived neurotrophic
366 factor (BDNF), a protein which encourages the development of new synapses (Ishibashi et al.,
367 2002). The upregulation of BDNF may be what changes the circuit structure around the bimodal
368 cells to enable purely visual activation without the corresponding somatosensory input. Thus, the
369 bimodal cells and their ability to become solely visually activated may be a driver of the known
370 object selectivity of the dorsal processing pathway (Vaziri-Pashkam & Xu, 2017; Kastner et al.,
371 2017; Freud et al., 2016) and lead to the dorsal pathway processing bias evoked by manipulable
372 objects (Chao & Martin, 2000). The object-specific neural activity in the dorsal processing
373 pathway, divorced from its need for somatosensory input, and largely derived from
374 magnocellular input, could then be read out during an identification task with high temporal
375 resolution, leading to heightened temporal precision for manipulable objects.

376 Taken together, our results demonstrate that object semantic knowledge determines the
377 processing bias of the object (via dorsal or ventral bias) and evokes subsequent behavioral
378 repercussions for perception and for action. Our work underscores the need for careful
379 consideration of object semantic knowledge and its subsequent possible bias to either dorsal or
380 ventral pathway processing when object images are used not only in psychological research, but
381 in applied settings such as display and product designs, environmental design, and in the design
382 of various cognitive assistants.
383
384

Methods

Participants. All participants were recruited from The George Washington University participant pool, gave informed consent according to the George Washington University's institutional review board (IRB), were naïve to the purpose of the experiment, and all reported normal or corrected-to-normal vision. In experiment 4, which utilized color stimuli no participant reported colorblindness.

For experiment 1, 26 undergraduate students (19 female; average age: 19.2; 6 left-handed) were recruited. No participant was removed from the analyses. For experiment 2, 27 undergraduate students were recruited. Twenty-six participants' data (14 female; average age: 19.0; 1 left-handed) were analyzed after one participant was cut for below chance accuracy in one of the conditions. For experiment 3, 33 undergraduate students were recruited. Thirty participants' data (26 female; average age: 19.07, 3 left-handed) were analyzed after eight participants were cut for below chance accuracy in at least one of the conditions. For experiment 4, 34 undergraduate students were recruited. Twenty-five participants' data (14 female; average age: 19.0; 1 left-handed) were analyzed after six participants were cut for not finishing the experiment and nine participants were cut for having less than chance accuracy in at least one of the conditions. For experiment 5, 26 undergraduate students were recruited. Twenty-five participants' data (18 female; average age: 19.5, 0 left-handed) were analyzed after one participant was cut for chance accuracy in all conditions.

Apparatus and Stimuli. All experiments were presented on a 24" Acer GN246 HL monitor with a refresh rate of 144 Hz, positioned at a distance of 60 cm from the viewer in a dark room. The experiment was generated and presented using PsychoPy v1.82.

The stimuli in Experiments 1, 2, 4, and 5 consisted of line drawings of real-world, everyday objects drawn both from The Noun Project, an online repository of object icons and clip art (https://thenounproject.com). The object stimuli consisted of 10 line-drawings of manipulable objects, and 10 line-drawings of non-manipulable objects. The manipulable objects were as follows: snow shovel, handsaw, plunger, screwdriver, hammer, wrench, knife, bottle opener, spatula, and mug. The non-manipulable objects were: fire hydrant, picture frame, window, toilet, candle, garbage can, water fountain, potted plant, fan, and lamp. The stimuli were displayed as large as possible in a 4° x 4° area and all stimuli were presented in black (HSV = 0, 0, 0) on a dark gray background (HSV = 0, 0, 50). All objects are displayed in Figure 1.

Objects were controlled for low-level differences by calculating the mean luminance, size, and aspect ratio (i.e., measure of elongation) for each object. There was no mean luminance difference between object groups, an independent samples t-test ($t(18) = -0.960$, $p = 0.350$). There was no significant difference in mean size (t-test ($t(18) = 1.043$, $p = 0.311$), or aspect ratio ($t(18) = 1.209$, $p = 0.242$). The width of the bottom line was controlled for each object on which the gap appeared. There was no significant difference between manipulable and non-manipulable objects in bottom line width in an independent samples t-test ($t(18) = 0.922$, $p = 0.369$).

For Experiment 3, the stimuli consisted of images of real-world, everyday objects drawn from Google image search and manipulated in GIMP 2.10.4. The object stimuli consisted of 10 images of the same manipulable objects, and 10 images of the same non-manipulable objects used in Experiments 1,2, 4, and 5. The stimuli were displayed as large as possible in a 4° x 4° area and all stimuli were presented in color on a dark gray background (HSV = 0, 0, 50). All objects are displayed in Figure 1.

Additionally, colored objects used in Experiment 3 were similarly controlled for low-level differences by calculating the mean size, hue, saturation, value, aspect ratio, and visual clutter. In analyzing mean size, there was no significant difference between manipulable and non-manipulable objects in an independent samples t-test ($t(18) = -1.027$, $p = 0.318$). Additionally, there were no significant differences for hue ($t(18) = -0.309$, $p = 0.761$), saturation ($t(18) = -0.031$, $p = 0.976$), value ($t(18) = 0.032$, $p = 0.975$), aspect ratio ($t(18) = -0.094$, $p = 0.927$), or visual clutter ($t(18) = 0.616$, $p = 0.545$). Additionally, we controlled the width of the bottom line of each object on which the gap would appear. There was no significant difference between manipulable and non-manipulable objects in bottom line width in an independent samples t-test ($t(18) = 0.557$, $p = 0.584$).

Design and Procedure. In Experiment 1, each trial began with a single central fixation point, which subtended a visual angle of 1° x 1°. The central fixation point was rendered in white (HSV = 0, 0, 100). After 1000 ms of fixation presentation, a single object line drawing would appear 4° to the left or right of the fixation point. The side of presentation was counterbalanced such that each participant saw an equal number of stimuli on the left and on the right. The stimuli were displayed as large as possible within a 4° x 4° area and all stimuli were presented in color on a dark gray background (HSV = 0, 0, 50). All objects are displayed in Figure 1.

In one half of the experiment, the object appeared with or without a spatial gap in the center of the bottom line of the object. The objects had an equal probability of having a spatial gap or not having a spatial gap. The objects appeared for 100 ms and participants were to report the presence of the spatial gap by pressing the right control button (present) or the left control button (absent) on the keyboard. Feedback was presented on incorrect trials only.

A staircase procedure was used to calibrate the size of the gap to each object to ensure that the gap was equally perceptible across each object regardless of each objects' individual characteristics (Pelli and Bex, 2013). Sixteen undergraduate students (13 female; average age: 18.8; 4 left-handed) from the George Washington University participated in exchange for course credit. In each trial the object would be presented with or without the spatial gap which would begin with a size of 0.025° visual angle. If the gap was detected correctly for two consecutive trials, the gap decreased by one 0.005° step. If the gap was missed, or a false alarm was made to the absence of a gap, for two consecutive trials, the gap was increased by one 0.005° step. The gap was calibrated until twenty trials had been completed or until the staircase reversed direction (2 correct followed by 2 incorrect or vice versa) three times. The gap size for each object is displayed in figure 1.

In the other half of the experiment, the object appeared with or without a temporal blink. The objects had an equal probability of having a temporal blink or not having a temporal blink. The blinks were 16 ms long. The object first appeared for 96 ms, followed by the temporal blink, and the object then appeared a second time for 32 ms. Participants were to report the presence of the temporal blink by pressing the right control button and absence of the temporal blink by pressing the left control button on the keyboard. Feedback was presented on incorrect trials only.

The presentation of stimulus type was counterbalanced across participants such that half of the participants were first presented with spatial gaps and half of the participants were presented with temporal blinks first. Participants completed a total of 720 trials broken into 6 blocks, 360 trials of spatial gaps and 360 trials of temporal blinks.

Experiment 2 was identical to Experiment 1 except each stimulus was presented upside down. The spatial gap was presented in the same place as it was in experiment 1 relative to the object.

Experiment 3 was identical to experiment 1, except more realistic images were used instead of line drawings. Similarly to the line drawing stimuli, a staircase procedure was used to calibrate the size of the gap to each object to ensure that the gap would be equally perceptible across each object regardless of each objects' individual characteristics (Pelli and Bex, 2013). Twenty three undergraduate students (18 female; average age: 18.9; 4 left-handed) from the George Washington University participated exchange for course credit. In each trial the object would be presented with or without the spatial gap which would begin with a size of 0.025° visual angle. If the gap was detected correctly for two consecutive trials, the gap would be made smaller by one 0.005 ° step. If the gap was not detected, or a false alarm was made to the absence of a gap, for two consecutive trials, then the gap would be made larger by one 0.005 ° step. Calibration was done until twenty trials had been completed or until the staircase reversed direction (2 correct followed by 2 incorrect or vice versa) three times. The gap size for each object is displayed in figure 1.

Experiment 4 was similar in trial structure to the temporal blink condition of Experiment 1, except instead of temporal blink detection each trial had a temporal blink that was either short or long in duration. The objects had an equal probability of having a short or a long temporal blink. In the short blink condition, the object first appeared for 96 ms, followed by a 16 ms temporal blink, and then the object appeared a second time for 32 ms. In the long blink condition, the object first appeared for 64 ms, followed by a 48 ms temporal blink, and then the object was presented for a second time for 32 ms. Participants were to report a presence of a short temporal blink by pressing the 'c' key and a long temporal blink by pressing the 'm' key on the keyboard. Feedback was presented exclusively on incorrect trials. Participants completed a total of 720 trials broken into 6 blocks, 360 trials of short blink duration and 360 trials of long blink duration.

Experiment 5, was identical to the spatial gap procedure of Experiment 1 except the background color was either green (HSV = 110, 30, 90) or red (HSV = 5, 30, 90). The background color was counterbalanced across participants such that half of the participants would first be presented with the green background and half of the participants would first be presented with the red background. Participants completed a total of 720 trials broken into 6 blocks, 360 trials of green backgrounds and 360 trials of red backgrounds.

Data Analyses. Data for each experiment were analyzed using repeated-measures analysis of variance with an α set to 0.05. Two-sample t-test were also employed where indicated in the text and were two-tailed. Anticipatory response times faster than 250 ms and any response times longer than 2000 ms were removed from analysis (2.67, 2.4, 5.59, 12.1, and 2.95% of the data was removed from experiments 1, 2, 3, 4, and 5 respectively). Mean response times for each condition in each experiment were calculated for each subject. For each analysis, all assumptions, including normality and equality of variances, were formally tested and confirmed.

Code availability. The custom Python programs generated for this study are available from the corresponding authors on reasonable request.

Data availability. The data that support the findings of this study are available from the corresponding author upon reasonable request.

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